Ecology and Conservation of

Owls

Editors: Ian Newton,
Rodney Kavanagh,
Jerry Olsen & Iain Taylor

Ecology and Conservation of

Owls

*Dedicated to the memory of Norman Wettenhall for his loyal
and longstanding support of the Australasian Raptor Association*

Ecology and Conservation of

Owls

Editors: Ian Newton, Rodney Kavanagh, Jerry Olsen & Iain Taylor

CSIRO
PUBLISHING

The Norman Wettenhall Foundation

Australasian Raptor Association

Birds Australia

National Library of Australia Cataloguing-in-Publication entry

Ecology and conservation of owls.

Bibliography.
ISBN 0 643 06794 9 (paperback).
ISBN 0 643 06988 7 (eBook).

1. Owls – Congresses. I. Newton, Ian.

598.97

Available from
CSIRO PUBLISHING
150 Oxford Street (PO Box 1139)
Collingwood VIC 3066
Australia

Telephone: +61 3 9662 7666
Freecall: 1800 645 051 (Australia only)
Fax: +61 3 9662 7555
Email: publishing.sales@csiro.au
Web site: www.publish.csiro.au

Cover photographs by David Hollands
Front cover (left to right):
Rufous Owl (*Ninox rufa*) in threatening posture; pair of Grass Owls (*Tyto longimembris*) at nest in bladey grass; Powerful Owl (*Ninox strenua*) at daytime roost.
Back cover (top, left to right):
Masked Owl (*Tyto novaehollandiae*) hunting in cut sugar cane; female Boobook (*Ninox boobook*) at entrance of nest hollow; male Lesser Sooty Owl (*Tyto multipunctata*) at entrance of nest hollow with White-tailed Rat (*Uromys caudimaculatus*);
Back cover (bottom, left to right):
Sooty Owl (*Tyto tenebricosa*) at entrance of nest in cave; female Barking Owl (*Ninox connivens*) entering nest hollow with rabbit; Barn Owl (*Tyto alba*).

Set in Stone Sans
Cover and text design by James Kelly
Typeset by J&M Typesetting
Printed in Australia by Ligare

FOREWORD

The Australasian Raptor Association (ARA) is proud to have initiated and hosted *Owls 2000* which was held in Canberra at the Australian National University, 19–23 January 2000. More than 130 delegates attended the conference from ten different countries. Fifty-one papers, presentations and workshops, covering a broad perspective of owl conservation and scientific exploration were presented during the conference. Fourteen poster papers and technical tours to the Australian National Wildlife Collection, Tidbinbilla Nature Reserve and Kosciuszko National Park augmented the formal proceedings. Following the conference, some of the delegates took the opportunity to observe Australia's owls in the wild during the post-conference tour to New South Wales and Victoria. From all accounts our delegates found the event rewarding at many levels and without doubt the conference proved to be a huge success. From this conference the editorial team, led by Professor Ian Newton, has produced a significant repository of information on the owls of the world with a particular focus on the Australasian region. This will not only form a useful reference on what we currently know about owls but also serves as a benchmark on which to develop future scientific and conservation activities on this fascinating group of birds. The ARA will continue to support this important pursuit of knowledge and will endeavour to host similar conferences in the future.

I take this opportunity to thank our major sponsors, The Norman Wettenhall Foundation, State Forests of New South Wales, The Johnstone Centre (Charles Sturt University), Department of Natural Resources and Environment (Victoria), National Parks and Wildlife Service (NSW), Bayer Australia Ltd. and the Northwest Habitat Institute for their support. Without their generosity the publication of this book would not have been possible.

Finally, I would like to express my personal gratitude to the late Dr Norman Wettenhall for his loyal and longstanding support of the ARA. Norman, together with his companion and confidante, Joan, was a 'cornerstone' of Birds Australia (The Royal Australasian Ornithologists Union) and he tirelessly devoted much of his time to bird conservation and the pursuit of scientific knowledge. Norman and Joan attended most of the major bird conservation events in Australia and it is with a great sense of achievement that Norman conveyed to me that *Owls 2000* was one of the best conferences he had ever attended. Norman, above all, was a great friend and colleague to us all, and so with pride the ARA dedicates this important body of work to him.

Mark Holdsworth
President
Australasian Raptor Association

This Page Intentionally Left Blank

CONTENTS

Preface x

Acknowledgments xi

Referees xii

Introduction to Australian owls xiii
David Hollands

Part 1. Population ecology

1 Population limitation in Holarctic owls 3
Ian Newton

2 Occupancy in relation to site quality in Barn Owls (*Tyto alba*) in south Scotland 30
Iain R. Taylor

3 Natal dispersal distances of Finnish owls: results from ringing 42
Pertti Saurola

4 Natal and post-natal dispersal of Northern Spotted Owls (*Strix occidentalis*) 56
Eric D. Forsman

5 Home-range, movement and dispersal of Lanyu Scops Owls (*Otus elegans*) 58
Lucia Liv Severinghaus

6 Detrimental effects of blood parasites on parental effort and reproductive success of Tengmalm's Owls (*Aegolius funereus*) and Eurasian Kestrels (*Falco tinnunculus*) 68
Erkki Korpimaki, Harri Hakkarainen, Petteri Ilmonen & Jürgen Wiehn

7 Infertility as a cause of hatching failure in the Barn Owl (*Tyto alba*) in the Netherlands 74
Arnold B. van den Burg

8 Ecology and behaviour of the Forest Owlet (*Athene blewitti*) 80
Farah Ishtiaq, Asad R. Rahmani & Pamela Rasmussen

Part 2. Distribution, habitat and diet

9 Habitat quality in Powerful Owl (*Ninox strenua*) territories in the Box–Ironbark forest of Victoria, Australia 91
T.R. Soderquist, K.W. Lowe, R.H. Loyn & R. Price

10 Urbanisation and the ecology of Powerful Owls (*Ninox strenua*) in outer Melbourne, Victoria 100
Raylene Cooke, Robert Wallis & Alan Webster

11 Distribution and habitat of Barking Owls (*Ninox connivens*) in central Victoria, Australia 107
Iain R. Taylor, Indre Kirsten & Paul Peake

12 Habitat, breeding and conservation of the Barking Owl (*Ninox connivens*) in northeastern Victoria, Australia 116
Iain R. Taylor, Indre Kirsten & Paul Peake

13 Distribution, habitat and abundance of Masked Owls (*Tyto novaehollandiae*) in Tasmania 125
P. J. Bell & Nick Mooney

14 Spatial habitat characteristics of an insular Spotted Owl (*Strix occidentalis*) population in southern California 137
Richard B. Smith, William S. Lahaye, R.J. Gutiérrez & Guthrie S. Zimmerman

15 Effects of habitat fragmentation and slope on the distribution of three owl species in the Manitoba Escarpment, Canada – a preliminary analysis 148
Heather L. Hinam & James R. Duncan

16 Comparative habitat use by owls in a high altitude (1,700–3,000 m) Rocky Mountain forest 162
Sta*nley H. Anderson & Kathleen A. Clark*

17 Comparative diets of the Powerful Owl (*Ninox strenua*), Sooty Owl (*Tyto tenebricosa*) and Masked Owl (*Tyto novaehollandiae*) in southeastern Australia 175
Rodney P. Kavanagh

18 Notes on the diet and observations of the Southern Boobook (*Ninox novaeseelandiae)* in southern Victoria 192
Edward G. McNabb

Part 3. Conservation and management

19 Conservation and management of large forest owls in southeastern Australia 201
Rodney P. Kavanagh

20 Large forest owl conservation in the East Gippsland Forest Management Area, Victoria 220
Andrew D. McIntyre & Stephen R. Henry

21 Owls in the southwest forests of Western Australia 233
G.L. Liddelow, I.B. Wheeler & Rodney P. Kavanagh

22 Modelling distributions of large forest owls as a conservation tool in forest management: a case study from Victoria, southeastern Australia 242
Richard H. Loyn, Edward G. McNabb, Lioudmila Volodina & Rolf Willig

23 Monitoring large forest owls and gliders after recent logging in production regrowth forests in the mid-north coastal region of New South Wales 255
Brett Cann, Justin Williams & James M. Shields

24 Response to habitat fragmentation by the Powerful Owl (*Ninox strenua*), Sooty Owl (*Tyto tenebricosa*), Masked Owl (*Tyto novaehollandiae*) and other nocturnal fauna in southeastern Australia 265
Rodney P. Kavanagh & Matthew A. Stanton

25 Lessons learned in 30 years of research and management on the Northern Spotted Owl (*Strix occidentalis*) 277
Eric D. Forsman

26 Rodenticides in British Barn Owls (*Tyto alba*) 286
Ian Newton & Ian Wyllie

27 Racumin rodenticide – potential environmental impact on birds 296
Warwick Madden

Part 4. Voice, structure and taxonomy

28 Vocalisations used by Southern Boobooks (*Ninox novaeseelandiae*) in the Australian Capital Territory 305
J. Olsen, S. Trost & G. Hayes

29 Do Southern Boobooks (*Ninox novaeseelandiae*) duet? 320
J. Olsen, B.G. Marcot & S. Trost

30 Independent evolution of outer ear asymmetry among five owl lineages; morphology, function and selection 329
Åke Norberg

31 The taxonomy and conservation status of the owls of the world: a review 343
John M. Penhallurick

32 Distribution, taxonomy, status and major threatening processes of owls of the Australasian region 355
Stephen Debus

PREFACE

The chapters that comprise this book derive from papers presented at a five-day conference devoted to the study of owls, which was held under the delightful setting of the Australian National University campus at Canberra, in January 2000. The conference was the third in a series of international meetings on owls, the previous two of which had been held in Canada[1,2]. This had inevitably given major emphasis to northern hemisphere species, so the idea arose to hold a meeting in the southern hemisphere, in order to redress to some extent the regional imbalance.

For two main reasons, Australia seemed the most appropriate venu. First, the Australasian region itself is the main biogeographic centre for two major groups of owls, namely *Tyto* and *Ninox*, and most of these species are little known by biologists from outside the region. Second, the Australian owls themselves had been subject to much recent research, especially on habitat needs and status, most of which had not been previously published. The conference therefore provided an opportunity for the presentation of new findings, for northern and southern hemisphere owl researchers to meet and discuss issues of mutual concern, and also for northern biologists to see some of the markedly distinctive species of the region. These species are illustrated on the cover of this book by the excellent photographs of David Hollands.

Like any symposium volume, this one does not attempt to provide a comprehensive review of existing knowledge, but is dependent on the papers presented at the meeting. However, it contains much new material (especially on Australian owls), and a number of 'review' chapters which bring together findings from a wide range of previous research. The latter include recent developments in owl taxonomy and systematics, and studies of population limitation in northern hemisphere owls. In addition, the book contains a chapter on the recently re-discovered Forest Owlet of India. The book is divided into four main sections, under the headings 'Population ecology', 'Distribution, habitat and diet', 'Conservation and management', and 'Voice, structure and taxonomy'. All the chapters in the book were peer-reviewed and each chapter was sent to two or more referees. As a result of this process, not all papers presented at the conference were accepted for publication, and all the others were greatly improved. As editors, we are grateful to all the referees involved. Their names are listed on the following pages.

Besides the referees, we owe special thanks to Mark Holdsworth and his team who played such a crucial role in the initial planning and organisation of the conference, and in the associated fund-raising for both the conference and this publication. Important helpers and sponsors are listed in the acknowledgements. Without them, the conference could not have taken place, and this book could not have been published.

Ian Newton, Rod Kavanagh, Jerry Olsen and Iain Taylor

---

[1] **Duncan, J. R., Johnson, D. H. & Nicholls, T. H.,** (eds.) 1997. Biology and Conservation of Owls of the Northern Hemisphere. USDA Forest Service Gen. Tech. Rep. NC-190.

[2] **Nero, R. W., Clark, R. J., Knapton, R. J. & Hamre, R. H.,** (eds.) 1987. Biology and conservation of northern forest owls. USA, USDA Forest Service Gen. Tech. Rep. RM-142.

ACKNOWLEDGMENTS

The *Owls 2000* conference was hosted by the Australasian Raptor Association (ARA), a Special Interest Group of Birds Australia. The Organising Committee consisted of Mark Holdsworth (President, ARA), Iain Taylor (Charles Sturt University), Rod Kavanagh (State Forests of NSW), Jerry Olsen (University of Canberra), Bob Digan (ARA), Malcolm Fyfe (Canberra Ornithologists Group) and Nick Mooney (Nature Conservation, Tasmania). Sue Trost (Erindale College) and Sally Bryant (Birds Australia) provided invaluable assistance to the committee and David Johnson (Northwest Habitat Institute) was a vital contact in North America.

The Organising Committee would like to thank the Manitoba Gray Owl Research Foundation and Birds Australia for providing seeding funds to get the conference off the ground. The State Forests of New South Wales, The Norman Wettenhall Foundation and The Johnstone Centre of Charles Sturt University kindly provided major sponsorship for keynote speakers and Bayer Australia Ltd. sponsored the session relating to threatening processes. The Northwest Habitat Institute, Applied Ecology Research Group and the Raptor Research Foundation also provided supporter sponsorships. We would also like to acknowledge the encouragement of Birdlife International and the in-kind assistance of the Canberra Ornithologist's Group and the Department of Primary Industries, Water and Environment (Tasmania).

The conference was expertly coordinated by Conference Solutions, and in particular, we are grateful for the professional and enthusiastic commitment to the task by Brigitte Gunn and Claire Wilson. The conference artwork was produced by Mel Hills, and the logo, stationery and program booklet was produced by Di Walker Designs. Thanks also to Malcolm Fyfe for his orderly assistance with conference organisation and registration. Arthur Georges and Mike Palmer-Allen (Applied Ecology Research Group) kindly provided all the audiovisual equipment and Ben Kropp (University of Canberra) ably kept things operating throughout the conference.

Prof Harry Recher (Edith Cowan University) and Richard Schodde (CSIRO Wildlife & Ecology) presented eclectic and thoroughly entertaining dinner speeches on their perspective on conservation and scientific endeavour in the Australasian region. The free guided tours of the Australian National Wildlife Collection, hosted by Dr Schodde, provided delegates with an invaluable insight into Australia's most important reference collection.

Nick Mooney, Harry Recher, Richard Schodde, Ian Newton, Jim Shields, Penny Olsen, Iain Taylor, Eric Forsman, Richard Loyn and Mark Holdsworth ably chaired the conference sessions. We are also appreciative of Ian Newton who presented the keynote address and has donated his valuable time to editing the papers in this book. Our gratitude also goes to our other guest speakers, Eric Forsman, Erkki Korpimaki and Pertti Saurola, who provided a useful worldwide perspective on owls.

The publication of this book was funded through donations from The Norman Wettenhall Foundation, State Forests of New South Wales, The Johnstone Centre (Charles Sturt University), Department of Natural Resources and Environment (Victoria), National Parks and Wildlife Service (NSW), Bayer Australia Ltd. and the Northwest Habitat Institute.

Finally, the Organising Committee wishes to thank all the delegates with whom we shared common interests and had a great time celebrating our many and varied achievements. Without their enthusiastic attendance, the conference would not have been the success that it was.

REFEREES

Paul Bellamy, Stephen Debus, Jim Duncan, Eric Forsman, Peter Fullagar, Rhys Green, Ross Goldingay, Greg Haywood, Richard Hill, Graham Hirons, Denver Holt, Jim Hone, Peter Hudson, Darryl Jones, Rod Kavanagh, Erkki Korpimäki, Bill La Haye, Wayne Longmore, Richard Loyn, Mick Marquiss, Bruce Marcot, Ian Mason, Dominic McCafferty, Ed McNabb, Peter Menkhorst, Heimo Mikkola, Ian Newton, Jerry Olsen, Penny Olsen, Chris Pavey, Paul Peake, John Penhallurick, Richard Pettifor, Steve Petty, Hannu Pieitiäinen, Pamela Rasmussen, Ken Sanderson, Dennis Saunders, Dick Shodde, Richard Shore, Andrew Smith, Geoff Smith, Todd Soderquist, Dave Spratt, William Sutherland, Iain Taylor, Richard Zann.

INTRODUCTION TO AUSTRALIAN OWLS

David Hollands

For its size, Australia has a relatively small number (11) of owl species and only two genera (*Tyto* and *Ninox)* but they make up a richly varied group, as shown in the photographs on the cover of this book. Just how many species of owl there are in the world is a subject for some conjecture. In 1973, Burton's *Owls of the World* recognised 133. By the time the revised edition appeared in 1992, this number had risen to 143. A much greater increase was to come with the publication of *Owls* by König *et al*. (1999) which listed a total of 213 species. If this total is accepted, it produces a 60% increase in the world's recognised owl species in barely a quarter of a century.

Some of the increase is due to the discovery of new species in the wild, but most of it is due to further taxonomic subdivision of already known forms. Not everybody will agree with these taxonomic changes. Burton's new species were designated largely by the traditional methods of taxonomy and field observation, but König *et al.* (1999) relied heavily on sonograms and DNA analyses, producing many new species which are mostly hard to separate on appearance in the field.

Australia's owls have not escaped involvement and, in recent years, the number of species has increased from eight to eleven. One of these additions occurred in 1958 when Christmas Island in the Indian Ocean became part of Australia, thus adding the Christmas Island Hawk Owl to the Australian list. At that time, there was debate about its taxonomic status and it was assigned as a sub-species of the Moluccan Hawk Owl *Ninox squamipila.* This classification always appeared slightly illogical, and it took DNA studies to establish that it does indeed warrant full specific status as *Ninox natalis.*

The addition of the Lesser Sooty Owl *Tyto multipunctata* was much more conventional. This bird had long been known to be separable in the field from the Sooty Owl *T. tenebricosa*, but Schodde & Mason (1980) were the first authors to give it full specific status. The third addition, resulting from the splitting by König *et al.* (1999) of the Masked Owl into the Australian Masked Owl *Tyto novaehollandiae* and the Tasmanian Masked Owl *T. castanops*, is much more contentious, because many argue that southern mainland Masked Owls are inseparable in size and colour from Tasmanian ones.

Based on König *et al.* (1999), Australia's list of owl species is now as follows:

Tyto

Barn Owl *T. alba*

Eastern Grass Owl *T. longimembris*

Australian Masked Owl *T. novaehollandiae*

Tasmanian Masked Owl *T. castanops*

Sooty Owl *T. tenebricosa*

Lesser Sooty Owl *T. multipunctata*

Ninox

Powerful Owl *N. strenua*

Rufous Owl *N. rufa*

Barking Owl *N. connivens*

Boobook *N. boobook*

Christmas Island Hawk Owl *N. natalis*

The position of the genus *Tyto* in Australia is particularly fascinating. Although the genus is always listed as being cosmopolitan, this is almost entirely due to one species, the Barn Owl *T. alba*. The only other species to have wide distributions outside Australia are the African Grass Owl *T. capensis*, the Eastern Grass Owl and the Sulawesi Masked Owl *T. rosenbergii.* With the exception of one or two very small regions, nowhere in the world, apart from Australia, has more than two species of *Tyto.* The fact that Australia has at least five species (or six according to König *et al.* 1999) must raise the question of the evolutionary origins of *Tyto*. Some have placed this in Europe, but others favour Australia or even its ancient parent continent, Gondwana.

Australia offers a huge range of habitats and its owls have evolved to occupy a large number of these. However, most species occur in forested areas, making them vulnerable to timber operations, resulting in loss of habitat or at least the loss of the large old trees that provide nest-sites. The Barn Owl is probably the world's most successful owl. In Australia it inhabits a wide range of woodland, open farmland and lightly timbered country right through to semi-desert, but here (in contrast to some other regions) it always needs hollow trees for nesting.

The Grass Owl is ground-nesting, and hence the only one of Australia's owl species which has no need for trees. However, its range is strangely restricted to tropical coastal grasslands and, less commonly, to flood plain grasslands inland.

The two Masked Owls are forest-edge birds, needing large trees for nesting but preferring to hunt in more open country. The two other *Tyto* species live in forest, the Sooty Owl basing its territory around the deep, moist forest gullies of the south-east, while the Lesser Sooty is found in tropical rainforest.

The *Ninox* owls have a similar wide range of needs. The huge Powerful Owl, the largest owl in Australia, is a bird of the southeast forests, needing big trees, big prey and a vast territory. Its northern counterpart, the Rufous Owl, lives in tropical riverine forest and is considerably more scarce than its southern cousin.

The Barking Owl is something of an enigma. Although much smaller than the two biggest *Ninox*, it needs big nesting hollows and is an aggressive hunter of quite large birds with a preference for water birds. In Queensland, it regularly bases its territory around small patches of trees and there are many records of birds nesting in towns and close to farmhouses. In this State, the populations seem quite stable, but in Victoria the species is in decline.

The Boobook is both the commonest and the most widespread owl in Australia. Its population is immense and it occurs just about anywhere with trees, from the densest rainforest out to the deserts where the only trees are small and confined to dry watercourses.

Finally, the Christmas Island Hawk Owl is among the world's smallest, most isolated and most vulnerable owl species. It is found only on Christmas Island, and Hill & Lill (1997) estimated the total population at less than a thousand birds.

What is the future for Australia's owls? With the country's vast size and, by world standards, thinly spread human population, it might be assumed that all was well. However, that may not be the case. The Masked, Sooty, Powerful and Rufous Owls all need extensive forest areas and are thus vulnerable to clearing and timber operations. Already there are signs that Powerful Owls in central Victoria are suffering a marked drop in numbers which is possibly due to the residual areas of forest being too small to provide enough prey. In North Queensland, sudden dramatic falls in the populations of Barn, Masked and Grass Owls have been linked to the use of new rodenticides by sugar cane growers. Away from the forests, there are regions where the removal of trees is leaving very few nest hollows for Barn and Boobook Owls, and the shortage of nesting sites may be reducing their numbers.

On Christmas Island there is a devastating new problem where an introduced ant, known as the Crazy Ant, has gained a foothold and is spreading rapidly. With no natural controls on the island, it has the potential to destroy much of the native wildlife.

It is essential that any conservation strategies for Australian owls are based on a sound knowledge of the owls themselves. Yet owls are not easy to study. They need time, skill and enormous patience. Australia was late into the field with owl studies but some excellent work is now being undertaken. It is a start but it is nowhere near enough. The OWLS 2000 Conference was a strikingly successful meeting and gave some pointers to where work most needs to be done in the future. One can only hope that the conference and this volume will act as a catalyst to further work. The papers in this volume give a flavour of the most recent research undertaken on Australian Owls.

REFERENCES

Burton, J.A. 1973. Owls of the World. England: Peter Lowe/Eurobook.

Burton, J.A. 1992. Owls of the World (Revised edition). England: Peter Lowe/Eurobook.

Hill, F.A.R. & Lill, A. 1997. Density and total population estimates for the threatened Christmas Island Hawk-Owl *Ninox natalis. Emu* **98**: 209–220.

König, C., Weick, F. & Becking, J-H 1999. Owls A guide to the owls of the World. East Sussex, England: Pica Press.

Norman, J., Christidis L., Westerman, M. & Hill, F.A.R. 1998. Molecular data confirms the species status of the Christmas Island Hawk-Owl. *Emu* **98**: 197–208.

Schodde, R., & Mason, I.J. 1980. Nocturnal birds Of Australia. Melbourne: Lansdowne Editions.

Soderquist, T. 2002. Home range and habitat quality of the Powerful Owl (*Ninox strenua*) in Box-Ironbark forest of central Victoria, Australia. This volume.

This Page Intentionally Left Blank

Part 1

Population ecology

This Page Intentionally Left Blank

1

POPULATION LIMITATION IN HOLARCTIC OWLS

IAN NEWTON

Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon,
Cambridgeshire PE28 2LS, United Kingdom.

This paper presents an appraisal of research findings on the population dynamics, reproduction and survival of those Holarctic Owl species that feed on cyclically-fluctuating rodents or lagomorphs. In many regions, voles and lemmings fluctuate on an approximate 3–5 year cycle, but peaks occur in different years in different regions, whereas Snowshoe Hares *Lepus americanus* fluctuate on an approximate 10-year cycle, but peaks tend to be synchronised across the whole of boreal North America.

Owls show two main responses to fluctuations in their prey supply. Resident species stay on their territories continuously, but turn to alternative prey when rodents (or lagomorphs) are scarce. They survive and breed less well in low than high rodent (or lagomorph) years. This produces a lag in response, so that years of high owl densities follow years of high prey densities (examples: Barn Owl *Tyto alba*, Tawny Owl *Strix aluco*, Ural Owl *S. uralensis*). In contrast, prey-specific nomadic species can breed in different areas in different years, wherever prey are plentiful. They thus respond more or less immediately by movement to change in prey-supply, so that their local densities can match the local food-supply at the time, with minimum lag (examples: Short-eared Owl *Asio flammeus*, Long-eared Owl *A. otus*, Great Grey Owl *Strix nebulosa*, Snowy Owl *Nyctea scandiaca*).

Some owl species that exploit sporadic food-supplies move around mainly within the breeding range (examples: Tengmalm's Owl *Aegolius funereus*, Northern Hawk Owl *Surnia ulula*). In other species, part of the population migrates to lower latitudes for the winter, thereby avoiding the worst effects of snow cover, but returns to the breeding range each spring, settling wherever voles are plentiful (examples: Short-eared Owl, Long-eared Owl).

In all these species, as well as in the hare-eating Great Horned Owl *Bubo virginianus*, food-supply affects every aspect of demography, including age of first breeding, reproduction (proportion of pairs laying, hatching and fledging young, clutch and brood sizes), juvenile and adult survival, natal and breeding dispersal, and winter irruptions. In eastern North America, irruptions of Snowy Owls *Nyctea scandiaca* documented since 1880 have occurred every 3–5 years, at a mean interval of 3.9 years (SE O.13). In periods when information on lemmings was available from breeding areas, mass emigration of owls coincided with crashes in lemming numbers. Similar periodicity has been noted in the movements of some other owl species in both North America and Europe. In most (but not all) irruptions, juveniles predominated. Irruptions of Great Horned Owls (and Northern Goshawks *Accipiter gentilis*) in North America have occurred for 1–3 years at a time, at approximately 10-year intervals, coinciding with known lows in the hare cycle.

While food-supply is the primary limiting factor, nest-site shortages, adverse weather and other secondary factors can sometimes reduce owl breeding densities and performance below what food-supply would permit.

INTRODUCTION

Studies on Holarctic owls have contributed greatly to our understanding of the processes of population limitation in birds. About 33 different owl species breed in this region, 14 in the Palaearctic, 12 in the Nearctic, and a further seven in both regions. Nearly half of these species feed largely or entirely on microtine rodents (lemmings and voles), two on lagomorphs (rabbits and hares), one on fish, and the rest mainly on insects or other invertebrates. In this paper, I shall concentrate on the rodent and lagomorph feeders, partly because they have been better studied than the others, but also because they provide some of the best evidence available among birds for the role of food-supply in influencing densities and performance. Other factors important in the ecology of these owls include winter snow cover and nest site availability, the effects of which vary with the hunting methods, life style and dietary range of the species themselves (Korpimäki 1992). I shall be concerned only with the limitation of numbers within areas of suitable habitat, and not with the effects of habitat loss and fragmentation, which, although important in conservation, are outside the scope of this review (but see Lande 1988, Lamberson *et al.* 1992, La Haye *et al.* 1994, Redpath 1995).

Some familiar aspects of owl biology influence the way in which owls respond to food conditions, and are affected by shortages and other adverse factors, such as snow. Their acute hearing, and ability to see in poor light, enable owls to hunt nocturnal mammals hidden under ground vegetation or snow, in a way that diurnal raptors cannot, giving them a particular advantage at high latitudes in winter. Secondly, most species nest mainly or wholly in cavities which protect them to some extent against predation, while others defend their nests aggressively. In consequence, nest predation levels are often low compared with other birds (although exceptions occur, see later). Thirdly, clutch sizes in many species are large, and very variable, so that owls can take advantage of good food conditions when they occur. Most also start incubating from the first or second egg, so that hatching is asynchronous and broods typically contain young of different sizes. This in turn provides a means of rapid brood reduction if food becomes scarce, for the smallest young dies first, followed by the second smallest and so on.

THE PREY

Most of the mammal species eaten by owls are ground dwelling, hidden under thick grass or other low vegetation, and are active mainly at night (though some mainly or also by day). Typically, they fluctuate greatly in numbers, often in regular multi-year cycles of abundance. This means that their predators are exposed to a greatly fluctuating food-supply, both within and between years. Such marked changes in food-supply affect the reproductive and survival rates of owls, as well as their movements, which in turn can bring about rapid changes in their local densities.

Cycles in prey numbers

Two main systems are recognised: (1) an approximately 3–5 year cycle of small (microtine) rodents in the northern tundras, boreal forests and temperate grasslands; and (2) an approximately 10-year cycle of Snowshoe Hares *Lepus americanus* in the boreal forests of North America (Elton 1942, Lack 1954, Keith 1963). The numbers of certain grouse species also fluctuate cyclically, in some regions in parallel with the rodent cycle and in others in parallel with the hare cycle (Hörnfeldt 1978, Keith & Rusch 1988).

Populations of microtine rodents do not reach a peak simultaneously over their whole range, but the cycles may be synchronised over tens, hundreds or many thousands of square kilometres, out of phase with those in more distant areas. However, peak populations may occur simultaneously over many more areas in some years than in others, giving a measure of synchrony, for example, to lemming cycles over large parts of northern Canada, with few regional exceptions (Chitty 1950). In addition, the periodicity of vole cycles tends to increase northwards from about three years between peaks in temperate and southern boreal regions, increasing to 4–5 years in northern boreal regions. The amplitude of the cycles also increases northwards from barely discernible cycles in some temperate regions to marked fluctuations further north, where peak densities typically exceed troughs by more than 100-fold (Hansson & Henttonen 1985, Hanski *et al.* 1991). Further north, on the tundra, the periodicity of lemming cycles is in some places even longer (5–7 years between peaks on Wrangel Island, Menyushina 1997), and the amplitude is even greater, with peaks sometimes exceeding troughs by more than a thousand-fold (Shelford 1945). In most places, the increase phase of the cycle usually takes 2–3 years, and the crash phase 1–2 years. Importantly, the crash phase often overlaps with spring and summer, a time when owls and other rodent predators are breeding.

In research projects, the numbers of rodents in an area are usually monitored by regular trapping programmes, measuring the numbers caught per unit effort (such as ‘trap days’), or less directly by counting the numbers of signs (such as droppings, runs or cut grass stems) per unit area. Different measures of rodent abundance taken at the same dates in the same area are usually closely correlated with one another, giving reassurance over the validity of the different indices (e.g. Hansson 1979, Petty 1999). An example of results from the same Field Vole *Microtus agrestis* population trapped three times each year over a period of years is shown in Fig. 1. Peaks in abundance occur at regular intervals of 3–4 years, but the height of the peaks and the depths of the troughs vary from one cycle to the next. Moreover, the trend in numbers at particular seasons can vary from one year to another. In some springs, when owls are breeding, they face an increasing food-supply, whereas in other springs, as mentioned above, they face a sharply decreasing food-supply. As expected, these contrasting situations have markedly different effects on owl breeding success (see below). An overall rodent density of less than 2–4 individuals per hectare (or two captures per 100 trap-nights) has been estimated as the threshold in prey density below which rodent-eating birds of prey do not breed (Hagen 1969, Potapov 1997), but this figure could well vary between areas and between species.

The longer hare cycles have been less studied, but peaks in numbers can exceed troughs by

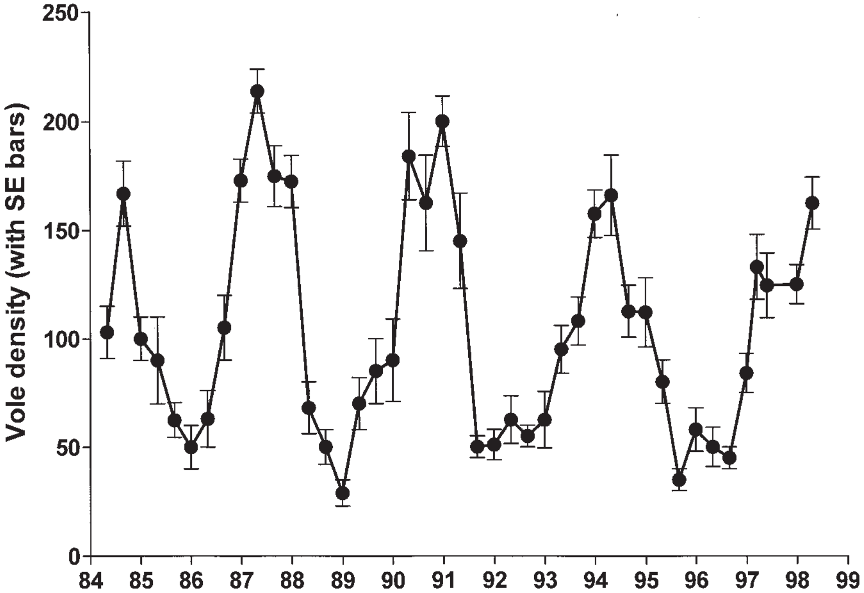


Fig. 1. Index of Field Vole *Microtus agrestis* densities in spring, summer and autumn in an area of northern England over 15 years. Note that in most years vole densities increased from spring to summer (the owl breeding season), but in some years they decreased from spring to summer. From Petty 1999.

more than 100-fold (Adamcik *et al.* 1978). Unlike the situation in rodents, the cycle is synchronised over much of boreal North America, with populations across the continent peaking in the same years (Keith & Rusch 1988). These animals, living above ground, are usually also counted by use of trapping programmes. In one study, no owl breeding occurred when hare densities fell below 0.9 animals per ha (Rohner 1996).

RESPONSES BY OWLS TO FLUCTUATIONS IN PREY ABUNDANCE

Owls show two main types of response to fluctuations in their food-supply (Fig. 2). One type is shown by resident species, which tend to stay on the same territories year-round and from year to year. While preferring rodents (or lagomorphs), they eat other prey, so they can remain in the same area through low rodent years. However, their survival may be poorer, and their productivity much poorer, in low than in high rodent years. In low prey years, the majority of territorial pairs may make no attempt to breed, and those that do, lay relatively small clutches and raise small broods. The Tawny Owl[1], Ural Owl, Barn Owl and Great Horned Owl are in this category, responding functionally to prey numbers, and numerically chiefly in terms of the numbers of young raised (Southern 1970, Saurola 1989, Petty 1992, Taylor 1994, Rohner 1996). This type of response, shown by resident owl populations, produces a lag between prey and predator numbers, so that high owl densities follow good food-supplies and low densities follow poor supplies (Fig. 2). Prey and predator densities fluctuate in parallel, but with the predator behind the prey (up to two years behind in the Snowshoe Hare – Great Horned Owl system, Rohner 1995). The lag period depends partly on the age at which first-breeding occurs. In the Tawny Owl, young produced in a peak vole year often breed in the following year, just before vole numbers crash

---

[1] *Scientific names of most owl species mentioned in the text are given in Table 1.*

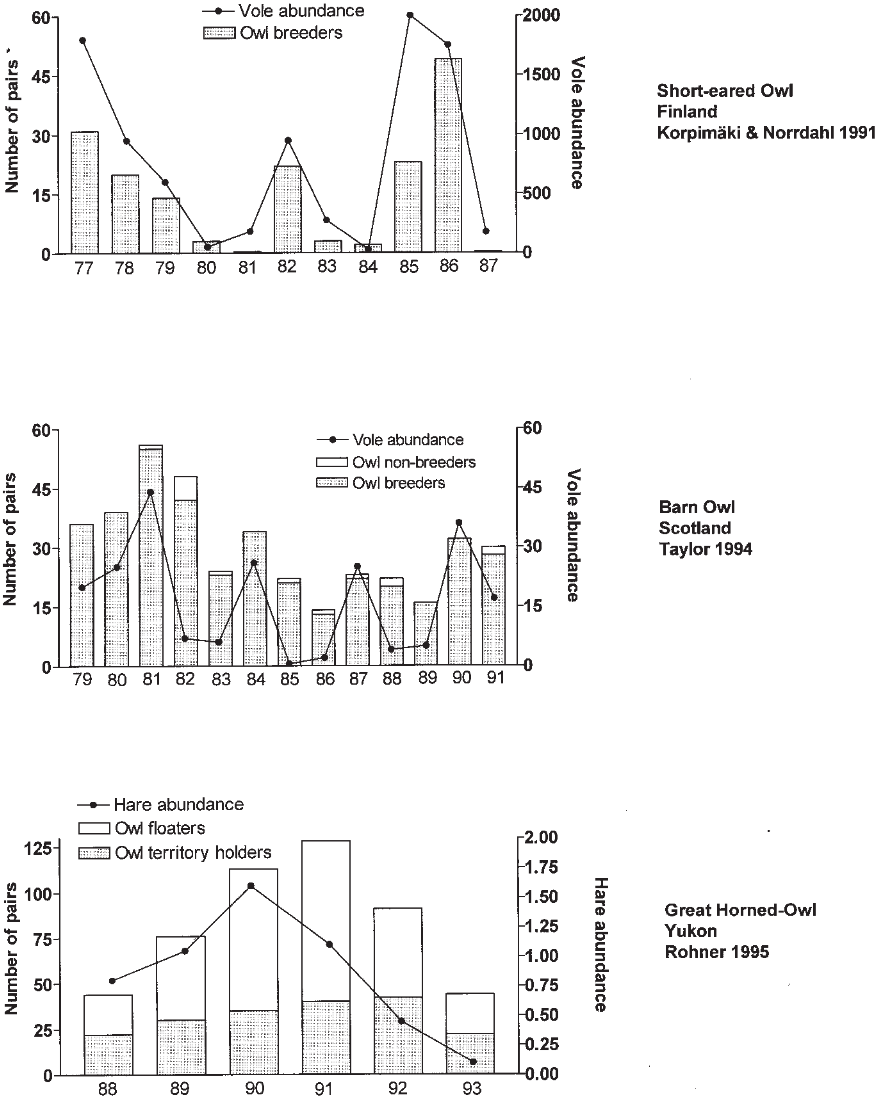


Fig. 2. Fluctuations in the numbers of breeding and non-breeding owls in relation to indices of vole densities. (a) Short-eared Owl, immediate response; (b) Barn Owl, lag in response in decline years; (c) Great Horned Owl, long lag in response, with the peak in total owl numbers one year behind the peak in prey numbers, and in breeding owl numbers two years behind. From Korpimäki & Norrdahl 1991, Taylor 1994, Rohner 1995.

(Petty 1992), but in the Great Horned Owl most individuals reach two or more years before they attempt to breed (Rohner 1995).

The extent of fluctuations in the spring densities of resident owl species depends largely on how much the birds have access to alternative prey, which allow them to survive through periods when their main prey are scarce. In the Tawny Owl, which in southern Britain has ready access to other mammals, birds and invertebrates, pair numbers in one study tended to remain fairly stable, changing by no more than about 15% from one spring to the next, unless affected by a hard winter (Southern 1970). In northern Britain, where a smaller range of prey is available, Tawny Owl pair numbers changed by up to 24% from one spring to the next (Petty 1992). Similarly in the Barn Owl, which in northern Britain has few alternative prey, year-to-year fluctuations were even greater, with numbers doubling or halving from one year to the next, in parallel with changes in rodent densities (Taylor 1994). In all the species mentioned, however, the proportion of the diet made up of the primary prey increased as the density of that prey increased in the environment (for Tawny Owl, see Southern 1970, Petty 1999; for Ural Owl, see Saurola 1989; for Barn Owl, see Taylor 1994; for Great Horned Owl, see Adamcik *et al.* 1978).

The second type of response is shown by 'prey-specialist' nomadic species, which concentrate to breed in different areas in different years, depending on where their food is plentiful at the time. Typically, individuals might have 1–2 years in the same area in each 3–5 year vole cycle, before moving on when prey decline. They thus respond to their food-supplies more or less immediately, so that their local densities can match food-supplies at the time, with minimal lag. The Short-eared Owl, Long-eared Owl, Northern Hawk Owl, and to some extent, Snowy Owl and Great Grey Owl are in this category. Their local densities can vary from nil in low rodent years to several tens of pairs per 100 km^2 in intermediate (increasing) or high rodent years. In an area of western Finland, for example, over an 11-year period, numbers of Short-eared Owls varied between 0 and 49 pairs, and numbers of Long-eared Owls between 0 and 19 pairs, in accordance with spring densities of *Microtus* voles (Korpimäki & Norrdahl 1991). When rodents are plentiful, such species tend to raise large broods, so if they are successful in finding prey-rich areas year after year, individuals could in theory breed well every year, buffered from effects of local fluctuations in their prey. In practice, however, they may not always find suitable prey-rich areas. In all the species mentioned, individuals have sometimes been seen in areas with low prey populations, typically as single wide-ranging non-breeders, rather than as territorial pairs (Pitelka *et al.* 1955, Menyushina 1997). In addition, if previously high rodent numbers crash during the course of a breeding season, nest desertion and chick mortality can be high. Under these conditions, 22 out of 24 nests of Short-eared Owls in south Scotland failed, and most of the adults left the area in early summer, when they would normally be raising young (Lockie 1955).

Nomadic species do not invariably appear each year in all areas where prey are plentiful: in parts of their breeding range they appear in numbers only at irregular intervals, far longer than the 3–5 years between rodent peaks. For example, several hundred pairs of Snowy Owls bred on the tundra of Swedish Lapland in 1978, where they had been rare to non-existent in many previous years (Andersson 1980). Snowy Owls bred in Finnish Lapland in 1974, 1987 and 1988, but before this date, none were seen breeding for several decades (Saurola 1997). Similarly, Hawk Owls bred in an area in Norway in the peak years of only four out of seven observed vole cycles (Sonerud 1997). This lack of response may arise because in many years the entire owl population can be absorbed in certain parts of the range with abundant prey, without needing to search out other parts. Breeding would then be dependent on an influx coinciding with a rodent peak (for Hawk Owl, see Sonerud 1997). In Fennoscandia, the numbers of Snowy and Hawk Owls at any time is determined largely by the arrival of large numbers from further east, recorded in Hawk Owls in the autumns of 1912, 1950 and 1984 (Sonerud 1997). Absence from specific localities in high rodent years has also been described in the Short-eared Owl (Maher 1970, Clark 1975) and Great Grey Owl (Hildén & Solonen 1987). Given the conditions they require, with exceptionally high microtine densities, it is not surprising that most nomadic species breed in northern boreal and tundra regions, and resident species mainly further south.

Some owl species that exploit sporadic food-supplies move around mainly within the breeding range, as exemplified by the Tengmalm's Owl and Northern Hawk Owl in forest. In other species, part of the population migrates to lower latitudes in winter, thereby avoiding the worst effects of snow cover, and returns to the breeding range each spring, settling in areas where voles happen to be numerous at the time. This pattern is exemplified by the Short-eared Owl and Long-eared Owl (Korpimäki & Norrdahl 1991). These two species hunt by quartering suitable vole habitat, a relatively expensive method compared to the sit-and-wait methods of most other owls (Sonerud 1984). This may be why they tend to leave areas with prolonged winter snow cover.

Local changes in nomadic owl densities from year to year are sometimes accompanied by changes in the size of territories (or foraging areas), with individuals ranging over larger areas when food is scarce (for Short-eared Owl, see Lockie 1955). In other species, they are also associated with changes in the occupancy of particular territories, with 'good' territories being occupied almost every year, and 'poor' territories only in high rodent years (Korpimäki 1988). Hence, through continuous nesting habitat, breeding distribution may expand and contract through each rodent cycle, and some places may be largely or entirely vacated in years when prey are scarce.

Relationships between nomadic owl and microtine densities have been studied mainly in particular areas, monitored over a number of years. Such studies have revealed temporal correlations between predator and prey numbers. However, spatial correlations were found by Wiklund *et al.* (1998), who counted predators and prey in 15 different localities on the Eurasian tundra in a single year. These areas extended from the Kola peninsula in the west, through 140° of longitude, to Wrangel Island in the east. Comparing areas, densities of Snowy Owls (and two skua *Stercorarius* species) were correlated with densities of lemmings, which were at different stages of their cycle in different areas.

The two responses (delayed and simultaneous) are not completely distinct, and different species of owls and raptors may be better described as forming a gradient in response, from the most sedentary at one end to the most mobile at the other. Moreover, the same species may show regional variation in behaviour depending on food-supply, and the extent to which alternative prey are available when favoured prey are scarce. The more varied the diet, the less the chance of all prey types being scarce at the same time. Korpimäki (1986) examined the population fluctuations, movements and diet of Tengmalm's Owls from studies at 30 different European localities extending from about 50°N to 70°N. The amplitude and cyclicity of owl population fluctuations increased northward, while diet breadth and degree of site fidelity decreased northwards. This fitted the fact that microtine fluctuations became more pronounced and more synchronised northwards, while the number of alternative prey decreased. Furthermore, snow conditions were more important in the north, because this small owl cannot easily get at voles protected by deep snow. In general, then, Tengmalm's Owl could be described as a resident generalist predator of small mammals and birds in central Europe, as partially nomadic (with males resident and females moving around) in south and west Finland, and as a highly nomadic microtine specialist in northern Fennoscandia, in areas with pronounced vole cycles. Similarly, the Long-eared Owl shows greater year-to-year site fidelity in the Netherlands than in Finland (Wijnandts 1984, Korpimäki 1992), as does the Great Grey Owl in different parts of North America (Collister 1997, Duncan 1997), while the Barn Owl is highly sedentary in Britain (Taylor 1994), but more dispersive in parts of continental Europe and North America (Marti 1999). In southeast Spain, Barn Owls fed on rats whose numbers did not fluctuate greatly between years; accordingly, and in contrast to Barn Owls elsewhere, they showed no significant annual variation in laying dates and clutch-sizes (Martinez & Lopez 1999).

Among lagomorph feeders, the Great Horned Owl would seem to show much greater fluctuation in the north of its range, where it depends primarily on Snowshoe Hares, than further south where it has a wider range of prey, but I know of no detailed studies in the southern parts. There would be little value in Great Horned Owls in northern areas breeding nomadically, because, as mentioned above, Snowshoe Hares seem to fluctuate in synchrony over their whole range. Owls leaving one area because of a shortage of hares would therefore be unlikely to find many more hares anywhere else. This is in marked contrast to the microtine feeding species.

Different species in the same area

The fact that several species of rodent-eating owls can breed simultaneously in the same area, all dependent on the same prey species, means that, in particular localities, their populations and breeding success usually fluctuate in synchrony with one another, and with those of diurnal rodent-eating raptors and mammalian carnivores (Hagen 1969, Korpimäki & Norrdahl 1991,Village 1992). In other places, several rodent eaters may occur together, but concentrate on different prey, depending on the habitats and times of day in which they hunt. Most species respond most strongly to their single primary prey, but the Hawk Owl in North America (as opposed to Europe) eats small hares (juveniles) as well as microtine rodents. Rohner *et al.* (1995) found that Hawk Owl breeding densities from year to year were better correlated with the combined densities of *Microtus* and *Lepus* than with either prey alone. Both these prey occurred in the open areas where the owls hunted. There was no correlation with the numbers of *Clethrionomys* voles which occurred in woodland.

DEMOGRAPHIC RESPONSES

The changes in reproduction, mortality and movements that bring about year-to-year changes in breeding density have been examined in relation to food supply in at least 11 Holarctic Owl species (Table 1). The following aspects have been most frequently studied: (1) age composition, with greater proportions of young birds among breeders in good food years than in poor ones; (2) breeding frequency, with greater proportions of territorial pairs nesting in good food years than in poor ones (annual variation from <5% to >95% in some populations); (3) among birds that lay, earlier mean laying dates in good food years than in poor ones (annual variation in first egg dates >4 weeks in some populations); (4) larger clutches in good food years than in poor ones (annual variation more than three-fold in some populations); and (5) greater fledgling production in good food years than in poor ones (annual variation in mean number of young raised per pair more than 10-fold in some populations); (6) lower mortality of both first-year and older birds in good food years than in poor ones (annual variation up to 2-fold or more in some populations); (7) shorter natal and breeding dispersal distances in good food years than in poor ones (annual variation apparent but hard to quantify accurately); and (8) irruptive migration, with smaller proportions of birds leaving the breeding range, or migrating shorter distances, in good food years than in poor ones (annual variation apparent, but again hard to quantify). In addition to these major aspects of performance, other aspects studied in only a small number of species include: (9) egg-size which is larger (or less variable) in good food-years than in poor ones (Pieitiäinen *et al.* 1986); (10) repeat laying after nest failure which is more frequent in good

Table 1. Responses of various Holarctic owl species to annual fluctuations in their food supply.

- no response, + slight response, ++ moderate response, +++ strong response, according to criteria listed below.

Species	Territorial pair density[a]	Age composition of breeders[b]	Proportion that breed[c]	Breeding performance			Mortality		Movements		
				Laying date[d]	Clutch size[e]	Young per pair[f]	First year[g]	Adult[g]	Natal dispersal[h]	Breeding dispersal[h]	Irruptive migration[i]
Microtine feeders											
1. Tawny Owl *Strix aluco*	+	+	+++	+++	++	+++	++	++	++	+	
2. Ural Owl *Strix uralensis*	++	++	++	+++	++	+++	+	++	++	+	–
3. Barn Owl *Tyto alba*	++		+	+++	++	+++	++	++	++	++	–
4. Tengmalm's Owl *Aegolius funereus*	+++	++	+	+++	+	+	++		+++	+++	–
5. Great Grey Owl *Strix nebulosa*	+++		++		+	+++			+++	+++	+++
6. Snowy Owl *Nyctea scandiaca*	+++	++	+++		+	+++			+++	+++	+++
7. Long-eared Owl *Asio otus*	+++		+	++	++	+++			+++	+++	++
8. Short-eared Owl *Asio flammeus*	+++			++		+++			+++	+++	++
9. Northern Hawk Owl *Surnia ulula*	+++				++				+++	+++	+++
Lagomorph-feeders											
10. Eurasian Eagle Owl *Bubo bubo*			++	+		++					–
11. Great Horned Owl *Bubo virginianus*	++		+++	+	+	+	++	++	+++		+++

References: (1) Southern 1970, Melée *et al.* 1978, Petty 1992, Petty & Fawkes 1997, Petty & Peace 1992, Jedrzejewski & Jedrzejewski 1998, Saurola 2002; (2) Saurola 1989, 1992, 2002, Pietiäinen *et al.* 1986, Pietiäinen 1989, Brommer *et al.* 1998; (3) Honer 1963, de Bruijn 1994, Taylor 1994, Marti 1997, 1999; (4) Korpimäki 1985, 1987, Korpimäki & Lagerstrom 1988, Löfgren *et al.* 1986, Sonerud *et al.* 1988, Saurola 2002; (5) Nero 1980, Hildén & Helo 1981, Mikkola 1983, Stefansson 1983, Hildén & Solonen 1987, Duncan 1992, Sulkava & Huhtala 1997: (6) Shelford 1945, Gross 1947, Chitty 1950, Pitelka *et al.* 1955, Watson 1957, Menyushina 1997; (7) Village 1981, 1992, Korpimäki & Norrdahl 1991, Korpimäki 1992a; (8),Lockie 1955, Holzinger *et al.* 1973, Village 1987, 1992, Schmidt & Vauk 1981, Arroyo & Bretagnolle 1999; (9) Korpimäki & Norrdahl 1991, Rohner *et al.* 1995, Sonerud 1997; (10) Olsson 1979, 1997, Martinez *et al.* 1992; (11) Adamcik *et al.* 1978, Houston 1978, 1999, Keith & Rusch 1988, Houston & Francis 1995, Rohner 1996; all species, Dementiev & Gladkov 1954, Cramp 1985.

Criteria for grading of response, according to annual variation in:

[a] Breeding density + = less than 2-fold, ++ = 2–10 fold, +++ = >10 fold

[b] Age composition ++ = no yearlings in poor food years

[c] Proportion that breed + = <2-fold, ++ = 2–10 fold, +++ = >10 fold

[d] Laying date + = <2 weeks, ++ = 2–3 weeks, +++ = >3 weeks

[e] Clutch size + = <2 fold, ++ = 2–3 fold, +++ = >3 fold

[f] Young per pair + = <2 fold, ++ = 2–4 fold, +++ = >5 fold

[g] Mortality + = <2 fold, ++ = >2 fold

[h] Natal and breeding dispersal ++ = longer or more obvious movement in poor food years, +++ = >2 fold, increase in mean or median distances, or total emigration in poor years

[i] marked variation in numbers of birds migrating in different years, usually in regular cycles, in some years extending beyond usual winter range

Other Holarctic mammal-eating owl species that are perhaps best classed as residents include Barred Owl *Strix varia*, Northern Spotted Owl *S. occidentalis*, Eurasian Pygmy Owl *Glaucidium passerinum* and Northern Pygmy Owl *G. californicum*, while nomadic species probably include Saw-whet Owl *Aegolius acadicus*, but insufficient information is available to be sure.

food-years than in poor ones (Melée *et al.* 1978); (11) female body mass during incubation and brooding which is larger in good years (Pieitiäinen & Kolunen 1993, Petty 1992); and (12) nest defence, which is more vigorous in good food years (Wallin 1987). With food-related variation in both breeding density and breeding performance, the number of young owls produced per unit area of habitat, even in resident species, can vary enormously from year to year: for example, from 12 to 336 young Ural Owls per year in the same area of Finland over a 25-year period (Saurola 1992).

As indicated earlier, resident owl species show year to year variation mainly in reproductive rate and to a lesser extent in mortality and movements, whereas in nomadic species, movements play a major role, and the main year-to-year variation is in settling patterns (Table 1). It is in the more nomadic species that clutch sizes and reproductive rates tend to be larger, but the effects of variation in food supply on reproduction and mortality are hard to assess because such species have been studied chiefly in good food areas, which they leave when prey densities fall. Not surprisingly, therefore, there are large gaps in our knowledge of these species (Table 1).

Food-supply permitting, at least three Holarctic owl species have been known to raise two broods in a season, namely Barn Owl, Long-eared Owl and Short-eared Owl (Cramp 1985). The first two species have also been recorded nesting into autumn, and the Short-eared Owl into winter (Dementiev & Gladkov 1954). In a study in France, 34% of 146 Barn Owl pairs raised two broods in one year (Baudvin 1975), and in a study in Utah, 11% of 262 raised two broods in one year (Marti 1997), while in tropical Malaysia some Barn Owls even raised three broods in a year (Lenton 1984). In addition, some owls in good prey conditions have been found to breed bigynously, as recorded in Barn Owl, Tawny Owl, Tengmalm's Owl, Great Grey Owl, Northern Hawk Owl, Snowy Owl, as well as Common Scops Owl, while biandry has been recorded in Barn Owl and Tengmalm's Owl (Watson 1957, Solheim 1983, Sonerud *et al.* 1987, Korpimäki 1988a, 1992, Taylor 1994, Menyushina 1997, Sulkava & Huhtala 1997).

Starvation is clearly a major cause of mortality in both nestling and adult owls, being especially prevalent in poor food years. For nestlings, it has been documented in most of the studies mentioned in this paper, but for adults much less information is available. However, starvation victims are often prevalent among owls found dead, especially in low rodent years, as recorded in Tawny Owl, Great Grey Owl, Ural Owl, Tengmalm's Owl, Short-eared Owl, and Barn Owl (Honer 1963, Southern 1970, Stefansson 1979, de Bruijn 1994). In addition, the proportions of starvation victims among dead owls found by members of the public (for Barn Owl, see Newton *et al.* 1997; for Tawny Owl, see Hirons *et al.* 1979; for Great Horned Owl, see Franson & Little 1996) were much higher than recorded among samples of other bird species (Newton 1998).

Overall, all eleven species listed in Table 1 have been found to respond to a lesser or greater extent to annual variations in their food supply (Table 2). Failures were usually much more frequent at the pre-laying and egg stages than at the nestling and post-fledging stages. Only in irruptive migration is a response shown by only a proportion of species. The responses are especially strong (and hence noticeable) in these microtine- and lagomorph-eaters, because they all experience huge year-to-year fluctuations in their food-supply, far greater than those experienced by most other kinds of birds. This does not imply, however, that food-supply is less important in the population dynamics of other owls, which eat other prey. Associated with more stable food-supplies, other Holarctic owl species show much less year-to-year variation in breeding densities and performance than some of the microtine and lagomorph feeders. Nor does the prevalence of food-related responses imply that other factors have only trivial influence

Table 2. Effect of food-supply on annual variations in breeding density and performance of eleven Holarctic owl species.

	Number examined	Effect shown:			
		Nil	Small	Moderate	Large
Breeding density	10	0	1	4	5
Age composition	4	0	1	3	0
Breeding performance					
Proportion laid	9	0	3	3	3
Laying date	8	0	2	2	4
Clutch size	9	0	4	5	0
Young raised per pair	10	0	1	2	7
Mortality					
First year	5	0	1	4	0
Adult	4	0	0	4	0
Movements					
Natal dispersal	10	0	2	1	7
Breeding dispersal	9	0	2	1	6
Irruptive migration	11	5	0	2	4

on the population ecology of rodent- and lagomorph-feeding owls, for all may sometimes be limited in density or performance by other factors, which prevent them from exploiting to the full a good food supply, as discussed below.

Modifying influence of weather

In much of northern Eurasia and North America, winter snow provides a protective blanket over small rodents that live and breed in the vegetation beneath. The level of protection that snow provides depends on its depth, the hardness of the surface crust, and the duration of lie, all of which tend to increase with latitude. Different species of owls vary in their ability to detect and secure rodents under snow, and in general the larger (heavier) species are better able to penetrate snow than smaller ones. The Great Grey Owl is renowned for its ability to smash through hard deep snow (45cm or more) to catch rodents which it apparently detects by ear (Nero 1980), while small species, such as Tengmalm's Owl, are affected by even very shallow snow (Sonerud 1984). The behaviour of the rodents themselves also affects their accessibility to owls, particularly the frequency with which they emerge and run along the surface. This activity is much reduced in spring, when pools of melt water can lie above the crust.

In these various ways, snow cover can greatly influence prey availability for owls. It can sometimes stop them responding in the usual way to a rodent peak in early spring, affecting breeding density, proportion of pairs nesting and clutch size (for Snowy Owl, see Menyushina 1997), and in some winters it can lead to large-scale starvation even when voles are plentiful (for Barn Owl, see Shawyer 1987, Taylor 1994; for Tawny Owl, see Jedrzejewski & Jedrzejewski 1998, Saurola 1997).

Nest sites

The numbers of some owl species (like those of some other bird species) can in certain areas be held by shortage of nest-sites below the level that food-supply would permit (Newton 1998). The evidence is of two kinds: (1) breeders may be absent from areas that lack nest-sites but which are suitable in other respects (non-breeders may live there), and (2) provision of artificial nest-sites can lead to an increase in breeding density, while removal of nest-sites can lead to a decrease in breeding density.

Some Holarctic owl species are obligate cavity nesters, and where natural sites are scarce, breeding densities can increase following the provision of nest boxes (for Little Owl *Athene noctua*, see Exo 1992; for Barn Owl, see Petty *et al.* 1994). The presence of Barn Owls in an area of northern Utah was attributed entirely to the presence of artificial structures, for the area had no natural nest sites (Marti 1997). Conversely, decline in Barn Owl numbers in parts of Britain has been attributed to the collapse or renovation of old buildings in which they nested (e.g. Ramsden 1998). Similarly, several owl species in northern Europe are thought to have declined following the felling of old growth forest, and the associated cavity-trees, together with the removal from young forests of dead snags likely to provide nest sites (cavities or broken tops). These species increased following widespread provision of nest boxes.

Other owl species, while preferring cavities, nest in a wide range of other sites where cavities are scarce, including the old stick nests of other birds. The Great Grey Owl is in this category, but has still responded to the provision of man-made stick nests in parts of Europe and North America where natural sites were scarce, and apparently increased in breeding density (Nero 1980, Mikkola 1983, Sulkava & Huhtala 1997). Yet other species, notably Short-eared and Snowy Owls, are obligate ground nesters, so are presumably not normally limited by shortage of sites, although available sites may vary in quality, as for other species.

A common experience is that, when boxes are provided, they are soon occupied, but care is needed to ensure that this represents a real increase in density, rather than merely a shift from other less preferred sites. It is mainly in managed forests, where trees are too young to contain cavities, that owls most readily take to nest boxes and where most population studies have been made. In contrast, Mossop (1997) erected more than 100 nest boxes in natural forest in the Yukon, and after five years only 1% had been used by Boreal Owls. He concluded that natural nest-sites were not in short-supply in this old-growth forest. Similarly, in planted conifer forests in northern England, all of 40 pairs of Tawny Owls switched from various non-cavity sites to nest boxes within four years of boxes being provided (Petty *et al.* 1994), whereas in old broadleaved woodland in southern England, where natural cavities were plentiful, no more than 56% of nesting attempts were in boxes (Southern 1970). In both studies more than one box was available in each territory.

Species that are flexible in type of nest site sometimes show better success in the more secure sites. For example, among Barred Owls in Michigan, 80% of 81 clutches in tree cavities or nest boxes produced young, at 2.0 young per productive nest, while only 31% of 13 clutches on hawk nests or other open sites produced young, at 1.0 young per productive nest (Postupalsky *et al.* 1997). Similar differences between different types of sites were noted in Northern Spotted Owls, Tengmalm's Owls and others (Forsman *et al.* 1984, Korpimäki 1984). Such differences were not due entirely to predation, but to the frequent tendency of nestling owls to leave open nests when half grown. This led some young to fall prematurely from stick nests, while in cavity nests they were contained for longer. Some stick nests also collapsed in part because the owls scraped out the bottom before laying.

Predation and disease

While owls fall prey to various predators, including other owls (Mikkola 1976), and to various pathogens, it is hard to assess whether predation or disease affect their breeding densities. Like other birds, owls may be more prone to predation and disease at times of food shortage. Adair (1892) recorded no less than eight adult and 68 young Short-eared Owls outside a single Red Fox *Vulpes vulpes* den during a vole plague. This occurred at the time of a vole crash, when many owls were nesting, but when foxes which (like the owls) had been feeding on voles suddenly switched to other prey. Losses of newly-fledged Tawny Owls from predation was greater in a poor food year, possibly because starving young allowed a closer approach then and females defended their young less well (Coles & Petty 1997). Similarly, deaths of nestling Great Horned Owls to the protozoan blood parasite, *Leucocytozoon*, occurred when hare numbers crashed and when the young owls were weakened by food-shortage (Hunter *et al.* 1997). Increases in blood parasite levels, associated with poor food-supplies or increased parental effort in feeding young, have been recorded for at least two owl species dependent on cyclic prey (for Tawny Owl, see Appleby *et al.* 1999; for Tengmalm's Owl, see Korpimäki *et al.* 1993, Ilmonen *et al.* 1999). Only in poor food conditions did blood parasites lower breeding success (Korpimäki *et al.* 2002).

Although some owl species have been suspected of limiting the distribution of others (for Eurasian Eagle Owl possibly affecting Ural Owl, see Saurola 1992; for Ural Owl possibly affecting Tengmalm's Owl, see Hakkarainen & Korpimäki 1996; for Tawny Owl possibly affecting Tengmalm's and Eurasian Pygmy Owls, see Koenig 1998; and for Ural Owl and Tawny Owl possibly affecting one another, see Lundberg 1980; for Barred Owl possibly affecting Northern Spotted Owl, see Dark *et al.* 1998), there is no conclusive evidence on whether their predation or competition has this effect. However, between Barred and Northern Spotted Owls, hybridisation has occurred repeatedly (Dark *et al.* 1998). It is clear, therefore, that, while food-supply is the primary limiting factor for the owls discussed in this paper, nest-site shortages, adverse weather or other secondary factors can sometimes reduce breeding densities and performance below what food supply would otherwise permit.

MOVEMENTS

For present purposes, it is helpful to distinguish three main types of movements: (1) natal dispersal, measured for each individual as the distance between birthplace and breeding place; (2) breeding dispersal, measured as the distance between the breeding sites of different years; and (3) irruptive migration to lower latitudes for the winter, involving varying proportions of birds, and varying distances, from year to year.

Natal dispersal

Differences in natal dispersal distances are apparent between resident and nomadic species. Most individuals of resident species move less than 20 km between birthsite and breeding site, and few move further than 100 km (for Tawny Owl, see Petty 1992, Saurola 2002; for Ural Owl see Saurola 1987, 2002; for Barn Owl see Taylor 1994). The movements may be longer in poor food years than in good ones, as noted in Barn Owl (de Bruijn 1994, Taylor 1994), Tawny Owl

(Saurola 2002), Ural Owl (Saurola 2002), Tengmalm's Owl (Saurola 2002) and Great Horned Owl (Adamcik *et al.* 1978, Houston 1978). Typically it is the young produced in peak food years that move further, because it is they that experience the crash that follows the peak; they are also more numerous than young produced in other years, which could further add to their difficulties.

Much less information is available for nomadic species, but much longer distances have been recorded than for resident ones. Movements exceeding 1,000 km have been documented for Short-eared Owl (up to about 4,000 km), Long-eared Owl (up to about 2,300 km) and Hawk Owl (up to 2,700 km) (Saurola 1983, 1997, 2002, Cramp 1985). In Tengmalm's Owl, which has provided more information, natal dispersal distances of females tend to be longer than those of males (as in many other birds, Greenwood 1980), and longer in poor vole years (following peaks) than in good ones (Sonerud *et al.* 1988). Other information on natal dispersal distances in all the above species are given in this volume by Saurola (2002).

Breeding dispersal

In sedentary owl species, such as Tawny, Ural and Barn Owls, adults usually remain in the same territories year after year, as mentioned above, with only small proportions moving to other territories, usually nearby (Saurola 1989, Petty 1992, Taylor 1994). One consequence of such strong site fidelity is strong mate fidelity, as partners remain together year after year, so long as neither dies or changes territory (for Tawny Owl, see Melée *et al.* 1978; for Ural Owl, see Saurola 1987).

Nomadic species, in contrast, may be present in particular localities at high densities for 1–2 years at a time, yet scarce or absent in the preceding and following years. The implication, that individual adults may breed in widely separated localities in different years, is supported by ring recoveries, although the proportions of individuals that move can vary from year to year, depending on food conditions.

Tengmalm's Owl, which nests readily in boxes and has been studied at many localities, has provided most information. In this species, males are mainly resident and females are highly dispersive (Fig. 3). Both sexes tend to stay in the same localities if vole densities remain high, moving no more than about 5 km between nest boxes used in successive years, but if vole densities crash, females move much longer distances. Many females have been recorded moving 100–580 km between breeding sites in different years (Fig. 3). Of females that moved shorter distances, two that bred as neighbours (1 km apart) in 1981 moved 70 km and bred again as neighbours (2 km apart) in 1982 (Löfgren *et al.* 1986). In contrast, few long movements were observed in males: most moved no more than 3 km (as did females during vole peaks), but one moved 21 km between breeding sites in 1982 and 1984 (Löfgren *et al.* 1986), and two moved more than 100 km (Fig. 3). As expected, females that moved long distances between breeding seasons also changed their mates. The greater residency of males has been attributed to their need to guard cavity nest-sites which are scarce in their conifer forest habitat, while their smaller size makes them better able than females to catch small birds, and hence to survive through low vole conditions (Lundberg 1979, Korpimäki *et al.* 1987).

In other species, both sexes may be inferred to move long distances, because areas can become almost deserted (or re-occupied) from one year to the next. Although the chances of recording marked individuals at places far apart are low, Short-eared Owls have provided some interesting records. In a study in south Scotland, 21 breeders were tagged in 1976. Vole numbers then

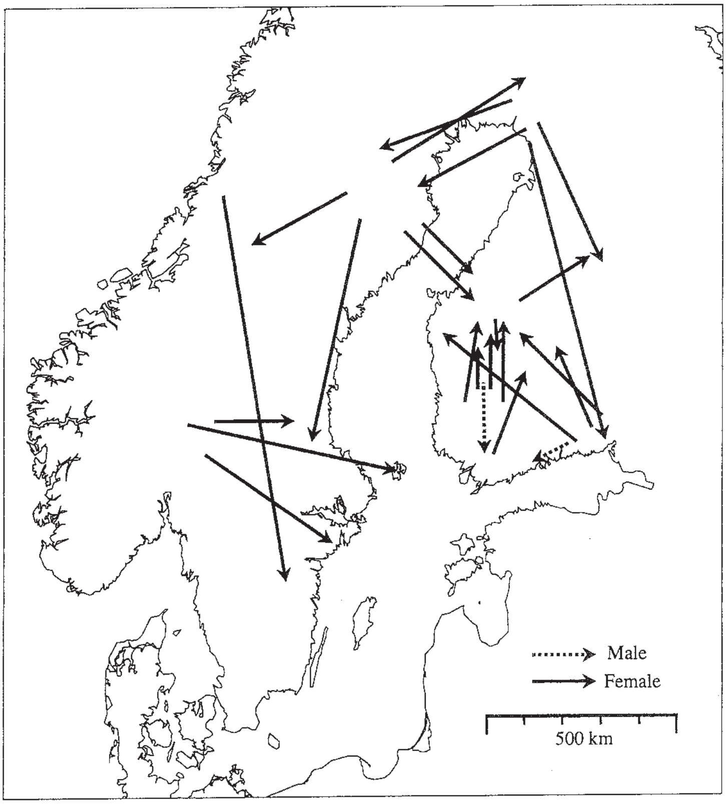


Fig. 3. Movements of >100 km recorded in marked adult Tengmalm's Owls between nest boxes used in different years. Compiled from data in Löfgren *et al.* 1986, Korpimäki *et al.* 1987 and Sonerud *et al.* 1988.

crashed, and only one of the tagged birds remained to breed in the area in 1977. However, two others were reported in spring 1977 in nesting habitat 420 km and 500 km to the northwest, and the latter, at least, was proved to breed there (Village 1987). In contrast, of seven breeders tagged in 1977, when vole numbers began to increase, three bred in the area in 1978. Hence, as in Tengmalm's Owl, individuals seemed more likely to remain to breed in successive years when voles were increasing than when they were declining.

Recoveries of Hawk Owls and Great Grey Owls ringed as breeding adults include examples of both males and females residing in an area from one nesting season to the next when microtine abundance remained high and of both sexes leaving when microtine populations declined (Sonerud 1997, Duncan 1992). Adult radio-marked Great Grey Owls in Manitoba and northern Minnesota dispersed 41–684 km (mean = 329, SD = 185, $N = 27$) between breeding sites in response to prey population crashes. Eleven marked birds that did not disperse did not survive (Duncan 1992, 1997). Two ringed Great Grey Owls in northern Europe were found at localities 300 km and 430 km apart in different breeding seasons (Hildén & Solonen 1987). The only other records for nomadic species known to me involve three adult Long-eared Owls in North America, which were found at localities more than 450 km apart in different breeding seasons (Marks *et al.* 1994), and further records from northern Europe given elsewhere in this volume (Saurola 2002).

Irruptive migration

Some owl species, as mentioned, respond to periodic crashes in their main prey by winter emigration, appearing south of their breeding range in much larger numbers than usual. Irruptions of Snowy Owls from the tundra to the boreal and temperate regions of eastern North America have

Table 3. Irruptions of Snowy Owls into eastern United States. From various sources.

1881–1920	1921–1960	1961–2000
—	1921	—
1882	—	—
—	—	—
—	—	1964
—	—	—
1886	1926	—
—	—	1967
—	—	—
1889	—	—
—	1930	—
—	—	1971
1892	—	—
—	—	—
—	1934	1974
—	—	—
1896	—	—
—	1937	—
—	—	1978
—	—	—
—	—	—
1901	1941	1981
—	—	—
—	—	—
—	—	—
1905	1945	—
—	—	1986
—	—	—
—	—	—
1909	1949	—
—	—	—
—	—	1991
1912	—	—
—	1953	—
—	—	—
—	—	—
—	—	1996
1917	1957	—
—	—	—
—	—	—
—	1960	2000

been documented since 1880. Throughout this 120-year period, irruptions have occurred every 3–5 years, at a mean interval of 3.9 (± SE O.13) years (Table 3). Moreover, in periods when information on lemmings was available from the breeding areas, mass movements of owls coincided with crashes in lemming numbers (Shelford 1945, Chitty 1950). In western North America, irruptions were not well synchronised with those in the east, presumably reflecting asynchrony in lemming cycles between breeding regions. The irruptions were also less regular and less pronounced in the west than in the east, with some birds appearing on the prairies every year (Kerlinger *et al.* 1985).

In eastern North America, two other vole-feeders, the Rough-legged Hawk *Buteo lagopus* and Northern Shrike *Lanius excubitor*, have irrupted at similar 3–5 year intervals, mostly (but not always) in the same years as Snowy Owls (Davis 1937, 1949, Speirs 1939, Shelford 1945, Lack 1954). Perfect synchrony between the three species would perhaps not be expected, because their breeding ranges only partly overlap. The hawk and the shrike breed mainly in the transition zone between forest and tundra, while the owl breeds on the open tundra, but part of the owl population winters in the transition zone. Nonetheless, with most invasions of each species coinciding with those of the other species, the level of synchrony is remarkable.

In North America, Great Grey Owl irruptions are also occasionally recorded south and east of the breeding range, with big flights noted in eastern regions in 1978, 1983, 1991 and 1995 (Nero *et al.* 1984, Davis & Morrison 1987, Bull & Duncan 1993, National Audubon Field Notes for later years), while Saw-whet Owl migrations are also more marked in some years than in others (National Audubon Field Notes). In Europe, the Great Grey, Long-eared, and Short-eared Owls seem to migrate on regular 3–5 year patterns (Harvey & Riddiford 1996, Schmidt & Vauk 1981, Hildén & Helo 1981). The same is true for the Snowy Owl further east, with invasions recorded in European Russia in 1911, 1915, 1919, 1922, 1926, 1932 and 1935 (Dementiev & Gladkov 1954), different years to those in eastern North America over the same period. Partly because irruptions tend to follow good breeding seasons, and partly because juveniles are more affected by shortages than adults, juveniles tend to predominate among irruptive migrants. They formed 85% of all Hawk Owls obtained in northern Europe in 1950, 100% of those obtained in 1976, and 88% of museum skins collected over several years (Cramp 1985). In Snowy Owls, juveniles predominated in invasion years, but in other years when few owls appeared, the majority were adults and many were underweight (Smith 1997). Not all owl invasions follow good breeding years, however, and after a known poor year, only four out of 126 Great Grey Owls trapped in Manitoba in 1995 were juveniles (Nero & Copland 1997).

Another example of the link between widespread winter emigration and food-supply is provided by the Great Horned Owl which, along with the Northern Goshawk *Accipiter gentilis*, is a major predator of the Snowshoe Hare in North America. Because Goshawks fly by day and are more readily seen, their invasions have been better documented than those of owls. They occur for 1–3 years at a time, but at about 10-year intervals (Table 4), coinciding with known lows in the hare cycle (Keith 1963, Keith & Rusch 1988, Mueller & Berger 1967, Mueller *et al.* 1977).

Great Horned Owls fly by night, and involve movement into more southern regions already well populated by resident Great Horned Owls, so their irruptions have been less well documented. However, all those that I could find recorded in the literature coincided with Goshawk invasions, and hence with low hare numbers, again providing strong circumstantial evidence that food-shortage stimulated large-scale emigration in this mainly resident species. Annual emigration rates of radio-marked Great Horned Owls from Kluan, Yukon Territory, increased from 0 to 33% for territory holders and from 0 to 40% for non-territorial floaters, as hares declined

Table 4. Irruptions of Goshawks and Great-Horned Owls in North America. From various sources.

1881–1920		1921–1960		1961–2000	
Owl	**Hawk**	**Owl**	**Hawk**	**Owl**	**Hawk**
—	—	—	—	—	—
—	—	—	—	1962	1962
—	—	—	—	1963	1963
—	—	—	—	—	—
—	—	1925	—	—	—
—	1886	1926	1926	—	—
1887	1887	1927	1927	—	—
—	—	—	1928	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	1972	1972
—	—	—	—	1973	1973
—	—	—	—	—	1974
—	—	—	1935	—	—
—	1896	1936	1936	—	—
1897	1897	1937	—	—	—
—	—	1938	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	1981	1981
—	—	—	—	1982	1982
—	—	—	—	—	1983
—	—	—	1944	—	—
—	—	—	—	—	—
—	1906	—	—	—	—
1907	1907	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	1992	1992
—	—	—	—	—	1993
—	—	—	1954	—	1994
—	—	—	—	—	—
1916	1916	—	—	—	—
1917	1917	—	—	—	—
1918	—	—	—	—	—
—	—	—	—	—	—
—	—	—	—	—	—

(Rohner 1996). To judge from ring recoveries, movement from northern Saskatchewan is mainly to the southeast, with some birds travelling more than 1,000 km from their breeding sites (Houston & Francis 1995, Houston 1999). As in other irruptive migrants, the survivors are presumed to return to their breeding range in later years.

Irruptive migrants do not necessarily remain in the same localities throughout a winter, as trapping has revealed some turnover in the individuals present at particular sites (for Great Grey Owl, see Nero *et al.* 1984; for Snowy Owl, see Smith 1997). The implication is that, in the non-breeding period, individuals move around, perhaps in continual search for good hunting areas. Local abundances of microtines can attract high densities of nomadic owls, and in these conditions some species form communal roosts, as recorded often in Long-eared and Short-eared Owls (Cramp 1985) and also in Great Grey Owls (Nero *et al.* 1984).

NON-TERRITORIAL FLOATERS IN OWL POPULATIONS

In addition to territorial pairs, owl populations may contain non-territorial floaters, which can arise in at least two types of circumstances. First, in years of low food-supply, some birds do not even attempt to defend territories, but live as single or grouped individuals that, although resident, range over large foraging areas. This is evident in Snowy Owls, but during low lemming years (Maher 1970, Pitelka *et al.* 1955) and in Long-eared Owls during low vole years (Korpimäki 1992). It is presumably the need to range widely for food and to hunt over much of each day that in poor food conditions prevents fixed-site, energy-expensive territorial defence. In these circumstances densities are low, and birds are under no obvious social pressure from other individuals. Secondly, non-territorial floaters can arise under conditions of good food-supply, when all available territories are occupied, and some individuals (mostly in the younger age groups) are excluded from gaining territories by the existing territorial occupants. Such birds do not normally advertise themselves, but are known to be present from the rapid replacement of territorial birds that die (Newton 1992). In the Great Horned Owl, such birds reached greatest numbers after good breeding years, and at a hare population peak, Rohner (1997) found by radio-tagging that floaters formed 40–50% of the local owl population.

This is not to suggest that floaters are always present in owl populations. They are seldom evident in Short-eared Owls, Long-eared Owls and Barn Owls during peak years, and among Tawny Owls in peak vole years, new recruits to the breeding population were mostly 2-year and 3-year birds. In the following years when vole numbers were declining, most of the new recruits were yearlings, suggesting that there were no older birds left in the non-territorial sector then (Petty 1992).

CONCLUDING REMARKS

These data for Holarctic owls show the marked affects of food-supply, not only on numbers, but on every aspect of demography, including age of first breeding, reproduction (proportion of pairs laying, hatching and fledging young, clutch and brood sizes), juvenile and adult survival, natal and breeding dispersal, and winter emigration. Few other types of birds have such a highly fluctuating and restricted (and hence measurable) food-supply, so few have shown the influence of food-supply so clearly. This is perhaps the main contribution that studies of Holarctic owls have made to our general understanding of avian ecology. Nonetheless, other factors, such as nest-sites or weather, influence their breeding densities and success, and in some species may achieve major importance in some areas or in some years.

Much the same could be said of some diurnal birds of prey, and nomadism in relation to a sporadic food-supply is well known in the Eurasian (Common) Kestrel *Falco tinnunculus* and Hen (Northern) Harrier *Circus cyaneus* (Hagen 1969, Newton 1979). It is also known in some nocturnal and diurnal birds of prey in other parts of the world; for example, in the Eastern Grass Owl *Tyto longimembris* and Letter-winged Kite *Elanus scriptus* in Australia (Hollands 1991, Olsen 1995).

In an earlier discussion of differences between resident and nomadic owl species, Korpimäki (1992) listed large body size, long life, strong territoriality and deferred maturity as associated with resident owl species, and small body size, short life, weak territoriality and non-deferred maturity as associated with nomadic species. Under the benefit of further information, none of these differences emerges as clear cut. In body size, the nomadic Snowy and Great Grey Owls are some of the largest species, while the resident Pygmy Owl is one of the smallest. On life-span and age of first breeding, insufficient data are available for most species. From their large clutch sizes, one might surmise, as did Korpimäki (1992), that the mortality rates of nomadic species must be higher than those of residents. This is not necessarily so, however, if some individuals of nomadic species refrain from breeding in some years. Unfortunately, ring recoveries of most nomadic species are still too few to allow reliable estimates of mortality rates and longevity. On territoriality, most nomadic species, such as Snowy, Short-eared, and Great Grey Owls, are strongly territorial, vigorously defending their hunting areas against conspecifics. Nonetheless, some nomadic species that use tree nests are often described as nesting close together (within 100m) in 'loose colonies'. This has been described for Long-eared and Great Grey Owls (Duncan 1997, Hildén & Solonen 1987), and probably occurs because nest sites are often clumped amid rich feeding areas. Typically these species nest in patches of forest and hunt on open land nearby. They mostly use old stick nests of other birds, which are themselves often clumped, having been constructed in different years in the same territories of the builder species. Hence, the differences listed by Korpimäki (1992) seem not to hold as generalisations, and some aspects need further study. On the other hand, the associations of nomadism with large clutch sizes and cyclic (as opposed to random) fluctations in food supply, that were predicted by Andersson (1980), have stood the test of time.

Looking to the future, more information is especially needed on the nomadic species, particularly on their movements. Because the chances of getting ring recoveries are so low, satellite-based radio-tracking seems to offer the best way forward. The main need is to track the same individuals over more than one year, to obtain information on the locations of their successive nesting attempts. Of all Holarctic species, the Hawk Owl, Snowy Owl, Great Grey Owl and Short-eared Owl are most in need of study in this way.

ACKNOWLEDGMENTS

I am grateful to Steve Petty, and to referees Hannu Pietiäinen and Iain Taylor for helpful comments on the manuscript. This paper was written while I was the grateful recipient of a Leverhulme Fellowship.

REFERENCES

Adair, P. 1892. The Short-eared Owl (*Asio accipitrinus*, Pallas) and the Kestrel (*Falco tinnunculus*, Linnaeus) in the vole plague districts. *Ann. Scot. Nat. Hist.* **1892**: 219–231.

Adamcik, R.S., Todd, A.W. & Keith, L.B. 1978. Demographic and dietary responses of Great Horned Owls during a Snowshoe Hare cycle. *Can. Field Nat.* **92**: 156–166.

Andersson, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. *J. Anim. Ecol.* **49**: 175–184.

Appleby, B.M., Anwar, M.A. & Petty, S.J. 1999. Short-term and long-term effects of food supply on parasite burdens in Tawny Owls, *Strix aluco*. *Functional Ecology* **13**: 315–321.

Arroyo, B.E. & Bretagnolle, V. 1999. Breeding biology of the Short-eared Owl (*Asio flammeus*) in agricultural habitats of southwestern France. *J. Raptor Res.* **33**: 287–294.

Baudvin, H. 1975. Biologie de reproduction de la Chouette effraie (*Tyto alba*) en Cote d'Or: premiers resultats. *Jean-de-Blare* **14**: 1–51.

Brommer, J.E., Pietiäinen, H. & Kolunen, H. 1998. The effect of age at first breeding on Ural Owl lifetime reproductive success and fitness under cyclic food conditions. *J. Anim. Ecol.* **67**: 359–369.

Bull, E.L. & Duncan, J.R. 1993. *Great Grey Owl. The Birds of North America.* **41**: 1–15.

Chitty, H. 1950. Canadian arctic wildlife enquiry, 1943–49, with a summary of results since 1933. *J. Anim. Ecol.* **19**: 180–193.

Clark, R.J. 1975. A field study of the Short-eared Owl *Asio flammeus* (Pontoppedon) in North America. *Wildl. Monogr.* **47**: 1–67.

Coles, C.F. & Petty, S.J. 1997. Dispersal behaviour and survival of juvenile Tawny Owls (*Strix aluco*) during the low point in a vole cycle. In Duncan J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997. Winnipeg, Manitoba, Canada*: 111–118. USDA Forest Service Gen. Tech. Rep. NCñ190.

Collister, D.M. 1997. Seasonal distribution of the Great Grey Owl (*Strix nebulosa*) in southwestern Alberta. In Duncan J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997. Winnipeg, Manitoba, Canada*: 119–122. USDA Forest Service Gen. Tech. Rep. NCñ190.

Cramp, S. 1985. *Handbook of the Birds of Europe, the Middle East and North Africa*, Vol 4. Oxford: Oxford University Press.

Dark, S.J., Gultiérrez, R.J. & Gould, G.I. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* **115**: 50–56.

Davis, D.E. 1937. A cycle in Northern Shrike emigrations. *Auk* **54**: 43–49.

Davis, D.E. 1949. Recent emigrations of Northern Shrikes. *Auk* **66**: 293–294.

Davis, D.E. & Morrison, M.L. 1987. Changes in cyclic patterns of abundance in four avian species. *Am. Birds* **41**: 1341–1347.

de Bruijn O. 1994. Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). *Ardea* **82**: 1–109.

Dementiev, G.P. & Gladkov, N.A. 1954. *Birds of the Soviet Union, Vol. 1.* Moscow: State Publishing House.

Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Grey Owl breeding dispersal. Unpub. PhD thesis, University of Manitoba, Winnipeg.

Duncan, J.R. 1997. Great Grey Owls (*Strix nebulosa nebulosa*) and forest management in North America: a review and recommendations. *J. Raptor Res.* **31**: 160–166.

Elton, C.S. 1942. *Voles, mice and lemmings.* Oxford: University Press.

Exo, K.M. 1992. Population ecology of Little Owls *Athene noctua* in Central Europe: a review. In Galbraith C.A., Taylor I.R. & Percival S. (eds.) *The ecology and conservation of European Owls*: 64–75. Peterborough: Joint Nature Conservation Committee.

Forsman, E.D., Meslow, E.C. & Wright, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* **87**: 1–64.

Franson, J.C. & Little, S.E. 1996. Diagnostic findings in 132 Great Horned Owls. *J. Raptor Res.* **30**: 1–6.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.

Gross, A.O. 1947. Cyclic invasions of the Snowy Owl and the migration of 1945–1946. *Auk* **64**: 584–601.

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. *Fauna* **22**: 73–126.

Hakkarainen, H. & Korpimäki, E. 1996. Competitive and predatory interactions among raptors: an observational and experimental study. *Ecology* **77**: 1134–1142.

Hansson, L. 1979. Field signs as indicators of vole abundance. *J. Appl. Ecol.* **16**: 339–347.

Hansson, L. & Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* **67**: 394–402.

Hanski, I., Hansson, L. & Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**: 353–367.

Harvey, P.V. & Riddiford, N. 1996. An uneven sex ratio of migrant Long-eared Owls. *Ringing & Migration* **11**: 132–135.

Hildén, O. & Helo, P. 1981. The Great Grey Owl *Strix nebulosa* – a bird of the northern taiga. *Ornis Fenn.* **58**: 159–166.

Hildén, O. & Solonen, T. 1987. Status of the Great Grey Owl in Finland. In Nero R.W., Clark R.J., Knapton R.J. & Hamre R.H. (eds.) *Biology and conservation of northern forest owls*: 116–120. USDA For. Serv. Gen. Tech. Rep. RMñ142.

Hirons, G.J.M., Hardy, A.R. & Stanley, P.I. 1979. Starvation in young Tawny Owls. *Bird Study* **26**: 59–63.

Hollands, D. 1991. *Birds of the night: owls, frogmouths and nightjars of Australia*. Balgowlah: Reed Books.

Hölzinger, J., Mickley, M. & Schilhansl, K. 1973. Untersuchungen zur Brut- und Ernahrungsbiologie der Sumpfohreule (*Asio flammeus*) in einem suddeutschen Brutgebeit mit Beinerkungen zum Auftreten der Art in Mitteleuropa. *Anz. orn. Ges. Bayern* **12**: 176–197.

Honer, R. 1963. Observations on the Barn Owl (*Tyto alba guttata*) in the Netherlands in relation to its ecology and population fluctuations. *Ardea* **51**: 158–195.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls and tularemia in northern Sweden. *Oecologia* **32**: 141–152.

Houston, C.S. 1978. Recoveries of Saskatchewan-banded Great Horned Owls. *Can. Field Nat.* **92**: 61–66.

Houston, C.S. 1999. Dispersal of Great Horned Owls banded in Saskatchewan and Alberta. *J. Field Ornithol.* **70**: 343–350.

Houston, C.S. & Francis, C.M. 1995. Survival of Great Horned Owls in relation to the Snowshoe Hare cycle. *Auk* **112**: 44–59.

Hunter, D.B., Rohner, C. & Currie, D.C. 1997. Black flies and *Leucocytozoon* spp. as causes of mortality in juvenile Great Horned Owls in the Yukon, Canada. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997. Winnipeg, Manitoba*, Canada: 260. USDA Forest Services Gen. Tech. Rep. NCñ190.

Ilmonen, P., Hakkarainen H., Koivunen, V., Korpimäki, E., Mullie, A. & Shutter, D. 1999. Parental effort and blood parasitism in Tengmalm's Owl: effects of natural and experimental variation in food abundance. *Oikos* **86**: 79–86.

Jedrzejewski, W., Jedrzejewski, B., Szymura, A. & Zub, K. 1996. Tawny Owl (*Strix aluco*) predation in a pristine deciduous forest (Bialowieza National Park, Poland). *J. Anim. Ecol.* **65**: 105–120.

Jedrzejewski, B. & Jedrzejewski, W. 1998. *Predation in Vertebrate Communities. The Bialowieza Primeval Forest as a Case Study*. Berlin:Springer-Verlag.

Keith, L.B. 1963. *Wildlife's ten-year cycle*. Madison: University Wisconsin Press.

Keith, L.B. & Rusch, D.H. 1988. Predation's role in the cyclic fluctuations of Ruffed Grouse. *Proc. Int. Orn. Congr*. **19**: 699–732.

Kerlinger, P., Lein, M.R. & Sevick, B.J. 1985. Distribution and population fluctuations of wintering Snowy Owls (*Nyctea scandiaca*) in North America. *Ecology* **63**: 1829–1834.

Koenig, C. 1998. Ecology and population of Pygmy Owls *Glaucidium passerinum* in the Black Forest (SW Germany). In Chancellor, R.D., Meyburg B.-U. and Ferrero J.J. (eds.) *Holarctic birds of prey*: 447–450. Berlin: World Working Group on Birds of Prey and Owls.

Korpimäki, E. 1984. Clutch size and breeding success of Tengmalm's Owl *Aegolius funereus* in natural cavities and nest boxes. *Ornis Fenn*. **61**: 80–83.

Korpimäki, E. 1985. Rapid tracking of microtine populations by their avian predators: possible evidence for stabilising predation. *Oikos* **45**: 281–284.

Korpimäki, E. 1986. Gradients in population fluctuations of Tengmalm's Owl *Aegolius funereus* in Europe. *Oecologia* **69**: 195–201.

Korpimäki, E. 1987. Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. *Ibis* **129**: 58–68.

Korpimäki, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol*. **57**: 97–108.

Korpimäki, E. 1988a. Factors promoting polygyny in European birds of prey – a hypothesis. *Oecologia* **77**: 278–285.

Korpimäki, E. 1992. Population dynamics of Fennoscandian Owls in relation to wintering conditions and between-year fluctuations of food. In Galbraith C.A., Taylor I.R. & Percival, S. (eds.) *The ecology and conservation of European Owls*: 1–10. Edinburgh: Joint Nature Conservation Committee

Korpimäki, E. 1992a. Diet composition; prey choice and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. *Can. J. Zool*. **70**: 2373–2381.

Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? *J. Anim. Ecol*. **63**: 619–628.

Korpimäki, E., Hakkarainen, H. & Bennett, G.F. 1993. Blood parasites and reproductive success of Tengmalm's Owls: detrimental effects on females but not males. *Functional Ecology* **7**: 420–426.

Korpimäki, E., Hakkarainen, H., Ilmonen, P. & Wiehn, E. 2002. Detrimental effects of blood parasites on parental effort and reproductive success of Tengmalm's Owls and European Kestrels. This volume.

Korpimäki, E. & Lagerström, M. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol*. **57**: 433–441.

Korpimäki, E., Lagerström, M. & Saurola, P. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scand*. **18**: 1–4.

Korpimäki, E. & Norrdahl, K. 1989. Predation of Tengmalm's Owls: numerical responses, functional responses and dampening impact on population fluctuations of voles. *Oikos* **54**: 154–164.

Korpimäki, E. & Norrdahl, K. 1991. Numerical and functional responses of Kestrels, Short-eared Owls and Long-eared Owls to vole densities. *Ecology* **72**: 814–825.

Lack, D. 1954. *The natural regulation of animal numbers*. Oxford: University Press.

Lahaye, W.J., Gutiérrez, R.J. & Akçakaya, H.R. 1994. Spotted Owl metapopulation dynamics in southern California. *J. Anim. Ecol*. **63**: 775–785.

Lamberson, R.H., McKelvey, R., Noon, B.R. & Voss, C. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. *Conserv. Biol*. **6**: 505–512.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia* **75**: 601–607.

Lenton, G.M. 1984. The feeding and breeding ecology of Barn Owls *Tyto alba* in peninsular Malaysia. *Ibis* **26**: 551–575.

Lockie, J.D. 1955. The breeding habits and food of Short-eared Owls after a vole plague. *Bird Study* **2**: 53–69.

Löfgren, O., Hörnfeldt, B. & Carlsson, B.-G. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus* (L)) in relation to cyclic food production. *Oecologia* **69**: 321–326.

Lundberg, A. 1979. Residency, migration and compromise: adaptors to nest-site scarcity and food specialisation in three Fennoscandian owl species. *Oecologia* **41**: 273–281.

Lundberg, A. 1980. Why are the Ural Owl *Strix uralensis* and the Tawny Owl *S. aluco* parapatric in Scandinavia? *Ornis Scand.* **11**: 116–120.

Maher, W.J. 1970. The Pomarine Jaeger as a Brown Lemming predator in northern Alaska. *Wilson Bull.* **82**: 130–157.

Marks, J.S., Evans, D.S. & Holt, D.W. 1994. *Long-eared Owl*. Washington, D.C: The American Ornithologists Union.

Marti, C.D. 1997. A 20-year study of Barn Owl *Tyto alba* reproduction in northern Utah. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997. Winnipeg, Manitoba*, Canada: 261. USDA Forest Services Gen. Tech. Rep. NC–190.

Marti, C.D. 1999. Natal and breeding dispersal in Barn Owls. *J. Raptor Res.* **33**: 181–189.

Martinez, J.A. & López, G. 1999. Breeding ecology of the Barn Owl (*Tyto alba*) in Valencia (SE Spain). *J. Orn.* **140**: 93–99.

Martinez, J.E., Sanchez, M.A., Carmona, D., Sanchez, J.A., Ortuño, A. & Martinez, R. 1992. The ecology and conservation of the Eagle Owl *Bubo bubo* in Murcia, south-east Spain. In Galbraith C.A., Taylor I.R. & Percival, S. (eds.) *The ecology and conservation of European Owls*: 84–88. Edinburgh: Joint Nature Conservation Committee

Melée, E., Dacky, P. & Simon, P. 1978. Quinze années d'observations sur la reproduction d'une population forestiere de Chouettes Hulottes (*Strix aluco*). *Le Gerfaut* **68**: 590–650.

Menyushina, I. E. 1997. Snowy Owl (*Nyctea scandiaca*) reproduction in relation to lemming population cycles on Wrangel Island. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 572–582. USDA Forest Services Gen. Tech. Rep. NCñ190.

Mikkola, H. 1976. Owls killing and killed by other owls and raptors in Europe. *Br. Birds* **69**: 144–154.

Mikkola, H. 1983. *Owls of Europe*. Calton: Poyser.

Mossop, D.H. 1997. The importance of old-growth refugia in the Yukon boreal forest to cavity-nesting owls. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 584–586. USDA Forest Services Gen. Tech. Rep. NC–190.

Mueller, H.C. & Berger, D.D. 1967. Some observations and comments on the periodic invasions of Goshawks. *Auk* **84**: 183–91.

Mueller, H.C., Berger, D.D. & Allez, G. 1977. The periodic invasions of Goshawks. *Auk* **94**: 652–63.

Nero, R.W. 1980. *The Great Grey Owl: phantom of the northern forest*. Washington, D.C.: Smithsonian Institution Press.

Nero, R.W., Copland, H.W.R. & Mezibroski, J. 1984. The Great Grey Owl in Manitoba, 1968–83. *Blue Jay* **42**: 129–190.

Nero, R.W. & Copland, H.W.R. 1997. Sex and age composition of Great Grey Owls (*Strix nebulosa*) winter 1995/1996. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 587–590. USDA Forest Services Gen. Tech. Rep. NCñ190.

Newton, I. 1979. *Population ecology of raptors*. Berkhamsted: Poyser.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biol. Rev.* **67**: 129–173.

Newton, I. 1998. *Population limitation in birds*. London: Academic Press.

Newton, I., Wyllie, I. & Dale, L. 1997. Mortality causes in British Barn Owls (*Tyto alba*) based on 1,101 carcasses examined during 1963–1996. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 299–307. USDA Forest Services Gen. Tech. Rep. NC–190.

Olsen, P.D. 1995. *Australian birds of prey*. Sydney: University of New South Wales Press.

Olsson, V. 1979. Studies on a population of Eagle Owls *Bubo bubo* (L.) in southeast Sweden. *Viltrevy* **11**: 1–99.

Olsson, V. 1997. Breeding success, dispersal, and long-term changes in a population of Eagle Owls *Bubo bubo* in southeastern Sweden. *Ornis Svecica* **7**: 49–60.

Petty, S.J. 1992. Ecology of the Tawny Owl *Strix aluco* in the spruce forests of Northumberland and Argyll. Ph.D thesis, Open University, Milton Keynes.

Petty, S.J. 1999. Diet of Tawny Owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *J. Zool. Lond.* **248**: 451–465.

Petty, S.J. & Fawkes, W. 1997. Clutch-size variation in Tawny Owls (*Strix aluco*) from adjacent valley systems: can this be used as a surrogate to investigate temporal and spatial variations in vole abundance? In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 315–324. USDA Forest Services Gen. Tech. Rep. NCñ190.

Petty, S.J. & Peace, A.J. 1992. Productivity and density of Tawny Owls *Strix aluco* in relation to the structure of a spruce forest in Britain. In Galbraith C.A., Taylor. I.R. & Percival S. *The ecology and conservation of European Owls*: 76–83. Edinburgh: Joint Nature Conservation Committee.

Petty, S.J., Shaw, G. & Anderson, D.I.K. 1994. Value of nest boxes for population studies and conservation of owls in coniferous forests in Britain. *J. Raptor Res.* **28**: 134–142.

Pietiäinen, H. 1989. Seasonal and individual variation in the production of offspring in the Ural Owl *Strix uralensis*. *J. Anim. Ecol.* **58**: 905–920.

Pietiäinen, H. & Kolunen, H. 1993. Female body condition and breeding of the Ural Owl *Strix uralensis*. *Functional Ecology* **7**: 726–735.

Pietiäinen, H., Saurola, P. & Väisänen, R.A. 1986. Parental investment in clutch size and egg size in the Ural Owl. *Orn. Scand.* **17**: 309–325.

Pitelka, F.A., Tomich, P.Q. & Treichel, G.W. 1955. Ecological relations of jaegers and owls near Barrow, Alaska. *Ecol. Monogr.* **25**: 85–117.

Postupalsky, S., Papp, J.M. & Scheller, L. 1997. Nest sites and reproductive success of Barred Owls (*Strix varia*) in Michigan. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 325–337. USDA Forest Services Gen. Tech. Rep. NC–190.

Potapov, E.R. 1997. What determines the population density and reproductive success of Rough-legged Buzzards, *Buteo lagopus*, in the Siberian tundra? *Oikos* **78**: 362–376.

Ramsden, D.J. 1998. Effect of barn conversions on local populations of Barn Owl *Tyto alba*. *Bird Study* **45**: 68–76.

Redpath, S.M. 1995. Habitat fragmentation and the individual: Tawny Owls *Strix aluco* in woodland patches. *J. Anim. Ecol.* **64**: 632–661.

Rohner, C. 1995. Great Horned Owls and Snowshoe Hares – what causes the time-lag in the numerical response of predators to cyclic prey. *Oikos* **74**: 61–68.

Rohner, C. 1995. Great Horned Owls and Snowshoe Hares – what causes the time-lag in the numerical response of predators to cyclic prey. *Oikos* **74**: 61–68.

Rohner, C. 1996. The numerical response of Great Horned Owls to the Snowshoe Hare cycle: consequences of non-territorial 'floaters' on demography. *J. Anim. Ecol.* **65**: 359–370.

Rohner, C. 1997. Non-territorial floaters in Great Horned Owls (*Bubo virginianus*). In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg, Manitoba, Canada*: 347–362. USDA Forest Services Gen. Tech. Rep. NC–190.

Rohner, C., Smith, J.N.H., Stroman, J., Joyce, M., Doyle, F.I. & Boonstra, R. 1995. Northern Hawk Owls in the Nearctic boreal forest: prey selection and population consequences of multiple prey cycles. *Condor* **97**: 208–220.

Rosen, M.N. & Morse, E.E. 1972. An interspecies chain in a fowl cholera epizootic. *Calif. Fish Game*. **45**: 51–56.

Saurola, P. 1983. Movements of Short-eared Owl (*Asio flammeus*) and Long-eared Owl (*A. otus*) according to Finnish ring recoveries. *Lintumies* **18**: 67–71.

Saurola, P. 1987. Mate and nest-site fidelity in Ural and Tawny Owls. In Nero, R.W., Clark, R.J., Knapton, R J. & Hamre, R.H. (eds.) *Biology and conservation of northern forest owls*: 81–86. USDA For. Serv. Gen. Tech. Rep. RM–142.

Saurola, P. 1989. Ural Owl. In Newton, I. (ed.) *Lifetime reproduction in birds*: 327–345. London: Academic Press.

Saurola, P. 1992. Population studies of the Ural Owl *Strix uralensis* in Finland. In Galbraith C.A., Taylor I.R. & Percival S. (eds.) *The ecology and conservation of European Owls*: 28–31. Edinburgh: Joint Nature Conservation Committee.

Saurola, P. 1997. Monitoring Finnish owls 1982–1996: methods and results. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 363–380. USDA Forest Services Gen. Tech. Rep. NC–190.

Saurola, P. 2002. Natal dispersal distances in Finnish owls: results from ringing. This volume.

Schmidt, R.C. & Vauk, G. 1981. Zug Ringfunde auf Helgoland durch ziehender Waldohreulen und Sunpfohreulen (*Asio otus* and *A. flammeus*). *Vogelwelt* **102**: 180–189.

Shawyer, C.R. 1987. *The Barn Owl in the British Isles. Its past, present and future*. London: The Hawk Trust.

Shelford, V.E. 1945. The relation of Snowy Owl migration to the abundance of the Collared Lemming. *Auk* **62**: 592–596.

Smith, N. 1997. Observations of wintering Snowy Owls (*Nyctea scandiaca*) at Logan Airport, East Boston, Massachusetts from 1981–1997. In Duncan, J.R., Johnson D.H. & Nicholls T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere, Second International Symposium, February 5–9, 1997, Winnipeg Manitoba, Canada*: 591–597. USDA Forest Services Gen. Tech. Rep. NCñ190.

Solheim, R. 1983. Bigyny and biandry in the Tengmalm's Owl *Aegolius funerus*. *Ornis Scand*. **14**: 51–57.

Sonerud, G. 1984. Effect of snow cover on seasonal changes in diet, habitat and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. *Holarctic Ecology* **9**: 33–47.

Sonerud, G. 1997. Hawk Owls in Fennoscandia: population fluctuations, effects of modern forestry, and recommendations on improving foraging habitats. *J. Raptor Res*. **31**: 167–174.

Sonerud, G.A., Nybo, J.O., Fjeld, P.E. & Knoff, C. 1987. A case of bigyny in the Hawk Owl *Surnia ulula*: spacing of nests and allocation of male feeding effort. *Ornis Fenn*. **64**: 144–148.

Sonerud, G.A., Solheim, R. & Prestrud, K. 1988. Dispersal of Tengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. *Ornis Scand*. **19**: 175–181.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Stix aluco*). *J. Zool. Lond*. **162**: 197–285.

Speirs, J.M. 1939. Fluctuations in numbers of birds in the Toronto Region. *Auk* **56**: 411–419.

Stefansson, O. 1979. The Great Grey Owl *Strix nebulosa* in the province of Norrbolten in 1975–78. *Vår Fågelvärld* **38**: 11–22.

Stefansson, O. 1983. Lappugglan *Strix nebulosa* i Sverige 1979–82. *Vår Fågelvärld* **42**: 245–250.

Sulkava, S. & Huhtala, K. 1997. The Great Grey Owl (*Strix nebulosa*) in the changing forest environment of northern Europe. *J. Raptor Res*. **31**: 151–159.

Taylor, I. 1994. *Barn Owls. Predator-prey relationships and conservation*. Cambridge: University Press.

Village, A. 1981. The diet and breeding of Long-eared Owls in relation to vole numbers. *Bird Study* 28: 215–224.

Village, A. 1987. Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. *Ornis Scand*. **18**: 198–204.

Village, A. 1992. *Asio* Owls and Kestrels in recently-planted and thicket plantations. In Galbraith C.A., Taylor I.R. & Percival S. (eds.) *The ecology and conservation of European Owls*: 11–15. Edinburgh: Joint Nature Conservation Committee.

Wallin, K. 1987. Defence as parental care in Tawny Owls *Strix aluco*. *Behav*. **102**: 213–230.

Watson, A. 1957. The behaviour, breeding, and food-ecology of the Snowy Owl *Nyctea scandiaca*. *Ibis* **99**: 419–462.

Wiklund, C.G., Kjellén, N. & Isakson, E. 1998. Mechanisms determining the spatial distribution of microtine predators on the Arctic tundra. *J. Anim. Ecol.* **67**: 91–98.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* **72**: 1–92.

2

OCCUPANCY IN RELATION TO SITE QUALITY IN BARN OWLS (*Tyto alba*) IN SOUTH SCOTLAND

IAIN R. TAYLOR

School of Biological Sciences, The University of Edinburgh, Mayfield Road, Edinburgh, Scotland. Present address: Applied Ornithology Group, Johnstone Centre, Charles Sturt University, PO Box 789, Albury, New South Wales, 2640, Australia.

There is considerable evidence from a range of species that birds preferentially occupy breeding areas of highest quality, where their productivity is greatest. To test if Barn Owls showed a similar tendency, data on occupancy collected over 20 years from a population in south Scotland, were compared with independent assessments of site quality. The owls hunted mainly along strips of long grassland at the edges of small woodlands surrounded by pasture. Their main prey were Field Voles *Microtus agrestis*, whose populations showed marked 3-year cycles of abundance. Sites varied in the amount of the preferred hunting habitat within the normal foraging range around nests. The mean number of young fledged per breeding attempt from each site was significantly correlated with the amount of such habitat within the foraging range. Despite such marked variation in breeding site quality, there was no correlation between the percentage of years each site was occupied by breeding owls and either the amount of foraging habitat around the nest or the mean number of young per attempt fledged from it. Possible explanations for this, and conservation implications, are discussed.

INTRODUCTION

For most, if not all, bird species that have been appropriately studied, there is local variation in the quality of habitat available for feeding, breeding or wintering. Our understanding of the responses of populations to such variations has been summarised by Newton (1998). Three lines of evidence suggest that habitat is occupied sequentially, with the best quality areas occupied in preference to the poorer quality areas. The first involves the settlement patterns of birds as they arrive in breeding or wintering areas, where the early arrivals occupy the better habitats (e.g. Lundberg *et al.* 1981, Arcese 1987, Aebischer *et al.* 1996). The second involves long-term patterns of occupancy, where densities are highest and numbers remain most stable from year to year in areas of better quality habitat, in which breeding performance is also higher (e.g. Kluijver & Tinbergen 1953, Lack 1966, O'Connor 1980, Newton 1991). Lastly, for a few species that have increased in numbers over several years, the better quality areas were occupied first, before the poorer quality areas (e.g. von Haartman 1971, O'Connor 1985, 1986).

In this paper, I examine the relationship between breeding site quality and occupancy in Barn Owls *Tyto alba*, in an agricultural area in south Scotland. Site quality is measured by the amount of suitable foraging habitat around nests, by the mean number of young produced per nesting attempt, and by occupancy as the number of years out of a total of 20 that the site was occupied. The study concentrates on the quality of foraging habitat around nesting places and not on the nesting places themselves. However, almost all pairs nested in farm buildings, in conditions that did not vary greatly among pairs. Most pairs nested in roof spaces, where they were undisturbed by humans or natural predators and where they experienced similar thermal conditions. There is no evidence that Barn Owls defend hunting areas, so the term 'site' is used here rather than 'territory' to refer to the birds' nesting places with associated foraging ranges.

In the study area, Barn Owls preyed almost entirely on small terrestrial mammals, with an average of around 60% by diet biomass comprised of Field Voles (*Microtus agrestis*) and the remainder mostly of Wood Mice (*Apodemus sylvaticus*) and Common Shrews (*Sorex araneus*). Field Vole populations were strongly cyclic, with 3-yearly intervals between successive peaks (Taylor 1994).

STUDY AREA

The study area comprised 110 km^2 of predominantly pastoral farmland at altitudes between 50 and 150 m above sea level, at the southern end of the Esk and Liddle river catchments in southern Scotland. Most fields in the area were short rotation pastures, silage and hay. Throughout, there were numerous small woods covering about 20% of the total area. Mostly, these were coniferous but there were also some deciduous and mixed coniferous-deciduous woods. Rough grassland areas that could support populations of small mammal prey were restricted mainly to edge habitats, especially woodland edges. Because livestock grazed most of the fields at some time during the year, not all fence-lines, hedges and ditches had rough grassland along their edges. The majority of farm buildings dated from the 19th century, and as a result of economic changes, many were no longer in use and were the main nesting places for the owls. Few trees had hollows large enough for Barn Owl nest sites.

METHODS

The quality of sites was assessed in two ways: firstly, by identifying the main components of habitat used by the birds for foraging and then quantifying the amount of such habitat within the potential foraging range of each pair; and secondly by examining the relationship between the amount of preferred habitat around each nesting place and the birds' mean breeding performance, in terms of young raised per nesting attempt. The quality of territories was assessed from the breeding performance of the occupants in earlier studies of European Sparrowhawks (*Acciper nisus*) in southern Scotland (Newton and Marquiss 1976, Newton 1991) and of Tengmalm's Owls *Aegolius funereus*) in west-central Finland (Korpimaki 1988).

From 1983 to 1985, twelve individual breeding Barn Owls were fitted with tail-mounted transmitters and followed during complete foraging trips. Observations began when a bird left its roost or nest site and ended when it either gave up hunting or returned to the nest with prey. The precise locations where prey were captured were recorded, this being possible because of the extended daylight at the latitude of the study area during summer. Potential foraging habitats were limited to woodland edges, hedge, fence and ditch lines and the field crops. The amount of each of these components within the range of each pair was quantified from 1:25000 maps and by ground survey. Because of limitation in battery life, tail-mounted transmitters operated for a maximum of six months and were therefore used only to determine foraging range sizes during the breeding season. In 1980, 18 pairs of owls were plumage-dyed with individual colour codes. Because moult of body feathers takes three years to complete (Taylor 1994), some birds were still alive with codes detectable up to 1983. From sightings of these birds made while travelling within the study area, additional data were obtained on the distances from the nest site at which individual birds foraged during summer and winter.

An assessment of the relative abundance of small mammals in each habitat component was made by trapping. In a sample of six areas of each habitat type, during May 1981, 40 Longworth traps were set out randomly with two traps at each of 20 trapping stations. Trapping was run for five days with traps checked and emptied each day. In addition, in April of each year, coinciding with the start of the owls' breeding season, an annual index of relative abundance of Field Voles was obtained by trapping. The method used for this aspect has been described elsewhere (Taylor 1994).

Each year the entire study area was searched for breeding pairs of owls by visiting all possible nesting places in buildings and in trees. As many as possible of the adults were trapped and ringed each year to enable estimates to be made of annual survival and site fidelity. Each site was visited up to eight times each year to determine occupancy, clutch size and number of young fledged, and to ring the young.

RESULTS

Foraging habitat and range size

The radio-tagged birds were seen catching prey along woodland edges, hedgerows, fence-lines and along ditches, and a few times from within field crops. The latter occurred where the crop had failed to grow allowing small patches of weedy vegetation to develop. Eighty-seven percent of all observed captures occurred along woodland edges, even though these made up only 53% of the total length of linear habitats available. Comparing numbers of captures made along all linear habitats with the lengths of each available, the preference for woodland edges and avoidance of other edge habitats was highly significant ($\chi^2 = 208.2$, d$F = 2$, $P < 0.001$, Table 1). Data obtained from spot locations of foraging birds, that is, single locations made without following individuals and that involved foraging in general rather than prey capture locations, gave similar results (Table 1).

Depending on the individual bird, between six and ten hours of continuous tracking was needed for estimates of range size to reach asymptotic values, calculated by the minimum convex polygon method. Mean range size for males, estimated in this way, was 318.5 ± 24.2 ha ($n = 6$) and for females 308.2 ± 17.5 ha ($n = 6$). For individual pairs, female and male ranges overlapped almost completely. Foraging range sizes did not differ significantly between a high vole year (1984) and low vole years (1983, 1985), although more prey were caught closer to the nest in the high vole year. The range size was equivalent to about 3 km? or a radius of 1 km around the nest. None of the ranges was perfectly circular, although their shapes were reasonably close to circular

Table 1. Foraging habitats of Barn Owls in the study area.

The data on prey captures are from nine radio-tracked birds and refer to locations where prey were seen to be captured. The data on foraging locations refer to casual observations of birds hunting, rather than only prey captures, in the same area. Expected values are calculated from the relative lengths of the linear habitats, assuming the birds foraged randomly in them. Comparing captures made along linear habitats, $\chi^2 = 208.2$, $P < 0.001$.

	Woodland edges	Hedges and fence-lines	Ditches	Field crops
Percentage of all prey captures observed (n)	86.8 (230)	7.1 (19)	1.9 (5)	4.2 (11)
Percentage of prey captures observed in linear habitats (n)	90.6 (230)	7.5 (19)	2.0 (5)	–
Percentage of prey captures expected in linear habitats (n)	50.4 (128)	41.5 (105.4)	8.5 (21.6)	–
Percentage of all spot foraging locations	80.2 (207)	10.9 (28)	2.7 (7)	6.2 (16)
Percentage of all spot foraging observations observed in linear habitats (n)	85.5 (207)	11.6 (28)	3.0 (7)	–
Percentage of spot foraging locations expected in linear habitats (n)	50.4 (122)	41.5 (100.4)	8.5 (20.6)	–

and nest sites were more often closer to the their centres than to their edges (Taylor 1994). Only 11% of prey captures observed during the radio-tracking ($n = 265$) were more than 1 km from the nest site. As these were obtained by tracking individuals continuously during complete hunting trips, there is unlikely to have been a bias in favour of items taken closer to the nest.

The data obtained from the plumage-dyed birds gave similar results to the radio-tracked birds for summer range sizes, but also revealed that range sizes during winter were considerably larger than in summer. During winter birds hunted up to 5 km from their nest sites. In summer 90% of 67 sightings were within 1 km of the nest, whereas in winter only 39% of 43 sightings were within 1 km and 90% were within 3 km of the nest (difference between means: Mann Whitney U-test, $z = -4.45$, $P < 0.001$). The birds' activity during the summer was clearly centred around their nest sites but in winter their roost sites became the focus of activity. Each bird had a single, favoured roost site, usually at an undisturbed location, which it used almost every day, but some were found at up to three sites when there were higher levels of disturbance. Forty-five percent of the females continued to roost around their nest sites in winter and 83% roosted within 500 m of the nest. Only 16% of males roosted close to the nest in winter and 61% within 750 m. The remainder roosted at distances up to 1.5 km. Thus individual winter foraging ranges might not have been quite as large as suggested by the distances in relation to their nest sites. Nevertheless, during winter, neighbouring birds frequently foraged over each other's breeding season ranges and sometimes into areas not used by any breeding birds during summer. Thus they had experience of the quality of foraging areas over a number of adjacent home ranges in addition to their own summer range.

Prey availability in relation to habitat

Small mammal trapping was done in edge habitats, woodland interiors and among various crops to obtain indices for comparison, rather than estimates of absolute abundance. The numbers of

Table 2. Relative abundance of Field Voles (the main prey of Barn Owls) in various habitats in the study area.

The values given are mean numbers trapped per sampling site over five consecutive days in May 1981. Six sites were sampled for each habitat. For field habitats all traps were within 25 m of the field boundary and for woodlands, all were within 25 m of the woodland edge. Testing for differences among sample sites, Kruskal–Wallis test, H = 43.6, $P < 0.001$

Habitat	Mean number of Field Voles trapped per site ± se
Woodland edge – coniferous forest	14.2 ± 2.6
Woodland edge – deciduous forest	12.7 ± 2.4
Hedgerow – grass 'headlands'	10.3 ± 2.2
Woodland interior – coniferous forest	0.5 ± 0.2
Woodland interior – deciduous forest	1.3 ± 0.6
Pasture	0
Silage	0
Hay	1.5 ± 0.7
Barley	0.2 ± 0.2

Field Voles, the most important prey, caught along woodland edges and hedgerows were significantly higher than those caught in any other habitats (Kruskal–Wallis test, H = 43.55, $P < 0.001$. Table 2). Most of the field crops supported few, or no voles, although slightly higher numbers were caught in some hay fields. Woodland interiors also supported only low densities of Field Voles. In woods, canopy cover was dense with little or no ground cover, and the grasses needed by the voles for food and runways were sparse. By contrast, the woodland edge habitats were mostly rank unmanaged grassland strips 3–5 m wide, between the trees and the field fence, offering an abundance of cover and food for voles and other small mammals. Shrub development was probably suppressed in these areas by browsing from Roe Deer *Capreolus capreolus*.

Variations in site quality and breeding performance

Although the birds lived in a complex mosaic of habitats, only one component, woodland edge, proved to be important for foraging, and the birds caught about 90% of their prey in this habitat, within 1 km of their nest sites. The quality of sites during the breeding season could therefore be quantified by determining the length of the woodland edge habitat within a 1 km radius around each nest. Site quality, assessed in this way, varied considerably, from a minimum of only 3.4 km of woodland edge to a maximum of 18 km.

Details of breeding performance were estimated from 8–20 years of information from each site, thus allowing for short-term variations in annual performance caused by the vole cycle and the quality of individual birds. Estimates of mean clutch size and fledged brood size for individual sites did not change significantly with increasing sample size beyond eight years. Mean clutch size for each site was not significantly correlated with the length of woodland edge within 1 km of the nest site ($r = 0.01$, NS, Fig. 1). However, the mean number of young fledged per attempt at each site was positively correlated with the length of woodland edge ($r = 0.69$, $P = 0.003$, Fig. 1). Food shortage was the main recorded cause of chick mortality, and there was no evidence of predation of nest contents. Later hatched chicks in a brood were the most likely to die, following signs of starvation. Usually, their remains were trampled into the nest debris, but sometimes they were eaten by their brood-mates and their remains recovered in pellets. Such

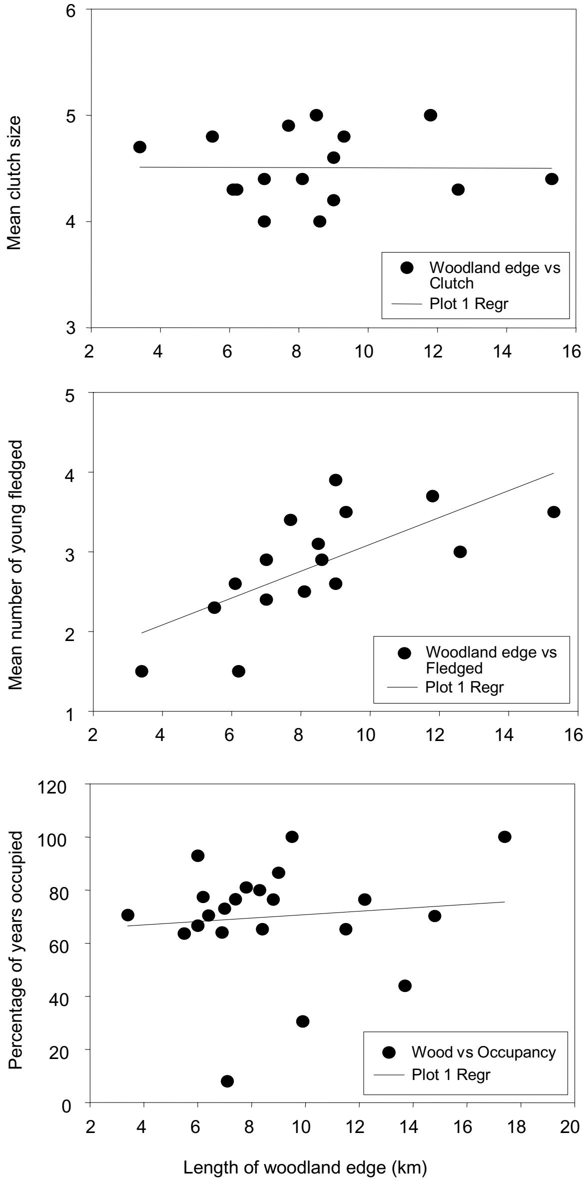


Fig. 1. Relationship between the length of woodland edge within a 1 km radius of Barn Owl nests and annual mean clutch size at each site (calculated over a minimum of eight years, $y = 4.5 - 0.001x$; $r = 0.01$, NS), mean number of young fledged per year (calculated over a minimum of eight years, $y = 1.41 + 0.17x$, $r = 0.69$, $P = 0.003$), and the percentage of years each breeding site was occupied ($y = 64.3 + 0.65x$, $r = 0.1$, NS).

losses were greater in low vole years than in high vole years (Taylor 1994). Thus, prey abundance within the birds' foraging range emerged as a significant factor in influencing chick survival.

From the variations in the amount of the preferred foraging habitat within the owls' feeding ranges and the significant relationship between the amount of this habitat and breeding performance, considerable variation in the quality of breeding sites was apparent within the study area.

Occupancy in relation to site quality

Almost all the Barn Owls nested in buildings, some of which were lost as breeding sites by collapse or renovation at various stages during the study. Also, at a few sites significant habitat changes within the birds' foraging range occurred over the 20 years of study. Site occupancy in relation to quality was examined, only for breeding sites that were available for at least eight years and around which no significant habitat changes occurred in the period covered. On this basis, 22 sites were available for comparison of percentage occupancy and length of woodland edge within 1 km of the nest. Occupancy by breeding owls ranged from 8% to 100% of the years the site was available, but was not correlated with the amount of woodland edge around the nest

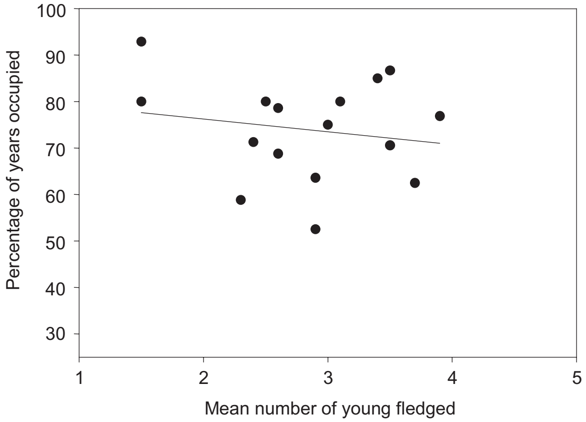


Fig. 2. Relationship between the percentage of years each breeding site was occupied and site quality, assessed as the mean number of young fledged from the site, calculated over a minimum of eight years (y = 81.8 – 2.76x, *r* = – 0.19, NS).

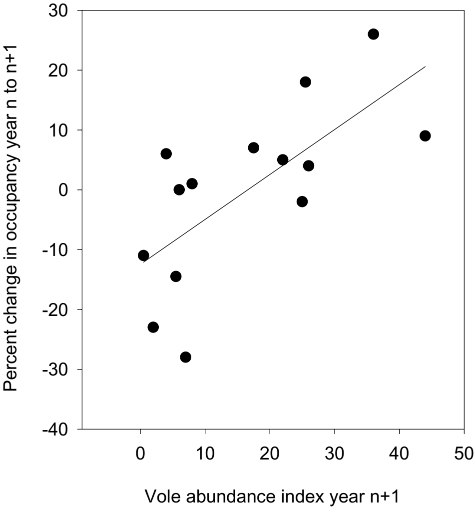


Fig. 3. Percentage change in the number of sites occupied by breeding pairs of Barn Owls between years *n* and *n+1*, and the index of vole abundance in the spring of year *n+1* (y = –12.5 + 0.75x, *r* = 0.70, *P* = 0.01).

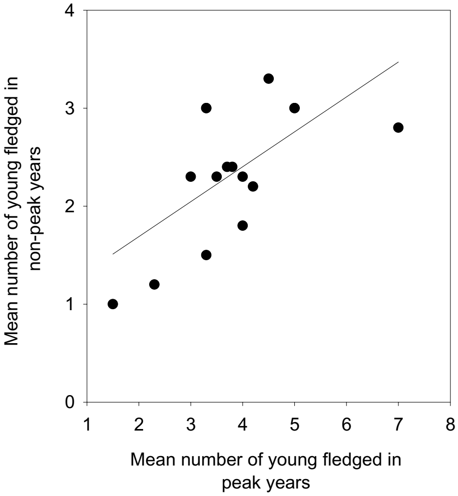


Fig. 4. Relationship between the mean number of young fledged per breeding attempt from each site in peak vole years and the mean number fledged per breeding attempt in non-peak years ($y = 0.98 + 0.36x$, $r_s = 0.54$, $P = 0.02$).

($r = 0.1$, $P = 0.65$). There was also no correlation between the percentage of years each site was occupied and the quality of the site as assessed by the mean number of young fledged from the site ($r = -0.19$, $P = 0.47$). Sites with the lowest amount of preferred foraging habitat and lowest long-term breeding success were occupied just as often as sites with the opposite characteristics (Figs. 1 and 2).

The number of breeding pairs in the study area, and hence the percentage of all sites occupied, varied significantly in relation to the vole cycle ($r = 0.70$, $P = 0.01$, Fig. 3). Occupancy was highest in vole peak years and declined progressively until the next peak year. These differences were caused mainly by fluctuations in the numbers of new birds recruited to the breeding population, with 68% ($n = 143$) of all new recruits joining the population in the high vole years and the remaining 32% ($n = 66$) in the low vole years. Thus, it is possible that new recruits may have been attracted to sites that were of reasonable quality during these high vole years but that in the long-term were poorer quality sites. This was not the case, however, as the average number of young fledged from individual sites during vole peak years was significantly correlated with production for those sites in low vole abundance years ($r_s = 0.54$, $P < 0.02$, Fig. 4). Thus, the quality of a site during high vole years was a good indicator of its long-term quality.

In the high vole years, occupancy averaged 66 ± 6% of all available sites in the study area, whereas in the years immediately preceding these high years, occupancy averaged only 48% ± 9% of sites. Thus, more than half of the total sites were available to the birds when the largest numbers were taking up new sites and almost a third of available sites, including high quality sites, were still vacant after the settlement had been completed.

Site and mate fidelity

Breeding adults were caught at the nest and ringed over the first 15 years of the study, during which there were 152 instances of males and 170 of females trapped in successive years. For most of the study, between 80% and 90% of the breeding adults were trapped each year. Of those retrapped, only one male and seven females changed nest sites between years, giving an overall annual site fidelity of 99.3% and 98.2% for the two sexes. Five of the females moved to adjacent sites following the loss of their mates during winter and two after breeding as the second female of bigynous males. Numerous instances were recorded throughout the study of both males and females, whose mates died during winter, remaining alone at their breeding sites as non-breeders the following season, and in some cases for two seasons. Overall, about 17% of all pairs that laid failed to fledge young. Despite this, there was no evidence that either males or females moved in response to breeding failure. In effect, therefore, once Barn Owls had selected a nest site, they kept it for life.

Barn Owls were also resident year-round in the study area with no evidence of migration. Of 54 ringed birds found dead, that were former breeders in the study area, all were recovered within seven kilometres of their former nesting places. Most of these deaths occurred during winter. All of the plumage-dyed birds were seen throughout the year at their roost or nest sites and the same was true of ringed birds that were trapped on many occasions throughout the study.

Survival in relation to site quality

The sedentary behaviour and almost total nest site fidelity of Barn Owls in the study area enabled annual survival estimates of breeding adults to be based on the presence or disappearance of individual ringed birds from their nesting sites between breeding seasons. No individual classed as dead in this way was ever subsequently found alive or breeding within the study area or elsewhere. Males were generally more difficult to trap than females which created frequent gaps in the records of individual male identities for particular sites. To obtain adequate sample sizes when testing for any effect of site quality on survival, I therefore decided to group data into only two classes: sites with less or more than 8 km of woodland edge within 1 km radius around nests. Approximately half of all sites fell within each category. There was no significant difference in the annual survival of males of females, so data for both were grouped. For the lower quality sites with less than 8 km of woodland edge foraging habitat, annual survival was estimated as 76.7% ($n = 120$), not significantly different from 71.4% ($n = 133$) for the higher quality sites with more than 8 km of woodland edge.

DISCUSSION

The quality of Barn Owl breeding sites within the study area, assessed either by the amount of preferred foraging habitat within the birds' summer feeding ranges, or by long-term variations in breeding performance at each site, varied greatly. The important habitat component was rough grassland edges around small woodlands, which supported high densities of the preferred prey, particularly Field Voles. Better quality sites had greater lengths of these edge habitats within the birds' foraging ranges, and presumably therefore higher numbers of prey. However, despite these strong differences in site quality, there was no relationship between the percentage of years each site was occupied over the 20-year study period and the quality of the site. The poorer sites were occupied just as frequently as good ones.

Survival rates of breeding adults were not related to breeding site quality. Most deaths occurred in winter when the birds were free of the spatial constraints imposed by the need to make frequent deliveries of prey to young or incubating mates, and consequently ranged over much larger areas. The birds seemed not to defend their foraging ranges, individuals with poor quality breeding season ranges often fed in adjacent better quality areas during winter (Taylor 1994). With such mobility, close relationships between survival and breeding season range quality would not be expected.

Once established at a site, male and female Barn Owls did not shift sites within the study area to any significant extent. This behaviour was similar to that recorded for male Tengmalm's owls *Aegolius funereus* which in some regions had high site fidelity (Schwerdtfeger 1984, Löfgren, Hörnfeldt & Carson 1986, Korpimaki 1988) and for Tawny Owls *Strix aluco* (Petty 1992). Strong site fidelity is a general characteristic of hole-nesting species, presumably because, under natural conditions, there is usually a shortage of suitable holes in good quality feeding areas (von Haartman 1968, Lundberg 1979). Birds that remain at a site, having bred there once, would also benefit from familiarity with local hunting conditions. For Barn Owls, two other factors would also encourage residency: relatively low annual survival rates and cyclic food supplies. The annual survival rate of breeding Barn Owls in the study area was around 75%, so that most birds bred for only one to three seasons. Most mortality occurred in winter, in the four months before the start of the next breeding season (Taylor 1994), so that vacancies in better quality sites might not have become available until close to the breeding season. If familiarity with local feeding conditions brings significant advantages, then presumably there is at least a temporary disadvantage in moving to a new site. Incurring such a disadvantage close to the start of breeding could result in later breeding and reduced success. This might not be important for a long-lived species that has ample opportunity to make up for it in subsequent breeding seasons, but for short-lived species such as the Barn Owl it might negate any gain obtained from the increased quality of the site. This might be especially so if Field Vole populations were in the low phase of their cycle, so that food was hard to find when individual birds shifted sites. In many predatory birds males have an essential provisioning role during breeding, so that familiarity of the male with local foraging conditions may be more important than that of the female. This may be why, in some species, such as Tengmalm's Owl (Korpimaki 1988) and to a lesser extent Sparrowhawk (Newton & Marquiss 1982, Newton 1988), females tend to move sites significantly more, and over longer distances than do males. Presumably, any temporary disadvantage for these females from a lack of familiarity with local conditions is more than offset by the experience of their new mates who have remained on their sites. Why then do female Barn Owls not move more often? One possibility is that the birds' behaviour is adapted to a set of environmental conditions that no longer exists within the study area. Possibly, nests sites may have been much scarcer in the past than they are today, so that finding places to breed was more important than differences in the quality of the habitat around them. Alternatively, the large spatial variations in habitat quality demonstrated in this study may be a relatively recent development in the farmed landscape, to which the birds' site-related behaviour has not yet adapted. Until relatively recently, most farms supported higher densities of commensal rodents and birds, and populations of non-commensal species were probably also higher (Taylor 1994). Hence, spatial variations in the quality of the landscape as hunting habitat for Barn Owls may not have been so pronounced then as now.

Variations in occupancy would also have been affected by the settlement pattern of new recruits to the breeding population. Most recruits were first year birds and there was a tendency towards assortative mating, so that 56% of first year breeders had mates that were also first year birds and 44%, spread approximately equally among males and females, bred with previous breeders whose mates had died (Taylor 1994). The number recruited each year varied according to the stage of the vole cycle, with 68% of all new recruits joining the population in four peak vole years and the remaining 32% in the low vole years (Taylor 1994). Thus, young birds mostly occupied new sites when food conditions were good. Variations in breeding performance among sites in high vole years were strongly correlated with variations at the same sites during non-peak years. Thus, conditions in high vole years were predictive of longer-term conditions, but the birds still failed to select the better quality sites. Even in the peak vole years about a third of all sites available, which included good quality sites as well as poor ones, remained unoccupied.

If the failure of the birds to settle preferentially in the better quality breeding sites, demonstrated in this study, is widespread among Barn Owl populations, there may be significant conservation implications. Barn Owls have declined over much of Europe and North America since the 1930s and 1940s (e.g. Prestt 1965, Guttinger 1965, Straeten & Asselberg 1973, Braaksma & de Bruijn 1976, de Jong 1983, Illner 1988, Shawyer 1987), with many local populations have reaching critically low levels or having become extinct. A failure to select the best of the remaining habitat would further exacerbate the problems by lowering total population productivity below the maximum possible. In many areas, artificial nest sites are provided in an attempt to reverse population declines, but if the factors that determine habitat quality are not understood and these artificial sites are not placed in the better quality areas, the productivity of the population could be reduced and recovery slowed. In the worst possible cases, it might even exaggerate declines, eventually leading to local extinction. Further research is needed to determine the characteristics of good quality Barn Owl habitat, and the response of the birds to this habitat, more widely over the species' range.

ACKNOWLEDGMENTS

I am grateful to all who helped with fieldwork during this study, including the late Tom Irving, Ian Langford, Mairi Osborne, Donna Kreft, Murray Grant, Laurel Hanna, Aleem Chaudhary, Fiona Slack and Sarah Taylor. Many thanks also to Ian Newton for his valuable comments on the draft. It is a great pleasure to thank all of the landowners, especially Buccleuch Estates, and farmers who kindly gave permission to study owls on their land. The research was funded by grants from the Natural Environment Research Council, World Wide Fund for Nature, and Edinburgh University. This paper was written while I was a visitor at The Centre for Ecology and Hydrology, Hill of Brathens, Banchory, Scotland. Many thanks to Steve Albon and his colleagues for providing a stimulating environment.

REFERENCES

Arcese, P. 1987. Age, intrusion pressure and defence against floaters by territorial male Song Sparrows. *Anim. Behav*. **35**: 773–784.

Aebischer, A., Perrins, N., Krieg, M., Struder, J. & Meyer, D.R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*. *J. Avian Biol.* **27**: 143–152.

Braaksma, S. & de Bruijn, O. 1976. De Kerkuilstand in Nederland. *Limosa* **49**: 135–187.

De Jong, J. 1983. *De Kerkuil*. Kosmos: Utrecht.

Güttinger, H.R. 1965, Gur winterstblichkeit schweizerischer Schleiereulen (*Tyto alba*) mit besonder berucksichtingung des winters 1962–63. *Orn. Beob*. **62**: 14–23.

Haartman, L. von. 1968. The evolution of residency versus migratory habit in birds. Some considerations. *Orn. Fenn*. **45**: 1–7.

Haartman, L. von. 1971. Population dynamics. In Farner, D.S. & King, J.R. (eds.) *Avian Biology Vol 1*: 391–459. London: Academic Press.

Illner, H. 1988. Langfristiger Ruekgang von Schleiereule *Tyto alba*, Waldohreule *Asio otus*, Steinkaus *Athene noctua* und Waldkaus *Strix aluco* in der Agrarlandschaft, Mittelwestfalens, 1974–1986. *Vogelweldt* **109**: 145–151.

Korpimaki, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol.* **57**: 97–108.

Kluijver, H.N. & Tinbergen, L. 1953. Territory and the regulation of density in titmice. *Arch. Neél. Zool.* **10**: 265–289.

Lack, D. 1966. *Population studies of birds*. Oxford: Oxford University Press.

Lundberg, A., Alatalo, R.V., Carlson, A. & Ulfstrand, S. 1981. Biometry, habitat distribution and breeding success in the Pied Flycatcher *Ficedula hypoleuca*. *Orn. Scand*. **12**: 68–79.

Newton, I. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. *Proc. Int. Orn. Cong.* **19**: 125–154.

Newton, I. 1998. *Population limitation in birds*. London: Academic Press.

Newton, I. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis*. **133**, Supplement 1: 76–88.

Newton, I. & Marquiss, M. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* **51**:327–341.

O'Connor, R. J. 1980. Population regulation in the Yellow Hammer *Emberiza citrinella* in Britain. In Oelke. H (ed.). *Bird census work and nature conservation*: *190–200*. Gottingen, Germany: Dachverbandes Deutscher Avifaunisten.

O'Connor, R.J. 1985. Behavioural regulation of bird populations: a review of habitat use in relation to migration and residence. In Sibley, R.M. & Smith, R.H. (eds.) *Behavioural Ecology*. *Ecological consequences and adaptive behaviour*: 105–142. Oxford: Blackwell Press.

O'Connor, R.J. 1986. Dynamic aspects of habitat use. In Verner, J., Morrison, M.L. & Ralph, C.J. (eds.) *Wildlife Zoo*: *Modelling habitat relations of terrestrial vertebrates* Madison: University of Wisconson Press.

Petty, S. J. 1992. *The ecology of the Tawny owl*, Strix aluco, *in the spruce forests of Northumberland and Argyll*. Unpubl. PhD thesis, Milton Keynes: The Open University.

Prestt, I. 1965, An enquiry into the recent breeding status of some smaller birds of prey and crows in Britain. *Bird Study* **12**: 196–221.

Shawyer, C.1987. *The Barn owl in the British Isles-its past present and future*. London: The Hawk Trust.

Straeten, E. van der & Asselberg, R. 1973. Het voedsel van de Kerkuil in Belgie. *Giervalk* **63**:149–159.

Taylor, I.R. 1994. *Barn Owls*: *predator prey relationships and conservation*. Cambridge: Cambridge University Press.

3

NATAL DISPERSAL DISTANCES OF FINNISH OWLS: RESULTS FROM RINGING

PERTTI SAUROLA

Ringing Centre, Finnish Museum of Natural History, P.O.Box 17, Fin-00014 University of Helsinki, Finland.

Since 1974, Finnish ringers have been especially encouraged to work on birds of prey. More than 30,000 potential nest sites for owls are checked annually; and up to 1999, more than 190,000 owls have been ringed in Finland. I calculated dispersal distances by using recoveries of owls found dead in the breeding season, as well as of those recaptured at the nest. As predicted, natal dispersal distances were much shorter (median values 20–50 km, maximum values 300 km) in the more generalist feeders, the Eagle Owl (*Bubo bubo*), Pygmy Owl (*Glaucidium passerinum*), Tawny Owl (*Strix aluco*) and Ural Owl (*Strix uralensis*), than in the microtine specialists, the Northern Hawk Owl (*Surnia ulula*), Great Grey Owl (*Strix nebulosa*), Long-eared Owl (*Asio otus*), Short-eared Owl (*Asio flammeus*) and Tengmalm's Owl (*Aegolius funereus*), which may breed several hundreds or even thousands of kilometres away from their natal area. In the Tengmalm's Owl, the natal dispersal distances of males were significantly shorter than those of females, but in the Tawny and Ural Owls no corresponding sexual difference was found. The owlets hatched in peak microtine years, which were followed by a microtine population crash, seem to have bred, in general, farther from their natal sites than owlets hatched in other phases of the 3–4 year vole cycle.

INTRODUCTION

'Lack of information about dispersal has begun to limit progress on several biological fronts' (Walters 2000). Adequate knowledge of dispersal is of crucial importance in understanding population dynamics, as well as in planning adequate conservation measures. In this paper I will examine information on the natal dispersal distances of Finnish owls using the database of ring (band) recoveries and recaptures of the Finnish Bird Ringing Centre. I will (a) compare the natal dispersal distances of different species (b) examine whether the distances differ between sexes, and (c) explore the effects on distances of the phase of the vole cycle in the year of fledging. In

Finland the voles that form the major food source of owls normally fluctuate with a regular periodicity, the peaks every third year being followed by crashes. By *natal dispersal distance*, I mean the distance from fledging site to first breeding or potential breeding site (Greenwood 1980).

MATERIAL AND METHODS

Ringing effort

Since 1974, as the Head of the Finnish Ringing Centre, I have encouraged the ringing of nestlings and breeding adults of birds-of-prey. There were several reasons for this (Saurola 1987a). Many bird-of-prey species have suffered from various human activities: habitat destruction, deliberate killing, use of pesticides, and so on. All conservation efforts must be based on sound data on the biology of the species to be protected. Ringing is one of the methods used to gather data on population ecology and movements of the species concerned. Further, ringing of birds-of-prey has in many ways a high 'cost-benefit-ratio' from the point of view of the Ringing Centre and science. It is normally quite laborious to find and reach a brood of a bird-of-prey to be ringed; there is much (voluntary) fieldwork behind every ringed individual compared with many other species. In addition, the recovery rate (number of recoveries per number ringed) is relatively high.

During 1913–1999, a total of 198,887 owls was ringed in Finland (Table 1). This almost entirely voluntary work has so far produced a total of 25,492 recoveries and 'interesting' recaptures (see Table 1 for the definition of 'interesting'). Finland spans 1,100 km from south to north, 600 km from east to west, and is located in the far north of Europe, at latitudes 60º–70º N. The vast majority of people, including 600 ringers, live in the southern half of the country, where most ringing takes place (as an example, see Fig. 1). For this reason, species which breed in the north of the country, such as the Snowy Owl *Nyctea scandiaca*, Northern Hawk Owl *Surnia ulula*, Great Grey Owl *Strix nebulosa* and Short-eared Owl *Asio flammeus*, have been ringed in much smaller numbers than the more southerly species (Table 1).

During the last three decades, the ringers have tried to compensate the losses caused by intensive forestry by offering nest-boxes for hole-nesting owls. In 1999, 4,200 nest-boxes intended for Eurasian Pygmy Owls *Glaucidium passerinum*, 4,800 for Tawny Owls *Strix aluco*, 4,200 for Ural

Table 1. Ringing and recovery totals of owls ringed in Finland in 1913–1999.

	Number ringed	Number recovered*
Eurasian Eagle Owl *Bubo bubo*	12,024	2,604
Snowy Owl *Nyctea scandiaca*	7	65
Hawk Owl *Surnia ulula*	2,473	50
Eurasian Pygmy Owl *Glaucidium passerinum*	12,676	661
Tawny Owl *Strix aluco*	33,111	8,732
Ural Owl *Strix uralensis*	30,779	8,108
Great Grey Owl *Strix nebulosa*	1,971	122
Long-eared Owl *Asio otus*	10,649	460
Short-eared Owl *Asio flammeus*	5,368	247
Tengmalm's Owl *Aegolius funereus*	89,829	4,443

* Note. The number of recoveries includes here (a) all birds found dead and (b) birds recaptured alive if the distance moved is longer than 10 km or if time elapsed is longer than 3 months from ringing or from the previous recapture.

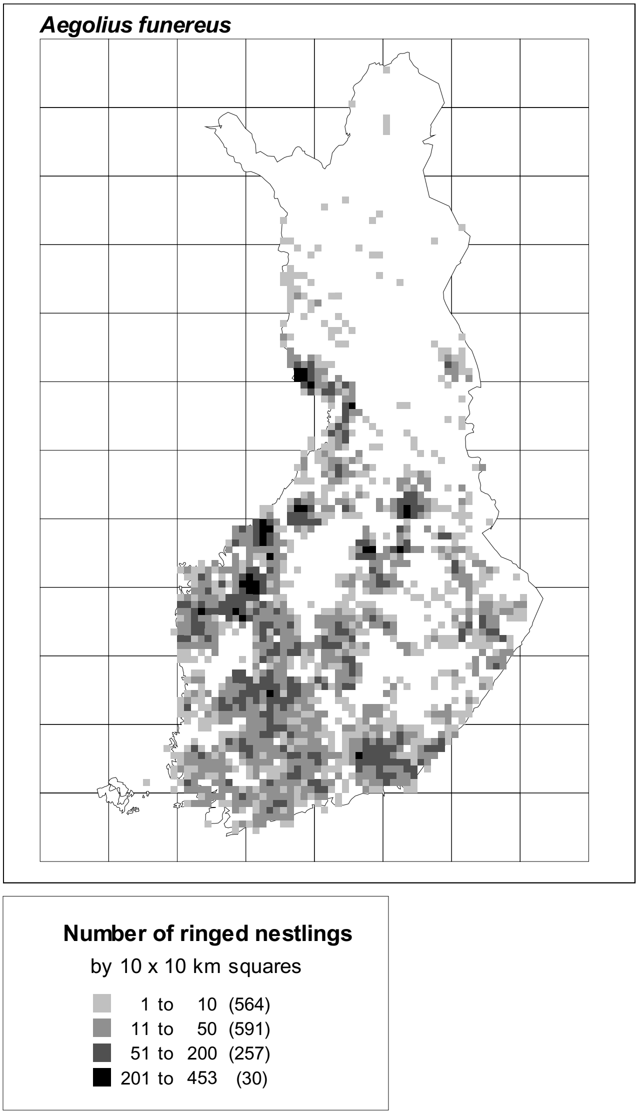


Fig. 1. Numbers of Tengmalm's Owl *Aegolius funereus* nestlings ringed in 1973–1999 in different 10x10 km squares of the Finnish National Grid. Scale from light grey to black: = 1–10, = 11–50, = 51 – 200 and = 201–453 nestlings ringed. Total nestlings ringed = 49,347.

Owls *Strix uralensis* and 10,000 for Tengmalm's Owls *Aegolius funereus* were checked by Finnish ringers, in addition to almost 6,000 natural holes. These widescale nest-box programmes explain the high numbers of nestlings ringed and adults recaptured of hole-nesting species (Tables 1and 2).

Recaptures and recoveries

In addition to ringing nestlings, I have strongly encouraged ringers to capture breeding adults at the nest, having worked out the safest and most effective procedure beforehand. It is easy to catch by hand or with a butterfly net incubating or brooding females from nest-boxes, but the

Table 2. Maximum annual numbers of active nests reported by ringers, nestlings banded, and adults captured (= banded or recaptured) at the nest of Finnish owls during 1986–1999.

The respective record years are given in parentheses. 'Active nest' includes here, in addition to nests found, broods detected after fledging. The proportion of fledged broods is low, however, except in the Long-eared Owl in which it may be up to 70% of the total. 'Population estimate' means for the non-nomadic species the average number of territories occupied annually and for the nomadic species (indicated by asterisks) the range in which the number of breeding pairs is thought to vary depending on the phase of the vole cycle (Saurola 1985 & unpublished data).

Species	Active nests	Nestlings banded	Adults captured at the nest		Population estimate
			Females	Males	
Eurasian Eagle Owl *Bubo bubo*	537 (94)	803 (94)	5 (88)	3 (89)	2,000
Snowy Owl *Nyctea scandiaca*	15 (88)	20 (88)	0	0	0–50*
Northern Hawk Owl *Surnia ulula*	119 (88)	399 (89)	10 (89)	4 (88)	50–2,000*
Eurasian Pygmy Owl *Glaucidium passerinum*	390 (99)	1,924 (99)	293 (98)	22 (91)	6,000
Tawny Owl *Strix aluco*	548 (94)	1,535 (94)	265 (91)	119 (94)	2,000
Ural Owl *Strix uralensis*	917 (99)	2,162 (99)	623 (94)	72 (89)	3,000
Great Grey Owl *Strix nebulosa*	100 (89)	200 (89)	20 (96)	13 (96)	50–1,000*
Long-eared Owl *Asio otus*	578 (91)	531 (86)	2 (88)	1 (89)	200–5,000*
Short-eared Owl *Asio flammeus*	132 (86)	322 (88)	8 (99)	14 (99)	200–5,000*
Tengmalm's Owl *Aegolius funereus*	2,265 (89)	6,691 (89)	1,336 (89)	191 (89)	1,000–15,000*

differences in sensitivity between species must be known. For instance, it is safe to catch Ural Owl or Tengmalm's Owl females at any stage of breeding, but it is risky to catch Tawny Owl or Pygmy Owl females before the young are about one week old, because at an earlier stage they are liable to desert the nest. Catching of males of hole-nesting species is possible with a trap described by Saurola (1987b), but much more difficult and time-consuming than catching of females. A safe and efficient method to catch the breeding adults of many open-nesting species, such as the European Eagle Owl *Bubo bubo* and Long-eared Owl *Asio otus*, is still to be developed. Only then could the numbers of adults caught at the nest of open-nesting species become large enough for useful analysis (Table 2).

In this paper, I used for analysis two types of recovery data of owls ringed as nestlings, namely (a) recaptures of owls caught alive at the nest as breeding adults; and (b) recoveries of owls found dead (EURING codes 1 and 2) or sick during the breeding season (April-July for the Long-eared and Short-eared Owls, March-July for the remaining species).

For resident species, it would have been possible to use all recoveries after the post-fledging period, but I wanted to use the same selection criteria for both resident and migratory or irruptive species. In some cases I have separated the records of owls which were in their second calendar year (owls which were in the breeding season about one year old) from those of older individuals.

Potential biases

Dispersal distances based on recaptures at the nest may be biased low if ringing of nestlings is restricted to the same small study area where the breeding birds are captured. This problem has been well known and various correction methods have been suggested (e.g. Barrowclough 1978, van Noordwijk 1984, Baker *et al.* 1995, Koenig *et al.* 1996). This is less of a problem in this study

Table 3. Average natal dispersal distances (km) of owls ringed as nestlings and found dead during the breeding season (April–July for the Long-eared Owl and Short-eared Owl, March–July for the remaining species).

Species	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum
European Eagle Owl *Bubo bubo*	563	71.9 (2.8)	52	26	94	416
Northern Hawk Owl *Surnia ulula*	2*	(490.0) –	–	–	–	(869)
Eurasian Pygmy Owl *Glaucidium passerinum*	10	65.0 (24.5)	8	6	147	183
Tawny Owl *Strix aluco*	1 126	38.4 (1.4)	22	10	50	386
Ural Owl *Strix uralensis*	538	41.0 (1.9)	28	14	52	339
Great Grey Owl *Strix nebulosa*	16	254.0 (56.4)	227	101	296	912
Long-eared Owl *Asio otus*	48	436.5 (68.4)	287	44	643	1,759
Short-eared Owl *Asio flammeus*	16	1007.1(248.5)	822	73	1,556	3,453
Tengmalm's Owl *Aegolius funereus*	96	153.5 (18.4)	71	19	247	874

*The distances in these two breeding season recoveries were 111 km and 869 km.

Table 4. Average natal dispersal distances (km) of owls ringed as nestlings and recaptured at the nest during their first breeding attempt.

Species	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum
European Eagle Owl *Bubo bubo*	20	48.2 (6.2)	47	31	57	114
Eurasian Pygmy Owl *Glaucidium passerinum*	131	30.1 (3.5)	15	8	33	288
Tawny Owl *Strix aluco*	1 288	28.1 (0.9)	17	8	35	270
Ural Owl *Strix uralensis*	1 036	29.4 (0.8)	22	13	38	205
Great Grey Owl *Strix nebulosa*	6	130.7 (46.7)	124	15	224	315
Tengmalm's Owl *Aegolius funereus*	541	125.0 (5.39)	78	22	200	588

because owls in large parts of the country are under study. In this paper, therefore, the distances based on recaptures are presented in non-corrected form and compared with the data based on recoveries of birds found dead.

In principle, recoveries of birds found dead by members of the general public are more random and do not suffer from the same bias as the local recaptures made by ringers. Instead the recoveries are dependent on the density of the human population. Thus, in species which often breed close to human settlements, the distances based on birds found dead may be biased low, while in species which normally breed in remote forests the equivalent distances may be biased high. It is also possible that birds which move longer distances suffer from higher mortality and, for this reason, are found dead with higher probability than are birds that have moved short distances.

Table 5. Natal dispersal distances (km) of Great Grey Owls *Strix nebulosa* ringed in Sweden, calculated from data in Stefansson (1997).

(Mann–Whitney = two tailed, p-value for normal approximation with continuity correction in Mann–Whitney U-test).

Recaptures at the nest	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum	Mann–Whitney
Males	18	36.4 (7.2)	27	15	56	100	ns.; $P = 0.76$
Females	36	63.4 (18.6)	30	10	94	650	
Total	54	54.4 (12.7)	29	10	68	650	$P < 0.0001$
Recoveries	26	166.6 (31.9)	100	38	263	530	

RESULTS

For comparing the species one with another, I calculated the average natal dispersal distances of the owls ringed as nestlings and either found dead during a subsequent breeding season (Table 3) or recaptured at the nest during the presumed first breeding attempt (Table 4).

Nomadic species

Finnish ring recoveries do not give much accurate information on the natal dispersal distances in the nomadic or semi-nomadic species. There are no relevant recoveries of the Snowy Owl and only two breeding season recoveries of the Northern Hawk Owl (Table 3). In addition to these, some interesting recoveries outside the breeding season give an idea of the scale of the movements. Of the Northern Hawk Owls ringed as nestlings in Finland two were found dead east of the Ural Mountains at 2,795 and 2,659 kilometres from their natal sites and three others in southern Norway at 1,200–1,400 kilometres from their natal sites.

To give a better picture of the movements of the Great Grey Owl (Tables 3 and 4) than is possible on Finnish records alone, I compiled Table 5 from the raw data presented by Stefansson (1997), derived from his long-term study in northern Sweden.

The Long-eared Owl and Short-eared Owl are both regular migrants in Finland, and only a small number of individuals may winter successfully when the circumstances are favourable. Recoveries indicate that, on average, the Long-eared Owls and especially the Short-eared Owls reported dead during the breeding season were several hundred kilometers away from their natal area (Table 3). With the information available, it is impossible to judge how many of these recoveries are relevant to natal dispersal and how many are likely to result from delayed migration of handicapped individuals. However, my selection criteria for recoveries was the same for all species in Table 3.

Resident species

There was a highly significant difference in average natal dispersal distances between the two types of data in the Tawny Owl and Ural Owl (Tables 3 and 4; Mann–Whitney test; $P < 0.0001$ in both cases) but not in the other species. However, when the Tawny and Ural Owl recoveries and recaptures were analysed separately for second calendar year owls and older ones, the highly

Table 6. Natal dispersal distances (km) for the Tawny Owl *Strix aluco* and Ural Owl *Strix uralensis* calculated for birds in their second calendar year (= about one year old birds) and later breeding seasons (older birds).

Recaptures = recaptures at the nest during the first breeding attempt; recoveries = recoveries of birds found dead during the breeding season; Mann–Whitney = two tailed p-value for normal approximation with continuity correction in Mann–Whitney U-test.

Species and season	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum	Mann–Whitney
Tawny Owl *Strix aluco*							
Recaptures, second calendar year	454	24.5 (1.4)	14	7	29	207	$P = 0.0001$
Recoveries, second calendar year	618	42.5 (2.1)	22	11	55	386	
Recaptures, later breeding seasons	833	30.2 (1.2)	19	9	38	270	ns.; $P = 0.054$
Recoveries, later breeding seasons	508	33.5 (1.6)	21	10	45	239	
Ural Owl, *Strix uralensis*							
Recaptures, second calendar year	80	26.9 (3.2)	18	9	35	153	$P < 0.0001$
Recoveries, second calendar year	243	49.2 (3.5)	31	15	59	339	
Recaptures, later breeding seasons	956	29.6 (0.8)	23	13	38	205	ns.; $P = 0.7$
Recoveries, later breeding seasons	295	34.3 (1.8)	26	13	45	216	

significant difference between recoveries and recaptures remained among the second calendar year owls but not among the older age classes. This was true both for the Tawny Owl and the Ural Owl (Table 6).

Comparisons between the two sexes

In general, breeding females of hole-nesting owls have been captured at the nest widely in various parts of Finland, but males have been captured at the nest only in certain intensive study areas (for example, see Figs.s 2 and 3). There were highly significant differences in natal dispersal distances between the two sexes of the Tawny Owl, Ural Owl and Tengmalm's Owl if all recaptures from the entire country were included in the analysis (Table 7). However, if the analysis was restricted only to the intensive study areas, where efforts were made to catch both sexes, the difference between the sexes remained significant only in the Tengmalm's Owl (Table 7).

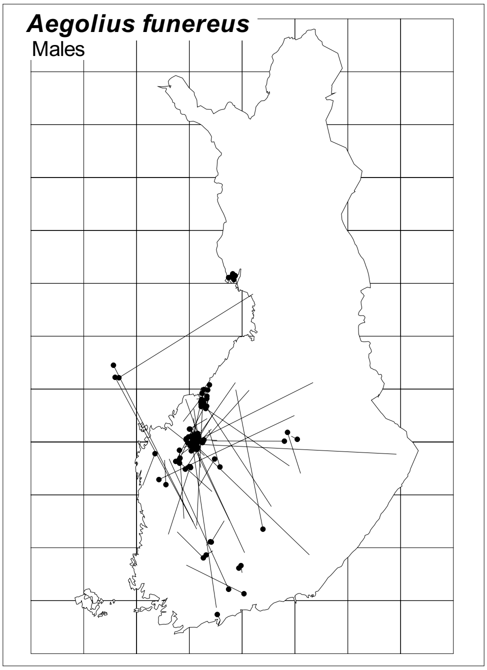


Fig. 2. Movements of 105 male Tengmalm's Owls *Aegolius funereus* between natal sites and breeding sites (indicated by dots). Grid = 100x100 km, Finnish National Grid.

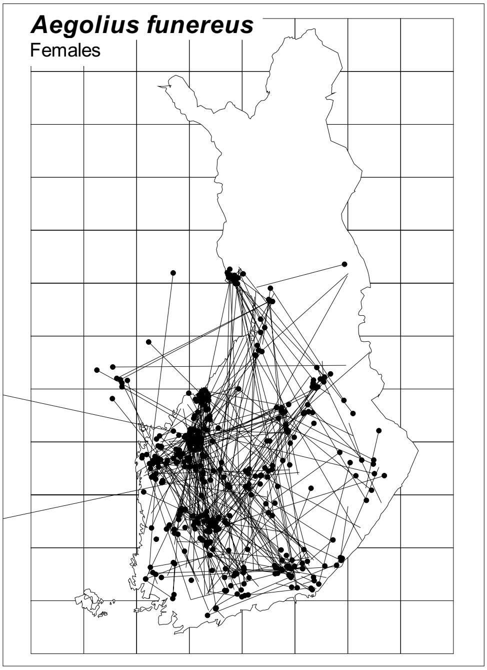


Fig. 3. Movements of 422 female Tengmalm's Owls *Aegolius funereus* between natal sites and breeding sites (indicated by dots). Grid = 100x100 km, Finnish National Grid.

Table 7. Natal dispersal distances (km) of males and females of the European Eagle Owl *Bubo bubo*, Eurasian Pygmy Owl *Glaucidium passerinum*, Tawny Owl *Strix aluco*, Ural Owl *Strix uralensis* and Tengmalm's Owl *Aegolius funereus* calculated both from recaptures at the nest of breeding adults and recoveries of birds found dead.

Mann–Whitney = two tailed p-value for normal approximation with continuity correction in Mann–Whitney U-test.

Species	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum	Mann–Whitney
European Eagle Owl *Bubo bubo*							
Recaptures							
Male	7	33.3 (8.1)	34	12	54	64	
							(ns.; $P = 0.11$)
Female	13	56.3 (7.8)	50	37	76	114	
Recoveries							
Male	52	62.3 (8.3)	46	16	85	280	
							$P < 0.05$
Female	37	79.4 (9.3)	58	11	101	238	
Eurasian Pygmy Owl *Glaucidium passerinum*							
Recaptures							
Male	10	11.5 (2.1)	11	7	19	21	
							(ns.; $P = 0.39$)
Female	117	31.6 (3.8)	16	8	35	288	

Table 7. *(continued)*

Species	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum	Mann–Whitney
Tawny Owl ***Strix aluco***							
All recaptures							
Male	358	23.7 (1.4)	15	7	30	178	*P* = 0.01
Female	898	29.7 (1.2)	18	9	37	270	
Recaptures in intensive studies							
Male	264	21.3 (1.4)	14	6	27	150	ns.;*P* = 0.43
Female	238	24.0 (1.8)	14	7	31	151	
Recoveries							
Male	31	49.3 (9.4)	28	11	62	179	ns.; *P* = 0.23
Female	23	30.0 (7.1)	23	11	34	154	
Ural Owl ***Strix uralensis***							
All recaptures							
Male	189	21.6 (1.3)	16	9	29	120	*P* < 0.0001
Female	836	31.2 (0.9)	25	14	40	205	
Recaptures in intensive studies							
Male	146	21.1 (1.4)	16	9	29	84	ns.; *P* = 0.22
Female	249	22.7 (1.1)	19	11	29	140	
Recoveries of dead birds							
Male	14	48.0 (13.3)	35	11	64	183	ns.; *P* = 0.43
Female	27	31.0 (4.9)	25	10	43	119	
Tengmalm's Owl ***Aegolius funereus***							
All recaptures							
Male	105	47.7 (9.0)	19	9	74	382	*P* < 0.0001
Female	422	140.0 (6.3)	110	33	214	588	
Recaptures in intensive studies							
Male	76	57.3 (9.4)	19	9	67	382	*P* < 0.0001
Female	110	107.9 (9.6)	66	22	181	376	

Comparisons between the different phases of the vole cycle

For studying the potential effects of food supply (i.e. the phase of the three-year vole cycle) on natal dispersal distances, I classified the years during 1980–1997 as low, increase and peak phase. In that period the cycle of two good and one bad seasons was quite clear in the southern part of Finland (Saurola 1997), from where almost all ringing data originate. In the late 1970s and late 1990s, the cycle was more obscure. Average natal dispersal distances in the three year classes are shown in Table 8. Recaptures and recoveries during the first potential breeding season (when the

Table 8. Natal dispersal distances (km) of the Eagle Owls *Bubo bubo*, Tawny Owls *Strix aluco*, Ural Owls *Strix uralensis* and Tengmalm's Owls *Aegolius funereus* fledged in low, increase and peak phases of the vole cycle.

Owls living their second calendar year excluded. Recoveries of birds found dead include only recoveries from the breeding season (March–July.) Mann–Whitney = two tailed p-value for normal approximation with continuity correction in Mann–Whitney U-test.

Species	Number	Mean (s.e.)	Median	Quartile 1	Quartile 3	Maximum	Mann–Whitney
Eagle Owl							
Recoveries of birds found dead							
Low phase	50	64.5 (7.9)	45	29	90	267	
Increase phase	101	70.0 (5.9)	53	28	95	295	
							ns.; *P* = 0.96
Peak phase	105	69.0 (5.5)	53	28	88	285	
Tawny Owl							
Recaptures at the nest							
Low phase	87	30.7 (3.5)	23	10	38	191	
Increase phase	217	27.3 (2.1)	18	8	34	186	
							P < 0.02
Peak phase	220	33.7 (2.4)	21	11	42	269	
Recoveries of birds found dead							
Low phase	34	30.5 (4.2)	25	12	41	96	
Increase phase	117	34.3 (3.7)	25	10	48	239	
							ns.; *P* = 0.32
Peak phase	75	31.1 (4.1)	20	9	33	152	
Ural Owl							
Recaptures at the nest							
Low phase	69	32.0 (2.9)	23	14	45	120	
Increase phase	383	28.6 (1.2)	22	13	36	160	
							P < 0.01
Peak phase	233	33.1 (1.6)	28	15	44	157	
Recoveries of birds found dead							
Low phase	27	36.7 (4.8)	31	19	45	102	
Increase phase	93	32.6 (3.5)	23	13	39	209	
							ns.; *P* = 0.51
Peak phase	52	35.5 (4.6)	29	12	53	205	
Tengmalm's Owl							
Recaptures at the nest							
Low phase	37	126.0 (23.9)	46	11	260	499	
Increase phase	166	122.1 (8.1)	118	26	182	489	
							P < 0.01
Peak phase	83	179.1 (14.5)	143	60	282	579	

owl is in its second calendar year and is roughly one year old) were analysed separately from later breeding seasons and excluded from Table 8 because of the differences found above (Table 6).

On the basis of recapture data, the average distance from the natal site to the first breeding site was significantly longer in young hatched in vole peak years than in increase years in the Tawny Owl, Ural Owl and Tengmalm's Owl (Table 8). Only for these three species was the recapture data set large enough to examine this point. In the Tawny Owl and Ural Owl the result was the same when analysis was based on all recoveries of owls found dead during the breeding season. However, if the recoveries of second calendar year (one year old) birds were excluded, there was no statistically significant difference between peak and increase years (Table 8). In the Ural Owl, there still was the expected difference in the numerical values of both means and medians.

In the Eagle Owl, recoveries of birds found dead gave almost exactly the same numerical values for peak and increase years (Table 8), but this species depends much less on voles than the others.

DISCUSSION

Natal dispersal distances in different species

Some comparative published information on natal dispersal distances of owls is given in Table 9. The average natal dispersal distance of the Tawny Owl was about three times longer in Finland than in Britain and southwest Sweden (Tables 3, 4 and 9). The average distance between nests (diameter of territories) in southwest Sweden was 2.7 times, and in Scotland 3.2 times, longer than in Finland (based on data in Saurola 1995, Wallin *et al.* 1988 and Petty & Peace 1992). Thus, the natal dispersal distances of birds in these three populations seem to be closely related to territory densities, with birds moving further where territories were larger.

The natal dispersal distances of the three resident *Strix* species, the Tawny Owl and Ural Owl in Finland and the Spotted Owl *Strix occidentalis* in the northwestern United States (Forsman *et al.* in press), were perhaps even more similar to one another than could be expected (Tables 4, 6 and 9).

Table 9. Published information on natal dispersal distances (km) of selected owl species.

Species and area	Number	Mean (s.e.)	Median	Reference
Barn Owl *Tyto alba*				
Britain, recoveries	445	23.9 (1.7)	-	Paradis *et al.* 1998
Pygmy Owl *Glaucidium passerinum*				
Germany, recaptures of females	33	16.8		Wiesner 1992
Germany, recaptures of males	19	11.6		Wiesner 1992
Little Owl *Athene noctua*				
Britain, recoveries	82	14.5 (2.9)	-	Paradis *et al.* 1998
Tawny Owl *Strix aluco*				
Britain, recoveries	282	8.3 (0.8)	-	Paradis *et al.* 1998
SW Sweden, recoveries	111	10.9 (1.3)	5.5	Wallin *et al.* 1988
SW Sweden, recaptures of females	137	8.6 (0.8)	6.0	Wallin *et al.* 1988
SW Sweden, recaptures of males	69	6.9 (0.7)	5.0	Wallin *et al.* 1988
Spotted Owl *Strix occidentalis*				
NW USA, recaptures of males	376	19.5 (0.8)	14.6	Forsman *et al.* in press
NW USA, recaptures of females	328	28.6 (1.0)	24.5	Forsman *et al.* in press
Long-eared Owl *Asio otus*				
Britain, recoveries	38	47.8 (9.2)	-	Paradis *et al.* 1998

From British recoveries Paradis *et al.* (1998) gave information on natal dispersal distances of the Barn Owl *Tyto alba*, Little Owl *Athene noctua*, Tawny Owl and Long-eared Owl. Wiesner (1992) carried out an extensive study on the Pygmy Owl in Germany, Wallin (1988) wrote his Ph.D. thesis on the population biology of the Tawny Owl in southwest Sweden, and Forsman *et al.* (in press) analysed the extensive data collected in the northwestern USA on the Spotted Owl *Strix occidentalis*.

The average natal dispersal distances differed significantly between the partly resident British and the migratory/semi-nomadic Finnish Long-eared Owl populations (Tables 3 and 9). But the numerical values of distances, especially for the Finnish population, may be unreliable because of potentially unrepresentative samples. The same is probably true for the data sets of other nomadic species, except the Tengmalm's Owl (see above).

Sexual differences in natal dispersal distances

Clarke *et al.* (1997) reviewed the literature on sex differences in natal and breeding dispersal in birds, strengthening the conclusion already drawn by Greenwood (1980): in most bird species, both natal and breeding dispersal distances were longer in females than in males. In their summary, natal dispersal distances were longer in females in 22 species, and in males in five species, while no sex difference was detected in 20 species.

A significant tendency for females to disperse further than males has been found in the following owl species: Barn Owl (Scotland, Taylor 1994; Utah, Marti 1999), Little Owl (Germany, Kämpfer & Lederer 1988), Spotted Owl (NW USA Forsman in press) and Tengmalm's Owl (Finland, Korpimäki *et al.*1987). These studies support the hypothesis that selection favours greater philopatry in the sex that defends the territory (see Greenwood 1980). This study strongly confirmed the greater female natal dispersal in the Tengmalm's Owl already detected in the above study with far fewer data (Table 7).

The distances calculated from the recoveries of Eagle Owls found dead during the breeding season were greater for females, but recoveries of Pygmy Owls and Great Grey Owls are too few to be sure (but see also Tables 5 and 9).

When comparisons between the two sexes of the Tawny Owl and Ural Owl were based on all recaptures from the entire country, there was a highly significant difference between the distances moved by males and females (Table 7). In contrast, when the analysis was based only on areas where both males and females were recaptured, no sexual difference was detected in either species. Clearly, all recaptures give more representative distributions of distances moved than do recaptures from restricted intensive study areas. But for the unbiased comparison between the sexes, the capture probability must be about the same for both males and females originating from near and far. Hence, the conclusion is that, in spite of the relatively extensive data, no significant sexual difference was found in the natal dispersal distances of Finnish Tawny Owls and Ural Owls. So far I have not found any good explanation for this somewhat unexpected result, which differs from what would be expected.

Effect of the phase of the vole cycle

Recoveries of birds found dead have shown that the extent of post-fledging dispersal of many species of owls depends on food supply (Newton 2002, this volume). For example, Adamcik and Keith (1978) showed that the post-fledging movements of Canadian Great Horned Owls *Bubo virginianus* were dependent on stage of the Snowshoe Hare *Lepus americanus* cycle, with longer movements in years when hares were scarce. In contrast, in very few studies of owls, have representative natal dispersal distances (= calculated from recaptures at the nest or from reliable recoveries in the breeding season) been related to measures of food supply or the density of the owl population.

Taylor (1994) found no difference between the high and low vole years in the distances moved by young Scottish Barn Owls, and further, in his review of continental Barn Owls, he gave no data on verified breeding in new areas as a result of increased dispersal in 'Wanderjahren'. With a small data set, Korpimäki & Lagerström (1988) found in the Tengmalm's Owl no differences in the natal dispersal distances between the phases of the vole cycle. Wallin *et al.* (1988) found that Tawny Owls in southwestern Sweden increased their natal dispersal distances in autumns rich in small mammals.

According to the recapture data from this study and in contrast to the findings of Wallin *et al.* (1988), the Finnish Tawny Owls, as well as Ural Owls and Tengmalm's Owls, moved longer distances when food supply was poor. In Finland, during the period analysed here, the peak phase of the vole cycle was followed by a crash, sometimes in early spring, but more often in summer. This meant that after a peak breeding season, the density of owls was high but the density of voles was low in the autumn, when post-fledging dispersal of juveniles started. In such circumstances, a young owl probably had to search larger areas, on average, to find a good vacant territory than in other phases of the vole cycle. For this reason, the average natal dispersal distances of owls fledged in a peak year should have been longer than the distances moved in an increase year when the food supply was improving towards its peak.

It is understandable that no difference emerged between the peak and increase years in distances calculated from the recoveries of dead Eagle Owls, because the Eagle Owl is less dependent on voles than the other three species (Table 8). But at the moment I cannot understand why the result from the recoveries of dead Tawny Owls (one-year-old owls excluded) was so different from the result based on recaptures at the nest.

Unfortunately there are insufficient recapture or recovery data for similar comparisons between the different phases of the vole cycle in other Finnish owl species. Further discussion of the natal and breeding dispersal distances of owls is given in the paper by Newton (2002) in this volume.

REFERENCES

Adamcik, S. R. & Keith, L. B. 1978. Regional movements and mortality of Great Horned Owls in relation to Snowshoe Hare fluctuations. *Can. Field-Nat.* **92**:228–234.

Baker, M., Nur, N.& Geupel, G.R. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using wrentits. *Condor* **97**:663–674.

Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* **49**:333–341.

Clarke, A.L., Saether, B.-E. & Roskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* **79**:429–438.

Forsman, E., Reid, J.A., Biswell, B. Loschl, P.J., Anthony, R.G., Ellingson, A., Meslow, E.C., Miller, G.S., Swindle, K., Thrailkill, J., Wagner, F. & Seaman, E. In press. Natal and post-natal dispersal of Northern Spotted Owls. *Wildlife Monograph Series.*

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* **28**:1140–1162.

Koenig, W.D., van Vuren, D. & Hooge, P.N. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *TREE* 11:514–517.

Korpimäki, E., Lagerström, M. & Saurola, P. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scand.* **18**:1–4.

Korpimäki, E. & Lagerström, M. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol.* **57**:433–441.

Kämpfer, A. & Lederer, W. 1988. Dismigration des Steinkauzes *Athene noctua* in Mittelwestfalen. *Vogelwelt* 109:155–164.

Marti, C.M. 1999. Natal and breeding dispersal in Barn Owls. *J. Raptor Res.* **33**:181–189.

Newton, I. 2002. Population limitation in Holarctic owls. In Newton, I., Kavanagh, R., Olsen J. & Taylor I. (eds.). This volume.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. 1998. Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* **67**:518–536.

Petty, S.J. & Peace A.J. 1992: Productivity and density of Tawny Owls *Strix aluco* in relation to the structure of a spruce forest in Britain. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds.) *The ecology and conservation of European owls*: 76–83. Peterborough: Joint Nature Conservation Committee.

Saurola, P. 1985. Finnish birds of prey: status and population changes. *Orn. Fenn.* **62**:64–72.

Saurola, P. 1987a. Bird ringing in Finland: status and guide-lines. *Acta Reg. Soc. Sci. Litt. Gothoburgensis. Zoologica.* **14**:189–201.

Saurola, P. 1987b. Mate and nest-site fidelity in Ural and Tawny Owls. In Nero, R.W., Clark, R.J., Knapton, R.J. & Hamre, R.H. (eds.) *Biology and conservation of northern forest owls. Symposium proceedings, February 3–7, 1987 Winnipeg, Manitoba*: 81–86. USDA Forest Service Gen. Tech. Rep. RM–142.

Saurola, P. 1995. *Suomen pöllöt. Owls of Finland.* Helsinki: Kirjayhtymä. In Finnish with English summary.

Saurola, P. 1997. Monitoring Finnish Owls 1982–1996: methods and results. In Duncan, J.R., Johnson, D.H. & Nichols, T.H. (eds.) *Biology and conservation of owls of the northern hemisphere. 2nd International Symposium, February 5–9, 1997, Winnipeg, Manitoba, Canada*: 363–380. USDA Forest Service Gen. Tech. Rep. NC–190.

Stefansson, O. 1997. *Nordanskogens vagabond. Lappugglan* (Strix nebulosa lapponica). *Vagabond of the northern forest.* Boden. In Swedish with English summaries.

Taylor, I. 1994.*Barn Owls. Predator–prey relationships and conservation.* Cambridge University Press.

Wallin, K., Carlsson, M. & Wall, J. 1988. Natal dispersal in female and male Tawny Owls (*Strix aluco*). In Wallin, K. 1988. *Life history evolution and ecology in the Tawny Owl* Strix aluco. Ph. D. thesis. University of Gothenburg.

van Noordwijk. A.J. 1984. Problems in the analysis of dispersal and a critique on its 'heritability' in the Great Tit. *J. Anim. Ecol.* **53**:533–544.

Walters, J.R. 2000. Dispersal behavior: an ornithological frontier. *Condor* **102**: 479–481.

Wiesner, J. 1992. Dismigration und Verbreitung des Sperlingskautzes (*Glaucidium passerinum* L.) in Thüringen. *Naturschutzreport* **4**:62–66.

4

NATAL AND POST-NATAL DISPERSAL OF NORTHERN SPOTTED OWLS (*STRIX OCCIDENTALIS*)

ERIC D. FORSMAN

U. S. Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis Oregon 97332 US

This paper was delivered at the conference, but because it has been published elsewhere, only the abstract has been printed here.

We studied the behaviour of 1,475 Northern Spotted Owls (*Strix occidentalis caurina*) that dispersed during banding and radio-telemetry studies in Oregon and Washington in 1985–1996. The sample included 324 radio-marked juveniles, and 1,151 banded individuals (711 juveniles, 440 non-juveniles) that were recaptured or resighted after dispersing from the initial banding location. Natal dispersal was typically initiated with a series of rapid movements away from the natal site during the first few days or weeks of dispersal. Thereafter, most juveniles settled into temporary home ranges in late October or November, and remained there for several months. Then, in February-April there was a second surge of dispersal, with many owls moving considerable distances before settling again in their second summer. Subsequent dispersal patterns were highly variable, with some birds settling permanently in their second summer, and others occupying a series of temporary home ranges before eventually settling on territories when they were 2–5 years old. On average, females dispersed farther than males. Differences between dispersal distances of radio-marked and banded owls were so small that we considered them biologically insignificant. Maximum and final dispersal distances were largely independent of the number of days that juveniles were tracked.

A minimum of 6% of the banded, non-juvenile owls on our study areas changed territories each year. The likelihood of post-natal dispersal was higher for females, young owls (1–2 yrs old), owls that did not have a mate in the previous year, and owls that lost their mate from the previous year through death or divorce. Mean distances moved by post-natal dispersers were shorter than distances moved by natal dispersers, and did not differ between the sexes or study areas.

One- and 2-year-old owls tended to disperse farther than owls that were more than 2 years old. The directions of post-natal dispersal did not differ from random.

Our data fit the general pattern observed in birds in that females dispersed farther than males and that dispersal distances were negatively skewed towards short distance dispersers. Our comparison of data from radio-marked and banded owls demonstrates that the negatively skewed distribution of dispersal distances represents the actual distribution of dispersal distances, i.e. it is not the result of small study area bias on recaptures of banded owls. Our findings were similar to those of other studies of birds in that there appeared to be little correlation between dispersal distance and individual reproductive rates, at least as measured by age at first breeding. We observed only three cases of inbreeding between siblings or between parents and offspring, which indicates that dispersal results in very low rates of close inbreeding.

5

HOME-RANGE, MOVEMENT AND DISPERSAL OF LANYU SCOPS OWLS (*OTUS ELEGANS*)

LUCIA LIV SEVERINGHAUS

Institute of Zoology, Academia Sinica, Taipei, Taiwan, 115

Lanyu is a subtropical island of 46 km^2, lying southeast of Taiwan. The small and primarily insectivorous Lanyu Scops Owl (*Otus elegans*) inhabits wooded areas on the island. Juveniles disperse at independence. Some adults also change their breeding locations from year to year. There is no sexual difference in the distances moved from natal to re-sighting site or from breeding site to re-sighting site.

The number of owls seen in good habitat shows large seasonal fluctuations, with very high densities during the breeding season. The small number of adults that remain in the breeding area year-round were mostly males of 3–6 year old. Radio-tracking of owls was conducted to select among three hypotheses capable of explaining this fluctuation. Many non-resident owls were found to winter in shrubby habitat nearby. Apparently, breeders crowd into suitable habitat before each breeding season, and disperse into wintering habitat after the breeding season.

INTRODUCTION

Important tasks when studying any rare or endangered bird species are to estimate its population size and to understand its population dynamics. The overall numbers of any bird species reach their highest level at the end of breeding, and then decline to reach their lowest level near the start of the next breeding season (Newton 1998). However, when studying the endemic Lanyu Scops Owl (*Otus elegans botelensis*) on Lanyu Island, I found its annual fluctuation within nesting habitat was opposite to this pattern, with peak numbers appearing just before breeding and lowest numbers just after breeding (Severinghaus 1992).

There are three possible explanations for this pattern: (1) owls alter their behaviour during the year, so that they are most detectable just before breeding and least detectable in the non-breeding season; (2) owls from peripheral locations not monitored by my team move in to the study area at the onset of the breeding season, and out again later; or (3) although this species has been considered an endemic resident on Lanyu Island, it is in fact partially migratory, departing each autumn and returning in spring.

This paper reports on a study aimed to understand the nature of the seasonal fluctuation in counts, and find which of the three hypotheses is the most likely cause of the fluctuation.

THE SPECIES

Lanyu Scops Owl was first collected in June 1926 by Kuroda who named it *Otus sunia botelensis* (Kuroda 1928). It was later accepted as a unique subspecies (*botelensis*) of the widely distributed Eurasian Scops Owl *Otus scops* (Hachisuka and Udagawa 1951). Based on vocalizations, Marshall (1978) reclassified it as *O. elegans botelensis*, being one of four subspecies, the other three of which were found respectiviely on Ryukyu Island (*O. e. elegans*), Daito Island (*O. e. interpositus*), and the Batanes Islands of the Philippines (*O. e. calayensis*). To my knowledge, none of the other subspecies has been studied.

Lanyu Scops Owl weighs 120 g, on average, and stands about 20 cm tall, with no size dimorphism between the sexes (Severinghaus 1986). It lives in forest, nests in tree cavities, and eats large insects, other invertebrates, and small vertebrates. It is monogamous, lays 2–3 eggs per clutch, and the female does all the incubation. The incubation and nestling periods each last about one month.

Lanyu Scops Owl was common on Lanyu Island historically (Kano 1931), but was considered endangered by 1978 (Marshall 1978, King 1981). In the 1980’s, the species was found in most parts of the island, but at higher densities in forests (up to 20 birds per survey site) than in disturbed habitat near villages (1–2 pairs per site) (Severinghaus 1989). Owl territories may overlap but, except for members of a pair, two birds do not normally use common areas of their ranges simultaneously (Severinghaus 2000). Although the population has been relatively stable in recent years (Severinghaus 1992), habitat loss is accelerating. So given its small distributional range, the subspecies is vulnerable in the longer term.

STUDY AREA

Lanyu Island (latitude 22^0 0’N, longitude 121^0 5’E) is volcanic in origin, about 46 km^2 in area, and lies 61 km southeast of Taiwan. It has very narrow coastal flatlands with a central plateau area. Soil on Lanyu is generally shallow and the topography steep. The climate of the island is humid sub-tropical (mean annual temperature 22.5°C, mean annual rainfall 3,055 mm). Three out of four days the wind speed reaches above 10 m/sec. The island is also hit by typhoons several times each year.

The coastal area of Lanyu Island is covered by littoral vegetation, including forbs, pandanas, shrubs and a few large trees (Su & Ho 1982). Shrubs form a dense cover on the cliffs, while windward slopes are covered by grasses, with small patches of meadows growing on wet areas at the bottoms of slopes. Besides small agricultural fields on flat ground scattered throughout the island, most of the down slope areas are covered by pandanas, small trees, and tall shrubs around 5 m in height. Forests typically contain only three layers, but epiphytes and lianas are common. Typical species include *Pometia pinnata*, *Palaguium formosanum*, and *Artocarpus altilis*. The forest canopy on slopes is only around 8 m tall, while that in river valleys can reach 20 m.

My study area includes both core habitat and peripheral habitat. Core sites include five patches of mature forest (Yung I, Yung II, Chungai, Hungtou, Chungshan), while peripheral sites are the smaller patches of woods around the island, such as at the Hsiang Office, Houtou, Command Office, Nursery, Lide, and Langdao. In this paper, each of these patches of woods is referred to as a study site, while the total is referred to as the study area. The total area monitored by my team is about 20 ha. The vegetation structure of the core and peripheral habitats were described in Severinghaus (1989).

The Human Factor

Lanyu Island is inhabited by the indigenous Yami people living in six villages with some Chinese mixed in. The Yamis have a sea-going culture and traditionally did not hunt the owls which they considered as bad omens. A brief history of human pressure on Lanyu Scops Owl was given in Severinghaus (1989).

Events in the past 15 years have had a mixed effect on the owl population. On the one hand, modern development and tourism accelerated habitat alteration, and brought in more motor vehicles which increased the frequency of road kills. Expanded contact with outsiders also brought in modern hunting and a gradual loss of traditional beliefs. On the other hand, conservation education efforts have heightened public awareness of this species of rare owl, which brought both protection and extra disturbance. The net effect of habitat alteration, human disturbance, and human interest on the owl population is difficult to assess.

STUDY METHODS

From August 1985, my assistants and I have mist-netted and colour-ringed owls almost every month. We also spent about seven days each month searching for ringed owls and recording their behaviour. The colour-ring combinations of all owls seen were recorded by location, while the numbers of unringed owls found in each location were also noted. In order to sex these owls, we collected a blood sample from every owl caught after 1997. Sexing protocol follows Griffiths *et al.* (1996, 1988).

In order to determine whether fluctuations in the counts were caused by seasonal variation in owl behaviour, we set mist nets in the same locations for the same number of nights each month from July 1988 through June 1989. The monthly capture rate was taken as an index of owl population size that was not biased by vocalisations or other display behaviour. In 1993, besides monitoring the core sites intensively, we selected 73 locations at roughly 500 m apart around the island and along the cross-island road, and conducted monthly population censuses by playing a taped owl call. Efforts were made to reduce the likelihood of double counting at adjacent playback stations. This gave us a monthly population estimate for owls living in peripheral habitat.

From 1999 to the present, we have been radio-tracking owls with Biotrack transmitters. From January to May 1999, we tracked four owls, while seven owls were tracked from August to January 2000. Usually two or three persons tracked simultaneously to determine the location of the focal owls. When tracking, we took a reading every ten minutes on each bird, in order to map out the paths of their activities.

RESULTS

Owl movements on the island

More than 80% of the birds in our study population have been colour-ringed, and close monitoring of the birds provided information on their movements. Accumulated data from 1986 to 1998 showed that owls moved between all parts of Lanyu Island (Fig. 1). Some birds banded on

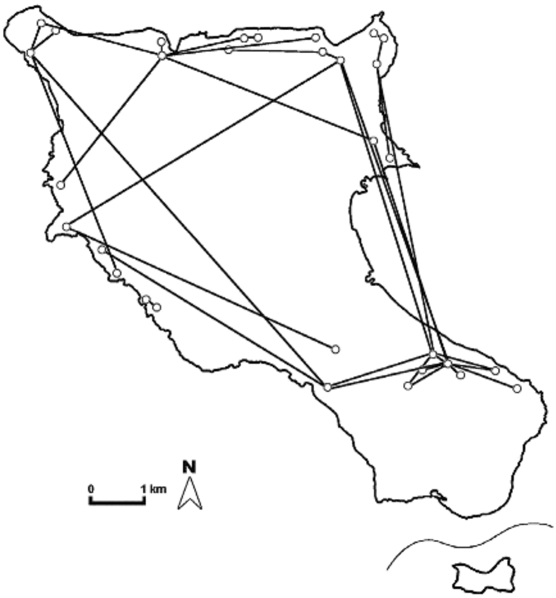


Fig. 1. Cumulative movements of owls recorded between 1985 and 1999.

Table 1. The **mean** distances moved by Lanyu Scops Owls from natal or breeding site to re-sighting site.

	n	Mean ± SD	Mann–Whitney U Statistic	P
Natal to re-sighting site				
Male	6	1.13 ± 1.14	32	0.70
Female	12	1.14 ± 1.09		
Breeding to re-sighting site				
Male	21	1.73 ± 1.54	80.50	0.52
Female	9	1.80 ± 1.18		

the east side of the island were found breeding on the west or north sides, while other owls from the north moved to the central part.

Records included the movements of juveniles from natal to re-sighting sites, as well as the movements of adults from breeding to re-sighting sites (in some but not all cases the next breeding site). Among owls ringed as nestlings, 13 females and six males were found away from their natal sites. On this small sample, the mean dispersal distance did not differ between the sexes (Table 1). Among owls ringed as breeding adults, the mean distances moved by the nine females and 20 males also did not differ from one another (Table 1).

Population fluctuation

Results of mist-netting in 1988–89 showed a monthly variation in capture rate which was similar to the monthly variation in the number of owls observed (Fig. 2). This result suggests that the observed population fluctuation in the study area was real, and did not merely reflect differences in detectability.

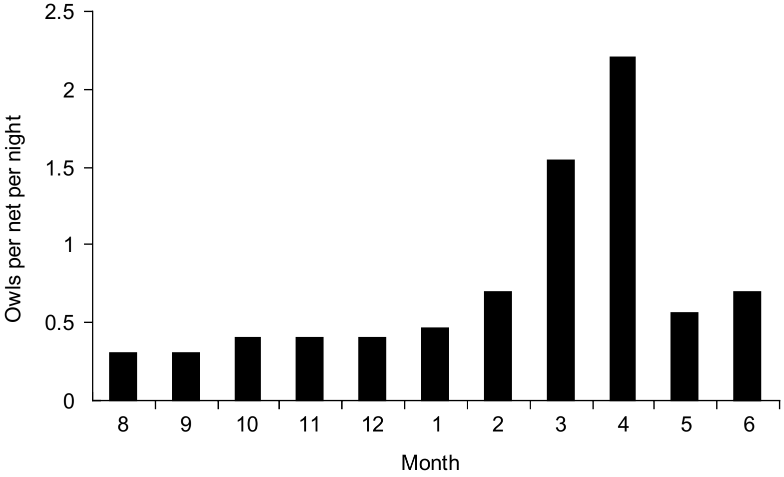


Fig. 2. Monthly variation in the number of owls caught, using the same number of mist nets in the same locations for the same number of nights each month. Data were from August 1988 to June 1989.

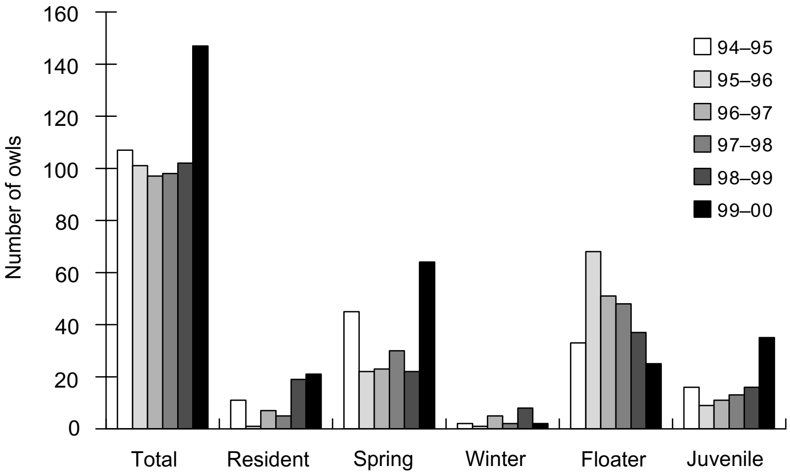


Fig. 3. Number of owls counted in core habitat between 1994 and 2000. Resident owls remained in the area year round. Spring owls showed up only in the breeding season. Winter owls appeared only in winter. Floaters appeared irregularly and infrequently. Population sizes fluctuated seasonally with the arrival and departure of non-resident owls.

Analysing the sightings of colour-ringed owls, it emerged that the population peaked when some owls moved into our study sites in spring and summer every year and decreased when some owls departed in autumn (Fig. 3). Between 1994 and 1999, the number of year-round residents, winter visitors, and juveniles produced in our core study sites showed little annual variation. However, the number of owls showing up each spring to breed, and the number of floaters seen each year, showed substantial variation from year to year. In addition, a higher number of unringed owls appeared in January through the breeding season than in autumn and

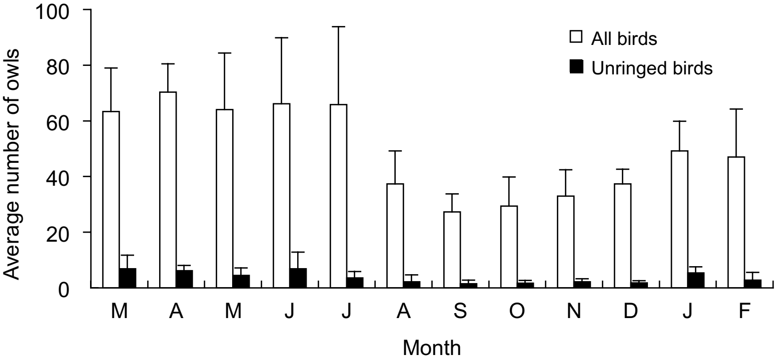


Fig. 4. Monthly variation in the mean number of owls counted in core habitat. One standard deviation is given above each column. Months are shown from March to February because March is the beginning of the breeding season. Averages are for 1994 through 1999.

winter (Fig. 4). Thus, the seasonal population fluctuations was caused by the arrival of both ringed and unringed owls in spring, and their departure in autumn.

Owls that moved

Using presence-absence records, each owl could be assigned to one of four categories: resident, spring visitor, winter visitor or floater. In core habitat, the proportion of birds assigned to each category varied from year to year. For example, in 1998, 22% of the owls were year-round residents, 26% were spring visitors, 9% were winter visitors and 43% were floaters. In 1999, however, 19% of the birds were residents, 58% were spring visitors, 13% were winter visitors and 11% were floaters.

Among owls of known age that occurred in core habitat between 1994 and 1999 ($n = 93$), six of the eight resident birds were 3–6 years old, with only one 2-year and one 8-year old bird (Table 2). Those returning in spring to breed in core habitat ($n = 26$) were primarily 3–6 year olds (81%). Winter visitors were few ($n = 5$), with only two birds in the 3–6 year category. Floaters spanned 1–9 years of age, but 50% were less than two years old, and 37% were 3–4 years old. In addition, there were 186 adults of unknown age present in core habitat.

The sex of all the owls present in the core habitat in 1998 and 1999, except 2.3% and 4.5% respectively, was known. Year-round residents were mostly males, while spring arrivals were

Table 2. Age distribution of birds in different status categories.

Status	1–2 year old	3–6 year old	>6 year old	Total	%
Resident	1	6	1	8	8.6
Spring visitor	4	21	1	26	28.0
Winter visitor	2	2	1	5	5.4
Floater	27	20	7	54	58.0
Total	34	67	10	93	100

Age composition did not differ significantly among residents, spring visitors and winter visitors ($\chi^2_4 = 4.13$, $P > 0.25$). It did, however, differ between these three groups (lumped) and floaters, which included a greater proportion of 1–2 year-olds ($\chi^2_2 = 12.93$, $P < 0.005$). Similarly, age composition among residents and spring visitors (i.e. potential breeders) differed significantly from winter visitors and floaters (i.e. those not recorded breeding) ($\chi^2_2 = 15.45$, $P < 0.005$).

mostly females. Winter visitors were practically all males, while floaters were more evenly divided by sex. The difference in residence status between male and female owls was highly significant in both 1998 and 1999 (Chi-square, $P < 0.0001$ and $P = 0.0013$ respectively). Considering only owls of known age, the difference in residence status between the sexes was significant (Chi-square test, $P < 0.0001$).

Of the seven females that were resident during 1994–2000, five paired with resident males the following spring and occupied nest cavities. The other two females were not known to breed. Most territories (86%, $n = 35$) contained only one resident bird, except for the five pairs mentioned above. In the last six years, only 35% of the 26 territories held year-round resident birds in more than one year, while other territories were occupied only once. Among the 40 resident male owls of the last six years, six birds were resident for two years, and five birds for three years, while the others were resident only in one year. No female was resident in more than one year. Most of the resident males were among the regular breeders.

Destination of movements

Results from tape-playback indicated that owl numbers did not decrease from the peripheral locations during the spring months, even though the owl responses varied with the wind or rain conditions of the time (Fig. 5). On the contrary, the pattern of population variation in the peripheral locations paralleled that of the core area, ruling out the possibility that the population fluctuation resulted from owls moving between the core habitat and peripheral locations sampled.

Among the seven owls that we were radio tracking at the end of the breeding season in 1999, only two remained in the breeding area through the winter, while three adults (two males and one female) and two juveniles moved to elsewhere on the island (Fig. 6). Their moves to their wintering quarters took place in stages, and sometimes followed circuitous routes.

Some of these wintering locations were not forested, but covered by shrubs and bushes up to 5 m tall. The fact that owls would use this type of habitat was previously unknown to us, and such locations were not included in our study area. These areas could not be used as breeding sites (because of lack of nest cavities), so if they are to breed, birds wintering in such places must

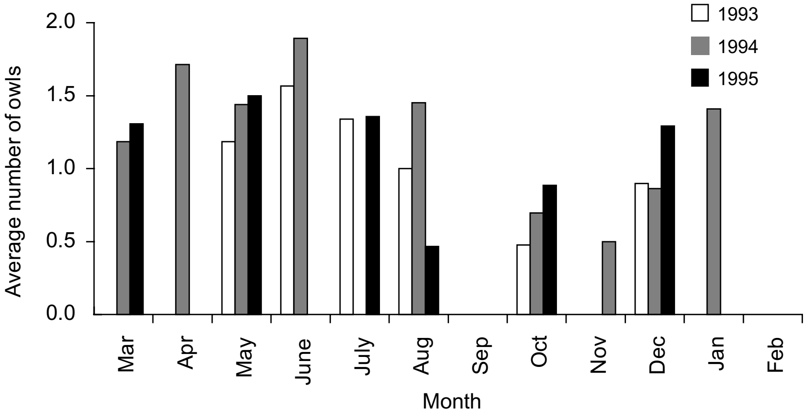


Fig. 5. Average number of owls at each peripheral playback location. The pattern of fluctuation in numbers detected paralleled that found in core habitat.

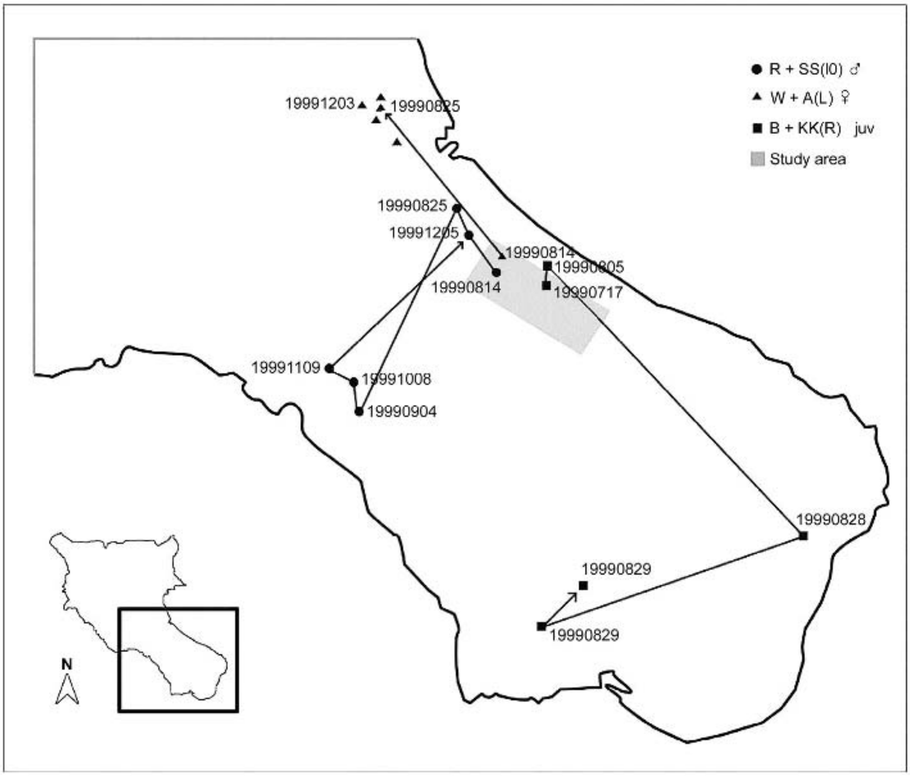


Fig. 6. Juvenile dispersal and post-breeding movements of two adults and a juvenile Lanyu Scops Owl in 1999. The date that each location was determined by radio-tracking is given.

move to locations that provide breeding opportunities. The three adults returned to their breeding sites in December 1999 and January 2000 respectively.

In conclusion, radio-tracking showed that some owls migrated locally between wintering and breeding sites, while a small number of owls were year-round residents in the prime nesting habitat of my study area.

Regional migration

If some Lanyu Scops Owls migrate off the island during the autumn and winter, the most likely wintering places would be the northern islands of the Philippines, immediately south of Lanyu. In order to search for Lanyu Scops Owls on these islands, I made a trip there with my research team in March 1999, which was the season when the islands were most accessible by boat. Although March was the beginning of the breeding season, not all spring visitors would have returned to their breeding sites by then, so some of the Lanyu Scops Owls should still be on those islands then if they went there at all.

We found a small number of owls of the local subspecies on Itbayat and Batan Islands, but not on Luzon Island. None of the owls we saw on either island were definitely identifried as Lanyu Scops Owls (*O. e. botelensis*) and none carried any leg rings. The different subspecies can be distinguished by call. Forests on these islands had already been largely destroyed. Given the fact that good habitat was much more limited on these islands than on Lanyu Island, it is highly unlikely that any Lanyu Scops Owl would migrate there.

DISCUSSION

The dispersal distances of neither juveniles nor adult Lanyu Scops Owls differed between the sexes. This agrees with findings on natal dispersal distances in some other owl species but contrasts with findings on yet others, in which females move furthest (Saurola 2002). Lanyu Scops Owl is a food generalist. But the fact that it lives year-round on a small island probably influenced its dispersal behaviour, because the farthest that any individual could move away from its natal site could not exceed the long axis of the island.

Only around 20% of Lanyu Scops Owls remained in their breeding locations year-round in a given year. Most of those that stayed were males, while more females made annual movements between wintering and breeding locations. This is similar in some respects to the partial migration found in many bird species (for example, Hawk Owl *Surnia ulula*, Byrkjedal & Langhelle 1986; Blue Tit *Parus caeruleus*, Smith & Nilsson 1987; European Robin *Erithacus rubecula*, Adriaensen & Dhondt 1990; House Finch *Carpodacus mexicanus*, Belthoff & Gauthreaux 1991), but the Lanyu Scops Owls moved over shorter distances and in various directions.

In most species, it is the larger and more dominant sex that remains close to the breeding grounds (Newton 1998). In Lanyu Scops Owls, however, there is no sexual size dimorphism and it is difficult to determine which sex is more dominant. Besides, Lanyu Island is subtropical in climate, so survival considerations are less important than at high latitudes. However, the breeding season for males appears to be longer than for females, because males start competing for nest cavities long before many of the females return to the breeding locations. The number of suitable tree cavities on Lanyu Island is very limited. Competition for nest sites probably advanced the date when males returned to the breeding habitat. Kokko (1999) pointed out that strong competition for high quality nest sites can lead to earlier arrival than would otherwise be optimal. The fact that male Lanyu Scops Owls suffer 7% higher annual mortality than females (Severinghaus & Rothery 2001) probably results from this sex difference in breeding behaviour.

Competition for nest sites is extremely strong among Lanyu Scops Owls, and resident birds had higher reproductive success than those wintering elsewhere (unpublished data). Strong competition for high quality territories can lead to partial migration, and birds in good condition are most likely to remain resident (Kokko 1999). Perhaps only the strongest owls are able to gain resident status.

The varying proportion of the Lanyu Scops Owl population that moved from breeding locations each year could be a reflection of the varying conditions of the breeding habitat from year to year. The number of owls remaining as residents may reflect the capacity of the habitat in winter. This variation may be influenced by the population size each year, which determines the levels of competition. Partial dispersal would then serve as a conditional strategy with frequency-dependent choices (Lundberg 1987).

The seasonal shift in habitat use could also reflect changes in the conditions of food resources in the different habitats. In the Barnacle Goose (*Branta leucopsis*), shifts in habitat use paralleled changes in the food quality in those habitats (Prins & Ydenberg 1985). Hazel Grouse *Bonasa bonasia* habitat shifts coincided with changes in diet (Drovetski, 1997), while in the Narcissus Flycatcher *Ficedula narcissina* habitat shifts corresponded to changes in the abundance and distribution of lepidopterous larvae (Murakami 1998). There are thus plenty of examples from other species that relate movements, and density changes in different habitats, to changes in the spatial distribution of food-supplies.

REFERENCES

Adriaensen, F. & Dhondt, A. A. 1990. Population dynamics and partial migration of the European Robin (*Erithacus rubecula*) in different habitats. *J. Anim. Ecol.* **59:** 1077–1090.

Belthoff, J. R. & Gauthreaux, S. A. Jr. 1991. Partial migration and differential winter distribution of House Finches in the eastern United States. *Condor* **93:** 374–382.

Byrkjedal, I. & Langhelle, G. 1986. Sex and age biased mobility in Hawk Owls *Surnia ulula*. *Orn. Scand.* **17:** 306–308.

Drovetski, S. V. 1997. Spring social organisation, habitat use, diet, and body mass dynamics of Hazel Grouse *Bonasa bonasia* in northeastern Asia. *Wildl. Biol.* **3:** 251–259.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7:** 1071–1075.

Griffiths, R., Daan, S. & Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proc. Roy. Soc., B.* **263:** 1251–1256.

Hachisuka, M. & Udagawa, T. 1951. Contribution to the ornithology of Formosa, Part II. *Quart. J. Taiwan Museum* **4:** 1–180.

Kano, T. 1931. The ecological distribution of birds of Kotosho. *Bull. Biogeographical Soc. Japan* **1(3):** 135–154. (In Japanese)

King, W. B. (ed.) 1981. *Endangered Birds of the World. ICBP Bird Red Data Book*. Washington, D. C.: Smithsonian Institution Press.

Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68:** 940–950.

Kuroda, N. 1928. Some new additions to the avifauna of Formosa and the Island of Botel Tobago. *Tori* **5(25):** 25–28.

Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. *J. Theor. Biol.* **125:** 340–351.

Marshall, J. T. 1978. Systematics of smaller Asian night birds based on voice. *AOU Orn. Monog.* No. 25.

Murakami, M. 1998. Foraging habitat shift in the Narcissus Flycatcher, *Ficedula narcissina*, due to the response of herbivorous insects to the strengthening defenses of canopy trees. *Ecol. Res.* **13:** 73–82.

Newton, I. 1998. *Population Limitation in Birds*. London: Academic Press.

Prins, H. H. & Ydenberg, R. C. 1985. Vegetation growth and a seasonal habitat shift of the Barnacle Goose (*Branta leucopsis*). *Oecologia* **66:** 122–125.

Saurola, P. 2002. Natal dispersal distances of Finnish owls: results from ringing. This volume.

Severinghaus, L. L. 1986. *An ecological study of the Lanyu Scops Owl* (*Otus elegans botelensis*). Ecological Research Series No. 15. Taipei: Council of Agriculture. In Chinese.

Severinghaus, L. L. 1989. The status and conservation of Lanyu Scops Owl *Otus elegans botelensis*. In Meyburg, B.U. & Chancellor, R.D. (eds.) *Raptors in the Modern World:* 423–432. Berlin: World Working Group on Birds of Prey.

Severinghaus, L. L. 1992. Monitoring the population of the endangered Lanyu Scops Owls (*Otus elegans botelensis*). In McCullough, D.R. & Barrett, R.U. (eds.) *Wildlife 2001*: *Populations*: 790–802. London: Elsevier Applied Science.

Severinghaus, L. L. 2000. Territoriality and the significance of calling in the Lanyu Scops Owl *Otus elegans botelensis*. *Ibis* **142:** 297–304.

Severinghaus, L. L. & Rothery, P. 2001. The survival rate of Lanyu Scops Owls. *Ibis* 143: 540–546.

Smith, H. G. & Nilsson, J. 1987. Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk* **104:** 109–115.

Su, H. C. & Ho, M. C. 1982. *Survey and analyses of plant resources on Lanyu and Green Islands*. Taipei: Forest Institute of National Taiwan University. In Chinese.

6

DETRIMENTAL EFFECTS OF BLOOD PARASITES ON PARENTAL EFFORT AND REPRODUCTIVE SUCCESS OF TENGMALM'S OWLS (*AEGOLIUS FUNEREUS*) AND EURASIAN KESTRELS (*FALCO TINNUNCULUS*)

ERKKI KORPIMÄKI, HARRI HAKKARAINEN, PETTERI ILMONEN & JÜRGEN WIEHN

Section of Ecology, Department of Biology, University of Turku, FIN-20014
Turku, Finland (e-mail: *ekorpi@utu.fi*)

Defenses against parasites and pathogens are expected to be beneficial in some circumstances, but also costly. We studied the benefits and costs of defence against blood parasites among Tengmalm's Owls *Aegolius funereus* and Eurasian Kestrels *Falco tinnunculus* breeding in western Finland. These birds of prey feed mainly on voles, whose population densities fluctuate in a cyclic manner, with 3–4 years between successive peaks. Blood parasite infections (intracellular *Haemoproteus* spp., *Leucocytozoon* spp. and extracellular *Trypanosoma* spp.) were more prevalent in poor food years. Parasitism was sometimes costly, as seen in (a) the reduced clutch sizes of female owls infected with leucocytozoids, (b) the later start of laying in Kestrel females mated with haemoproteid-infected males, and (c) the less vigorous defense of offspring by trypanosome-infected male owls. With supplementary food experiments and brood size manipulations, we showed that the costs of defence against blood parasites may be modified by food supply, and that the expected costs can vary between the sexes due to their different parental roles. The prevalence of trypanosomes among female owls was lower at nests where supplemental food was provided than at control nests, whereas trypanosome and haemoproteid prevalence was reduced in female Kestrels with food supplements only in a year of low natural food supply. Manipulations of Kestrel brood sizes revealed that trypanosome prevalence in males increased with experimental brood size, and the difference in prevalence between males with reduced and enlarged broods increased with decreasing natural food supply. We conclude that defence against blood parasites is costly, and that costs may vary with the sex of the avian host species and with prevailing environmental conditions.

INTRODUCTION

Costs of reproduction are defined as allocation trade-offs between current reproductive effort and future reproductive potential. When organisms invest in current reproduction their future survival and/or reproductive output may be reduced (e.g. Williams 1966), possibly because of somatic deterioration or increased predation risk. Actual mechanisms underlying reproductive costs are still largely unknown (Lessells 1991), but it has been suggested that parasites may modify the costs of reproduction (e.g. Møller 1993). Because reproduction and immune defence are both thought to be energetically costly (Keymer & Read 1991, Toft 1991, Ilmonen *et al.* 2000, Råberg *et al.* 2000), the birds may face a trade-off between allocation of resources to reproduction and immunity. The magnitude of reproductive costs vary with temporal and spatial variation in environmental conditions. Costs of reproduction may emerge only when resource levels are limited, but not if resource intake can be increased (Tuomi *et al.* 1983). In captivity, poor nutrition has often been found to be associated with impaired immunocompetence and susceptibility to diseases and parasites (Chandra & Newberne 1977, Gershwin *et al.* 1985), but in the field annual variation in food levels has mostly been ignored in studies of host-parasite interactions.

Our study birds are the Tengmalm's Owl *Aegolius funereus* and the Eurasian Kestrel *Falco tinnunculus*. Tengmalm's Owl is a small nocturnal species of holarctic coniferous forests which breeds in natural cavities or nest-boxes. The Kestrel is a small widespread diurnal raptor of open-country, which breeds on stick-nests, cliff ledges or in nest-boxes. In both species, the sexes have distinct roles in parental care. Males are responsible for all hunting from before egg-laying until the young are half-grown, whereas females produce and incubate eggs and brood the young, and help with the hunting only when the young are large. In our study area in western Finland (63°, 23°E), both species mainly feed on voles; in particular, the Field Vole *Microtus agrestis*, the Sibling Vole *M. rossiaemeridionalis* and the Bank Vole *Clethrionomys glareolus*. Population densities of all these voles fluctuate in a cyclic manner, with 3–4 years between successive peaks (Korpimäki & Krebs 1996, Korpimäki & Norrdahl 1998, Klemola *et al.* 2000). This situation provides an excellent opportunity to study the effects of varying food supply on reproductive effort and success (e.g. Korpimäki 1988, Korpimäki & Hakkarainen 1991, Hakkarainen & Korpimäki 1994a, 1994b, 1994c, Tolonen & Korpimäki 1994, 1995, 1996, Korpimäki & Rita 1996, Korpimäki & Wiehn 1998). In this paper, we summarize the results of our studies on the benefits and costs of defence against blood parasites in Tengmalm's Owls and Kestrels breeding in western Finland (for full details, see Korpimäki *et al.* 1993, 1995, Hakkarainen *et al.* 1998, Wiehn & Korpimäki 1998, Ilmonen *et al.* 1999, Wiehn *et al.* 1999).

Parasites found in the blood of Tengmalm's Owls and Kestrels included intracellular haemosporidians of the genera *Haemoproteus*, *Leucocytozoon* and *Plasmodium*, and extracellular haemoflagellates of the genus *Trypanosoma*. Their most important vectors are ornithophilic culicine mosquitos, simulid and hippoboscid flies, and dermanyssic mites. Two methods were applied to quantify different taxa of haematozoa. First, for determining intracellular haemosporidians, a drop of blood was collected in a microcapillary tube, transferred to a clean glass slide, smeared, air-dried, and fixed in absolute ethanol some hours later (Bennett 1970). Second, flagellated trypanosomes which circulate in the blood stream were quantified by means of a hematocrit centrifuge method (Woo 1970).

RESULTS

Most breeding Tengmalm's Owl parents trapped in the mid-nestling period were infected with leucocytozoids and trypanosomes, whereas the most prevalent parasites in the blood of Kestrels in the mid-nestling period were haemoproteids and trypanosomes (Table 1).

Clutch size was reduced in female owls infected with leucocytozoids at intermediate vole densities (in 1991), but not at peak vole densities (in 1992) (Fig. 1 in Korpimäki *et al.* 1993). On average, partners of infected male Kestrels started to lay eggs five days later, and produced 0.5 eggs fewer than partners of non-infected males (Figs. 1–2 in Korpimäki *et al.* 1995).

In the poor vole year of 1993, most (>80%) breeding parent owls trapped in the mid-nestling period were infected with trypanosomes, whereas in better vole years (1994–95) the prevalence of trypanosomes was lower (30% to 70% (Fig. 1 in Ilmonen *et al.* 1999). In 1993, most (>60%) breeding parent Kestrels were infected with trypanosomes in the mid-nestling period, whereas in better vole years (1994–95) the prevalence of trypanosomes was lower (20 to 30%) (Fig. 2 in Wiehn *et al.* 1999).

Investment in immunological response may occur at the expense of reduced investment in other functions. Because the defence of offspring entails a risk of serious physical harm to the parent, it is assumed to be a good measure of parental effort. In both 1994 and 1995, infected male owls defended their offspring against a live caged American Mink *Mustela vison* less vigorously than uninfected males, whereas the intensity of female nest defence was not connected with the prevalence of trypanosomes (Fig. 1 in Hakkarainen *et al.* 1998). In size, colour and movements, a mink is similar to a Pine Marten *Martes martes* which is the main predator at Tengmalm's Owl nests (Korpimäki 1987).

To study experimentally the effects of food levels on the susceptibility of parent owls and Kestrels, we provided extra food at owl nests during two years of relatively low natural food availability and at Kestrel nests during three years with low, intermediate and high levels of main food supply. Trypanosome prevalence was lower among supplemented than control female owls, whereas no effect of supplementary feeding was found in males (Table 2). In addition, food-supplementation did not have obvious effects on the prevelance of leucocytozoids and haemoproteids in the blood of parent owls. Blood parasite prevalence was reduced in female Kestrels given food supplements in a year of low food supply (1993), but not in those given food supplements in years of intermediate (1992) and high (1995) food supply. In contrast, no effect

Table 1. Prevalence (percentage of infected individuals) of parasites in the blood of Tengmalm's Owls (50 females and 65 males, data from Ilmonen *et al.* 1999) and Kestrels (84 females and 87 males, Wiehn *et al.* 1999).

Pooled data from 1993–95.

	Females	**Males**
Tengmalm's Owl		
Leucocytozoon ziemanni	100	94
Haemoproteus noctuae/syrnii	12	8
Trypanosoma avium	47	64
Kestrel		
Leucocytozoon toddi	1	0
Haemoproteus tinnunculi/brachiatus	41	23
Trypanosoma spp.	33	39

Table 2. Prevalence (% of individuals infected) of blood parasites among parent Tengmalm's Owls at food-supplemented (S) and control (C) nests during the nestling period in 1996–97.

Number of individuals within parentheses (data from Ilmonen *et al.* 1999).

Parasite	Females		Males	
	S (11)	C (11)	S (11)	C (10)
Trypanosomes	36	82	73	80
Leucocytozoids	100	100	91	90
Haemoproteids	9	0	9	20

was found in male kestrels (Fig. 1 in Wiehn & Korpimäki 1998) that do not usually alter their parental effort as a response to food-supplementation (Wiehn & Korpimäki 1997).

The influence of parental effort on susceptibility to blood parasitism was investigated by manipulating the brood sizes of Kestrels. Brood sizes were either enlarged or reduced by 1–2 young on days 5–7 after hatch while unmanipulated broods served as controls. Among female Kestrels, the effect of brood enlargement on trypanosome prevalence was apparent in the relatively good vole year (1994) only. Trypanosome prevalence in male Kestrels increased with experimental brood size, and the difference in prevalences between reduced and enlarged broods increased with decreasing natural food supply (Fig. 5 in Wiehn *et al.* 1999).

DISCUSSION

The main findings from our observational and experimental studies on blood parasites of Tengmalm's Owls and Kestrels can be summarized as follows. First, most parent owls and Kestrels were infected with trypanosomes in poor food years, whereas in better food years trypanosome prevalence was low. Second, we found that blood parasitism may be costly, as seen in the reduced clutch size of female owls infected with leucocytozoids, and later start of laying and smaller clutches in Kestrel females mated with haemoproteid infected males. Moreover, trypanosome-infected male owls defended their offspring less vigorously than uninfected males, whereas this difference was not found in female owls. Third, with supplementary food experiments and brood size manipulations, we showed that defending against blood parasites is costly, that the costs may be modified by food supply, and that the expected costs can vary between the sexes due to their different parental roles. The prevalence of trypanosomes among female owls was lower at food supplemented nests than at control nests, whereas trypanosome and haemoproteid prevalences were reduced in female Kestrels given food supplements only in a year of low natural food supply. In male owls and Kestrels, food supplements did not have obvious effects on blood parasite prevalence. Trypanosome prevalence in male Kestrels increased with experimental brood size, and the difference in prevalence between reduced and enlarged broods increased with decreasing natural food supply. Among female Kestrels, the effect of brood enlargement on trypanosome prevalence was apparent in the relatively good vole year only.

To conclude, trypanosomes appeared to have more detrimental effects on reproductive effort and success of owls and Kestrels than did haemoproteids. Our results support the idea that increased parental effort may make avian hosts susceptible to haematozoan infection. Our results also are the first to suggest that the levels of natural food supply can modify vulnerability to blood parasite infection. Female owls and kestrels appeared to be more vulnerable to blood parasite infection than males. The reasons may be that breeding females are dependent on the food provision of males and are also more exposed to parasite vectors when they incubate and brood in nest-boxes. Our results also provide new insight into why the appearance of reproductive costs may be linked to gender or to variation in environmental conditions. Finally, our results may have implications for the conservation of owl and raptor populations, because blood parasitism may be increased by habitat fragmentation which in turn may augment vector abundance and/or reduce food abundance (e.g. Loye & Carroll 1995). More field studies are therefore needed on the interactions between habitat fragmentation, food abundance, vectors and parasitism, and parasitism needs consideration in species survival and recovery plans.

ACKNOWLEDGMENTS

We would like to thank Ian Newton and two anonymous referees for valuable comments on the draft ms. These studies were financially supported by the Academy of Finland (to EK).

REFERENCES

Bennett, G.F. 1970. Simple techniques for making avian blood smears. *Can. J. Zool.* **48**: 585–586.

Chandra, R. & Newberne, P.M. 1977. Nutrition, immunity, and infection. New York: Plenum Press.

Gershwin, M.L., Beach, R.S. & Hurley, L.S. 1985. Nutrition and immunity. Orlando, FL: Academic Press.

Hakkarainen, H. & Korpimäki, E. 1994a. Does feeding effort of Tengmalm's owls reflect offspring survival prospects in cyclic food conditions? *Oecologia* **97**: 209–214.

Hakkarainen, H. & Korpimäki, E. 1994b. Environmental, parental and adaptive variation in egg size of Tengmalm's owls under fluctuating food conditions. *Oecologia* **98**: 362–368.

Hakkarainen, H. & Korpimäki, E. 1994c. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Anim. Behav.* **48**: 843–849.

Hakkarainen, H., Ilmonen, P., Koivunen, V. & Korpimäki, E. 1998. Blood parasites and nest defence behaviour of Tengmalm's Owls. *Oecologia* **114**: 574–577.

Ilmonen, P., Hakkarainen, H., Koivunen, V., Korpimäki, E., Mullie, A. & Shutler, D. 1999. Parental effort and blood parasitism in Tengmalm's Owl: effects of natural and experimental variation in food abundance. *Oikos* **86**: 79–86.

Ilmonen, P., Taarna, T. & Hasselquist, D. 2000. Experimentally activated immune defence in female Pied Flycatchers results in reduced breeding success. *Proc. R. Soc. Lond. B* **267**: 665–670.

Keymer, A.E. & Read, A.F. 1991. Behavioural ecology: the impact of parasitism. In Toft, C.A., Aeschlimann, A. & Bolis, L. (eds.) Parasite-host associations. Coexistence or conflict?: 37–61. Oxford: Oxford University Press.

Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. 2000. Experimental tests of predation and food hypotheses for population cycles of voles. *Proc. R. Soc. Lond. B* **267**: 351–356.

Korpimäki, E. 1987. Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's Owl *Aegolius funereus*. *J. Anim. Ecol.* **56**: 185–196.

Korpimäki, E. 1988. Costs of reproduction and success of manipulated broods under varying food conditions in Tengmalm's Owl. *J. Anim. Ecol.* **57**: 1027–1039.

Korpimäki, E. & Hakkarainen, H. 1991. Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. *Oecologia* **85**: 543–552.

Korpimäki, E. & Krebs, C.J. 1996. Predation and population cycles of small mammals. A reassessment of the predation hypothesis. *BioScience* **46**: 754–764.

Korpimäki, E. & Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* **76**: 2448–2455.

Korpimäki, E. & Rita, H. 1996. Effects of brood size manipulations on offspring and parental survival in the European Kestrel under fluctuating food conditions. *Ecoscience* **3**: 264–273.

Korpimäki, E. & Wiehn, J. 1998. Clutch size of Kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos* **83**: 259–272.

Korpimäki, E., Hakkarainen, H. & Bennett, G.F. 1993. Blood parasites and reproductive success of Tengmalm's Owls: detrimental effects on females but not on males? *Funct. Ecol.* **7**: 420–426.

Korpimäki, E., Tolonen, P. & Bennett, G.F. 1995. Blood parasites, sexual selection and reproductive success of European Kestrels. *Ecoscience* **2**: 335–343.

Lessells, C.M. 1991. The evolution of life histories. In Krebs, J.R. & Davies, N.B. (eds.) Behavioural Ecology. An Evolutionary Approach: 32–68. Oxford: Blackwell Science.

Loye, J. & Carroll, S. 1995. Birds, bugs and blood: avian parasitism and conservation. *Trends Ecol. Evol.* **10**: 232–235.

Møller, A.P. 1993. Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol.* **62**: 309–322.

Råberg, L., Nilsson, J.-Å., Ilmonen, P., Stjerman, M. & Hasselquist, D. 2000. The cost of immune response: vaccination reduces parental effort. *Ecology Letters* **3**: 382–386.

Toft, C.A. 1991. Current theory of host-parasite interactions. In Loye, J.E. & Zuk, M. (eds.) Bird-parasite interactions: 3–15. Oxford: Oxford University Press.

Tolonen, P. & Korpimäki, E. 1994. Determinants of parental effort: a behavioural study in the European Kestrel, *Falco tinnunculus*. *Behav. Ecol. Sociobiol.* **35**: 355–362.

Tolonen, P. & Korpimäki, E. 1995. Parental effort of Kestrels (*Falco tinnunculus*) in nest defense: effects of laying time, brood size and survival prospects of offspring. *Behav. Ecol.* **4**: 435–441.

Tolonen, P. & Korpimäki, E. 1996. Do Kestrels adjust their parental effort to current or future benefit in a temporally varying environment? *Ecoscience* **3**: 165–172.

Tuomi, J., Hakala, T. & Haukioja, E. 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *Am. Zool.* **23**: 25–34.

Wiehn, J. & Korpimäki, E. 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. *Ecology* **78**: 2043–2050.

Wiehn, J. & Korpimäki, E. 1998. Resource levels, reproduction and resistance to haematozoan infections. *Proc. R. Soc. Lond. B* **265**: 1197–1201.

Wiehn, J., Korpimäki, E. & Pen, I. 1999. Haematozoan infections in the Eurasian Kestrel: effects of fluctuating food supply and experimental manipulation of parental effort. *Oikos* **84**: 87–98.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.

Woo, P.T.K. 1970. The hematocrit centrifuge technique for the detection of trypanosomes in blood. *Can. J. Zool.* **47**: 921–923.

7

INFERTILITY AS A CAUSE OF HATCHING FAILURE IN THE BARN OWL (*TYTO ALBA*) IN THE NETHERLANDS

ARNOLD B. VAN DEN BURG

Division of Genetics, University of Nottingham, Queens Medical Centre, Nottingham NG7 2UH, United Kingdom.

In the Barn Owl *Tyto alba*, many eggs fail to hatch (average *ca* 20%). As a first step towards understanding the causes of egg hatching failures, this study was established to quantify the contribution of unfertilised eggs to total hatching failures. Unhatched eggs of Barn Owls (1998–9, *n* = 204) were collected throughout the Netherlands and the yolk membranes were subjected to fluorescent microscopy to check for excess sperm cells that indicate that fertilisation had taken place. 57% of eggs that showed no sign of embryonic development contained sperm cells adhering to these membranes, and were considered fertile. The outbred status of the Dutch Barn Owl population (which makes the occurrence of haploid and homozygous parthenogenones unlikely) and the absence of triploid embryos (which would indicate the presence of heterozygote ova, that could result in heterozygote parthenogenones) suggest that eggs containing embryos have been fertilised, and that parthenogenesis is negligible in Barn Owls. Infertility was found to contribute 20% to all egg hatching failures, and to affect an average of 4% of all eggs laid.

INTRODUCTION

The number of Barn Owls *Tyto alba* in the Netherlands has risen from an estimated 200 breeding pairs in the early 1980's to 1,400 breeding pairs in 1996 (De Jong 1997). This increase was aided by conservation efforts: by 1997, 800 volunteers worked nationwide to provide and check Barn Owl nest boxes, or were active in other aspects of conservation. It became increasingly apparent that Barn Owl clutches frequently suffer from complete or partial egg hatching failure; it is not uncommon for 20% of eggs laid by a population to fail to hatch (Taylor 1994). This lowers the number of hatchlings produced and could slow the rate of population increase. Because little is known about hatching failure in wild bird populations, its cause is a matter for speculation. This study aimed to quantify the contribution of infertility to total egg inhatchability, which may also help to focus research to clarify alternative causes. So far, little is known about the occurrence of egg infertility in wild bird populations (Lifjeld *et al.* 2000).

In this study, an egg is considered fertile after its nucleus has fused with sperm DNA to form a zygote. Before fertilisation, sperm cells have to be transferred from the male to the female, and then transported through the oviduct towards the ovary. During the first stage of oviductal transport (in the vagina) sperm cells have to propel themselves; inviable sperm cells are selected against by immunological attack and abovarial beating cilia (Bakst *et al.* 1994). Within the oviduct, from the region adjacent to the vagina, sperm cells are transported by antiperistaltic movement of the oviduct itself. In birds, sperm cells can be stored in the oviduct, but in species such as the Barn Owl, with high mating frequency (Taylor 1994), the need to store huge quantities of sperm may be reduced. The male that provides the last sperm cells to enter the storage sites will be the most likely father of the offspring, because his sperm will be the first out to fertilise the egg (Compton *et al.* 1978). After ovulation, some sperm cells hydrolyse the single layered yolk membrane (= perivitelline membrane) to fertilise the egg, but many others are caught in two more layers that are deposited by the infundibulum and cannot be hydrolysed (Wishart 1987, Howarth 1990, Bramwell & Howarth 1992).

Sperm cells that are caught in the yolk membrane provide a means of estimating the number of fertilised eggs among a sample of unhatched eggs, in the absence of embryonic development (Wishart 1987; chapter 4.). In this study, sperm cells were scored histologically in yolk membranes of eggs from Dutch Barn Owls that failed to hatch. Genetic variation among Dutch Barn Owls was assessed to discuss the likelihood of parthenogenesis – development of the ovum without fertilisation (Kosin & Sato 1960; Romanoff 1972).

MATERIAL AND METHODS

The majority of the unhatched Barn Owl eggs came from Friesland (25% of all examined eggs), Wieringermeer (19%), and the Flevopolder (15%). The number of unhatched eggs collected from each of several other regions did not exceed 10% of the total of eggs examined. Eggs were collected in 1998 and 1999. The nest boxes in which the owls lay their eggs were usually examined when the young were ready to be ringed, starting in the last week of May. Sometimes, eggs were buried in a heap of pellets produced by the nestlings and were difficult to recover. After the eggs were collected, they were stored at 4^0C until analysis. In total, 204 unhatched eggs were examined.

Egg shells were broken in the laboratory and samples of the yolk membrane were collected and washed in saline solution (0.15 M NaCl) to remove yolk debris. Cleaned samples were kept at 4^0C for at most two days before microscopic inspection. Recovered embryonic tissue was stored at -20^0C. Each egg was classified as 'embryo present', 'embryo absent', or 'not usable' if the egg was highly infected and no remains of embryonic development or yolk membrane could be found.

Prior to the microscopic analysis, the yolk membranes were rinsed in phosphate buffered saline (PBS) and spread out on a microscope slide. The membrane was stained by a few (3–4) drops of DAPI solution in PBS (4,6-diamidino–2-phenyindole, 1 µg/ml). Samples were inspected at 200x magnification (Nikon microphot FXA, exciting wavelength 350 nm, emission cut-off 450–500 nm). In order to avoid possible misinterpretation due to adherent debris, the presence of three recognisable sperm cells was used as a threshold to classify the sample as 'sperm present'.

Samples were also checked for the presence of embryonic membrane, and the yolk membrane was assessed for bacterial growth and yolk debris.

Embryo tissue was finely chopped and incubated at 55^{0}C for two nights in a lysis buffer comprising 650µl 1xSET (0.15M NaCl, 0.05M Tris, 1mM EDTA.Na$_2$), 30µl proteinase K (10 mg/ml in SET), 15µl SDS (25% in water). The samples were then cleaned using standard phenol/chloroform methods. To recover the DNA, the samples were spun through QIAquick columns (from the QIAGEN gel-isolation kit) in accordance with the manufacturer's manual. The DNA was eluted in a volume of 40µl.

Genetic variation was measured using intron size and sequence variation in two genes by SSCP (Fan *et al.* 1993; Hayashi & Yandell 1993; Lessa & Applebaum 1993). The first sequence was intron XI of the glyceraldehyde–3-phosphate dehydrogenase gene (Gapd), and the second included introns III and IV of the B-fructose 1,6-bisphosphate aldolase gene (Ald) (Friesen *et al.* 1997). PCR's were performed in accordance with standard procedures. 2–10µl of eluted DNA was used as template and annealing temperatures were as in Friesen *et al.* (1997). PCR product (8µl) was run on 1.5% TBE-agarose gell at 10V/cm to assess the product yield. Based on the amount of DNA on the agarose gel, 5–17 µl of PCR product was used for SSCP analysis. SSCP gels were prepared using MDE gel solution (FMC) (25%, v:v), 0.6x TBE, 0.6ml/ml TEMED, and 15ml/ml 10% (w:w) ammonium persulfate (APS). To each sample, 10µl loading buffer (0.025% bromophenolblue, 10mM NaOH, in formamide) was added. The products were subsequently denatured (95^{0}C, 3 min). The samples were then run on the gel for 16–24h, at 150–300V (7.5–15V/cm), at constant temperature (4^{0}C). After running, the SSCP gels were silver-stained to visualise the PCR products. Products were scored from the gel before drying it on Whatman paper.

Chi-square tests were used to test year differences among egg categories, and the occurrence of Ald homo- and heterozygotes. The year differences were tested given the year and category totals (in a 3x2 Table). The Ald allele frequencies were used to calculate the proportions of the population with a particular allelic make up, assuming Hardy–Weinberg equilibrium. This was tested against the observed frequency of individuals with these genotypes.

RESULTS

Almost all unfertilised eggs that were found in this study came from clutches that suffered partial infertility (usually one egg per clutch). In only one case was a complete clutch found to be unfertilised.

In total, 21% of the eggs were decayed to an extent that made them useless for analysis. Remains of yolk membrane were hard to recover, especially in eggs that showed embryonic development. In eggs lacking a visible embryo, the yolk membrane was usually fragmented, but pieces large enough for analysis could frequently be found sticking to the thick albumen. Membranes that showed too much background staining for reliable analysis were treated the same as eggs that did not yield a membrane sample. In total, 57% of eggs lacking a visible embryo had sperm cells in their yolk membranes (Table 1). Embryonic mortality peaked around day 3 of development (20% of total embryo deaths). At no other developmental stage did mortality exceed 6%. Embryonic development could not be detected before day 3, because all eggs were decayed to some extent.

As 57% of the eggs that did not contain an embryo were in fact fertilised, 43% of all eggs that did not show embryonic development were considered infertile. This included the eggs that were

Table 1. Egg content and the presence of sperm cells in the yolk membranes of unhatched Barn Owl eggs.

N values in section I indicate the number of eggs collected, in sections II and III the numbers of eggs that were used for fluorescence microscopy analyses. Year differences in section I were not statistically significant (χ^2_2: $P = 0.09$). The year difference in the number of analysed eggs was caused by a higher collection effort in 1999. Secton II shows the percentage eggs that were fertilised but would have been considered unfertile without the results of fluorescence sperm detection. Section III depicts the eggs with embryos that were candidates to be parthenogenones.

		1998		1999		Total	
		%	N	%	N	%	N
I	Not usable	13	70	25	134	21	204
	Embryo	57		53		54	
	No embryo	30		22		25	
II	No embryo, Sperm present	71	21	36	14	57	35
III	Embryo, No sperm	71	7	75	4	73	11

‘not usable’, for reasons given below. In total, egg hatching failure due to infertility (43% of the first and third category in the top section of table 1) accounted for 20% of all eggs examined.

Eleven different haplotypes were revealed using Gapd among 24 random individuals; these can be interpreted as 11 diploid genotypes related to seven alleles. Due to allele overlap on the gel, one haplotype, found in five individuals, could not be translated to a genotype. Four alleles had a frequency above 10%. The Aldolase introns revealed three haplotypes among 29 individuals, probably derived from two alleles (frequencies: 0.74 and 0.26). The number of homozygotes and heterozygotes fitted the Hardy–Weinberg equilibrium (χ^2: $P = 0.58$). No evidence of triploid embryos was found from the putative Gapd alleles.

DISCUSSION

Using fluorescence microscopy to identify sperm cells proved to be crucial in recognising egg infertility. Without this, 14% of the eggs would have been wrongly classified as infertile. In total, 20% of the eggs were estimated to be infertile. There may have been some unfertilised eggs that contained sperm cells and some fertilised eggs in which no sperm cells could be found. However, by setting a threshold of three detected sperm cells before an egg was classified as ‘fertilised’, it is likely that the estimate of 20% is maximal.

Eggs containing an embryo might become addled to such an extent that the remains of the embryo or the embryonic membranes cannot be detected. If this happened, such eggs would be classed as ‘not usable’. However, this is an unlikely scenario because embryonic development slows the addling process. The embryonic membranes replace the yolk membrane before it bursts (as it usually does) and thus prevent the yolk mixing with the albumen. Such mixing will provide nutrients for bacteria and will also block defensive enzymes in the albumen (personal observation).

It is to be expected that the percentage of fertilised eggs in the ‘not usable’ category will equal the percentage in those eggs that did not show embryonic development. Evidence of support for this comes from the year differences in Table 1. Egg addling was more pronounced in 1999, which matches a decrease in the number of eggs that did not show embryonic development. On average, eggs were collected at a later stage of the season in 1999, due to the owls starting to lay earlier in that year although the nest box inspections were held around the same date. Thus, the eggs had been lying in the nests for longer in 1999, causing a larger proportion to decay. Similarly, the number of eggs that could be used for reliable yolk membrane analyses was considerably less in 1999.

A yolk membrane degenerates in a matter of days after it has been replaced by the embryonic yolk sac. Thus, absence of sperm cells from the yolk membranes in embryonated eggs should not be interpreted as evidence of parthenogenetic development. DNA studies in Sparrowhawks *Accipiter nisus* revealed that most embryos have arisen from a fertilised egg (Van den Burg, *in prep*.). In inbred populations, haploid or fully homozygous parthenogenetic progeny may occur more frequently than in outbred populations (Zartman 1972), due to the loss of deleterious alleles during the inbreeding process. In Dutch Barn Owls, genetic diversity was slightly less than in Sparrowhawks at the same loci. More individuals were examined in the Sparrowhawk; six alleles were found in a sample of 54 birds at the Ald site, and 11 alleles were discovered at the Gapd locus among 74 birds (Van den Burg, *in prep*.). Although there is a difference in allele numbers, the genetic diversity among Dutch Barn Owls does not indicate an inbred situation, as might have been hypothesised on the basis of the low population numbers in the early nineteen-eighties. Therefore, it is unlikely that 3-day-old haploid or homozygous parthenogenones occurred frequently among the observed embryos. Heterozygote parthenogenones (Zartman 1972) are very hard to detect, but after fertilisation, heterozygous oocytes would become triploids. The absence of triploids at the Gapd site indicates that heterozygous parthenogenones are also unusual in Barn Owls.

Functional male or female infertility is considered to be very rare, because infertility of all eggs in a clutch was only observed once. The occurrence of infertile eggs may be related to a decrease in mating frequency, in combination with a depletion of stored sperm cells in the oviduct, at the end of the laying period. Although Barn Owls have a high mating frequency before egg laying starts (Taylor 1994), this may drop after the onset of laying, as was reported for two passerine species (Lifjeld *et al.* 2000). In accordance with the sperm competition hypothesis (Birkhead & Møller 1992), multiple copulations within the pair would increase the chance of the male being the father of the offspring, because his sperm would outcompete sperm from an extra-pair copulation. Female Barn Owls start incubating from the first egg and may be less available for copulation with other males, which may reduce the need for the male to keep his copulation efforts at a high level. Especially if the female is also not very motivated to copulate (e.g. because her conditional status is decreasing), infertile eggs may be produced. Lifjeld *et al.* (2000) reported that the number of sperm cells in the yolk membrane and oviductal storage sites decrease during the laying period in two passerine species. In domestic chickens, egg infertility is also biased towards the last eggs of a series, perhaps due to an increased vaginal immune response against sperm cells towards the end of egg production (Bakst *et al.* 1994). Regrettably, it is unknown whether the unfertilised eggs found in this study were indeed the last of a clutch.

If 20% of unhatched eggs failed due to egg infertility, 80% must have failed from other causes. This study revealed a large group of fertilised eggs that did not show embryonic development. Assuming that this is caused by very early embryonic deaths that could not be traced, the total embryonic mortality in inviable eggs during the first three days rises to 34%. This study emphasises that the first three days should play an important role in influencing the 80% of the eggs that failed from causes other than infertility.

ACKNOWLEDGMENTS

Many people were involved in the collection of unhatched eggs (under licence of the Dutch Ministry of Agriculture, Nature and Fisheries), and here I would like to thank them all. I especially thank the co-ordinators of the Dutch Barn Owl conservation network, for making all necessary arrangements within their districts. I am very grateful to Johan de Jong for his support and involvement in starting up the collection efforts on a nationwide scale. The Experimental Zoology section at the Wageningen University and Research Centre, welcomed me in both years to open the eggs in their laboratory and let me use the fluorescence microscope; without this support, organising the entire project would have been very difficult and therefore, my gratitude towards the members of this research group is great. I thank David Parkin for his support and comments on the manuscript.

REFERENCES

Bakst, M.R. & Howarth, B. 1977. Hydrolysis of the hen's perivitelline layer by cock sperm *in vitro*. *Biol. Reprod.* **17**: 370–379.

Bakst, M.R., Wishart, G. & Brillard, J.-P. 1994. Oviductal sperm selection, transport, and storage in poultry. *Poultry Sci. Rev.* **5**: 117–143.

Bramwell, R.K. & Howarth, B. 1992. Preferential attachment of cock spermatozoa to the perivitelline layer directly over the germinal disc of the hen's ovum. *Biol. Reprod.* **47**: 1113–1117.

Birkhead, T.R. & Møller, A.P. 1992. *Sperm competition in birds-evolutionary causes and consequences*. London: Academic press.

Compton, M.M., van Krey, H.P. & Siegel, P.B. 1978. The filling and emptying of the uterovaginal sperm-host glands in the domestic hen. *Poultry Sci.* **57**: 1696–1700.

Fan, E., Levin, D.B., Glickman, B.W. & Logan, D.M. 1993. Limitations in the use of SSCP analysis. *Mutation Res.* **288**: 85–92.

Friesen, V.L., Congdon, B.C., Walsh, H.E. & Birt, T.P. 1997. Intron variation in Marbled Murrelets detected using analyses of single-stranded conformational polymorphisms. *Molec. Ecol.* **6**: 277–289.

Hayashi, K. & Yandell, D.W. 1993. How sensitive is pcr-sscp? *Human Mutation* **2**: 338–346.

Howarth, B. 1990. Research note: avian sperm-egg interaction: perivitelline layer possesses receptor activity for spermatozoa. *Poultry Sci.* **69**: 1012–1015.

de Jong, J. 1997. De kerkuil in Nederland 1996. *Vogelnieuws* **10.3**: 2–3.

Kosin, I.L. & Sato, I. 1960. A study of abnormalities in parthenogenetically developing germ discs and embryos of the domestic turkey. *Morphol.* **106**: 263–276.

Lessa, E.P. & Applebaum, G. 1993. Screening techniques for detecting allelic variation in DNA sequences. *Molec. Ecol.* **2**: 119–129.

Lifjeld, J.T., Aas, C.K., Birkhead, T.R., Fletcher, F., Kroneke, C. & Rigstad, K. 2000. Variation in number of spermatozoa in Blue tit and Great tit Eggs. *Auk* **117**: 246–249.

Romanoff, A.L. 1972. *Pathogenesis of the avian embryo*. Wiley inter-science: New York.

Taylor, I. 1994. *Barn Owls*; *predator prey relationships and conservation*. Cambridge: University Press.

Wishart, G.J. 1987. Regulation of the length of the fertile period in the domestic fowl by numbers of oviductal spermatozoa, as reflected by those trapped in laid eggs. *Reprod. Fertil.* **80**: 493–498.

Zartman, D.L. 1972. An aberrant parthenogenetic chicken embryo. *Poultry Sci.* **31**: 803–808.

8

ECOLOGY AND BEHAVIOUR OF THE FOREST OWLET (*ATHENE BLEWITTI*)

FARAH ISHTIAQ[1]*, ASAD R. RAHMANI*[1] *& PAMELA C. RASMUSSEN*[2]

[1]Bombay Natural History Society, Hornbill House, Shaheed Bhagat Singh Road,
Mumbai-4000 23, INDIA
E-mail: *bnhs@bom4.vsnl.net.in*

[2]Division of Birds, NHB E607 MRC 116, Smithsonian Institution, Washington, DC 20560,
and Michigan State University Museum, East Lansing, MI 48824, USA; e-mail:
rasmussen.pamela@nmnh.si.edu

From June 1998 to June 1999 studies were conducted on the Forest Owlet *Athene blewitti* to ascertain its current status and distribution and to evaluate its ecological requirements. Playback of vocalisations resulted in the location of seven pairs at two different sites in tropical deciduous forest at 400–500 m elevation near Shahada, Maharashtra, India; playback at higher altitudes failed to elicit any response. Previously unknown vocalizations were documented, and the first data were obtained on courtship and breeding biology of this species. Three pairs were found nesting beginning in October, and one pair renested. Their habitat is open mixed teak-dominated forest with grass understory. The male provided the food for both the female and young during the breeding season. Of 183 prey capture attempts observed, 58.8% involved skinks and non-skink lizards, 15.8% field mice and rats, 2.3% birds, 1.8% grasshoppers, 0.6% frogs, 0.6% caterpillars and 20.5% were unidentified. Adults cached food in hollow trunks of dead trees (diameter 72.3 ± 0.6 cm; hole depth of 105 ± 90.9 cm; $n = 3$). The owlets normally perched at a height of 20.6 ± 4.6 m ($n = 50$), but their hunting perches were only 1–5 m ($n = 100$) in height. Seasonal differences in perching behaviour were probably related to shade and temperature. The Forest Owlet resembles pygmy-owls, *Glaucidium* species, in its diurnality, tail-flicking, relatively large, primarily reptilian prey, and relatively high wing loading typical of owls that adopt a sit-and-wait foraging strategy. The forest at sites where the owl was found is rapidly being degraded by illegal encroachment for cultivation and grazing, and requires protection if the Forest Owlet is to survive there.

INTRODUCTION

The Forest Owlet (or Forest Spotted Owlet) *Athene blewitti* is one of the rarest and least-known endemic birds of India. In the nineteenth century, only seven specimens were collected, five from northern Maharashtra, one from eastern Madhya Pradesh, and one from western Orissa. None have been obtained since then (Rasmussen & Collar 1998). The species had purportedly been last reported from Mandvi, Gujarat, by Richard Meinertzhagen who claimed to have collected a specimen there in 1914. In the 1970s, a team from the Bombay Natural History Society (BNHS) failed to find any forest or Forest Owlets in Mandvi (Ripley 1976). Later it was found that the specimen reported to have been collected by Meinertzhagen had actually been stolen from The Natural History Museum (NHM, UK) and restuffed, and that there had been no acceptable records since 1884 (Rasmussen & Collar 1998, 1999). The Forest Owlet thus remained unreported for 113 years, and was listed as extinct by several authors until its rediscovery in November 1997 (King & Rasmussen 1998).

The Forest Owlet is totally protected under the Indian Wildlife Protection Act of 1972, and is listed as critically endangered (Collar *et al.* 1994). Until recently, the only information on its life history was from anecdotal nineteenth century accounts (Ali & Ripley 1987; Rasmussen & Collar 1998; Rasmussen & Ishtiaq 1999). The need to determine the Forest Owlet's ecological requirements and conservation status led to the present study (Ishtiaq 1998) of its vocalisations, behaviour, feeding habits, breeding biology, and habitat utilisation.

STUDY AREA

The study was conducted in the Toranmal Forest Range of Shahada in Maharashtra at the site of the Forest Owlet's rediscovery in 1997 (King & Rasmussen 1998). Toranmal lies in the Akrani Range (822.7 km^2; Choudhury 1991), a western outlier of the Satpura Mountains which stretch across north-central India. The altitude in the Toranmal Forest Range extends from plains level to about 1100 m elevation. The forest is dominated by Teak *Tectona grandis* plantations, with other trees mixed in and grass understory (see 'Elevation and Habitat' for species composition), and lies in the tropical dry deciduous forest zone (Champion & Seth 1968). Most of the area has already been deforested by shifting cultivation and settlements, resulting in many barren patches due to the unsuitability of the rocky soil for long-term cultivation.

The only previous survey of the Toranmal's avifauna was by Davidson (1881), who formed a representative collection from West Khandesh. Since then there has been a sharp decline in the population of game birds (e.g. Grey Junglefowl *Gallus sonneratii* and Red Spurfowl *Galloperdix spadicea*) due to hunting, and several ungulate species are now extinct in the forest. In a one year study period, we came across no Red Spurfowl, Grey Junglefowl or any ungulate species. The plains forest, where Davidson did most of his collecting (including his five specimens of the Forest Owlet), has now been almost entirely cleared.

METHODS

Observations were made from June 1998 to June 1999 of two pairs of Forest Owlets at the rediscovery site. We started with a status survey but, due to the monsoon, the owlets were very quiet and difficult to locate, so we discontinued for about a month in August, and resumed the survey in October. Behaviours were documented photographically and on videotape, and vocalizations were tape-recorded mainly of two pairs found at the rediscovery site. In order to locate Forest Owlets at new sites, we used playback of pre-recorded owlet calls. Upon confirming the presence of a Forest Owlet, the call was never played again at that site in order to avoid disturbance of their natural behaviour. Once an individual was located, we followed it until we lost track of it in the forest. The owlets often perched for long periods, facilitating observation, but when active they were usually quickly lost to sight. Field observations and plant identifications were made primarily by FI.

Throughout the study we continued to search for more Forest Owlets in other localities. A total of seven pairs was located at two locations in Maharashtra (near both of Davidson's 1870–1880s sites). Davidson (1881) reported that he had never seen Forest Owlets in the higher hills. To check his finding, we played the tape-recorded song and territorial calls of the Forest Owlet at higher elevations (1,100 m near Toranmal village), but had no response. We conducted morning surveys of the avifauna of the Toranmal area in which eight transects of 200 m at different elevations were monitored every month. The recorded call was played at all the transects in mixed dense forest. This paper deals with general observations made near Shahada on ecological and behavioural aspects. Other findings will be presented elsewhere.

RESULTS

Elevation and Habitat

The seven pairs of Forest Owlets were all located at 400–500 m altitude with none at higher elevations. They were mainly found in the tropical dry deciduous forest zone, mostly in areas dominated by teak *Tectona grandis* along with other tree species such as *Boswellia serrata*, *Dalbergia latifolia*, *Bombax ceiba* and *Lagerstroemia parvifolia*, interspersed with grass species such as *Cymbopogon martini*, *Sehima nervosa*, *Soymida febrifuga*, *Anogeissus latifolia*, *and Lania grandis*.

Diet and Foraging

Most feeding observations were made on one pair of Forest Owlets at the time of nesting. Of 183 observed prey captures, the diet expressed as percentage of total items consisted of 58.5% skinks and non-skink lizards, 15.8% field mice and rats, 2.3% birds, 1.8% grasshoppers, 0.6% frogs, 0.6% caterpillars and 20.5% unidentified items. The owlets typically hunted using a sit-and-wait strategy. If the intended prey was on the ground, they usually dived upon it from a perch 1–5 m above ground ($n = 100$). Insects were captured either on the ground (e.g. grasshopper) or from branches by pouncing on them with the feet or landing beside them and picking them up in the bill. Lizards and rodents were seized in the claws, then killed by tearing at the base of the cranium or the neck. The heads of vertebrate prey were usually eaten first, then the forequarters, then the visceral organs, and the hindquarters were swallowed last.

During the breeding season, the male did most of the hunting and food provisioning at the nest. He passed prey to the female, who then tore off pieces and fed the begging owlets. The female remained at the nest until nearly all the young had fledged at 30–32 days. The young were dependent on the parents for at least 40–45 days after leaving the nest. Males were not seen to feed the young directly, but left the food with them while inside the nest. However, females always helped to feed the young for up to 40–45 days after leaving the nest and later males took over the responsibility of feeding the juveniles.

The young fed much as the adults did but they tore large prey into much smaller pieces before swallowing and required more time to consume it. Smaller prey such as skinks were swallowed whole while the larger *Calotes* lizards (up to 36–40 cm) were torn up and swallowed in pieces. We never saw Forest Owlets drinking.

When adults captured large prey items, they habitually brought them to regular feeding perches for consumption. These feeding sites were well within the pair's core territory. During courtship and rearing of the young, prey itmes were transported for longer distances in the claws, being switched to the bill before landing.. The males always transferred prey to the females by beak. Forest Owlets regularly cached food during the breeding season. Adults cached prey in small hollow tree trunks (mean diameter 72.3 ± 0.6 cm and mean hole depth of 105 ± 90.9 cm, $n = 3$), and juveniles sometimes left uneaten prey lying on a branch of the nest tree.

Habitat Usage

Perching and roosting sites

During early morning in winter, Forest Owlets were found perched on top of tall trees, facing the sun, often for 2–3 hours. Mean perching height was 20.6 ± 4.56 m ($n = 50$). They descended to lower strata to search for prey, sometimes only about one metre from the ground.

Forest Owlets used habitual diurnal roosts. In the winter, they roosted on bare branches, with closed eyes, sometimes resting on one leg for 4–5 hours at a time. Conversely, in the summer, after the leaves had fallen and no shade was available, the owlets avoided direct sun by perching with the underparts as close as possible to the tree trunk, changing their positions frequently depending on the movement of shade. During early summer, while leaves were still abundant, they spent much of the day well inside the leafy shade. The mean roosting height, observed during the breeding season, was 11.9 ± 3.5 m ($n = 10$). We were unable to locate any nocturnal roosts.

Nesting sites

The Forest Owlet's breeding season extended from October to May. Four cavity nests were located, two in *Soymida febrifuga* trees and two in *Anogeissus latifolia* trees. One pair re-nested in a *Lania grandis* tree. The mean height of the nests was 7.8 ± 2.0 m ($n = 4$).

Disturbance by people

The Forest Owlet appeared as a shy, elusive bird that always maintained a distance from people. However, one nest was found on a roadside at 8 m height, and the male owlet often perched on a teak on the opposite side of the road from the nest hole. When villagers, tourist vehicles, and buses passed by on the road, these owlets showed no response.

Auditory Displays

We confirmed that the Forest Owlet is primarily a diurnal species but that it shows at least some crepuscular activity. One song type and one call type were tape-recorded for the first time during the non-breeding season in June 1998 (Rasmussen & Ishtiaq 1999). This song, which now seems likely to be a secondary song, was made up of quick, clear, musical, usually bisyllabic '*oh…owow*' notes given in series of variable length and with variable intervals depending on intensity. The song was typically given by either sex from a treetop perch, and in calm weather, this song was audible for at least 1 km. On one occasion a male owlet gave a series of more than 80 notes while perched on top of a large tree in a valley, where we found it nesting a few days later.

Territorial Song

A second song type, not heard during June 1998, appears to be the main territorial song. It can be written as '*kwaak…kk*, *kwaa..k*', and first rises in pitch and then falls. This song is clear and easily distinguishable in the field but is not of very high pitch. This song was heard for up to 25 minutes at a time, but birds sometimes sang for only 5 minutes. Paired birds commonly duetted, calling back and forth in their territories and during territorial disputes. This song was the principal one used in locating pairs at new sites.

The call type already reported upon (Rasmussen & Ishtiaq 1998) consisted of a low flat buzzing '*shreee*' lasting for 2–3 seconds and rising slightly near the end; this was given when the birds were perching and otherwise quiet.

Contact call

This vocalisation was given only by the male whenever it brought food near the nest or did not find the female there. The call can be written as '*kee..yah*, *kee…yah*'. This call was used at the time of diurnal roosting. Every day before departing for roost, the male gave the same '*kee...yah*' call, possibly to make the female aware of his presence around the nesting site.

The male often gave a very subdued version of this call when he arrived near the nest with food. On hearing this call, the female would immediately fly in to receive the food from the male.

Alarm Call

A screech was frequently given by adults, usually in response to other predators. This call resembles the '*chirrur…chirrur*' call of the Spotted Owlet *Athene brama*, but is nevertheless quite different. The '*chirrur*' call of the Spotted Owlet ends with a repeated '*cheevak…heevak*', while the corresponding call of the Forest Owlet has '*chirr…chirr*' notes. This call of the Forest Owlet is given by both sexes as an alarm call in response to the presence of predators such as White-eyed Buzzard *Butastur teesa*, Shikra *Accipiter badius* and Black Eagle *Ictinaetus malayensis*, especially when these were near the owlet's nesting site. We also heard this call given by a 52-day-old juvenile Forest Owlet outside the nest in alarm when a Rufous Treepie *Dendrocitta vagabunda* was near the nest hole.

Begging Call

A begging call was given by female and juvenile Forest Owlets to incite the male to bring food for them. This call sounds like '*kee…k*, *kee…k*' and was higher in frequency with greater volume than for the '*shree*' call given by resting birds. The female frequently gave this call, especially when the male was nearby but also sometimes while searching for prey on the ground. We never heard this call from the adult male. However, similar calls were given by juveniles from inside the nest when they reached 15 days of age, but they lacked the clarity and volume of the adult female. When the juveniles left the nest, their begging calls were given as frequently as were the adult females' calls during the incubation and courtship periods. Frequently a juvenile continued giving begging calls after it had received food from the adult male.

Courtship Displays

On 16 October 1998, at 09.22 hrs, we saw a Forest Owlet flying to a tall *Boswellia serrata* tree and giving its '*oh…owow*' song. Four minutes later the call of another individual was heard from a different direction. At 09.26 hrs, these two Forest Owlets were found perched together on a branch, which confirmed that they were paired. This vocal communication seemed to mark the beginning of their courtship.

The next day, a Forest Owlet was found perched at 12m on a tall teak by the side of the road, giving '*kee…k*, *kee…k*' begging calls which could be heard from a distance of 60 m. Although it was drizzling, the owlet continued to sit in the rain, calling frequently. A day later, we found an owlet on the same branch, clutching a *Calotes* lizard in its feet, and making begging calls. At 08.40 hr, a second individual approached it, looked around and started flicking its tail rapidly, while the bird holding the lizard fluffed its feathers and started to call more loudly and frequently. The second bird then mounted the first one, which raised its tail slightly and continued calling. During mating, which lasted for 3–4 seconds, the male closed its eyes and rubbed its beak over the female's neck; afterwards the male flew to another branch but kept flicking its tail while the female called.

After this mating event, the male returned at 08.59 hr with a frog, which it gave to the continuously calling female. The male then flew to a nearby branch, flicking its tail. At 09.00 hr they mated again for 3–4 seconds, and soon after mating the male flew off. These copulations, at the beginning of the breeding season, confirmed that the second owlet was a male, while the one holding a lizard and calling was the female.

Aggressive Displays

In aggressive displays, an owlet gave a *chirr*.. *chirr* call, fluffed its body feathers, and made its head look very broad and flat. They adopted this display when they locate a predator near their nest site or when they were being mobbed by other birds, such as Jungle Babblers *Turdoides striatus*, Red-vented Bulbuls *Pycnonotus cafer*, Common Wood-Shrikes *Tephrodornis virgatus*, and Rufous Treepies *Dendrocitta vagabunda*. These birds mobbed owlets any time of the day, but usually in the morning or just before going to their nocturnal roost. Sometimes Forest Owlets chased treepies and woodshrikes away if they are struck more than 3–4 times on the head, but usually the owlets remained passive and silent.

Tail-flicking

The short, conspicuously banded tail of the Forest Owlet was frequently flicked in a rapid side to side movement while perched. The tail was also often flicked when the bird was chasing prey on the ground, and the flicking became more frequent as the bird became more excited. Sometimes after an owlet had been still-hunting for as long as an hour, it would begin flicking its tail, while staring intently at the ground, which seemed to indicate that it had spotted potential prey. In addition, the male flicked its tail a great deal both before and after mating.

Head Bobbing

The Forest Owlet frequently engaged in repeated and exaggerated head-bobbing. This behaviour was usually performed when a human or potential predator approached the owlet. When we approached within 10–15 m, the owlets began bobbing their heads, and either flew to a higher branch, or remained on their perch if no threat seemed imminent.

Maintenance Behaviour

Resting

The adults rested in one of two basic postures that were correlated with the birds' need to dissipate or conserve body heat. We never saw them sleeping with their heads buried in their back feathers. During warm weather or while perched in the sun in summer, they augmented heat loss by gular fluttering as well as by exposing their legs and feet pads, sleeking their contour feathers, and drooping their wings. Conversely, for conserving body heat in relatively cool weather, the birds crouched, frequently on one leg, the other being drawn up in the feathers of the abdomen, the neck withdrawn and feathers fluffed.

DISCUSSION

Our study provided the first data on the ecology and behaviour of the Forest Owlet. In a number of behavioural respects, as well as some morphological ones, the Forest Owlet is more similar to pygmy-owls *Glaucidium* than it is to *Athene* owls (Rasmussen & Collar, in prep.). Its wings are broader and its body is much heavier than in *Athene brama*, and hence its wing loading must be higher, as is typical of forest-living, sit-and-wait hunting owls, such as *Glaucidium* species (Marks *et al.* 1999). Pygmy-owls tend to prey more on reptiles than do most owls, and by far the largest portion of the diet of the Forest Owlet is comprised of lizards (Proudfoot 1997, Marks *et al.* 1999). It should be noted, however, that most other studies have used analysis of pellets, while we counted prey taken to the nest area, so the data from the different studies may not be strictly comparable. The Spotted Owlet also takes a small amount of reptile prey, but these are of very small size (Suresh Kumar 1985: 103). The Forest Owlet has extraordinarily stout tarsometatarsi and large claws compared with other *Athene* species, again suggesting a reptile diet (R. W. Storer, pers. comm.). The Forest Owlet resembles pygmy-owls in its preference for relatively large prey (including quail and lizards up to 40 cm); its strongly diurnal habits and its tail-flicking (Solheim 1984, Proudfoot 1997, König *et al.* 1999, Marks *et al.* 1999).

The genus *Athene* (including *Speotyto*) is the sister group to the pygmy-owls and the Northern Hawk-Owl *Surnia ulula* (Wink & Heidrich 1999), but *A. blewitti* was not included in the analysis. Further systematic studies will be necessary to settle the generic allocation of the Forest Owlet. Resurrection of the monotypic genus *Heteroglaux* in which the Forest Owlet was described by Hume (1873) may be found necessary.

The much more heavily feathered toes of the Forest Owlet, as compared with those of the Spotted Owlet, are almost certainly related to the larger and more dangerous prey of the Forest Owlet. Both species occur at low elevations in the same parts of India that are seasonally extremely hot, so a thermoregulatory explanation following 'Kelso's Rule' (Kelso & Kelso 1936) seems unlikely. Also, the Spotted Owlet is a mostly nocturnal predator that roosts diurnally in holes and crevices, so it would mostly be exposed to cool night air.

The increasing human pressure on the habitat of the Forest Owlet is of great concern. Illegal tree cutting, land encroachment for cultivation and settlement are ongoing practices at these sites, so that the habitat has become fragmented and patchy. There is an urgent need to declare the Forest Owlet site as a protected area. It remains unclear why the species is so restricted in its known range, and why it has been missed since its discovery in 1872. In the 1870s and 1880s, it was collected by only three people at four sites, and there are considerably fewer museum specimens of the Forest Owlet than of any other resident bird species of central India. A more detailed investigation of the ecology and status of the Forest Owlet is urgently required to assess the factors limiting its populations and the degree of its endangerment.

ACKNOWLEDGMENTS

Financial support was provided by the Biological Surveys and Inventories (BSI) program and the Office of the Secretary Emeritus, National Museum of Natural History, Smithsonian Institution, and Mr. Hans Sigg-Forycki, Switzerland. Thanks go to the Maharashtra Forest Department for permission to work in the Shahada reserve forest, especially to Mr. Moi Pokkyim (ex-Deputy Conservator of Forest, Shahada), Mr. S. H. Patil, Deputy Conservator of Forests, Shahada, and Mr. Jeet Singh, Deputy Conservator of Forests, Taloda. Mr. R. J. Gaikwad, Ranger of Ranipur and staff helped us set up our base camp and in other ways. We also thank Mr. J. C. Daniel (Hon. Secretary) Mr. Naresh Chaturvedi (Curator), Mr. S. R. Nayak, Mr. T. K. Bharatan, and other staff of the BNHS for their help and cooperation during the study. Special thanks go to Mr. Mehboob Alam for his continuous help in the field and with data collection.

REFERENCES

Ali, S. & S. D. Ripley. 1987. *Handbook of the birds of India and Pakistan*. Compact Ed. Delhi: Oxford University Press.

Champion, H. G. & Seth S. K. 1968. *A revised survey of the forest types of India*. Manager of Publications, Delhi.

Choudhury, R. L. 1991. Working plan for the forests of North Dhulia divisions. Part 1. Unpublished Forest Department Report.

Collar, N.J., Crosby, M. J. and Stattersfield, A. J. 1994. *Birds to watch 2*. Cambridge: BirdLife International.

Davidson, J. 1881. Rough list of the birds of Western Khandesh. *Stray Feathers* **10**: 279–327.

Hume, A. O. 1873. *Heteroglaux blewitti*, Sp. Nov. *Stray Feathers* **1**: 468–469.

Ishtiaq, F. 1998. Status survey of the Forest Owlet *Athene blewitti* in India. Bombay Natural History Society, Mumbai, Unpublished report.

Kelso, L. & Kelso E. H. 1936. The relation of feathering of feet of American owls to humidity of environment and to life zones. *Auk* **53**: 51–56.

King, B. & Rasmussen P. C. 1998. Rediscovery of the Forest Owlet *Athene blewitti*. *Forktail* **14**: 51–53.

König, C., F. Weick, & Becking J.-H. 1999. *Owls. A guide to the owls of the world*. Sussex: Pica Press.

Marks, J.S., Cannings R. J., & Mikkola H. 1999. Family Strigidae (typical owls). In del Hoyo, J., Elliott, A., and Sargatal, J. (eds.). *Handbook of the birds of the World*. Vol. 5: 76–151. Barcelona: Lynx Edicions.

Proudfoot, G. A. & Beasom S. L. 1997. Food habits of nesting Ferruginous Pygmy-Owls in southern Texas. *Wilson Bull*. **109**: 741–748.

Rasmussen, P.C. & Collar N. J. 1998. Identification, distribution and status of the Forest Owlet *Heteroglaux blewitti*. *Forktail* **14**: 41–49.

Rasmussen, P.C. & Collar N. J. 1999. Major specimen fraud in the Forest Owlet *Heteroglaux* (*Athene* auct.) *blewitti*. *Ibis* **141**:11–21.

Rasmussen, P. C. & Ishtiaq F. 1999. Vocalizations and behaviour of the Forest Owlet *Athene* (*Heteroglaux*) *blewitti*. *Forktail* **15**: 61–65.

Ripley, S. D. 1976. Reconsideration of *Athene blewitti* (Hume). *J. Bombay Nat. hist. Soc.* **73**: 1–4.

Solheim, R. 1984. Caching behavior, prey choice and surplus killing by pygmy-owls (*Glaucidium passerinum*) during winter, a functional response of a generalistic predator. *Ann. Zool. Fenn.* **21**: 301–308.

Suresh Kumar, T. 1985. *The life history of the Spotted Owlet* (Athene brama brama, *Temminck*) *in Andhra Pradesh*. Raptor Research Centre Monogr. Publ. No. 4, Hyderabad, India.

Wink, M. & Heidrich P. 1999. Molecular evolution and systematics of the owls (Strigiformes). In König, C., F. Weick, and J.H. Becking. *Owls. A guide to the owls of the world*: 39–57 Sussex: Pica Press.

Part 2

Distribution, habitat and diet

9

HABITAT QUALITY IN POWERFUL OWL (*NINOX STRENUA*) TERRITORIES IN THE BOX–IRONBARK FOREST OF VICTORIA, AUSTRALIA

T. R. SODERQUIST[1,2], *K. W. LOWE*[3], *R. H. LOYN*[1] *& R. PRICE*[4]

[1] Arthur Rylah Institute, Department of Natural Resources and Environment, 123 Brown St, Heidelberg, Victoria, Australia 3084.

[2]Current address: Threatened Species Unit, NSW National Parks and Wildlife Service, PO Box 2111 Dubbo, New South Wales 2830

[3]Parks, Flora and Fauna Division, NRE, PO Box 500, East Melbourne, Victoria 3002

[4]Flora and Fauna, NW Region, NRE, PO Box 3100, Bendigo, Victoria 3554

Box–Ironbark forests in central Victoria have been extensively cleared, fragmented and subjected to intensive timber harvesting. The remnant population of Powerful Owls *Ninox strenua* is this region is widely distributed but at very low densities. Comparative habitat analyses between areas occupied by breeding pairs and the forest at large suggest that owls select areas with more large old trees and more hollows than are available on average in the forest. These two environmental attributes have been demonstrated previously to correlate with densities of the owl's preferred prey, hollow-dependent arboreal mammals. Conservation of the Powerful Owl in this region requires protection and enhancement of currently occupied territories, and expansion of the population through sympathetic management of the wider forest to return it to a more natural state.

INTRODUCTION

Large owls may act as 'umbrella species' (Simberloff 1997) because, as high-order carnivores, their population density and stability reflect the abundance and viability of a suite of prey species, and thus of numerous habitat parameters. The largest Australian owl, the Powerful Owl

Ninox strenua, is widespread but rare in the eucalyptus forests of eastern Australia (Higgins & Davies 1999). Recent assessment of its conservation status in Victoria has identified habitat clearing and degradation as the primary causes of the species' population decline (NRE 2000), leading to its listing as an Endangered species (NRE 1998a). Within its current range, breeding pairs are particularly sparse in the dry eucalyptus forests of central Victoria.

Until recently, the Powerful Owl in Victoria was assumed to be associated solely with wetter forests south of the Great Dividing Range (e.g. Fleay 1968). During the past decade, growing awareness of the species in dry eucalyptus forests has promoted a re-evaluation of its habitat requirements (Traill 1993). About 85% of potential Powerful Owl habitat has been cleared in the Box–Ironbark region of central Victoria, with forests and woodlands on the most fertile soils removed first (ECC 1997). The remaining forest is fragmented and has been intensively harvested. Only one small patch of old growth exists in over 300,000 ha of public land (ECC 1997), and less than 7% of the remaining Box–Ironbark forest currently has a density of large, old trees that approaches levels present before European settlement (Soderquist & Rowley 1995, Holland & Cheers 1999). The loss of large trees has meant a decline in tree hollows (Soderquist 1999a), and a concomitant decline in the main prey of the Powerful Owl, hollow-dependent arboreal marsupials (Traill 1991). These factors may explain the current low densities of Powerful Owls in the region. They further suggest that the Box–Ironbark forest was formerly much better habitat for the species than now, and that the declining regional populations should not be dismissed as marginal or unrepresentative. This project was designed to identify aspects of the habitat requirements of Powerful Owls in the Box–Ironbark forest of central Victoria, and to guide land management protocols.

METHODS

The Box–Ironbark region

Soils of the Box–Ironbark region are predominantly shallow, infertile clays, and the landscape is mostly undulating with widely scattered hills. Precipitation increases from west to east, with 400–700 mm of rain per year falling mostly during winter. Temperatures exceeding 35°C are common during summer and frosts are frequent in winter.

Grey Box *Eucalyptus microcarpa* and Red Ironbark *E. tricarpa* are the most common tree species, followed by Yellow Gum *E. leucoxylon*. Red Box *E. polyanthemos*, Red Stringybark *E. macrorhyncha* and Long-leaved Box *E. goniocalyx* are also common, and predominate on the low ridges. Yellow Box *E. melliodora* has been conserved for many decades as an important source of nectar for commercial bee keepers, and is therefore disproportionately well represented among the large remnant trees of the region (Soderquist 1999a). Other less common species include River Red Gum *E. camaldulensis*, White Box *E. albens*, and Green Mallee *E. viridis*.

Study sites

The study area was approximately defined by the towns of Murchison (145°10′ E, 36°40′ S), Tooborac (144°50′ E, 37°00′ S), Dunolly (143°40′ E, 36°50′ S) and Logan (143°30′ E, 36°40′ S). Only owls occupying the Box–Ironbark Broad Vegetation Class (ECC 1997) were considered for analysis. Fifteen sites were chosen for study where there were recent records of owls (Gibbons 1995, Soderquist 1999b). Because the eastern sections of the Box–Ironbark forest are more

Table 1. Habitat attributes of 15 Powerful Owl home ranges measured for the density of large old trees (LOT).

Sites are designated as those E and W of the Loddon River.

Site designation	Site Name	Mean density of LOT ha^{-1}	Standard Deviation	Percent of plots with > one LOT
W	Bolangum	8.2	5.0	91
W	Big Tottington	5.0	4.6	80
W	Wehla	4.8	5.0	74
W	Kooyoora	5.3	4.6	84
W	Dalyenong	6.8	5.3	84
W	Moorl Moorl	2.9	3.4	59
W	Tarnagulla	0.7	1.6	26
E	Lyell	0.9	1.6	30
E	Pilchers Bridge	1.7	2.6	47
E	Crosbie	2.4	3.8	48
E	Dargile	1.1	1.9	36
E	Costerfield	1.6	2.1	49
E	Mt Black	3.5	4.2	68
E	Darrochs Dam	5.0	3.7	83
E	Spring Plains	2.2	3.1	52

degraded than the western (NRE 1998b), due primarily to the closer proximity of higher-density human settlements in the east and the resulting more intensive exploitation of the forest, the sites were divided into two geographical groups lying east or west of the Loddon River.

General locality names of each owl territory are provided in Table 1. Powerful Owls are highly susceptible to human disturbance, so the exact locations of these territories are not disclosed here. Records of the study sites are on file with the Victorian Department of Natural Resources and Environment, and are available for scientific or management purposes.

Playback survey

The continued residency of Powerful Owls at these Box–Ironbark sites was verified using playback survey (e.g. Debus 1995) conducted during autumn 1998. The surveyor initially listened at a site for at least 10 min in order to detect ‘voluntary’ calling of the resident birds. A tape was then played of both male and female calls for 5 min, followed by 15 min of listening, 5 min of further tape playing, then spotlighting within 50 m whilst listening for a distant response. In some instances, the period of listening was extended 1–2 h after the second tape playing, which on several occasions revealed reticent birds.

Playback surveys were also used in an attempt to define the core home range of each pair as an improvement upon single-point records more commonly used in management of this species. New survey points were chosen so as to expand upon previously identified owl locations. While this technique enhanced single-point records for the purposes of habitat analysis, subsequent radio-tracking of owls demonstrated that playback survey was not a precise technique in defining home range (Soderquist 1999b), and it would have required extensive, long-term effort to gradually define the extent of an owl pair’s home range (Fleay 1968, McNabb 1996).

Home range definition

Four breeding adult owls (two males and two females), occupying four geographically separate territories in the Box–Ironbark forest, were trapped and radio-tagged as part of a broader study. Based on minimum convex polygon mapping (Soderquist 1999b), the home ranges of these four owls were 1380, 1770, 2900 and 4770 ha (radio-tracking data will be fully presented elsewhere). Flight patterns and activity of these birds indicated that their hunting was best described as a continuous path of searching in the large home range. Individual trees or sites were often investigated by the radio-tagged owl when it was in a particular section of the territory, but in general nearly the whole area was used regularly.

Because the territory boundaries of non-radio-tagged owls were uncertain, a conservative estimate of foraging habitat was made by delineating an area of approximately 1000 ha of public forest around the multiple points where owl pairs responded to playback survey. Given the large home range demonstrated by radio-tagged owls, these hypothetically delineated territories were likely to be encompassed by the resident birds' actual home range.

Habitat analyses

As in many areas, the main prey of Powerful Owls in the Box–Ironbark forest was arboreal marsupials, specifically the Common Ringtail Possum *Pseudocheirus peregrinus*, Common Brushtail Possum *Trichosurus vulpecula* and Sugar Glider *Petaurus breviceps* (e.g. Seebeck 1976, Lavazanian *et al.* 1994). Large birds (including hollow nesters such as Galahs *Cacatua roseicapillus*) were also taken, especially in areas where arboreal mammals were rare (Soderquist 1999b). The density of arboreal mammals in the Box–Ironbark forest is very low and highly variable as a result of habitat degradation and the loss of trees with hollows (e.g. Meredith 1984, Deacon & Mac Nally 1998). Direct assessment of habitat quality based on prey abundance was thus extremely difficult. However, two habitat variables have proven to be surrogate measures of prey density: the densities of large old trees and of hollows. Recent studies in the Box–Ironbark forest have shown these surrogates to be directly correlated with the population density of arboreal mammals and hollow-nesting birds (e.g. Traill 1991, Soderquist & Mac Nally 2000). Although other factors may influence the selection of a home range by Powerful Owls, these two attributes have been repeatedly identified as potentially important from both a biological and management perspective (Silveira 1997). Large hollows are also important to the owls for nesting, but only one is needed for breeding each year compared to the many that are needed by the prey populations.

Within each delineated territory area of 1000 ha, ten points were randomly located, each serving as the initial location of a randomly orientated 1 km transect. Consecutive plots of 0.5 ha were sampled along these transects, each 50 m on either side of the transect and 50 m along its length. Thus the total area sampled in each of the 15 presumed owl core areas was 100 ha in 200 plots.

Large old trees greater than 60 cm diameter at breast height over bark (DBH) were enumerated, and any tree for which size was uncertain was measured with a diameter tape. The exact distance from the transect line was measured for any tree that was debatably within the 50 m boundary. Dead trees were not counted, and any of doubtful status was examined for live branches deriving from the bole more than 1.3 m above ground.

At four points along each transect, hollow trees were recorded on a 20 m radius circle (0.125 ha). Hollow determination followed that used in the Box–Ironbark Timber Assessment (BITA)

(NRE 1998b). Any hole greater than 10 cm in depth was classified by entrance diameter size as Small (2–5 cm), Medium (5–10 cm), Large (10–20 cm) and Very large (>20 cm). Holes present in dead trees were recorded separately from those in live trees. Habitat values in the Powerful Owl home ranges were subsequently compared to those of the forest at large, based on data collected in the BITA (NRE 1998b, Soderquist 1999a). However, the density of dead trees, and hollows within them, could not be calculated from data collected in the BITA (F. Cumming, pers. comm.), so only live trees were used for comparison. Plot size in the BITA was not consistent due to the use of Variable Probability Sampling, so densities of habitat attributes were calculated using a standard formula (NRE 1998b) before comparison. Extrapolation of the mean size of large trees measured in the BITA indicates that plots were, on average, equivalent to the 0.5 ha plots measured in the owl territories. Thus, although the two methods of sampling trees differed somewhat, they both yielded comparable measurements of large tree density.

RESULTS

Based on the two surrogate measures of prey density, the abundance of large old trees and hollows, Powerful Owls occupied significantly better habitat than the average available in the Box–Ironbark forest. The mean density of large old trees in owl territories was 3.5 ha^{-1} compared to the regional average of 2.1 ha^{-1} (NRE 1998b). This difference was consistent when owl sites are divided geographically (Table 1). The mean density of large trees in the seven western sites was 4.8 ± 4.9 ha^{-1} (S.D.) versus the forest average in the west of 2.7 ± 4.4 ha^{-1}. The equivalent eastern values were about half of the western ones: 2.3 ± 3.3 ha^{-1} and 1.2 ± 2.6 ha^{-1}, respectively. Owl territories had significantly more large trees than the average forest in both western and eastern areas (Mann–Whitney U = 389866 and 424387, respectively; both $P < 0.0001$). In addition, the percentage of plots lacking large trees was significantly greater (proportional contingency table, Z = 12.6 and 11.7, both $P < 0.001$) in the forest at large than in sites chosen by owls (Fig. 1).

Hollows were also significantly more common in areas selected by owls. The mean density of hollows in live trees in the western owl territories was 32.3 ± 47.7 ha^{-1} and in the eight eastern

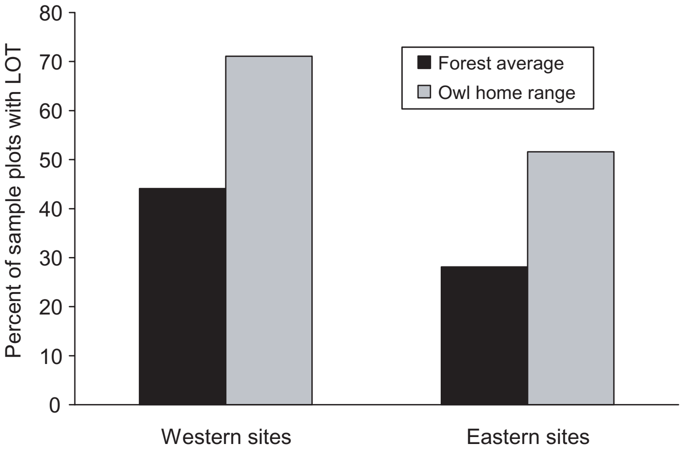


Fig. 1. The percentage of total sample plots that contained any large old trees (LOT) in 15 Powerful Owl territories and in the forest at large. Geographical divisions are west and east of the Loddon River.

Table 2. Attributes of hollow availability in 15 Powerful Owl territories.

Large hollows are >10 cm diameter, and so serve as shelter for several of the larger prey species and as nest sites for the owls themselves. Sites are designated as E or W of the Loddon River.

Site designation	Site Name	Hollows ha^{-1} live trees	Standard Deviation	Hollows ha^{-1} dead trees	Standard Deviation	Total large hollows ha^{-1}
W	Bolangum	47.2	38.2	3.2	6.4	20.6
W	Big Tottington	41.4	51.6	1.4	4.3	15.8
W	Wehla	45.0	62.0	8.2	19.1	16.8
W	Kooyoora	48.8	67.2	4.6	12.3	22.4
W	Dalyenong	18.6	25.1	9.8	23.1	8.6
W	Moorl Moorl	22.2	34.5	7.8	12.5	11.0
W	Tarnagulla	3.2	6.2	0.4	2.5	0.2
E	Lyell	8.6	16.1	14.6	28.6	6.6
E	Pilchers Bridge	17.8	29.9	2.8	8.1	7.0
E	Crosbie	12.0	32.7	3.8	9.1	6.2
E	Dargile	5.2	9.0	0.6	2.8	1.2
E	Costerfield	8.4	18.2	1.6	5.4	4.0
E	Mt Black	29.4	41.9	10.0	17.5	9.0
E	Darrochs Dam	21.6	26.0	2.8	7.5	8.2
E	Spring Plains	31.4	34.9	8.2	16.4	11.0

sites it was 16.8 ± 29.2 ha^{-1}. Comparative average values for the whole forest were 11.1 ± 24.8 ha^{-1} and 5.9 ± 17.7 ha^{-1}, respectively. The differences were significant (Mann–Whitney U = 78083 and 80309 for west and east, respectively; both $P < 0.0001$).

Considering Large and Very large hollows only – which serve as nests for both the owl and its prey – the western owl sites averaged 12.0 ± 20.4 ha^{-1}, and the eastern sites averaged 4.7 ± 10.9. The forest average in the west was 4.3 (±9.9) and in the east 1.6 (±8.5). Again, comparisons were significantly different (for west and east, Mann-Whiney U = 92110 and 94485; $P < 0.0001$). Although hollows were more common in owl territories than elsewhere on average, the density was still often low even there (Table 2) when compared to areas where large trees were present at more natural densities.

DISCUSSION

These analyses suggest that Powerful Owls select areas in the Box–Ironbark forest that are potentially better habitat than available in the forest at large. Owl territories had significantly more hollows and large old trees than the surrounding forest. These two attributes may be surrogate measures for the densities of arboreal mammals that are the preferred prey of Powerful Owls. (It should be noted that Ringtail Possums, significant items in the owls' diet, almost never build dreys in the Box–Ironbark forest, and are therefore hollow dependent, Traill 1991.)

In this region, large trees (>60 cm DBH) are three times more likely to be hollow-bearing than trees which are 40–60 cm DBH (Soderquist 1999a). After decades of intensive harvest and ringbarking, these legacy trees currently exist at about one-tenth of their historical densities (Soderquist 1999a). Thus, populations of hollow-dependent prey have greatly declined in the past century due not just to the clearing of most of their habitat (85%), but also to the loss of nest sites. Powerful Owl densities may once have been higher in this region but are now critically sparse.

Prior to this study, the assumed home range size of Powerful Owls was 300–1000 ha (Higgins & Davies 1999). In this study, some Powerful Owls used over four times this area (1380–4770 ha, $N = 4$ radio-tracked owls). These large home ranges apparently resulted from the low prey densities in this forest. Although hot spots for prey exist in the Box–Ironbark forest (Soderquist & Mac Nally 2000), they are limited in number and extent, and may be transitory owing to exploitation by the owls themselves (Kavanagh 1988, Traill 1993). Although owls selected the better habitat available in the region, even these territories were apparently in poor condition compared to the natural state, with fewer large trees and hollows.

As in the case of habitat previously occupied by Barking Owls *Ninox connivens* (Debus 1997), forest clearing in Powerful Owl habitat targeted areas of highest productivity (ECC 1997), where arboreal mammals were more abundant (Deacon and Mac Nally 1998, Soderquist and Mac Nally 2000). Subsequent harvesting has reduced habitat quality in the remaining forest, and prey are currently scarce. These factors may be the cause of the apparently low reproductive rate of Powerful Owls in the Box–Ironbark region of Victoria compared to elsewhere. Two studies in moist forests of New South Wales estimated that Powerful Owls fledged 0.8–1.2 young per nesting attempt (Debus and Chafer 1994, Kavanagh 1997). In southern Victoria, McNabb reported that 1.4 young were fledged per year per pair. Conversely, Hollands (1991) summarised records indicating that Powerful Owl pairs in central Victoria fledged only 0.4–0.5 young per year. This disturbing contrast is supported by the early findings from a planned long-term program designed to monitor breeding success in the Box–Ironbark area (Soderquist 1999b).

Even though the home ranges of Powerful Owls in the Box–Ironbark area are much larger than those reported elsewhere, presumably in response to low prey densities, these owls apparently raise less than half as many chicks as their conspecifics in wetter forests elsewhere. It is uncertain at what threshold of habitat degradation reproduction and adult survival will be inadequate to sustain the population. Habitat selection by dispersing juveniles is probably made on a local or perhaps regional basis. Therefore, one would expect the Powerful Owl population in the eastern Box–Ironbark forest to continue inhabiting the best available habitat locally (even though apparently better habitat exists 200 km to the west).

The goals of conservation management for Powerful Owls in the Box–Ironbark forest should include the improvement of sites where owls reside, and an increase in population density throughout the region. The selection by Powerful Owls of higher quality areas within the remaining forest suggests that it is important to identify and protect those sites currently occupied by owls. This study supports the management approach described in the Powerful Owl Action Statement (NRE 2000) in which emphasis is placed on conserving remaining pairs of owls and their particular home ranges (Loyn *et al.* 2001). Delineation of Powerful Owl Management Areas (POMA) around known owl sites should be based on the biological value of existing habitat in maintaining prey populations. If each POMA were 1000 ha, the protected site would serve as a core home range managed to improve the supply of prey so that foraging was successful even during environmentally stressful years, and reproduction was more consistent. Preliminary observations suggest that Powerful Owls which rely on large birds for the majority of their diet are less likely to breed successfully (Soderquist 1999b), so that management for each POMA should aim to increase the densities of arboreal mammals. Sensitive management of the adjacent areas would further improve the survival and reproduction of owl pairs.

The ultimate aim of Powerful Owl conservation should be to increase the numbers of this species (NRE 2000). The site-specific approach of POMA establishment differs from the Habitat

Conservation Area (HCA) model adopted for Spotted Owls *Strix occidentalis* (Doak 1989, Thomas *et al.* 1990) in North America, and recently proposed for Powerful Owls in Victoria (Silveira 1997). The HCA model emphasises large reserves managed to sustain locally viable and interacting meta-populations. However, such large reserves are not available in much of the Box–Ironbark forests considered in this paper. If habitat quality in the Box–Ironbark forest as a whole improves significantly during the next half-century, allowing for the establishment of new owl breeding territories, flexibility in reserve design may permit a more biologically meaningful emphasis on localised population foci, as in the HCA model. Consistent, long-term monitoring of Powerful Owl populations in this region will provide the knowledge needed by forest managers to judge the benefit of habitat improvements or propose further conservation measures.

ACKNOWLEDGMENTS

This research was funded through the Commonwealth Regional Forests Agreement process. Special thanks are owed to Dale Gibbons for volunteering hundreds of hours in the effort to capture and radio-track owls. Ed McNabb, Steve Craig, Alan Webster, Rod Kavanagh, Paul Peake and Barry Traill provided valuable insights on Powerful Owls.

REFERENCES

Deacon, J. N. & Mac Nally, R. 1998. Local extinction and nestedness of small-mammal faunas in fragmented forest of central Victoria, Australia. *Pac. Conserv. Biol.* **4:** 122–131.

Debus, S. J. S. 1995. Surveys of large forest owls in northern New South Wales: methodology, calling behaviour and owl responses. *Corella* **19:** 38–50.

Debus, S. J. S. 1997. The Barking Owl in New South Wales. *Aust. Birds* 30: 53–80.

Doak, D. F. 1989. Spotted Owls and old growth logging in the Pacific Northwest. *Conserv. Biol.* **3:** 389–396.

ECC 1997. *Box–Ironbark Forests and Woodlands Investigation, Resources and Issues Report.* Fitzroy, Victoria: Environment Conservation Council.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain.* Brisbane: Jacaranda Press.

Gibbons, D. 1995. *Survey of Powerful Owls* (Ninox strenua) *in central Victoria.* Unpublished report. Bendigo: Victorian Department of Natural Resources & Environment.

Higgins, P. J. & Davies, S. J. J. F. (eds). 1999. *Handbook of Australian, New Zealand and Antarctic birds, Vol. 4.* Melbourne: Oxford University Press.

Holland, G. & Cheers, G. 1999. *Identification of large old tree sites and fauna refuges in the ECC's Box–Ironbark study area.* Melbourne: Victorian Department of Natural Resources & Environment.

Kavanagh, R. P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans. Aust. J. Ecol.***13:** 445–450.

Lavazanian, E., Wallis, R. & Webster, A. 1994. Diet of Powerful Owls (*Ninox strenua*) living near Melbourne, Victoria. *Wildl. Res.* **21:** 643–646.

Loyn, R.H., McNabb, E.G. Volodina, L. & Willig, R. 2001. Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. *Biol. Conserv.* **97:** 361–376.

McNabb, E. G. 1996. Observations on the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16:** 267–295.

Meredith, C. W. 1984. Possums or poles? – the effect of silvicultural management on the possums of Chiltern State Park, northeast Victoria. In Smith, A. P. and Hume, I. D. (eds). *Possums and Gliders*: 575–577. Sydney: Australian Mammal Society.

NRE 1998a. *Threatened Vertebrate Fauna in Victoria – 1998*. Unpublished report. Melbourne: Victorian Department of Natural Resources & Environment.

NRE 1998b. *Box–Ironbark Timber Assessment Project*. Forests Service Technical Report 98–3. Melbourne: Victorian Department of Natural Resources & Environment.

NRE 2000. *Powerful Owl* Ninox strenua. *Action Statement No. 92*. Melbourne: Victorian Department of Natural Resources & Environment.

Seebeck, J. H. 1976. The diet of the Powerful Owl *Ninox strenua* in western Victoria. *Emu* **76:** 167–170.

Silveira, C. E. 1997. *Targeted assessments of key threatened vertebrate fauna in relation to the North East and Benalla–Mansfield Forest Management Areas, Victoria: Powerful Owls*. Unpublished report. Melbourne: Victorian Department of Natural Resources & Environment.

Simberloff, D. 1997. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol. Conserv*. **83:** 247–257.

Soderquist, T. R. 1999a. *Tree hollows in the Box–Ironbark forest*. Forests Service Technical Report 99–3. Melbourne: Victorian Department of Natural Resources & Environment.

Soderquist, T. R. 1999b. *Home range and habitat quality of the Powerful Owl in the Box–Ironbark forest*. Unpublished report. Melbourne, Australia: Victorian Department of Natural Resources & Environment.

Soderquist, T. R. & Mac Nally, R. 2000. The conservation value of mesic gullies in dry forest landscapes: mammal populations in the Box–Ironbark system of southern Australia. *Biol. Conserv*. **93:** 281–291.

Thomas, J. W., Forsman, E. D., Lint, J. B., Meslow, E. C., Noon, B. R. & Verner, J. 1990. *A conservation strategy for the Northern Spotted Owl*. Portland: U.S. Government Printing Office.

Traill, B. J. 1991. Box–Ironbark forests: tree hollows, wildlife and management. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 119–123. Sydney: Royal Zoological Society of New South Wales.

Traill, B. J. 1993. The diet and movements of a pair of Powerful Owls *Ninox strenua* in dry eucalypt forest. In Olsen, P. (ed.) *Aust. Raptor Studies*: 155–159. Melbourne: Royal Australasian Ornithological Union.

10

URBANISATION AND THE ECOLOGY OF POWERFUL OWLS (*NINOX STRENUA*) IN OUTER MELBOURNE, VICTORIA

RAYLENE COOKE[1], *ROBERT WALLIS*[2] *& ALAN WEBSTER*[3]

[1]School of Ecology & Environment, Deakin University, Melbourne, Victoria 3125.

[2]School of Ecology & Environment, Deakin University, Warrnambool, Victoria 3280

[3]Department of Natural Resources & Environment, Port Phillip Region, Box Hill, Victoria 3128

Historically, the Powerful Owl (*Ninox strenua*) has been seen as a southeastern Australian species restricted to, or most numerous in, dense gullies of tall open forests in hilly or mountainous areas of the coast and Great Divide. However, recent research has revealed that Powerful Owls may breed numerously and successfully in a wider range of habitats than previously believed, including the forests and woodlands within the metropolitan areas of some major cities.

Here we report on the breeding of a number of pairs of Powerful Owls in the Yarra Valley, Victoria. Study sites ranged from relatively undisturbed, wet sclerophyll forest 80 km from central Melbourne, through dry sclerophyll, eucalypt-dominated open forest with some disturbance, to a highly disturbed urban parkland only 18 km from central Melbourne.

We found that Powerful Owls breed successfully in some urban areas, but are limited in the amount of human disturbance they can tolerate near their nesting hollow. In the most heavily utilized section of the urban parkland, all breeding attempts were unsuccessful and in one year the young were apparently eaten by one of the parents. This followed construction of a timber boardwalk under the nest tree during the breeding season. The Powerful Owls subsequently moved to a more secluded nesting hollow and raised two young.

Recommendations for management of Powerful Owls in urban areas are discussed in the context of these results.

INTRODUCTION

The Powerful Owl *Ninox strenua* is Australia's largest owl. In Victoria its conservation status is listed as threatened under the Flora and Fauna Guarantee Act 1988, while nationally the species

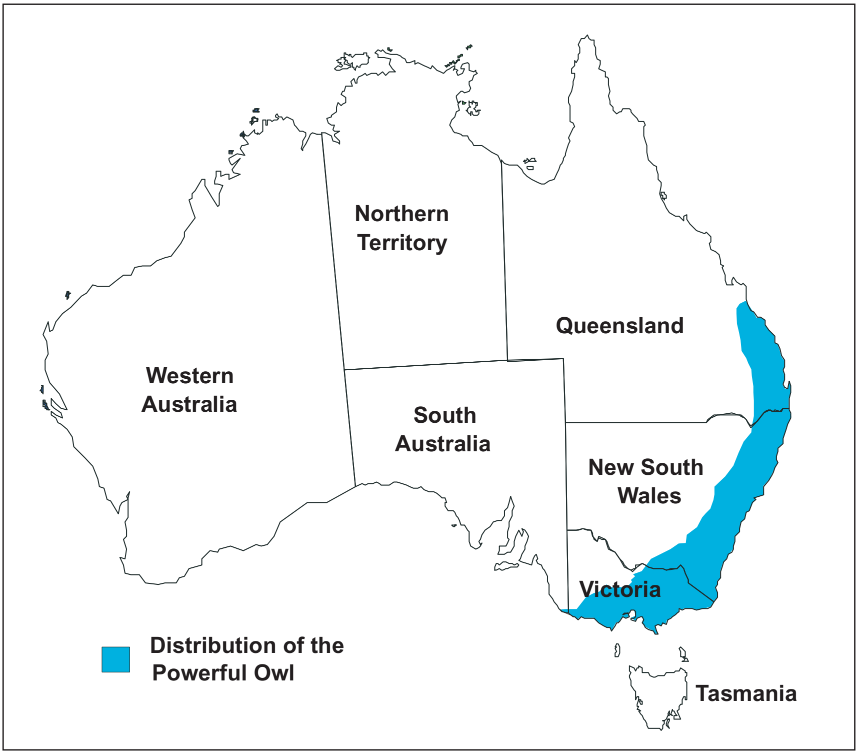


Fig. 1. The distribution of the Powerful Owl in Australia. From Simpson & Day 1999.

is considered in the category of 'least concern' (Garnett & Crowley 2000). Previous work on Powerful Owls suggested that they preferred living in dense gullies of tall open forests with old-growth characteristics in the higher altitude regions of the Great Dividing Range (Debus & Chafer 1994). Recent studies have questioned the species' reliance on old growth forests, and have argued that Powerful Owls can breed successfully in a wider range of habitats, including urban settings, provided that suitable prey species and nesting/roosting cavities are available (Pavey 1993; Quinn 1993; Debus & Chafer 1994; McNabb 1996; Cooke *et al.* 1997; Kavanagh 1997; Webster *et al.* 1999a).

The Powerful Owl has a relatively restricted distribution in southeastern Australia (Fig. 1). Here we report on studies in the Yarra Valley, near Melbourne, Victoria. Study sites ranged from relatively undisturbed Wet Sclerophyll forest 80 km from central Melbourne, through Dry Sclerophyll, eucalypt-dominated open forest with moderate disturbance, to a highly disturbed urban parkland located 18 km from central Melbourne. In particular, we report on the relationship between habitat disturbance and breeding success, as well as some more general aspects of the owl's ecology.

STUDY SITES

The six study sites are located in Melbourne's eastern corridor in the Yarra Valley (Fig. 2, Table 1).

Toolangi State Forest is a Wet Sclerophyll forest with gullies of old growth that provide suitable nesting sites for owls and their prey. The other sites consist of drier forests with varying

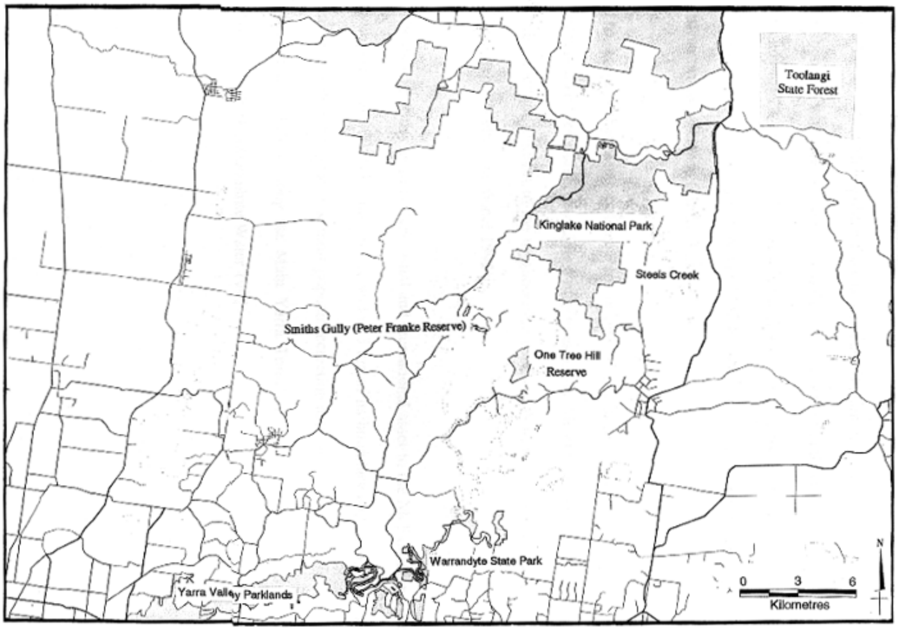


Fig. 2. Powerful Owl study sites in the Yarra Valley. From Parks Victoria 1999.

Table 1. Powerful Owl study sites in the Yarra Valley.

Study Site	Distance from Melbourne (km)	Forest Structure	Level of Disturbance	Dominant Eucalypt species
Toolangi State Forest	80	Wet Sclerophyll Forest	Relatively Undisturbed	Mountain Grey Gum *E. cypellocarpa* Mountain Ash *E. regnans* Messmate *E. obliqua*
Steels Creek (privately owned)	65	Dry Sclerophyll Forest	Low	Messmate *E. obliqua* Broad-leaved Peppermint *E. dives* Manna Gum *E. viminalis* Red Stringybark *E. macrorhyncha*
Smiths Gully (Peter Franke Reserve)	35	Dry Sclerophyll Forest	Moderate	Long-leaved Box *E. goniocalyx* Red Stringybark *E. macrorhyncha* Yellow Box *E. melliodora*
One Tree Hill Reserve	35	Dry Sclerophyll Forest	High	Red Stringybark *E. macrorhyncha* Red Box *E. polyanthemos* Long-leaved Box *E. goniocalyx* Messmate *E. obliqua*
Warrandyte State Park	24	Riparian	Very High	Red Box *E. polyanthemos* Manna Gum *E. viminalis* River Red Gum *E. camaldulensis* Messmate *E. obliqua*
Yarra Valley Metropolitan Park	18	Urban Parkland	Extensive	River Red Gum *E. camaldulensis* Red Box *E. polyanthemos* Manna Gum *E. viminalis*

degrees of disturbance. The most disturbed site is the Yarra Valley Metropolitan Park, with more than one million visitors per year (Melbourne Water 1992), few mature trees, modified vegetation and close proximity to housing and grazing pasture.

RESULTS

Requirements for successful breeding

To survive and reproduce Powerful Owls require suitable nesting hollows, roost trees with appropriate cover and suitable prey in the form of arboreal marsupials (Webster *et al.* 1999b). Nest hollows have to be large enough to house the adult female and up to two juveniles. Eleven nest hollows were measured during this study. Their mean height above ground was 13.48 m ± 2.80 m (mean ± 1.96 S.E) in large emergent eucalypts. The mean hollow depth was 1.12 m ± 0.34 m (mean ± 1.96 S.E), the mean entrance width 0.48 m ± 0.04 m (mean ± 1.96 S.E) and the mean entrance length 0.82 m ± 0.44 m (mean ± 1.96 S.E). The Powerful Owls at all sites changed nest trees at least once during this three year study, but at particular sites they used the same tree species.

Roost trees comprised mainly various *Eucalyptus*, *Acacia* and *Leptospermum* species which were common in the study areas. Roost trees in the breeding season were rarely more than 50 m from the nest hollow.

Diet

Powerful Owls consume those medium-sized arboreal marsupials which are most common in their territory. At Warrandyte State Park, the Common Ringtail Possum *Pseudocheirus peregrinus* and Common Brushtail Possum *Trichosurus vulpecula* were the most abundant arboreal marsupials surveyed, while at One Tree Hill Reserve Common Ringtail Possums and Sugar Gliders *Petaurus breviceps* were most common. In general, the percentage occurrence of mammals in the regurgitated pellets of Powerful Owls at these two sites (Table 2) reflected the relative abundance of the different prey species there (Wallis *et al.* 1998).

Previous authors have suggested that the future survival of Powerful Owls is dependent on there being high populations of hollow-dependent, arboreal, marsupial prey (Fleay 1968;

Table 2. Number of pellets containing mammalian prey collected from Warrandyte State Park (upper line) and One Tree Hill Reserve (lower line) for each of the seasons.

Figures in parentheses refer to the percentage of pellets found to contain remains of that species (from Wallis *et al.* 1998).

Mammalian Prey	Summer	Autumn	Winter	Spring	Total
Common Ringtail Possum	106	75	70	149	400 (64)
Pseudocheirus peregrinus	170	83	184	126	563 (92)
Common Brushtail Possum	29	14	31	110	184 (29)
Trichosurus vulpecula	1	0	1	13	15 (3)
Sugar Glider	12	12	0	21	45 (7)
Petaurus breviceps	18	14	25	19	76 (12)
Other mammals	1	2	1	0	4 (0.6)
	0	0	0	4	4 (0.6)
Total number of pellets	146	99	108	273	626
	199	101	204	182	686

Schodde & Mason 1980; McNabb 1996). We agree with these statements, but add that the Common Ringtail Possum and the Common Brushtail Possum occur in good numbers throughout suburban Melbourne, often residing in house roofs and nest boxes. Although both species are known to inhabit tree hollows when available, neither species is totally dependent on hollows in urbanized environments. We often observed Common Ringtail Possums utilizing dreys (leaf/stick nests) where the denser shrub-storey habitat of urban environments may favour this construction. Studies in southern coastal New South Wales (Chafer 1992; Kavanagh 1997) also found Powerful Owls feeding mainly on arboreal marsupials which were not restricted to old-growth forests. Although future management needs to ensure that potential prey species remain abundant if habitats are to support Powerful Owls, two of the main prey species are not wholly dependent on natural hollows and thrive in low level urbanization (Thomson & Owen 1964; Kerle 1984).

Breeding

Powerful Owls in the most disturbed site, the Yarra Valley Metropolitan Park, had the lowest breeding success of the six groups studied, with only three juveniles reared to fledgling stage in four breeding seasons (37.5% of all eggs laid, at two per year). In contrast, birds at the undisturbed Toolangi State Forest and Steels Creek sites each had high breeding success, with five juveniles fledged from six eggs laid (83.3%) over three breeding seasons (Table 3).

Despite its successful breeding in other semi-urban environments near Melbourne (Quinn 1993; McNabb 1996; Cooke *et al.* 1997), the degree of urbanization that the Powerful Owl can tolerate is still unknown. The Yarra Valley Metropolitan Park is one of Melbourne's busiest urban parklands (Webster *et al.* 1999a). In 1995, the Powerful Owls successfully hatched at least one egg but the young failed to fledge. During this time a timber boardwalk was constructed under the nest tree. On 11 September 1995, clumps of broken wing feathers of a young Powerful Owl were detected amongst fresh pellets (Webster *et al.* 1999a). Although siblicide is well recognised among both diurnal and nocturnal raptors, the ingestion of offspring by a parent had not been reported previously in the Australian owl literature (Webster *et al.* 1999a).

In 1996 the birds attempted to breed in the same hollow as in 1995. The female was seen to enter the hollow in the first week of June but had stopped using it by the first week of July. By mid-July both adults had left the area altogether. In 1997 what was presumed to be the same pair nested in a less disturbed forest 2.5 km east of the original nest tree in the park and successfully raised two juveniles. Although the extent to which disturbance adversely affected the pair's breeding attempts in 1995 and 1996 remains unknown, the successful fledging of two owlets in 1997 at a less disturbed site suggests that disturbance may have caused breeding failure in 1995 and 1996 (Webster *et al.* 1999a).

Table 3. Breeding data for Powerful Owls at the Yarra Valley Metropolitan Park, Steels Creek and Toolangi State Forest.

Numbers under each year represent number of young successfully reared to fledging. Success rate is calculated by dividing the total number of young raised by the total number of eggs laid (two per year).

Study Site	1995	1996	1997	1998	Total	maximum	success rate
Yarra Valley Metropolitan Park	0	0	2	1	3	8	37.5%
Steels Creek	n/a	1	2	2	5	6	83.3%
Toolangi State Forest	n/a	2	1	2	5	6	83.3%

MANAGEMENT

Management actions for Powerful Owl conservation across Victoria have been outlined in the Flora and Fauna Guarantee Action Statement for the species (Webster *et al.* 1999b). Initial emphasis is on ensuring that enough good quality habitat is maintained across the landscape on public land for at least 500 breeding pairs.

Powerful Owl protection in more urbanized environments is often more complex due to competing land-use, a variety of land tenures and increasing disturbance pressures. Key management mechanisms in such situations include close liaison with local Councils, use of environmental overlays and GIS registers in planning schemes, encouragement of landowners to enter into voluntary conservation agreements and a general increase in community awareness and appreciation of habitat corridors and bushland remnants.

ACKNOWLEDGMENTS

We thank the Holsworth Wildlife Research Fund, the M.A. Ingram Trust, Birds Australia and Deakin University for providing financial support. We also acknowledge the assistance of Victor Hurley, Mike Lauder, Peter Sexton and Glen Jameson for collecting data and providing on site assistance. Parks Victoria is also thanked for providing study maps.

REFERENCES

Chafer, C. J. 1992. Observations of the Powerful Owl *Ninox strenua* in the Illawarra and Shoalhaven Regions of New South Wales. *Aust. Bird Watcher* **14:** 289–300.

Cooke, R. M., Wallis, R. L., Webster, A. G. & Wilson, J. 1997. The diet of Powerful Owls *Ninox strenua* in Warrandyte State Park, Victoria. *Proc. Roy. Soc. Victoria* **109:** 1–6.

Debus, S.J.S. & Chafer, C. J. 1994. The Powerful Owl *Ninox strenua* in New South Wales. *Aust. Birds* (Supplement) **28**: 20–38.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Brisbane: Jacaranda Press.

Garnett, S.T & Crowley, G.M. 2000. The Action Plan for Australian Birds 2000. Canberra: Environment Australia, Australian Government.

Kavanagh, R. P. 1997. Ecology and management of large forest owls in south-eastern Australia. PhD Thesis. School of Biological Sciences, University of Sydney.

Kerle, J.A. 1984. Variation in the ecology of *Trichosurus*: its adaptive significance. In A.P. Smith and I.D. Hume (eds) *Possums and Gliders*: 115–128. Sydney: Surrey Beatty and Sons.

Melbourne Water. 1992. Yarra Valley Park Management Plan. Melbourne: Melbourne Water.

McNabb, E.G. 1996. Observations on the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16**, 267–297.

Pavey, C. R. 1993. The distribution and conservation status of the Powerful Owl *Ninox strenua* in Queensland. In P. Olsen (ed) *Australian Raptor Studies*: 144–154. Melbourne: Australasian Raptor Association, Royal Australasian Ornithologists' Union.

Quinn, D. 1993. Nesting Powerful Owls *Ninox strenua*. *Australasian Raptor Association Newsletter* **14,** 70–71.

Schodde, R. & Mason, I. J. 1980. *Nocturnal Birds of Australia*. Melbourne: Lansdowne.

Simpson, K. & Day, N. 1999. *Field Guide to the Birds of Australia*. Ringwood, Victoria: Penguin Books.

Thomson, J.A. & Owen, W.H. 1964. A field study of the Australian Common Ringtail Possum *Pseudocheirus peregrinus*. *Ecol. Monog.* **34,** 27–52.

Wallis, R., Cooke, R. & Webster, A. 1998. Diet of Powerful Owls *Ninox strenua* in the Yarra Valley, Victoria. *Aust. Bird Watcher* **17(8):** 395–397.

Webster, A., Cooke, R., Jameson, G. & Wallis, R. 1999a. Diet, roosts and breeding of Powerful Owls *Ninox strenua* in a disturbed, urban environment: a case for cannibalism? Or a case for infanticide? *Emu* **99:** 80–83.

Webster, A., Humphries, R. & Lowe, K. 1999b. Powerful Owl *Ninox strenua*. Action Statement No. 92, Flora and Fauna Guarantee Act. Melbourne, Victoria: Department of Natural Resources and Environment.

11

DISTRIBUTION AND HABITAT OF BARKING OWLS (*NINOX CONNIVENS*) IN CENTRAL VICTORIA

IAIN R. TAYLOR[1]*, INDRE KIRSTEN*[1] *& PAUL PEAKE*[2]

[1]Applied Ornithology Group, Johnstone Centre, Charles Sturt University, PO Box 789,
Albury, NSW 2640, Australia.

[2]Environment Conservation Council, 250 Victoria Parade, East Melbourne, Vic 3002, Australia.

This study supports earlier suggestions that the endangered Barking Owl is now extremely rare in the central area of Victoria. The species was recorded at only 11 (4.3%) of 257 sites surveyed in 1998–99 even though the sites were selected to maximise the chance of locating the owls. They were found at only 6.7% of 75 sites where they had previously been reported and listed in the Wildlife Atlas of Victoria during the 1980s and 90s. Thus, the accumulated Atlas records may not give an accurate representation of current distribution and abundance. The data may also suggest that the species has declined significantly in recent years. There seem to be only three possible concentrations of population; in the Northern Inland Slopes, the Goldfields, and the Greater Grampians with adjacent Dundas Tablelands. Further intensive surveys of each of these areas and other parts of the species' range in Victoria are needed to clarify the status of the species. Differences in some aspects of habitat were found at sites where Barking Owls were recorded compared with sites where they were not. Sites with owls had significantly higher densities of larger trees and also had higher densities of tree hollows of a range of sizes, including those suitable as nesting places for Barking Owls. Sites with owls were also more closely associated with hydrological features such as rivers and swamps.

INTRODUCTION

With an estimated population size of fewer than 50 pairs, the Barking Owl *Ninox connivens* is classed as endangered in Victoria and is listed on Schedule 2 of the Flora and Fauna Guarantee Act 1988 (Silveira *et al.* 1997, CNR 1995). There has been no major study of the species anywhere in Australia and little is known of its ecological requirements. It nests in large hollows of a range of tree species but is uncommon or absent in forest interior habitats, especially in extensive areas of moist forest, regardless of the availability of suitable nesting places (McNabb *et al.* 1997, Kavanagh & Stanton 1998, Debus 2001). The limited evidence available suggests that it occurs predominantly in drier woodland types, including Box–Ironbark, and in River Red Gum *Eucalyptus camaldulensis* habitats (Robinson 1994). It seems to prefer open woodlands, woodland edges and farmland–woodland mosaics. The few studies of the species' diet that have been made have shown a mixture of species associated with cleared or edge habitats, such as the European Rabbit *Oryctolagus cuniculus* and Eastern Rosella *Platycercus eximius*, and of species more characteristic of woodlands, such the Sugar Glider *Petaurus breviceps* (Calaby 1951, Fleay 1968, Schodde & Mason 1980, Barker & Vestjens 1989, Hollands 1991, Kavanagh *et al.* 1995, Debus *et al.* 1998, Debus *et al.* 1999, Debus 2001).

At present, our level of understanding of the species' ecological requirements falls far short of that needed to formulate an effective conservation strategy. There is a clear need for a more comprehensive assessment of the species' abundance and distribution, especially within its perceived preferred habitat types. Any areas of specific concentrations of population need to be identified, where conservation efforts might be most successful. Also, a greatly improved understanding is needed of all aspects of the species' requirements, especially those related to habitat structure, and consequently to management. In the long term, in order to provide for the establishment of sustainable populations, information will be required on its population dynamics and ecology and the relationships between population parameters and aspects of habitat quality.

This paper reports the findings of a recent survey of the status of Barking Owls in the central area of Victoria and compares some aspects of habitat at sites where owls were recorded with those at sites at which no owls were recorded.

METHODS

Selection of survey sites

Previous surveys for Barking Owls in Victoria have been combined with surveys for other species and hence have employed systematic rather than targeted procedures for the selection of survey sites. During such surveys in woodland and forest habitats throughout Victoria in 1996–97, Barking Owls were located at only 11 of 1445 (0.8%) sites (Loyn 1996a,b, McNabb *et al.* 1997, Silveira 1997). Systematic surveys have merit in that they may help to identify the habitat types in which the species does and does not occur. However, when the priority is the location of as many pairs as possible, they are not an efficient use of resources. In our study we used a targeted selection of survey sites so as to enhance the effectiveness of locating the birds. The targeting procedure consisted of the following elements, based on existing published and unpublished information:

Sites were selected along the edges of woodland habitat rather than in the interiors.

This was based on the failure to locate Barking Owls at forest interior sites during previous extensive surveys (Loyn 1996 a,b, McNabb *et al.* 1997), on evidence that most known Barking Owl sites in Box-Ironbark woodlands have been in edge areas (Taylor *et al.*2002), and from data on the species' diet showing both edge and woodland prey items (Kavanagh *et al.* 1995).

A sample of 75 sites where there were previous records of the species was re-checked.

Locations of these sites were taken from the Wildlife Atlas of Victoria supported by any details reported by the observers. Because of time limitations, not all reported sites could be re-examined and preference was given to records from the 1980s and 1990s and especially to sites where there was more than a single recording.

Sites were selected in each of the eight bioregions, approximately in proportion to their areas.

Nocturnal survey

This was based on standard methodology that has been used widely in surveys for large forest owls in southeastern Australia (Kavanagh & Peake 1993, Kavanagh & Bamkin 1995). It consisted of an initial listening for spontaneous calling for 15 minutes followed by the broadcasting of taped Barking Owl calls for 5 minutes and listening for up to 15 minutes for any responses. This was followed by searching with a spotlight for 5 minutes to check for the presence of any birds that were attracted to the taped broadcast, but did not call. Nocturnal surveys were completed between late October 1998 and March 1999. Known pairs in northeastern Victoria responded to broadcast calls throughout this period and it is assumed that birds in other parts of the state would also have responded.

Analysis of habitat characteristics at survey sites

Territory sizes of Barking Owls have not been quantified in southeastern Australia so a precise statement of the size of area that should be covered by habitat analyses cannot be given. However, a preliminary radio-tracking study revealed that the owls may use at least 226 ha (Taylor *et al.* 2002). In this study we decided to sample habitat within a 1.0 km radius of the point at which the owls were first detected, or, for sites where no owls were detected, from the survey point. Depending on the nature of each site, the landscape was divided into its major components of: (1) Woodland or forest interior habitats (>50 m from any edge); (2) Woodland edge habitat (<50 m from edge); (3) Wooded roadside habitat; (4) Wooded creek-side habitat; and (5) Cleared habitats.

Within each of the wooded components, a minimum of five sample areas was selected randomly. In linear habitats, including the woodland edge habitat, the sample areas were 20 ? 50 m rectangles; in woodland centre habitat, circular sample areas of 25 m radius were used. Within each sample area, the following aspects of habitat were quantified: (1) Stem diameter at breast height of all trees (DBH); (2) Percentage canopy cover; (3) Percentage understorey cover; (4) Proximity to nearest river or swamp; and (5) Numbers and sizes of potential hollows. This was assessed from the ground only, so hollows not visible from the ground would have been missed. Also, details of depth or other qualities were not quantified. Nevertheless, the method should have provided a valid index of hollow abundance for comparisons among sites

RESULTS

Distribution of survey sites and owl locations

A total of 257 sites was surveyed for the presence of owls, including 182 new sites and 75 where the owls had been reported previously, listed in the Wildlife Atlas of Victoria (Fig. 1). Of these, Barking Owls were recorded at only eleven (4.3%) sites, including six (3.3%) at new sites and five (6.7%) at sites with previous records (Fig. 2, Table 1). With such low numbers, it is not possible to test statistically for differences in the incidence of owls in different bioregions. However, there were no positive recordings for three bioregions: the Central Victorian Uplands, the Riverina and

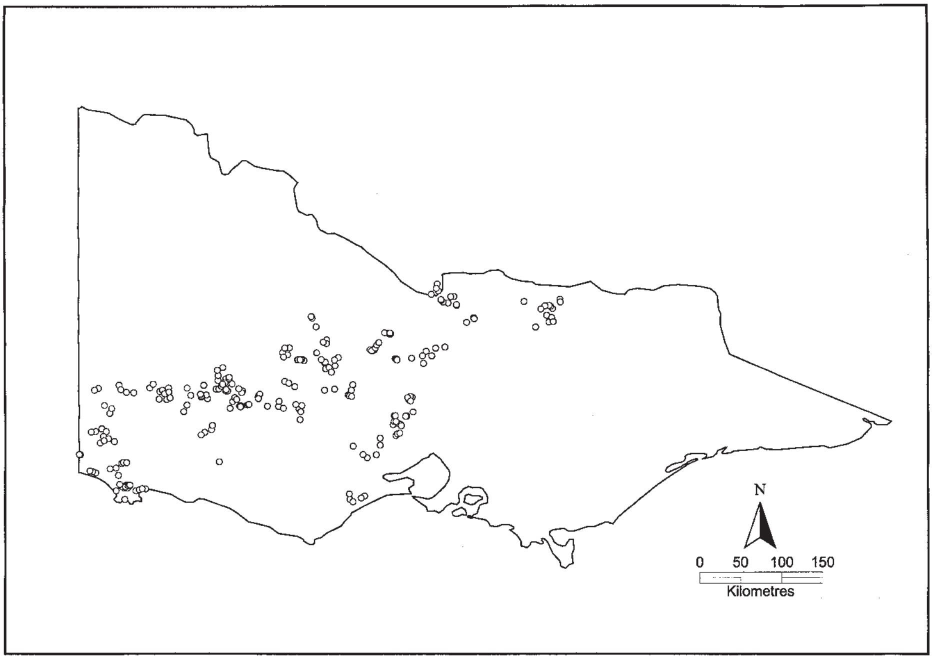


Fig. 1. Locations of all sites surveyed for Barking Owls in the Victorian study area, November 1998 to March 1999.

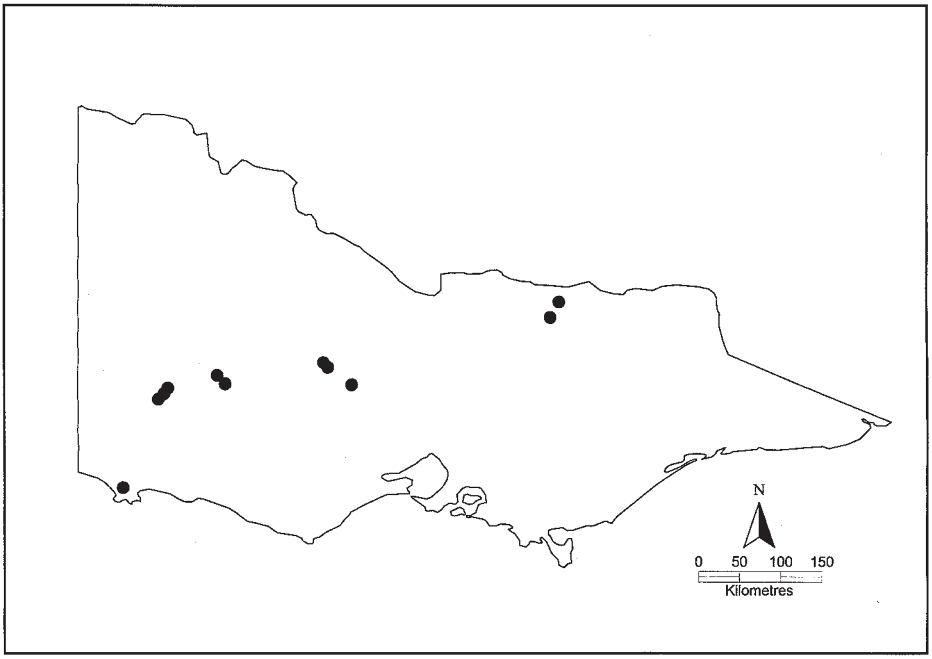


Fig. 2. Sites where Barking Owls were found during surveys conducted from November 1998 to March 1999.

Table 1. Numbers and distribution of sites surveyed for Barking Owls according to Bioregion, and sites at which owls were located.

Bioregion	New sites surveyed	New Barking Owl records	Old sites resurveyed	Old sites reconfirmed	Total sites surveyed	Total sites with Barking Owls
Goldfields	59	1	36	2	95	3
Central Victorian Uplands	32	0	7	0	39	0
Greater Grampians	20	2	7	0	27	2
Dundas Tablelands	21	3	0	0	21	3
Glenelg Plain	32	0	9	1	41	1
Northern Inland Slopes	11	0	4	2	15	2
Riverina	3	0	12	0	15	0
Otway Plain	4	0	0	0	4	0
Totals	182	6	75	5	257	11

the Otway Plain regions. Tentatively, it might be possible to suggest some degree of concentration of pairs in three areas: the Northern Inland Slopes, the Goldfields, and the Greater Grampians with the adjacent areas of the Dundas Tablelands (Table 1, Fig. 2). Seven of the Barking Owl sites recorded were in State Forests, three in State Game Reserves and one on Crown Land at the edge of a reservoir.

Habitat characteristics of Barking Owl sites

In the following analysis, the habitat characteristics of sites with Barking Owls are compared with those of a sub-sample of 30 sites at which the species was not recorded. This sub-sample was selected randomly from the total set of negative owl survey sites using a stratified procedure from all of the bioregions. In the analyses, data collected for woodland interior habitats (>50 m from edges) and for edge habitats were treated separately. All edge habitat data, including woodland edges, and wooded strips along watercourses and roads were lumped.

Tree size class distribution. There were no significant differences in the densities of trees in the 0–20, 21–40 and 41–60 cm diameter classes between sites where Barking Owls were recorded and sites where they were not recorded. However, for both edge and interior habitats, there were significantly higher densities of trees greater than 60 cm diameter (at breast height) in the sites where Barking Owls were recorded (Table 2). Overall, sites with owls had about twice the densities of these larger trees.

Abundance of potential nest and roost hollows. For both woodland interior and edge habitats, the recorded densities of hollows of all size classes were significantly greater at sites that had Barking Owls compared with sites that did not, with the sole exception of hollows in excess of 20 cm diameter in woodland interior habitat where the differences did not reach statistical significance. Sites with owls mostly had more than twice the densities of hollows than sites without owls (Table 3).

Canopy cover and understorey cover. All of the sites surveyed had between 20% and 40% canopy cover, with no significant differences between sites where owls were recorded and sites where they were not. All sites had relatively open understoreys with no statistically significant differences in cover for any stratum of understorey between sites with and without owls.

Table 2. A comparison of the densities of trees (number/ha) of different diameter classes (cm) between sites where Barking Owls were recorded and sites where they were not recorded

Significance levels for Kruskal–Wallis tests given.

a) Edge habitats

	Stem diameter class (cm)				
	0–20	**21–40**	**41–60**	**>60**	**n**
Owls recorded	289.0 ± 147.1	90.1 ± 13.4	14.2 ± 2.8	29.6 ± 6.2	11
Owls not recorded	152 ± 34.3	112.5 ± 10.4	14.6 ± 1.4	18.3 ± 2.1	30
P difference	0.21	0.23	0.82	0.03	

b). Woodland interior habitats

	Stem diameter class (cm)				
	0–20 cm	**21–40 cm**	**41–60 cm**	**>60 cm**	**n**
Owls recorded	85.7 ± 18.5	82.1 ± 20.0	7.6 ± 2.0	20.5 ± 7.8	11
Owls not recorded	99.9 ± 17.0	67.7 ± 6.3	6.6 ± 0.9	8.9 ± 1.5	30
P difference	0.98	0.93	0.67	0.05	

Table 3. Comparison of the densities of hollows (number/ha) in edge habitats and woodland centre habitats for sites where Barking Owls were recorded and sites where they were not recorded

Significance levels for Kruskal–Wallis tests given.

a). Edge habitats

	Hollow diameter (cm)		
	0–10	**11–20**	**>20**
Owls recorded	21.3 ± 4.8	16.7 ± 3.7	3.2 ± 0.9
Owls not recorded	12.5 ± 1.6	6.1 ± 1.0	1.3 ± 0.2
P difference	0.001	0.003	0.013

b). Woodland interior habitats

	Hollow diameter (cm)		
	0–10	**11–20**	**>20**
Owls recorded	14.8 ± 3.5	12.8 ± 2.5	2.6 ± 0.9
Owls not recorded	6.6 ± 1.2	3.4 ± 0.8	1.0 ± 0.4
P difference	0.009	0.001	0.13

Association with hydrological features

The sites where Barking Owls were found showed a strong spatial association with major hydrological features. All seven of the localities where the owls were discovered in State Forests were in floodplains and within 100 m of permanent rivers. The three sites in State Game Reserves were in swamps and the single remaining site was at the edge of a reservoir. By contrast, of the sample of sites at which Barking Owls were not found, only four (12.9%) were close to permanent streams. Of the remainder, 19 (61.3%) were within 1 km of minor, ephemeral drainage lines and seven (22.6%) were greater than 1 km away from any hydrological feature. Comparing sites with and without owls on the basis of close association (within 100 m) with major hydrological features, or no close association with such features, the difference was statistically highly significant ($\chi^2 = 31.6$, $P < 0.001$, Table 4).

Table 4. Comparison of close association (within 1 km) with major hydrological features between sites where Barking Owls were recorded and sites where they were not recorded.

	Number close to major hydrological feature	Number not close to major hydrological feature
Owls recorded	11 (100%)	0
Owls not recorded	4 (12.9%)	26 (87.1%)

DISCUSSION

Even though this study yielded a higher percentage of positive locations for Barking Owls than previous surveys, probably because it was targeted rather than systematic, the number of pairs discovered was still low. Some birds or pairs may have been missed, as the method of detection relied mainly on birds responding to the broadcasting of taped calls. Studies of the frequency with which Barking Owls that are known to be present actually respond by calling back are currently being undertaken. Preliminary results suggest that, although there are occasions when known residents have not responded, most birds respond most of the time (I. Kirsten & I.R. Taylor). Instances of lack of response may have arisen from seasonal or diurnal variations in responsiveness or simply because the birds happened to be far from the broadcast site at the time. Whatever the reason, the evidence suggests that relatively few sites might have been wrongly classified during the survey. The most reasonable conclusion from the survey is that the species is extremely rare throughout most of the study area, confirming previous perceptions (Silveira 1997).

The higher frequency (6.7% of 75 sites) of records at sites where the owl had been reported during the 1980s and 1990s was expected, but the apparent absence of them at most of these sites was not. For most of the sites there was little detailed information on the status of the birds when the original recordings were made and it is not known with certainty whether most records involved pairs or individuals, residents or transients. Nevertheless, there must be concern that the owls were not recorded at the majority of sites where they were known to occur in the recent past. Even if some of the former records were of non-resident birds, the evidence suggests that the species is in decline and that the rate of loss may be considerable. The accumulated historical records provided in the Wildlife Atlas of Victoria clearly cannot be used to give an accurate assessment of current distribution and abundance; they are liable to overestimate both. Classification of the species as endangered in Victoria seems to be strongly supported by this study.

Several clear associations between the presence of Barking Owls and environmental variables were recorded. A significantly higher density of larger trees (>60 cm diameter) occurred in a 1 km radius around sites where owls were detected than around sites where the owls were not recorded. There may be a number of possible explanations for this, but the most likely is that larger trees were more likely to have adequate-sized hollows for the owls to nest in. The presence of many large trees might also be indicative of a reduced level of human disturbance in the past and hence related to other aspects of the quality of the environment for the owl and its prey.

The densities of hollows of all size classes at sites where owls were recorded were also about twice those at sites where the owls were not recorded. The abundance of hollows could have been important as potential nest sites for the owls and also as nest and resting sites for potential prey. Most recorded Barking Owl nest hollows were in excess of 15 cm diameter (Taylor *et al.* 2002), so the two largest size categories used in this study could have contained suitable breeding hollows. The largest size class of hollows occurred at very low densities even in the sites with owls, and presumably not all of these would have been suitable as nesting places. They were assessed from the ground and no information was obtained on their depth or dryness or other characteristics that might be important. There is clearly a need for more detailed research into the precise qualities of hollows that determine their suitability as nesting places for the owls and into the possibility that owl densities may be limited in some areas by a shortage of suitable nest sites. However, even in the absence of such information, it is still possible to conclude that such hollows are extremely rare and that the owls only occur at sites that have an exceptionally high density of them.

Studies of Barking Owl diet have shown that in addition to ground-living prey, they take a variety of hollow-requiring species, including gliders, bats, parrots, and European Starlings *Sturnus vulgaris* (Calaby 1951, Fleay 1968, Schodde & Mason 1980, Barker & Vestjens 1989, Hollands 1991, Kavanagh *et al.* 1995). Presumably, areas that have a high density of hollows also have relatively high densities of these prey. This might be especially so in edge habitats, with adjacent cleared land, as several possible prey such as some of the parrots and the European Starling can reach high densities at the interfaces of such habitats.

The strong association recorded between the presence of Barking Owls and hydrological features such as rivers and swamps might be explained by the seasonal and long-term availability of prey in such areas. The population biology of Barking Owls is almost completely unknown but they are likely to be relatively long-lived, as are most medium to large forest owls that have been studied in detail (McCarthy *et al.* 1999) The oldest known captive Barking Owl was 16 years old (G. Thompson, in Silveira 1997). Barking Owls are also likely to be sedentary and probably remain in the same territory all year round, and from year to year. Pairs of Barking Owls must have to survive not only seasonal dry periods but also longer term periods of severe drought. The general availability of prey is reduced during such periods but is likely to remain highest in areas that either retain water or some level of soil moisture. It is quite likely that many potential prey species may concentrate in these areas during droughts. Added to this, areas in floodplains generally have better soil quality and higher primary production which is likely to promote higher productivity of potential prey species. Thus, such sites probably offer the optimal habitat for Barking Owls where adult survival is highest. Historically, Barking Owls might have occurred in a wider range of drier woodlands away from rivers and other wetlands, but following habitat fragmentation and degradation from logging, overgrazing and fuelwood collection, with the subsequent reduction in terrestrial and arboreal mammal populations (Menkhorst 1995), such habitats can no longer support the birds, especially during drought periods.

In a study of Barking Owl diet in New South Wales, Kavanagh *et al.* (1995) noted that all five of the breeding sites they studied were close to rivers or other wetlands and they suggested that this might be a general habitat requirement for the species. The results of the present study agree well with Kavanagh *et al.* and combining both gives a sample of 16 sites fitting a model of association with hydrological features. Nevertheless, more work is needed to test and refine this idea and to assess its applicability to other parts of the species' range in southeast Australia.

ACKNOWLEDGMENTS

We thank the large number of Parks Victoria and Department of Natural Resources and Environment staff, and members of Field Naturalist groups throughout the region who helped in many ways. The research was funded by the Department of Natural Resources and

Environment. We thank Kim Lowe for his help on various aspects of the study. We also thank Ian Newton, Rod Kavanagh and an anonymous referee for their improvements to the manuscript.

REFERENCES

Barker, R.D. & Vestjens, W.J.M. 1989. *The Food of Australian Birds. I Non-passerines.*Melbourne: CSIRO.

Calaby, J.H. 1951. Notes on the Little Eagle; with particular reference to rabbit predation. *Emu* **51**: 33–56.

Debus, S.J.S. 2001. Surveys of the Barking Owl and Masked Owl on the north-west slopes of New South Wales. *Corella* **25**:5–11.

Debus S.J.S. Shepherd, R.B., & Rose, A.B. 1998. Diet of the Barking *Owl Ninox connivens* near Armidale, New South Wales. *Aust. Bird Watcher* **17**: 302–305.

Debus, S.J.S., Shepherd, R.B. & Rose, A.B. 1999. Non-breeding diet of the Barking Owl near Armidale, New South Wales. *Aust. Bird Watcher* **18**: 43–45.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Milton, Queensland: Jacaranda Press.

Hollands, D. 1991. *Birds of the night*: *owls*, *frogmouths and nightjars of Australia*. Sydney: Reed Books.

Kavanagh, R.P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Aust. Zool.* **30**:449–466.

Kavanagh, R.P. & Peake, P. 1993. Survey procedures for nocturnal forest birds: an evaluation of variability in census results due to temporal factors, weather and technique. In Olsen, P. (ed.), *Australian Raptor Studies*: 86–100. Melbourne: Australian Raptor Association, Royal Australian Ornithologists' Union.

Kavanagh, R. P. & Stanton, M.A. 1998. Nocturnal forest birds and arboreal marsupials of the southwestern slopes, New South Wales. *Aust. Zool.* **30**: 449–466.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B. & Turner, R.J. 1995. Diet and habitat of the Barking Owl *Ninox connivens* in New South Wales. *Aust. Bird Watcher* **16**: 137–144.

Loyn, R.H. 1996a. *Owl update*, *10 July 1996*. (unpubl.), Melbourne: Arthur Rylah Institute for Environmental Research.

Loyn, R.H. 1996b. *Owl and Mammal update*, *Central Highlands*, *Spring 1996*. (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

McCarthy, M.A., Webster, A., Loyn R.H. & Lowe, K.W. 1999. Uncertainty in assessing the viability of the Powerful Owl *Ninox strenua* in Victoria, Australia. *Pac. Conserv. Biol.* **5**: 144–54.

McNabb, E. G., Hill, R. J., Robinson, J & Loyn R. H. 1997. *Survey of Midlands Forest Management Area for Powerful Owl*, *Barking Owl and Masked Owl* (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

Menkhorst, P.W.1995. *Mammals of Victoria*: *distribution*, *ecology and conservation*. Melbourne: Oxford University Press.

Robinson, D. 1994. *Research plan for threatened woodland birds of south eastern Australia*. Melbourne: Arthur Rylah Institute for Environmental Research, Technical Report Series No. 133.

Schodde, R. & Mason, I.J. 1980. *Nocturnal birds of Australia*. Melbourne: Landsdowne.

Silveira, C.E. 1997. *Targetted assessments of key threatened vertebrate fauna in relation to the North East and Benalla-Mansfield forest management areas*, *Victoria*: *Barking Owl* (*Ninox connivens*). Report prepared for flora and Fauna Branch, Dept. of Natural Resources and Environment (unpubl.), Melbourne: Arthur Rylah Institute for Environmental Research.

Silveira, C.E., Yen, A.L., Bennet, A.F., Brown, G.W., Hinkley, S.D., Loyn, R.H., Lumsden, L.F. & Smith, W. 1997. *Fauna of the Box-Ironbark study area. Report for the Land Conservation Council* (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

Taylor, I.R., Kirsten, I. & Peake, P. 2002. Habitat, Breeding and Conservation of the Barking Owl *Ninox connivens* in northeastern Victoria, Australia. This volume.

12

HABITAT, BREEDING AND CONSERVATION OF THE BARKING OWL *NINOX CONNIVENS* IN NORTHEASTERN VICTORIA, AUSTRALIA

IAIN R. TAYLOR[1]*, INDRE KIRSTEN*[1] *AND PAUL PEAKE*[2]

[1]Applied Ornithology group, The Johnstone Centre, Charles Sturt University, PO Box 789, Albury, New South Wales 2640, Australia.

[2] Environment Conservation Council, 250 Victoria Parade, East Melbourne, Vic 3002, Australia.

Twenty pairs of Barking Owls were located in a 170 km^2 study area in northeast Victoria in 1999. The area was a mosaic of pastoral farmland and Box-Ironbark forest. The birds showed a strong selection for forest edge areas. Mean distances of nest sites to the nearest edge was 101.7 ± 46.9 m, significantly different from a mean of 455.2 ± 50.1 m for 30 locations selected randomly across the forest area. Nest sites were also more associated with relatively productive valley habitats than with less productive ridge habitats. Mean nearest neighbour distance between nest sites was 4.5 km, with some pairs nesting as close together as 1.8 km. The most frequently used nest trees were Apple Box *Eucalyptus bridgesiana* and Red Box *E. polyanthemos*. Mean nest tree diameter (DBH) was 120 cm and mean hollow height was 10.0 m. Mean hollow entrance was 31.4 × 24.1 cm and mean depth 103.6 cm. Seventy-seven percent of nest hollows had a southerly aspect. Laying was from the last week of July to the second week of August. Twenty young were fledged from 17 pairs whose productivity was known, or 1.2 young per pair, with 53% of pairs rearing young. Territory size of a single radio-tracked female was 226 ha. This individual spent only 15% of its foraging time in forest interior areas with the remainder in forest edges, creek lines and from trees in paddocks.

INTRODUCTION

The Barking Owl *Ninox connivens* is classed as endangered in Victoria and listed under Section 2 of the Flora and Fauna Guarantee Act 1988 (CNR 1995). Little is known of the species' ecology and recent surveys to locate the birds in various parts of the state have given few positive records (Loyn 1996 a,b, McNabb *et al.* 1997). However, the results of one survey (Taylor *et al.* 2002) suggest that the Northern Inland Slopes bioregion, in the northeast of Victoria, may be one of the few remaining strongholds of the species. This paper presents preliminary results from the first year of a study of Barking Owls in northeast Victoria to assess their status and ecology in more detail. Data are given on the abundance, spacing and location of breeding pairs, on nest site characteristics and breeding performance, and on the results of radio-tracking a single breeding female over three months during spring.

STUDY AREA

The study area covered approximately 170 km^2 around the towns of Beechworth and Chiltern in northeast Victoria (146°40´E, 36°20´S). There were two major blocks of continuous forest within the area: Chiltern Box-Ironbark National Park and Mt. Pilot State Recreation Area with adjacent Mt Barambogie State Forest Reserve (Fig 1). Around these areas there were numerous small, fragmented woodlands, with strips along creeks and roadsides. Non-forested land was mostly grassland for cattle and sheep production with many small hobby farms. Altitude ranged from about 200 m above sea level around Chiltern to just over 500 m at Mt. Pilot. The higher areas were granitic outcrops surrounded by areas of poor quality skeletal granitic soils. Lower altitude areas had richer alluvial soils. The predominant vegetation type at lower elevation was Box-Ironbark Forest characterised by Red Ironbark *Eucalyptus sideroxylon*, Grey Box *E. microcarpa*, Yellow Box *E. melliodora*, Apple Box *E. goniocalyx*, Red Box, *E. polyanthemos* and Red Stringybark *E. macrorhyncha*. This graded into drier forest types with increasing altitude characterised by Red

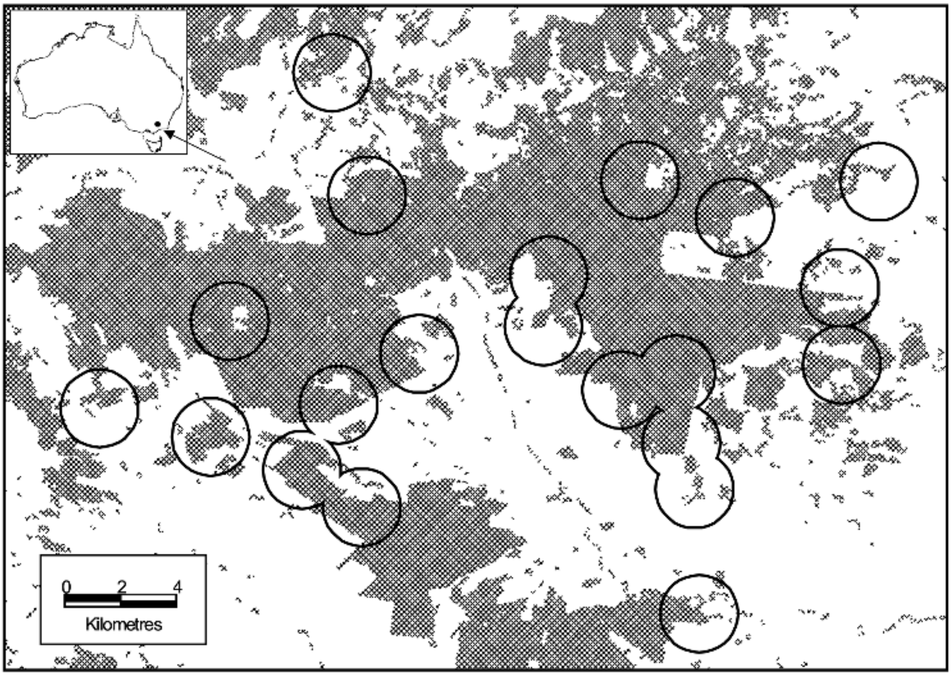


Fig. 1. Locations of breeding areas of Barking Owls within the study area in northeast Victoria, showing the spatial relationship with forest edges. Forest areas are shaded. For security reasons, the exact locations of Barking Owl nests are not given and locations are represented by circles of 1 km radius, within which the nests occurred.

Box, Blakely's Red Gum *E. blakelyi*, Red Stringybark and Black Cypress-pine *Callitris endlicheri*. Throughout, the woodland had an open structure with poorly developed ground and shrub layers.

Mean annual rainfall for the area ranged from 600 mm in the lowest areas to 900 mm at the highest points, with most falling in winter and spring from May to October. Temperatures varied seasonally, with highest mean daily values of about 30°C in January and February and lowest values of around 12°C in July.

METHODS

Before the start of our project, five breeding sites were already known in the study area. To locate all remaining pairs, between April and July 1999 standard Barking Owl nocturnal survey methods were employed at 100 sites spread evenly over the entire study area. The method used was modified from that developed by Kavanagh & Peake (1993) and Kavanagh & Bamkin (1995), and involved spending 15 minutes listening for owls calling, followed by broadcasting of taped Barking Owl calls for 10 minutes at sites where no calling was heard, listening for responses for up to 15 minutes and finally scanning by spotlight for 5 minutes at sites where no auditory responses were elicited to check for the possibility of birds being attracted without calling.

At sites where birds were found, intensive searching and following of adult owls were undertaken to locate nest sites. Nest hollows were not examined directly while the birds were thought to be incubating, because their response to disturbance was unknown, but they were observed from a distance to obtain evidence on whether they were breeding or not. The prolonged occupation of a hollow by a female with the male roosting close by and providing food were taken as evidence of attempted breeding. Once the young were 3 – 4 weeks old, sites were visited to determine the number of young and to collect pellets and prey remains. Each successful site was checked several times to determine the number of young eventually raised. After the end of breeding, each nest tree was climbed and details taken of the nest hollow dimensions, height and aspect.

A single breeding female was radio-tracked from October to December 1999. She was trapped by canopy netting and the use of tape playback of calls under the net, and fitted with an 18 g harness transmitter. She was tracked regularly over three months and her exact locations and activities recorded. The bird showed no signs of adverse reactions to the harness attachment.

RESULTS

Numbers and distribution of breeding pairs

A total of 20 pairs was located. Of these, 18 pairs were known to breed and their nest sites found. The remaining two pairs were unpredictable in their behaviour and no nest sites were found. They may have been nonbreeders or they may have attempted to breed, but failed at an early stage. The distribution of pairs within the area was distinctly non-random. All nest sites (and main roosting areas for the pairs that did not breed) were in major forest blocks or in areas where the forest was broken but with many remnants close together. Small forest remnants isolated from others, narrow strips of trees along roads and tracks, and isolated trees within paddocks, were not used for nesting. Although the birds were clearly associated with forest, they also avoided nesting in the interior of closed forest. They showed a highly significant preference for nesting close to the forest edge. The mean distance of known nests in 1999 to the nearest edge was 101.7 ± 46.9 m ($n = 18$), compared with a mean of 455.2 ± 50.1 m for 30 locations selected randomly using computer generated co-ordinates, across the forest area (Mann–Whitney U statistic = 34.0, $P < 0.001$). One nest was 900 m from any edge but this was in an unusual section of forest that contained a significant drainage line with an open canopy of exceptionally large, well spaced Apple Box trees and a lush understorey of grasses and herbs. The territories of two pairs were centred around small cleared areas of 0.5 km^2 and 0.8 km^2 within the main forest block. Nine pairs were on private land and eleven pairs on state land, but as all but one of the pairs on state land were at the edges, it is likely that they also foraged extensively over private land.

Previous studies have shown significant associations between Barking Owl nest sites and hydrological features such as rivers and swamps (Kavanagh *et al.* 1995, Taylor *et al.* 2002). There were no major rivers or swamps in the study area but there were many small creeks and areas of springs. Generally these were seasonal, with maximum flows in winter and spring, and most dried by mid summer. Eighteen of the nest sites were in small valleys or relatively low-lying parts of the area and all were within 300 m of creeks or spring areas. Nine of these were within 100 m of a creek.

The average nearest neighbour distance between pairs (taking the geographic centres of activity for pairs for which nest sites were not found) was 4.5 km ($n = 20$) but the smallest distance between adjacent pairs was only 1.8 km and there were two cases of only 2.5 km between pairs.

Nest site characteristics

Combining sites used in 1999 with sites known to have been used in previous years, data were available for 23 nest hollows. Eight of these were in Apple Box, six in Red Box, four in River Red Gum *E. camaldulensis*, and three in Blakely's Gum, all living trees. The remaining three were in dead trees of unidentified species.

The mean diameter at breast height (DBH) of nest trees was 120.0 cm, with a range from 60.0 to 260.0 cm, and the estimated mean height of nest trees was 20.0 m. The mean height of nest hollows was 10.0 m with a range from 4.8 to 19.0 m. The average size of the entrance to hollows was 31.4 × 24.1 cm with the smallest recorded at 16.0 × 14.0 cm. In most cases the entrance was slightly smaller than the cavity within, and the minimum cavity dimensions were 23.0 × 15.0 cm. Average hollow depth was 103.6 cm, ranging from 30.0 to 200.0 cm (Table 1). More nest hollow entrances had a southerly aspect than a northerly one (77.3% compared with 22.7%, $n = 22$; $\chi^2 = 6.54$, $P < 0.02$), although it is not known if this represents a selection for south facing hollows or whether there was a southerly bias in the availability of nest hollows. South-facing hollows would have given protection from the heating effects of the sun, especially in early summer when large chicks were in the nests.

Table 1. Characteristics of Barking Owl nest trees and hollows, northeast Victoria

DBH – diameter at breast height.

	Nest tree			Nest hollow				
	DBH (cm)	height (m)	Hollow height (m)	Entrance widest dimension (cm)	Entrance narrowest dimension (cm)	Cavity widest dimension (cm)	Cavity narrowest dimension (cm)	Cavity depth (cm)
Mean ± SD	120.2 ± 56.9	20.0 ± 5.0	10.0 ± 3.5	31.4 ± 12.9	24.1 ± 9.2	41.4 ± 23.7	24.2 ± 5.4	103.6 ± 56.0
Range	60.0–259.6	10.0–28.0	4.8–19.0	16.0–76.0	14.0–55.0	23.0–125.0	15.0–35.0	30.0–200.0
n	22	22	22	19	19	17	17	19

Breeding performance

Seventeen pairs were monitored for breeding performance and the outcome was known with certainty for 15 pairs. The remaining two pairs had well grown chicks in the nest hollow but at the next visits neither chicks nor parents could be found. Barking Owl chicks were found to leave the nest hollow when around 35 days old with winglengths of about 210 mm, which is about two thirds of adult winglength. At this stage of development, the young were able to climb well and make clumsy short flights in the canopy and onto the ground. It seems likely that at these two nests the young had fledged and moved away from the immediate nest area.

Eight of the remaining 15 pairs failed to produce any fledged young. Five of these were known to have hatched chicks (from food being carried in by parents and calling of chicks), but to have lost them later. The timing of loss for the remaining three pairs was unknown. There was no clear evidence of the cause of chick loss, as nest hollows were not inspected until after failure. The condition of chicks was unknown so any role of food supply could not be determined. At all failed nests there were no remains of either eggs or chicks and this, combined with the total rather than partial loss of broods, might suggest that predation was the cause. Throughout the study area, there was a high density of the predatory Lace Monitor lizard *Varanus varius* which habitually climbs trees to feed and take refuge. At a maximum length of 2.0 m, this lizard would probably be capable of withstanding defensive attacks from the adult owls. Lace Monitors have been observed leaving Barking Owl nest hollows in the study area.

The seven successful pairs reared on average 2.3 ± 0.5 young per pair, with five broods of two and two broods of three. If the two pairs whose young were probably missed at fledging are included as successful breeders, and the two young each had just before fledging are taken as the number produced, the overall production of the study population was 20 young from 17 pairs or 1.18 young per pair, with 53% of pairs rearing young. If these two pairs are counted as failed breeders the equivalent figures are 16 young, or 0.94 young per pair with 41% rearing young.

The approximate dates, accurate to within about 3–5 days, at which the young left the nest hollows was established for eight pairs. All were in the second and third weeks of October. The ages at fledging were obtained for three broods each of two young, at around 35 days, when wing lengths were about 200–210 mm. Preliminary wing-length growth data were determined for four chicks from two broods in the two weeks before fledging at 6.0, 4.7, 5.9 and 5.9 mm per day. Assuming this growth rate, averaging 5.6 mm per day, was maintained for most of the growth period, the birds would have reached adult wing-lengths of around 300 mm (Higgins 1999) when about 50–55 days old. Also, assuming growth rate to have been reasonably constant from about day ten after hatching to fledging and slightly slower during the initial ten days (Taylor 1994), it is possible to back date from fledging dates to approximate hatching dates. For all pairs this fell in the first half of September. With incubation taking about 36 days (Higgins 1999), laying dates would have been from the last week of July to second week of August.

Diet

A detailed assessment of the diet of the study population is in progress. A preliminary list of vertebrate prey species from remains found at nest and roost sites during the breeding season includes the following: European Rabbit *Oryctolagus cuniculus*, Brush-tailed Possum *Trichosurus vulpecula*, Sugar Glider *Petaurus breviceps*, Autralasian Grebe *Tachybapyus novaehollandiae*, Eurasian Coot *Fulica atra*, Peaceful Dove *Geopelia humeralis*, Eastern Rosella *Platycercus eximius*, Tawny Frogmouth *Podargus strigoides*, Magpie Lark *Grallina cyanoleuca*, Australian Magpie *Gymnorhina tibicen*, Australian Raven *Corvus coronoides* and White-winged Chough *Corcorax melanorhamphos*. Many pellets contained remains of yet to be identified smaller bird and mammal species, suggesting that larger prey may have been over-represented in remains at the nest. The body weights of these vertebrate prey would have ranged from about 20 g to 500 g. Many pellets also contained insect remains, especially cicadas and beetles.

Territory size and foraging habitat

A single female which had failed in her breeding attempt was radio-tracked from October to December 1999. From a total of 559 night-time locations spread over many nights during this period, her territory size, estimated by the minimum convex polygon method, was 226 ha. The territory was approximately circular, centred on the nest site and equivalent to just under a 1 km radius around the nest site.

Considering all night time locations (*n* = 559), regardless of the bird's activity, 68.6% were at forest edges (defined here as within 100 m of the edge), 11.6% along wooded creeklines, 6.6% on single trees in paddocks, 3.4% in small patches of trees in paddocks and 9.8% in the forest interior areas away from edges. The bird spent an average of 30.5% of its time foraging. Of 170 locations of foraging, 35.3% were in forest edge areas, 30.6% along wooded creek-lines, 9.4% in single trees in paddocks, 9.4% in small clumps of trees and 15.3% in forest interior areas. The bird used three roost sites for both day-time and night-time resting. All were in tree canopies and within 300 m of the nest site.

DISCUSSION

With 20 pairs, the study area contained the highest density of Barking Owls found to date in Victoria. The only published estimate of the total population for the state suggested about 50 pairs (Silveira *et al.* 1997) and, while this number might be conservative, the study area is clearly important for the species.

Most of the pairs located were close to the edges of major forest blocks and adjacent to cleared land, which was mostly pasture for cattle and sheep. This agrees with conclusions reached by Kavanagh *et al.* (1995) that the species used mainly edge areas. The reasons for this apparent selection of forest edges and avoidance of interiors were not investigated in this initial study but several hypotheses can be suggested that would be amenable to future testing. The birds were shown to use large hollows for nesting so it is possible that trees of suitable size classes were either more abundant or available close to forest edges. Related to this, the birds were associated mostly with the more mesic parts of the study area, in small valleys and close to creeks. These were the areas that were most likely to be partly cleared for agriculture and so to include forest edges, but it is also likely that they were better for tree growth because of higher moisture levels and better soil quality, and hence were the areas where larger trees were mainly found. Almost half of the nest sites found (9 out of 20) were on private land which often has retained a relatively high proportion of mature trees (Bennet 1993).

Edge areas used by the owls may also have had higher densities of suitable prey The introduced European Rabbit often occurs at high densities along the edges of paddocks, while some avian prey species, such as the Australian Magpie and Eastern Rosella, feed in paddocks and nest in adjacent forest or wooded strips along creeks and tracks. There may also be complex inter-relationships between the quality of plant growth conditions, acting through soils and moisture, tree sizes, hollow abundance and the numbers of hollow-dependent birds and arboreal mammals, with edge areas having higher densities of these than forest interior areas. Such relationships would presumably also extend to other parts of the ecosystem, with increases in other food sources such as insects and nectar in the more fertile edge areas leading to higher densities of a wide range of bird, mammal and insect prey for Barking Owls. The owls were also shown to take some wetland species, such as Australasian Grebes and Eurasian Coot, which were found on farm dams and presumably would not have occurred in uncleared forest. The single bird that was radio-tracked spent only 15.3% of its foraging time in forest interior areas, further suggesting that such areas were less profitable for foraging. Present-day edge areas are the result of human activity and would not have existed in the original landscape. Farming has resulted in the removal of forests in the more low-lying fertile areas and it seems likely that these were probably also the areas of highest prey densities and hence, Barking Owl densities, in the original intact forests.

While human modification of the landscape over the past 150 years or so may have produced these artificially rich edge areas, it may also have reduced the attractiveness of forest interiors to Barking Owls. The abundance of several native species that presumably would have occurred more generally throughout forests and that may have been prey for Barking Owls in the past have now been severely reduced or in some cases eliminated. For example, the Rufous Bettong *Aepyprymnus rufescens*, the immatures of which would have been a suitable prey size for the owls, is believed to have become extinct in the study area about 1895 (McEvey, 1965). Also, most forests in the area have been subject to high levels of timber extraction, which has reduced average stem diameters and presumably also the number of hollows suitable for arboreal mammal prey, such as Sugar Gliders and possums, reducing their abundance (Meredith 1984, Traill 1991, Traill 1993, Soderquist 1999). Stem densities have been increased and growth forms simplified (Bennet 1993), which probably has reduced the structural suitability of forests for foraging Barking Owls.

The significance of nest sites as a factor limiting the abundance of Barking Owls, both at present and in the future, needs to be investigated. For a species with such a low Victorian state-wide population, the continued occupancy of all breeding areas used at present needs to be assured, and the overall number of suitable breeding areas needs to be increased. The loss of individual trees that are large enough to contain suitable nest hollows may be a significant factor determining the suitability of areas. Were large gaps in the distribution of breeding pairs in the present study area, such as around most of Chiltern Box-Ironbark National Park, caused by a lack of suitable nest hollows? Experimental supplementation of nest sites by the provision of artificial sites would be an appropriate direction for future research (Newton 1998), as would an assessment of the numbers of suitable hollows within the ranges of existing pairs.

Barking Owls in the study area laid in late July and early August, that is, during the latter half of winter. This resulted in young in the nest during early spring. Thus, breeding coincided with the season of relatively moist conditions of maximum plant growth when many of the prey species were also breeding. Most of the young were fully grown before the main dry summer months. It would be interesting to determine more precisely the relationships between the breeding periods of the owls and their prey and especially to assess the extent to which the owls rely on young or recently fledged mammals and birds, as do some raptors elsewhere (e.g. Newton 1986).

The reasons for breeding failure in the study population also need to be investigated and especially the role of Lace Monitor lizards. These large predators may be able to locate nest hollows more easily in a simplified environment where large trees are few and the number of options to be searched is greatly reduced, in which case the effect of their predation in present day landscapes may be greater than it was in the original natural landscapes. The overall effect of nest predators could be examined experimentally by the use of collars around trees to prevent access to nests.

ACKNOWLEDGMENTS

The work of Paul Peake in discovering the first Barking Owl nests in the area stimulated the present study. Much of the subsequent fieldwork was done by Indre Kirsten and project planning, data analysis and report production by Iain Taylor. We thank Matt O'Connell who assisted greatly with fieldwork, Victor Hurley for advice on tree climbing and Glen Johnson for help securing funds. The project was funded by Charles Sturt University and by generous grants from VicRoads and a Stuart Leslie Bird Research Award. An earlier draft of the paper was greatly improved by comments from Ian Newton and Steve Petty.

REFERENCES

Bennett, A.F. 1993. Fauna conservation in Box and Ironbark forests: a landscape approach. *Victorian Naturalist* 110: 15–23.

CNR. 1995. *Threatened fauna in Victoria – 1995*. Melbourne: Department of Conservation and Natural Resources.

Higgins, P. (ed.). 1999. Handbook of Australian, New Zealand and Antarctic Birds. Vol. 4. Parrots to Dollarbirds. Melbourne: Oxford University Press.

Kavanagh, R. P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biol. Conserv*. **71**: 41–53.

Kavanagh, R.P. & Peake, P. 1993. Survey procedures for nocturnal forest birds: an evaluation of variability due to temporal factors, weather and technique. In Olsen, P. (ed.) *Aust. Rapt. Studies*: 86–100. Melbourne: Australasian Raptor Association, R.A.O.U.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B. & Turner, R.J. 1995. Diet and habitat of the Barking Owl (*Ninox connivens*) in New South Wales. *Aust. Bird Watcher* **16**: 137–144.

Loyn, R.H. 1996a. Owl update, 10 July 1996. (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

Loyn, R. H. 1996b. Owl and Mammal update, Central Highlands, Spring 1996. (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

McNabb, E.G. Hill, R.J., Robinson, J & Loyn R.H. 1997. *Survey of Midlands Forest Management Area for Powerful Owl*, *Barking Owl and Masked Owl* (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

McEvey, A. 1965. The birds of the Rutherglen district. *Emu* **65**: 1–56.

Meredith, C.W. 1984. Possums or poles? – the effect of silvicultural management on the possums of Chiltern State Park, northeast Victoria. In Smith, A. P., and Hume, I. D. (eds.), *Possums and Gliders*: 575–577. Sydney: Australian Mammal Society.

Newton, I. 1986. *The Sparrowhawk*. Carlton: Poyser.

Newton, I. 1998. *Population limitation in birds*. London: Academic Press.

Silveira, C.E., Yen, A.L., Bennet, A.F., Brown, G.W., Hinkley, S.D., Loyn, R.H., Lumsden, L.F. & Smith, W. 1997. *Fauna of the Box–Ironbark study area*. Report for the Land Conservation Council (unpubl.). Melbourne: Arthur Rylah Institute for Environmental Research.

Soderquist, T.R. 1999. *Tree hollows in Box-Ironbark forest: analysis of ecological data from the Box-Ironbark Timber Assessment in the Bendigo Forest Management area and Pyrenees Ranges*. Forest Service Technical Reports 99–3. Melbourne: Department of Natural Resources and Environment.

Taylor, I.R. 1994. *The Barn Owl: predator-prey relationships and conservation*. Cambridge: Cambridge University Press.

Taylor, I.R., Kirsten, I. & Peake, P. 2002. The distribution and habitat of Barking Owls (*Ninox connivens*) in central Victoria, Australia. This volume.

Traill, B.J. 1991. Box-Ironbark forests: tree hollows, wildlife and management. In Lunney, D. (ed.), *Conservation of Australia's Forest Fauna*: 119–123. Mosman: Royal Zoological Society of NSW.

Traill, B.J. 1993. Forestry, birds, mammals and management in Box and Ironbark forests. *Victorian Naturalist* **110**: 11–14.

13

DISTRIBUTION, HABITAT AND ABUNDANCE OF MASKED OWLS (*TYTO NOVAEHOLLANDIAE*) IN TASMANIA

P. J. BELL & NICK MOONEY

Department of Primary Industry Water and Environment, GPO Box 44A, Hobart,
Tasmania, Australia 7001.

A dataset comprising 423 records (26 nesting, 42 roosting, 192 of birds found dead and 145 encounters (sighting and/or hearing) of Tasmanian Masked Owls *Tyto novaehollandiae castanops* were used to predict the distribution of the species in Tasmania. The predicted distribution was mainly in areas of low elevation, low annual mean rainfall and high annual mean temperature, corresponding with areas broadly mapped as dry sclerophyll forest and woodland. To supplement this incidental records dataset, we conducted a field survey of owls using a combination of listening, playback of taped calls and spotlighting. Eighty-six sites were surveyed over a range of forest vegetation types and bioregions in Tasmania. Masked Owls were detected at 13% of sites surveyed and Southern Boobooks *Ninox novaeseelandiae* at 21%. For Masked Owls, the findings on habitat preferences were not inconsistent with those from the incidental records.

INTRODUCTION

Two owl species breed in Tasmania, the Masked Owl *Tyto novaehollandiae castanops* and the Southern Boobook *Ninox novaeseelandiae leucopsis*. A third species, the Barn Owl *Tyto alba*, occurs as a vagrant with no confirmed reports of breeding. Both the Masked Owl and Southern Boobook are forest-dependent, requiring cavities in forest trees for nesting. Significant changes to the structure and floristics of the forest habitat as a result of logging could influence the distribution and abundance of these species. Influence may be direct through the removal or modification of essential habitat or indirect through changes in the abundance of prey species. Recent research in southeastern mainland Australia has added to our knowledge of the habitat requirements, distributions and abundance of some species of forest owls (Debus, 1995; Kavanagh & Peake 1993a; 1993b), but further studies are needed to quantify the effects of forestry practices on forest owls and their prey species.

Information on the distribution, population status and habitat requirements of owls in Tasmania is scarce and insufficient for assessments of conservation status, or impacts of forest modification. In 1996 the Comprehensive Regional Assessment for the Tasmanian Regional Forest Agreement provided an opportunity for a preliminary study of Tasmania's forest owls, especially the Masked Owl. The present study summarises the results from a dataset of incidental site records and a brief systematic survey of Masked Owls in Tasmania.

METHODS

Incidental site records

We compiled a database of Masked Owl site records from a number of sources, including information associated with specimens held at the Tasmanian Museum and Art Gallery and the Queen Victoria Museum and Art Gallery, the Tasmanian Parks and Wildlife Service Biological Records Scheme, published literature (including the Tasmanian Bird Report, Emu, Tasmanian Naturalist and Records of the Queen Victoria Museum), site records made by members of avian interest and research groups, and records from the general public following media publicity for the project.

Systematic survey site records

A stratified random sampling program was used to generate survey sites across mainland Tasmania. Sites were stratified by forest vegetation class using a Condensed Photo-interpretation Database prepared by Forestry Tasmania, and by biogeographic region using the Interim Biogeographic Regionalisation for Australia (Thackway & Cresswell 1994). Sites were selected on the basis that they fell within 200 m of a vehicular track but otherwise at random.

The survey protocol followed Kavanagh & Peake (1993), Debus (1995) and Loyn (pers. comm.). Sites were visited once during the day to describe habitat, then again at night to check for owls. The procedure at each site involved a 10-minute listening period followed by a 5-minute broadcast of pre-recorded Southern Boobook calls (repetitive double call), 5-minute listening period, 5-minute broadcast of pre-recorded Masked Owl calls (including several screeches and occasional chittering calls), 5-minute listening period and finally a 10-minute spotlight search of approximately one hectare surrounding the survey site.

A Sony TCM–359V *Cassette-Corder* Walkman Cassette Recorder connected to a 13W megaphone was used to play pre-recorded calls. Southern Boobook calls were of *N. novaeseelandiae boobook* recorded in Victoria by Ed McNabb (Ninox Pursuits, 1996), while Masked Owl calls were of *T. novaehollandiae novaehollandiae* recorded in New South Wales by Steven Debus (Department of Zoology, University of New England).

At each survey site records were made of precipitation, wind, nightlight and moon phase. Structure and floristic information on the surrounding forest was noted on standardised proformas, and included information on landform, topography, abundance of hollow-bearing trees and large hollows, tree stem diameters and tree densities.

Statistical analysis

Contingency Chi-squared analysis or Fisher Exact Tests (Zar 1984) were used to determine the effect of time of night and environmental variables on the frequency of owl detections. A probability level of 0.05 was used as the criterion for significance. Systematic survey results were reduced to presence/absence data prior to analysis. For the purposes of analysis an 'owl present' record was defined as a site where an owl was seen and/or heard and was either close or distant from the designated survey site. Continuous data were converted to categorical data and all categorical data were further lumped for statistical analysis.

Species distribution modelling

For modelling we used a module of the CORTEX system developed by the Tasmanian Parks and Wildlife Service. It was derived from BIOCLIM (Nix 1986) and GARP (Genetic Algorithms for Rule Set Prediction). The environmental data were based on the abiotic (physical) parameters of climatic, topographic and substrate surfaces developed jointly by the Tasmanian Parks and Wildlife Service and the Center for Resource and Environmental Studies, Australian National University.

Species environmental envelopes were formulated as conjunctions of environmental variable ranges (for continuous variables) and variable classes (for categorical variables). Initially, an environmental envelope which enclosed all the observations for the species was constructed. Then, one by one, outlying observations were identified and removed and new environmental envelopes were constructed by finding the observation which, when removed, most increased the certainty of finding the remaining observations in the new smaller environmental envelope within which they were located. Outlying observations were removed until only an inlying core of observations remained. The result of this procedure was an ordered set of species-environmental envelopes which reflected an increasing certainty of finding at least one record on any grid cell within each successive environmental envelope. Each grid cell for which a prediction was sought was tested to find the most inlying (highest ranking) environmental envelope within which it fell.

RESULTS

Incidental site records

Fig. 1 shows the distribution of 423 site records of Masked Owls in Tasmania. Sixty-five records were for birds calling (without a sighting). The remainder includes 80 sightings of live birds (with no information on the bird's activity), 18 foraging records, 26 nesting records, 42 roosting records and 192 records of birds found dead (predominantly birds killed on roads but also some killed by collision with powerlines or by electrocution). One hundred and fifty-eight site records were obtained from 1991 to 1996, 156 from 1981 to 1990, and 109 prior to 1980. One hundred and seventy-seven site records were determined to have a location accuracy within 100m; the remainder ranged from 200m to 5 km.

Twenty-six nest sites were known historically or currently to be active (including two probable). All nests were in live or dead eucalypt trees: 54% were in White Gum *Eucalyptus viminalis*, 27% in Brown-topped Stringy Bark *E. obliqua*, 4% in Mountain Gum *E. dalrympleana*, 4% in Candlebark *E. rubida*, 4% in Smithton Peppermint *E. nitida* (identification inferred from extant surrounding trees), 4% in *E. tenuiramis* Silver Peppermint (identification inferred from extant surrounding trees) and 4% in Swamp Gum *E. ovata*.

Nests were in live or dead eucalypts varying in their state of decay. Observations of extant

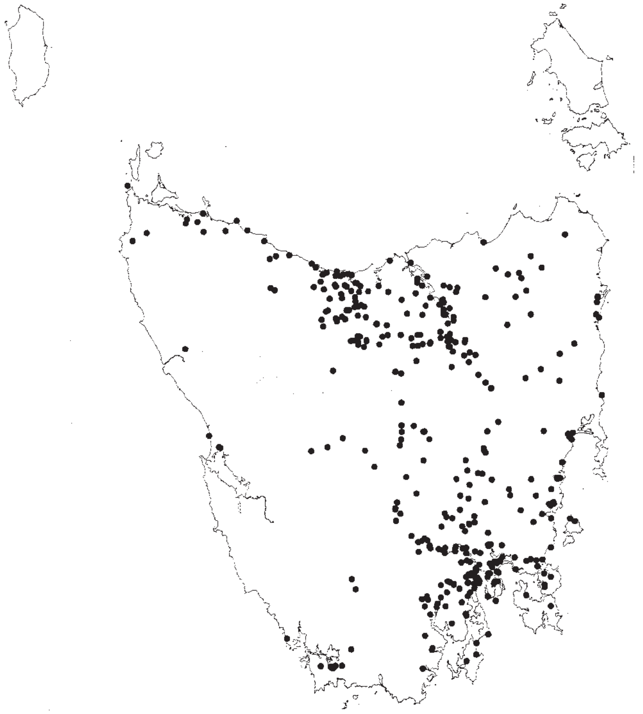


Fig. 1. Distribution of incidental site records of Masked Owls in Tasmania (n = 423).

nest-trees suggested that most were in excess of 150 years old. *E. viminalis* nest trees tended to be more youthful, robust and on average had suffered less crown damage than *E. obliqua* nest-trees which tended to have suffered considerable crown damage and were more often dead. Although *E. viminalis* is a common species with a similar distribution to that predicted for the Masked Owl, it is also the most common living tree used for nesting.

Only a single nest site occurred in a large patch of wet forest. Five were in open and closed forests in gullies supporting a dense understorey of mesic species such as Dogwood *Pomaderris apetala*, Musk *Olearia argophylla*, Stinkwood *Zieria arborescens*, Blanket Bush *Bedfordia salicina* and *Monotoca glauca*. The remainder were in open woodlands and closed forests with dry and generally sparse understories of shrub and heath species. Seven sites were in largely unmodified woodlands and open forests with a sparse understorey of shrubs including Bull Oak *Allocasuarina littoralis*, Native Cherry *Exocarpos cupressiformis* and Silver Wattle *Acacia dealbata* over dense heath. Seven occurred in open woodland to woodland habitats, in which tree density, understorey and/or ground cover may have been structurally modified. All had a pasture grass understorey.

Of 42 roost sites recorded, 44% were on external surfaces of trees or shrubs, 37% in holes on cliffs, 17% in buildings or other man-made structures and 3% in tree hollows. Tree and shrub roosts included *E. viminalis* (2), *E. cupressiformis* (2), *A. littoralis* (1), *E. obliqua* (1), *A. dealbata* (1), Paperbark *Melaleuca ericifolia* (1), Myrtle *Nothofagus cunninghamii* (1), *O. argophylla* (1), *P. apetala* (1) Teatree *Leptospermum sp.* (1) and exotic conifers (2). The only tree hollow roost recorded was in an unidentified dead stag. Cliff roosts were predominantly on sandstone (93%), with one site on mudstone. Roost sites in man-made structures included a shearing shed, wool shed, horse stable, blacksmiths shed, flour mill and buildings within the city of Hobart.

It appears that the densest canopy covers are favoured for roosting (e.g. *M. ericifolia* closed scrub and *A. dealbata* closed forest), the densest understorey components in gullies and along water courses (e.g. mesic species such as *P. apetala* and *O. argophylla*), or the most heavily foliated understorey shrub species (e.g. *E. cupressiformis* and *A. littoralis*) in extensive areas of dry forest/woodland in undulating country with few gullies or damp creek lines. The use of dense heavily foliated vegetation (usually associated with wet forest) may help to explain the apparent preference for a mesic forest or mesic understorey component as part of the home-range, as opposed to extensive areas of dry forest.

Systematic survey site records

No Masked Owls were heard during the initial listening period and ten of the eleven detections were calls and/or sightings in response to playback. Six detections of Masked Owls involved sightings in addition to calls and on three occasions both an adult male and an adult female owl were seen. One Masked Owl was sighted while we were leaving a survey site. Owls were detected at 28 (33%) of 86 sites surveyed across all biogeographic regions and forest types. The Masked Owl (Fig. 2) and the Southern Boobook were detected at 11 (13%) and 18 (21%) of sites respectively.

There was no significant association between the frequency of Masked Owl or Southern Boobook detections and time of night, wind strength, precipitation, phase of moon or brightness

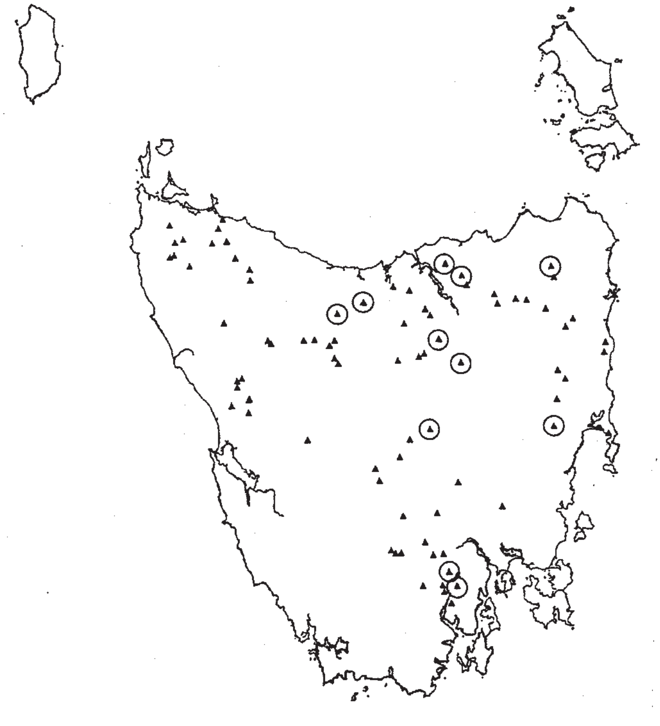


Fig. 2. Locations of sites surveyed in Tasmania for Masked Owls. ▲ = survey sites; Ⓐ = sites where Masked Owls were detected.

Table 1. Owl detectability at survey sites and time of night, moon phase and weather conditions.

Parameter and species	Categories and counts (present/absent)	Test value and probability
Time		
Masked Owl	1800h–2200h, 5/47; after 2200h, 6/28	Fisher Exact Test $P = 0.33$
Southern Boobook	1800h–2200h, 10/52; after 2200h, 8/34	$\chi^2 = 0.15$, d$F = 1$, $P = 0.70$
Wind		
Masked Owl	calm or light wind, 10/63; moderate or strong, 1/10	Fisher Exact Test $P = 1.0$
Southern Boobook	calm or light wind, 16/57; moderate or strong, 2/11	Fisher Exact Test $P = 0.73$
Precipitation		
Masked Owl	no precipitation, 7/58; precipitation, 4/17	Fisher Exact Test $P = 0.45$
Southern Boobook	no precipitation, 16/49; precipitation, 2/19	Fisher Exact Test $P = 0.22$
Moon Phases		
Masked Owl	new moon and first quarter, 6/36; last quarter and full moon 5/39	Fisher Exact Test $P = 0.75$
Southern Boobook	new moon and first quarter, 10/32; last quarter and full moon 8/36	Fisher Exact Test $P = 0.60$
Night Light		
Masked Owl	very dark or heavy cloud and detail seen, 7/66; bright and clear, 4/10	Fisher Exact Test $P = 0.07$
Southern Boobook	very dark or heavy cloud and detail seen, 15/58; bright and clear, 3/10	Fisher Exact Test $P = 1.0$

Table 2. Relationship between environmental parameters and the presence of owls.

Parameter and species	Categories and counts (present/absent)	Test value and probability
Slope		
Masked Owl	flat, 5/37; moderate and steep, 6/38	$\chi^2 = 0.06$, d$F = 1$, $P = 0.81$
Southern Boobook	flat, 7/35; moderate and steep, 11/33	$\chi^2 = 0.9$, d$F = 1$, $P = 0.47$
Aspect		
Masked Owl	northerly, 4/24; southerly 4/19	Fisher Exact Test $P = 1.0$
	easterly, 2/20; westerly 6/18	Fisher Exact Test $P = 0.12$
Southern Boobook	northerly, 6/22; southerly 4/19	Fisher Exact Test $P = 1.0$
	easterly, 5/17; westerly 5/15	Fisher Exact Test $P = 1.0$
Altitude		
Masked Owl	<700m asl, 10/61; >700m asl 1/14	Fisher Exact Test $P = 0.68$
Southern Boobook	<700m asl, 17/53; >700m asl 1/15	Fisher Exact Test $P = 0.17$
Tree density		
Masked Owl	absent, sparse, medium, 4/36; dense 7/39	Fisher Exact Test $P = 0.53$
Southern Boobook	absent, sparse, medium, 10/30; dense 8/38	Fisher Exact Test $P = 0.43$
Distance to forest edge		
Masked Owl	<500m, 9/34; >500m, 7/39	Fisher Exact Test $P = 0.03$
Southern Boobook	<500m, 10/30; >500m, 8/38	Fisher Exact Test $P = 0.43$
Distance to water		
Masked Owl	<500m, 6/30; >500m, 5/45	Fisher Exact Test $P = 0.33$
Southern Boobook	<500m, 9/27; >500m, 9/41	Fisher Exact Test $P = 0.43$

Level of significance $P = 0.05$

Table 3. Number of survey sites at which owls were detected in different habitats in Tasmania.

Records from all bioregions are pooled.

Forest type	Number of sites surveyed	Number of sites where Masked Owls were detected	Number of sites where Boobooks were detected
Rainforest	16	0	3
Dry sclerophyll forest	16	4	3
Wet eucalypt forest	13	1	3
Teatree scrub or forest dominated by native conifers, Sassafras, Blackwood and/or Silver Wattle	27	4	6
Cleared land and/or pasture	11	2	3
Pine plantation	3	0	0

Table 4. Number of survey sites at which owls were detected in different bioregions in Tasmania.

Records from all habitat types are pooled.

Bioregion	Number of sites surveyed	Number of sites where Masked Owls were detected	Number of sites where Boobooks were detected
Woolnorth	18	2	9
Ben Lomond	13	3	2
Freycinet	8	1	1
Midlands	8	2	3
Central Highlands	14	1	1
West and South West	12	0	0
D'Entrecasteaux	13	2	2

of nightlight (Table 1). No significant association was found between the frequency of Masked Owl detections across survey sites and the slope of the site, altitude, aspect, tree density or distance to a significant water body (Table 2).

Masked Owls were detected more frequently than expected <500 m from forest edges (moorland, grassland or cleared land of patch size >25 ha). They were found in wet eucalypt forest, dry sclerophyll forest, non-eucalypt-dominated forest, scrub and cleared land or pasture, but not in rainforest (within 16 survey sites) or pine plantation (within only three survey sites) (Table 3). They were found in all Tasmanian bioregions, except the West and Southwest region (Table 4). Too few were found to warrant statistical analysis for either habitat or regional variation; but Masked Owls were found at 20% of survey sites in the Ben Lomond and Midland bioregions (Fig. 3).

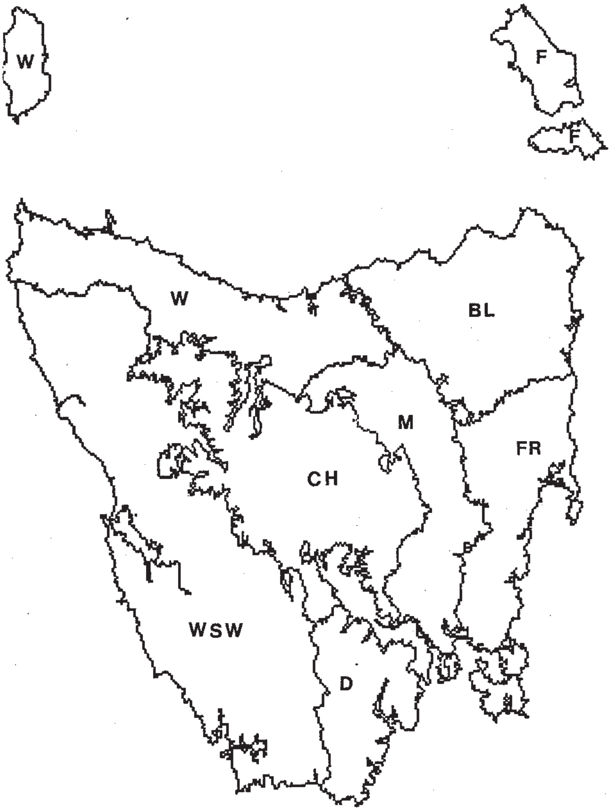


Fig. 3. Biogeographic regionalisation of Tasmania used in the present study (after Thackway & Cresswell, 1994). (BL) Ben Lomond, (CH) Central Highlands, (D) D'Entrecasteaux, (FR) Freycinet, (F) Furneaux, (M) Midlands, (W) Woolnorth, West and South West (WSW).

Predicted distribution of Masked Owls

On the basis of our model, the predicted distribution of Masked Owls in Tasmania including the Bass Strait islands, is shown in Fig. 4. The model was based on both historic and current Masked Owl site records of all types ($n = 423$), and included records with a location accuracy within 5 km. High probability areas tended to be at low elevation with a low annual mean rainfall and high annual mean temperature. They were concentrated in the lowlands of the north coast, midlands, east coast, Derwent and Huon river catchments and small fragmented patches on western Flinders Island. High probability distribution reflected areas mapped as cleared land, or as dry sclerophyll forest and woodland. An area of anomaly lies on the mid north coast and hinterland on the Forth and Mersey river catchments between the Rubicon River, Burnie and Mole Creek. This high probability area had a greater coverage of mixed forest and wet eucalypt forest, though fragmented due to clearing. Moderate probability areas extended the predicted distribution along the entire northwest coast, northern and central midlands and generally further inland.

Almost 70% of the predicted distribution of Masked Owls was on private land. The proportion of the predicted distribution that lay within dedicated reserves was about 6%. In fact, few large reserves overlapped this distribution.

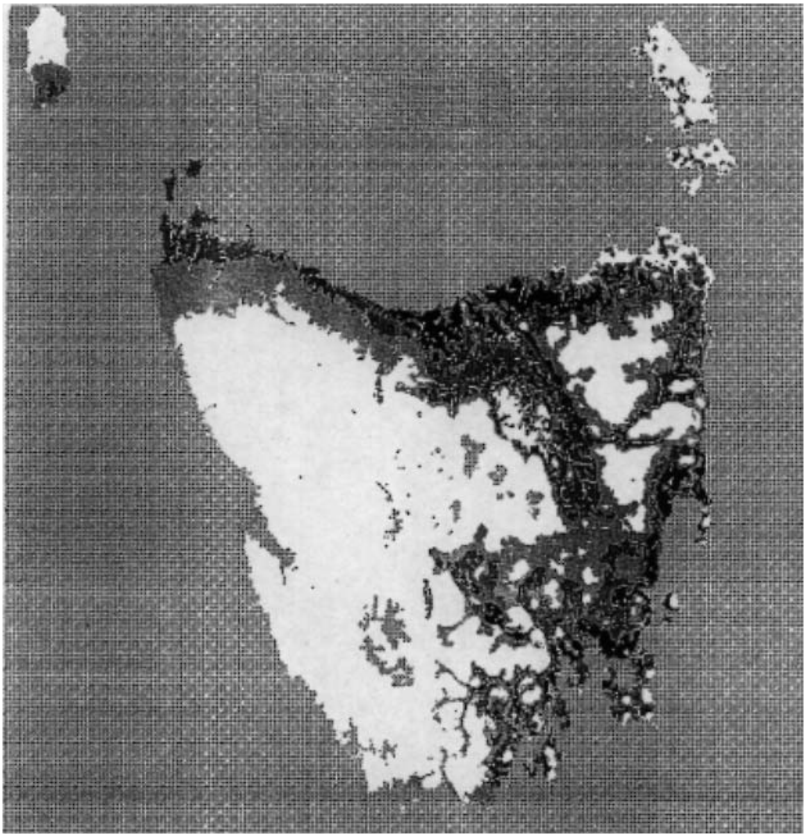


Fig. 4. Predicted distribution Masked Owls in Tasmania. The model is based on current and historic site records of all types, i.e. sightings, hearings, nest sites, roost sites, road kill and other accidental deaths (*n* = 423). Black represents areas where the probability of owl presence is at its highest, while grey, light grey and white represent areas where the occurrence of owls is predicted to be moderate, low or extremely low respectively.

DISCUSSION

Distribution and habitat

The model of predicted distribution suggests that the Masked Owl's preferred habitat in Tasmania is lowland areas (<600 m) with a high mean annual temperature and low mean annual rainfall. This distribution corresponds with the distribution of dry sclerophyll forest and woodland and 'cleared land'. This agrees with stochastic distribution models of the southern subspecies *T. n. novaehollandiae* in northeast New South Wales (NPWS 1994).

The survey data revealed a statistically significant association between the frequency of Masked Owl detections and their distance from forest edge indicating a preference for proximity to areas of cleared land, moorland, grassland or heathland habitats. From the analysis of incidental site records of *T. n. novaehollandiae* in Victoria, Peake *et al.* (1993) suggested a preference for ecotones, because nearly all their nocturnal sightings were within 300m of a boundary between two vegetation types. Peake and his associates found that the most prominent habitat type was lowland sclerophyll forest, almost half of which was associated with wet heathland

and/or riparian forest. In New South Wales, Masked Owl sites were most numerous in open forest and woodland with diverse vegetation structural types and a mosaic of dense and sparse cover types; they were least numerous in dense forests (Debus, 1993). Where we have detailed descriptions of vegetation associated with sighting records in Tasmania, and these are nest and roost sites only, there is some support for the importance of lowland dry sclerophyll forest, closeness to forest edge (natural ecotones or forest edge/cleared land) and a mosaic understorey from open to dense. In contrast, wet forest appears to provide only marginal habitat for Masked Owls. Over the last 20 years, no Masked Owl records have been reported from areas of current forestry operations in wet forest types. Nonetheless, wet gully and riparian forest, where it occurs in otherwise dry forest types, may be favoured for roosting and nesting and for its greater diversity of prey species.

Nesting

Mooney (1996) suggested that isolated nest trees in substantially cleared farmland are very old and remain from the original forest/woodland canopy, prior to clearing. They may even have been used for nesting prior to clearing. Most known nest trees occur in environments subject to development. This reflects the co-occurrence of preferred Masked Owl habitat with human habitation in eastern Tasmania (dry forest types in coastal lowlands) and the same may hold elsewhere. The very nature of Masked Owl nest trees on or near cleared land, and the species' preference for forest edge habitats, must increase the likelihood of nest destruction. Nest trees are usually very old or dead and often fragile. They are trees typically targeted for felling during landscaping, firewood collection and landclearing activities.

To add to the risk of targeted felling and land clearing of nesting trees is the problem of natural attrition. Several authors have recognised the fragility of Masked Owl nest sites (e.g. Mooney 1996, Hollands 1991) and empirical studies indicate the life expectancy of trees supporting large hollows may only be several years (e.g. Lindenmayer *et al.* 1990b). The fragility of nest trees increases the probability of destruction by fire and wind and isolated nest trees are particularly susceptible to wind action (Lindenmayer *et al.* 1990a; Debus 1993).

Roosting

Masked Owls appear to be versatile in their requirements for roost sites and the use of buildings for roosting is well known and typical in farming and urban areas lacking dense vegetation. Owls have been flushed from a range of trees (incidental site dataset), some representative of dry forest understorey, others of mixed forest, wet forest, wet gully and riparian forest understories. During the present study, a male Masked Owl was flushed from a small *E. cupressiformis* in otherwise dry woodland with a sparse understorey of shrubs offering little shelter. The owl was roosting at a height of only two meters.

Population estimates

There are no published estimates of the population of Masked Owls in Tasmania. However, Peake *et al.* (1993) provided an estimate of 600–800 breeding individuals for Victoria, including 60 breeding pairs for Gippsland and the East Gippsland Plains. The Comprehensive Regional Assessment for East Gippsland (1996) used an estimate of 85–275 pairs and, based on a median of 180 pairs, this gave a density of one bird per 1,389 ha for that area (Joint RFA Team 1996).

Based on the number of site records in our dataset and eliminating possible duplication at the individual and territory level (by allocating all records within a 2km radius of each other to the same territory), we estimated about 199 'territory' records for Tasmania. If we follow a similar procedure to Peake *et al.* (1993) and assume that we know of up to one half the actual number of territories occupied at one time, then a crude estimate of the size of the Tasmanian Masked Owl population is in the range of 200–400 pairs.

Owl survey procedure

Although the present study included only 86 survey sites, the frequency of detection of *T. n. castanops* appeared to be higher than that for *T. n. novaehollandiae* in New South Wales. However, many of our survey sites were outside the predicted distribution range of the species or in habitat generally considered unsuitable. If the survey focused in the drier areas of eastern Tasmania in forested and fragmented forest environments, the proportion of sites where owls were detected would almost certainly have been greater than 13%. Of 35 detections of *T. n. novaehollandiae*, Debus (1995) recorded no cases where a pair of birds responded, but in our survey three of eleven responses were from pairs (or two birds of different size). The Tasmanian survey data are currently too few for more detailed analysis, but the density of *T. n. castanops* on Tasmania may well be higher than that of *T. n. novaehollandiae* on the mainland.

Finally, our survey provides us with a useful basis from which to launch further systematic surveys of owls in Tasmania. The survey protocol appears to be appropriate for use on Tasmania's forest owls and the survey technology is tried and tested. Moreover the habitat measurements collected during our study will remain a useful addition to similar data collected in future.

ACKNOWLEDGMENTS

Funding for this project was provided by Environment Australia through the Comprehensive Regional Assessment for Tasmania's Regional Forest Agreement. We thank Steven Debus, Richard Loyn, Rod Kavanagh and Ed McNabb for advice on forest owl survey techniques.

REFERENCES

Bell, P. J. & Mooney, N. 1997. Predicting essential habitat for forest owls in Tasmania. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee.

Debus, S. J. S. 1995. Surveys of large forest owls in Northern New South Wales: methodology, calling behaviour and owl responses. *Corella* **19**: 38–50.

Debus, S. J. S. 1993. The mainland Masked Owl *Tyto novaehollandiae*: a review. *Aust. Bird Watcher* **15**: 168–191.

Hollands, D. 1991. Birds of the Night. Sydney: Reed.

Joint Commonwealth and Victorian Regional Forest Agreement (RFA) Steering Committee 1996. *Comprehensive Regional Assessment East Gippsland*, *Environment and Heritage Report*.

Kavanagh, R. P. & Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96**: 250–257.

Kavanagh, R. P. & Peake, P. 1993a. Survey procedures for nocturnal forest birds: an evaluation of variability in census results due to temporal factors, weather and technique. In Olsen, P. (ed.), *Australian Raptor Studies*: 86–100. Melbourne: Australasian Raptor Association, RAOU.

Kavanagh, R. P. & Peake, P. 1993b. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In Olsen, P. (ed.), *Australian Raptor Studies*: 101–125. Melbourne: Australasian Raptor Association, Royal Australian Ornithologists Union.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P. & Nix, H. A. 1990a. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia: I. Factors influencing the occupancy of trees with hollows. *Biol. Conserv*. **54**: 111–131.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P. & Nix, H. A. 1990b. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia: II. The loss of trees with hollows and its implications for the conservation of Leadbeater's Possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biol. Conserv*. **54**: 133–145.

Mooney, N. 1996. Habitat and seasonality of nesting Masked Owls in Tasmania. In Czechura, G. & Debus, S. (ed.). *Australasian Raptor Studies 11*: 34–39 Birds Australia Monograph 3, Birds. Melbourne: Australia.

Nix, H. A. 1986. BIOCLIM – a bioclimatic analysis and prediction system. CSIRO Division of Water and Land Resources Annual Report, pp. 59–60, Canberra: CSIRO.

Peake, P., Conole, L. E., Debus, S. J. S., McIntyre, A. & Bramwell, M. 1993 The Masked Owl *Tyto novaehollandiae* in Victoria. *Austr. Bird Watcher* **15**: 124–136.

Schodde, R. & Mason, I. J. 1980. *Nocturnal Birds of Australia*. Melbourne: Landsdowne.

Thackway, R. & Cresswell, I. D. Ed. 1994. *Toward an interim biogeographic regionalisation for Australia*: *a framework for setting priorities in the national reserves system cooperative program*. Proceedings of a technical meeting held in Adelaide at the South Australian Department of Environment and Natural Resources 7–11 February, 1994.

Zar, J. H. 1984. *Biostatistical Analysis*. New Jersey: Prentice-Hall, Inc..

14

SPATIAL HABITAT CHARACTERISTICS OF AN INSULAR SPOTTED OWL (*STRIX OCCIDENTALIS*) POPULATION IN SOUTHERN CALIFORNIA

RICHARD B. SMITH[1,2]*, WILLIAM S. LAHAYE*[1,3]*, R. J. GUTIÉRREZ*[1,4]*, &*
GUTHRIE S. ZIMMERMAN[4]

[1]Department of Wildlife, Humboldt State University, Arcata, California, 95521, USA

[2]Current address: 840 Little Neck Road, Cutchogue, New York 11935, USA

[3]Current address: P.O. Box 523, Big Bear City, California, 92314, USA

[4]Department of Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55108, USA

We studied the distribution of Spotted Owls *Strix occidentalis occidentalis* with respect to landscape cover types within the San Bernardino Mountains of southern California. We located 144 owl territories within the mountain range. Minimum crude density was 0.08 owl territories km^{-2} and ecological density was 0.29 owl territories km^{-2}. Owl territories ranged in elevation from 800 m to 2600 m and were found in three main forest types: Canyon Live Oak *Quercus chrysolepis*/ Big-cone Fir *Pseudotsuga macrocarpa* (56 territories), mixed conifer/hardwood (40 territories), and mixed conifer (48 territories). Ecological density of territories in each of the forest types was 0.39, 0.29, and 0.16 territories km^{-2}, respectively. The mean nearest neighbour distance of owl territories was 1,497 ± 63 m. The spatial distribution of owl sites was significantly different from random ($P < 0.01$) and characterized by vegetation associations that were different from those of random sample points. The area of forested vegetation was significantly greater at owl sites and occurred in larger patches than at random sites.

INTRODUCTION

The Spotted Owl *Strix occidentalis* occupies forested landscapes in western North America (Gutiérrez *et al.* 1995). It is a territorial, habitat specialist occupying mainly older seral stage forests (Forsman *et al.* 1984, Gutiérrez *et al.* 1992, Seamans & Gutiérrez 1995). This species has been the focus of much research in recent decades, because its preferred habitat has declined across its range (Gutiérrez *et al.* 1995). As a result, considerable effort has been devoted towards its conservation (Thomas *et al.* 1990; USDI 1990, 1992, 1993, 1995).

Two of the three subspecies (*S. o. caurina* and *S. o. lucida*) are listed under the U. S. Endangered Species Act as threatened because timber harvesting has either destroyed or threatens much of their primary habitat (USDI 1990, USDI 1993). The California subspecies (*S. o. occidentalis*) is not currently listed, even though it has similar habitat requirements (Gutiérrez *et al.* 1992, LaHaye *et al.* 1997). Thus, there is concern for the future of this subspecies (Verner *et al.* 1992a), particularly the insular populations found in southern California (Noon & McKelvey 1992, LaHaye *et al.* 1994). In order to better understand this subspecies' ecological relationships and to facilitate conservation planning, we assessed the distribution of owl territories in relation to landscape vegetation.

STUDY AREA AND METHODS

The 1,890 km^2 study area was located in the San Bernardino Mountains approximately 140 km east of Los Angeles. Elevations ranged from 500 m to 3500 m and supported a diverse assemblage of vegetation types, including desert and semi-desert scrub, relatively mesic conifer forests and alpine vegetation (Minnich 1998). However, most Spotted Owls occupied mixed evergreen (Sawyer *et al.* 1988) and montane forests (Thorne 1988) at 800–2,600 m elevation (Gutiérrez *et al.* 1992, LaHaye *et al.* 1997).

Regionally, forest was scarce, limited to higher elevations, and isolated from forests in adjacent mountain ranges by extensive areas of nonforest vegetation (Hanes 1988, Mooney 1988, Vasek & Barbour 1988, LaHaye *et al.* 1994). Even where forests occur, the vegetation is often heterogeneous, consisting of relatively small patches of forest, woodland, chaparral and bare ground.

Rainfall varied greatly within the study area and annual averages ranged between 400 and 1200 mm, depending on elevation, topography, and proximity to rain shadows (Minnich 1988). The climate was Mediterranean, with most precipitation occurring in winter (Fujioka *et al.* 1998).

Spotted Owl surveys

We located owl territories during 1987–96 using standard protocols (Franklin *et al.* 1996), which included multiple surveys of the entire study area annually to locate territorial owls and check their breeding success. Most of the owls within the population were colour-banded (LaHaye *et al.* 1992, 1994). Accurate locations of nests and roosts were obtained using a global positioning system (GPS), except where rugged terrain or forest interfered with access to satellites. Only locations with an error of ≤30 m were accepted for analysis. In addition, GPS and other locations were cross-checked or mapped using a compass, altimeter and topographic maps.

Nest locations were used to identify territory centres. When no nest locations were known, the territory centre was defined by a roost location. When multiple nests or roosts were known from a territory, we selected the most centrally located nest or roost to represent the territory centre. Only one location per territory was used for statistical comparisons and one random point was selected for each owl territory.

Image interpretation and development of the cover type map

We used an unsmoothed Landsat 5 Thematic Mapper image geocoded to a pixel size of 25 × 25 m. MicroImage Software was used for image analysis (Terra-Mar 1990). Data analysis proceeded by first extracting the area of interest from the entire data set, grouping pixels with similar reflectant values, and conducting an unsupervised classification to establish preliminary cover types (Richards 1993). Forested cover types were emphasized during image processing.

The development of a cover type map from the Landsat imagery followed an iterative process based on vegetation sampling. Forested cover types were sampled in the field using Bitterlich's variable plot method with a 20 basal area factor prism (Dillworth 1975). Trees were lumped into four diameter classes (0–30.5 cm dbh, 30.5–61.0 cm dbh, 61.0–91.5 cm dbh, and >91.5 cm dbh). Elevation, aspect, percent slope, and canopy closure were measured at each sample point using an altimeter, compass, clinometer and spherical densiometer, respectively. Ground cover was estimated visually within a 12 m radius surrounding each sample point, to the nearest 5%, in each of five categories: open, rock, dead and down, grasses and shrubs. All of the above attributes contributed to the spectral reflectance of cover features and affected values obtained by the Landsat sensor (Lillesand & Kiefer 1987). The final map was assessed for accuracy by comparing the actual cover type at 195 random sample points (exclusive of random sample points used for comparison with owl sites) to the cover type predicted by the final map. Both user and producer error rates were evaluated (Congalton 1991).

Statistical analyses

The spatial distribution of owl sites and random sample points and the relationship of owl sites and random sample points to the cover types were analyzed using FRAGSTATS (McGarigal & Marks 1995), ArcInfo (ESRI 1993) and ArcView software (ESRI 1996). A one km buffer around the entire study area was mapped to ensure that owl and random sites near the study area boundary could be included. Nearest neighbour distances between owl sites and random sites were compared using the formula of Clark & Evans (Krebs 1989).

We estimated the area of each cover type within the study area and the study area plus a one km buffer. The natural cover types were aggregated into a smaller set of cover classes based on their presumed value to Spotted Owls. The area of each cover class was estimated within circular plots of increasing area around owl sites and random sample points to evaluate the effect of scale when exploring the differences between these groups. These areas were: 3 ha, 20 ha, 79 ha, and 177 ha plots, derived from circle radii of 100 m, 250 m, 500 m, and 750 m, respectively. Spotted Owl home ranges in the San Bernardino Mountains varied in size from 300 to 800 ha during the breeding season (Zimmerman *et al.* 2001). The 177 ha plot was selected as our largest plot size because the radius of this plot (750 m) was approximately one half the mean nearest neighbour distance (see below). In addition, a Simpson's Diversity Index (SDI, Simpson 1949) was computed for each plot size using the proportion of habitats for each owl site and random location.

Crude (number of territories/total area of the study area, Tanner 1978) and ecological (number of territories/area of owl habitat, Tanner 1978, Franklin *et al.* 1990) territory densities were estimated based on all known territories and the amount of owl habitat within the study area, respectively. Spotted Owl habitat was defined as any cover type used for nesting or roosting. The frequencies of owl territory centres and of random sites in each cover class were compared to evaluate whether these sites were distributed similarly among the cover classes.

Fragmentation of the vegetation at owl sites and random sample points was estimated using the 20 ha plots (250 m radius)and defined as all natural and human caused heterogeneity in the vegetation. In general, if a site contained a large number of patches with a small mean patch size, this indicated greater fragmentation. A patch was defined as any contiguous area of the same cover class.

We developed a set of *a priori* models based on hypothesized relationships between Spotted Owl ecology and this species' potential use of the cover classes and employed logistic regression analysis to evaluate our ability to correctly classify owl sites and random samples. Four models composed of cover class variables were developed to analyze the data for each plot size. The models were closed canopied forest (CCF) + nonforest (NF), CCF + chaparral (CH), CCF + open forest (OF), and CCF. + OF + CH (see below for descriptions of cover classes). The most parsimonious model was selected by ranking model performance using Akaike's Information Criterion (AIC, Burnham & Anderson 1992). The model with the highest rank (lowest AIC value) was used to produce percent correct classifications using the jack-knife procedure. We tested for significance of correct classification rates by using a chance-corrected classification evaluation (Titus *et al.* 1984). In addition, we noted which variable(s) contributed most to classification success.

RESULTS

Image analysis

Seventeen cover types were delineated based on spectral signatures of the vegetation and exposed soils (Table 1). A quantitative assessment of accuracy of the cover type map resulted in 77.1% producer accuracy and 72.5% user accuracy. Accuracies by cover type ranged from 0% for unknown to 100% for water (Table 1).

One hundred and forty-four owl territories were located in eight forested cover types (Table 1). These eight cover types were subdivisions of the three main forest types found within the mountain range. Eighty-eight percent of the owl territories were located in only four forested cover types, whereas random sites were located in all cover types. At lower elevations, Canyon Live Oak *Quercus chrysolepis*/ Big-cone Fir *Pseudotsuga macrocarpa* was the dominant cover type and contained 39% of the owl sites. Areas at mid-elevations were primarily mixed conifer/hardwood, which included Canyon Live Oak and Big-cone Fir, as well as Sugar Pine *Pinus lambertiana*, White Fir *Abies concolor*, Coulter Pine *Pinus coulteri*, Incense Cedar *Calocedrus decurrens* and Black Oak *Quercus kelloggii*. Twenty-eight percent of the owl sites were found in this forest type. Mixed conifer was the dominant forest at higher elevations and was composed of White Fir, Jeffery Pine *Pinus jeffrey* and Incense Cedar. This forest type contained 33% of the owl sites. Mixed conifer stands occasionally merged into Pinyon Pine *Pinus monophylla*/Juniper *Juniperus sp*. forests (Vasek and Thorne 1988) on transmontane slopes and Lodgepole Pine *Pinus contorta*/Limber Pine *Pinus flexilis* forests (Thorne 1988) at higher elevations. In contrast to owl sites, brush/chaparral/rock and the chaparral cover types were most common at random sample points (Table 1).

The original 17 cover types were consolidated into four cover classes based on the structure of the vegetation and its presumed value to Spotted Owls, namely: nonforest, chaparral, open forest and closed canopied forest (Table 2). This was done to eliminate the effect of elevation, to simplify statistical analyses and to focus on the importance of forested vegetation.

Table 1. Ground-cover types at Spotted Owl sites and random sample points estimated from satellite imagery in the San Bernardino Mountains, California.

Vegetation Type	Study Area Km^2	 %	% Correct[12] classification	Owl sites	Random sites
Unknown	109.78	5.8	0	0	8
Water	19.29	1.0	100	0	7
Rock/Exposed Soils	210.20	11.1	94	0	13
Brush/Chaparral/Rock	445.66	23.6	96	0	40
Grass/Meadow	49.66	2.6	100	0	3
Chaparral	196.01	10.4	89	0	20
Big sage[1]/Rabbit brush[2]	96.39	5.1	75	0	3
Pinyon pine[3]/Juniper[4]	78.43	4.1	55	0	4
Coulter pine[5]/Limber pine[6]	89.83	4.8	11	1	8
Black oak[7]	34.55	1.8	86	6	4
Oak[8]	37.86	2.0	67	19	3
Oak[8]/Big-cone fir[9]	105.12	5.6	80	37	3
Oak[8] Scrub/Chaparral	99.03	5.2	80	0	7
Mixed conifer – Open[10]	20.04	1.1	100	5	1
Mixed conifer – Closed[11]	196.62	10.4	75	42	7
Mixed conifer/Hardwood/Low	23.37	1.2	0	5	3
Mixed conifer/Hardwood/High	78.19	4.1	50	29	10

[1] Big Sage, *Artemesia tridentata*; [2] Rabbit Brush, *Chrysothamnus nauseosus*; [3] Pinyon Pine, *Pinus monophylla*; [4] Juniper, *Juniperus* sp; [5] Lodgepole Pine, *Pinus contorta*; [6] Limber Pine, *Pinus flexilis*; [7] Black Oak, *Quercus kelloggii*; [8] Canyon Live Oak, *Quercus chrysolepis*; [9] Big-cone Fir, *Pseudotsuga macrocarpa*; [10] Open canopy, <65%; [11] Closed canopy >65%; [12] Producer accuracy: the probability that the cover type in the field matched the cover type on the map.

Table 2. Components of four cover classes from 17 natural cover types used in analyses of Spotted Owl habitat in the San Bernardino Mountains, California.

Nonforest	Chaparral	Vegetation Class Open forest	Closed canopied forest
Water	Brush/Rock/	Lodgepole Pine[4]/	Black Oak[9]
	Chaparral	Limber Pine[5]	
Unknown	Chaparral	Pinyon Pine[6]/	Canyon Live
		Juniper[7]	Oak[3]/ Big-cone fir[8]
Grass/	Canyon Live	Mixed Conifer/	Mixed Conifer/
Meadow	Oak[3] Scrub/	Open Canopy	Closed Canopy
	Chaparral		
Big Sage[1]/			Mixed Conifer/
Rabbit Brush[2]		Hardwood/Low	
			Elevation
Rock/Exposed			
Soils		Mixed Conifer/	
		Hardwood/High	
		Elevation	
			Canyon Live Oak[3]

[1] *Artemesia tridentata*; [2] *Chrysothamnus nauseosis*; [3] *Quercus Chrysolepis*; [4] *Pinus contorta*; [5] *Pinus flexilis*; [6] *Pinus monophylla*; [7] *Juniperus* sp; [8] *Psuedotsuga* ; [9] *Quercus kelloggii*

The nonforest cover class (Table 2) included cover types that were not forested or were unlikely to support prey densities sufficient to support Spotted Owls. The chaparral class was retained from the original classification because it was regionally abundant and known to harbor substantial prey populations (Horton & Wright 1944). The open forest cover class included forests that may have been used by Spotted Owls for foraging, but contained a small proportion of the owl territory centres. The closed canopied forest cover class consisted of the six cover types that contained the majority of Spotted Owl territory centres (Table 1).

Statistical analyses

The mean nearest neighbour distance between owl territory centres was 1,497 ± 63 m ($n = 144$, Range = 412 – 5541 m). The equivalent estimate between random sample points was 1,787 ± 79 m ($n = 144$, Range = 146 – 4,887 m). Owl sites were significantly closer to one another than were random sites ($t_{286} = 2.893$, $P < 0.01$). The Clark & Evans Test indicated that owl sites were clumped and not distributed in a random fashion within the study area ($z_{143} = –4.16$, $P < 0.01$).

The frequency of owl sites and random sample points within cover classes was significantly different ($\chi^2_{3} =$ 24.65, $P < 0.01$). The proportion of closed canopied forest at owl sites declined as plot size increased (Table 3), while the chaparral cover class increased. The amount of closed

Table 3. The **mean** proportions (SE) of four cover classes occurring within Spotted Owl and random plots in the San Bernardino Mountains, California.

Plot Size	Nonforest	Open forest	Chaparral	Closed canopied forest
Random Plots				
3 ha (n = 144)	0.24 (0.02)	0.10 (0.02)	0.41 (0.02)	0.24 (0.02)
20 ha (n = 143)	0.23 (0.02)	0.10 (0.01)	0.40 (0.02)	0.26 (0.02)
79 ha (n = 143)	0.24 (0.02)	0.09 (0.01)	0.40 (0.02)	0.27 (0.02)
177 ha (n = 141)	0.22 (0.02)	0.09 (0.01)	0.40 (0.01)	0.28 (0.02)
Owl Plots				
3 ha (n = 144)	0.06 (0.01)	0.04 (0.01)	0.20 (0.02)	0.70 (0.02)
20 ha (n = 143)	0.08 (0.01)	0.05 (0.01)	0.26 (0.02)	0.61 (0.02)
79 ha (n = 143)	0.10 (0.01)	0.06 (0.01)	0.30 (0.01)	0.54 (0.02)
177 ha (n = 141)	0.11 (0.01)	0.06 (0.01)	0.32 (0.01)	0.51 (0.02)

Table 4. Summary of the Simpson's Diversity Indices (SDI) and associated significance tests between plots at Spotted Owl sites and random sample points within the San Bernardino Mountains, California.

Plot Size	Mean Owl SDI	Mean Random SDI	*t*-value	P
3 ha	0.32	0.44	–5.77	<0.01
20 ha	0.43	0.51	–4.43	<0.01
79 ha	0.50	0.54	–2.52	0.01
177 ha	0.53	0.56	–2.45	0.01

canopied forest was significantly different between owl sites and random sample points for all plot sizes (t_{286} – values ranged from 66–183, $P < 0.01$ for all comparisons). At random sample points, all four of the cover classes showed no trend as the sampling radius increased (Table 3). Significant differences were found in the Simpson's Diversity Indices between owl sites and random sample points for all plot sizes (Table 4). Random sample points were typically more diverse than owl sites.

Crude and ecological territory densities were 0.08 territories km^{-2} and 0.29 territories km^{-2}, respectively. Ecological territory densities were 0.39, 0.29, and 0.16 km^{-2} for Canyon Live Oak/Big-cone Fir, mixed conifer/hardwood, and mixed conifer forests, respectively.

Owl sites were characterized by more hectares of closed-canopied forest in fewer, larger patches than occurred at random sample points (Table 5). The logistic regression analysis showed significant correct classification rates for all plot sizes (Table 6). The best model for each plot size always included closed canopied forest with a slope significantly different than zero, indicating a clear association between owl sites and this cover class. The sign of the associated

Table 5. **Mean** patch numbers, types and sizes of closed canopied forest and nonforest vegetation within 20 ha plots centered on Spotted Owl sites and random sample points in the San Bernardino Mountains, California.

Variable	Owl Sites (*N* = 95)	Random Sample (*N* = 130)	*t*-value (D*F* = 223)	P
Total number of vegetation patches	16.1	14.6	1.55	0.12
Number of nonforested vegetation Patches	10.6	9.2	6.44	<0.001
Number of patches of closed canopied forest	5.5	9.2	4.89	<0.001
Hectares of nonforested vegetation	5.7	12.6	12.00	<0.001
Hectares of closed canopied forest	6.5	2.1	5.66	<0.001
Mean patch size of nonforested vegetation (ha)	1.2	6.6	7.00	<0.001
Mean patch size of closed canopied forest (ha)	6.5	2.1	5.66	<0.001
Maximum patch size of nonforested vegetation (ha)	3.7	11.4	12.00	<0.001
Maximum patch size of closed canopied forest (ha)	12.9	5.6	12.00	<0.001

Table 6. Summary of the logistic regression analyses of Spotted Owl sites and random sample points in the San Bernardino Mountains, California.

Plot Size	Variables in Best Model	Variables with significant slopes	Sign of Beta	Percent Correct	P[1]
3 ha	CCF[2] + NF[3]	CCF	+	78.1	<0.01
20 ha	CCF + Chap[4]	CCF	+	75.9	<0.01
79 ha	CCF + NF	CCF	+	72.7	<0.01
177 ha	CCF + NF	CCF + NF	+,-	70.9	<0.01

[1] Significance of percent correct classification rate; [2] Area (ha) of closed canopied forest cover class; [3] Area (ha) of nonforest cover class; [4] Area (ha) of chaparral cover class.

parameter estimate was always positive (Table 6). This indicated that as the amount of closed canopied forest cover class in a sample increased, the probability that it was an owl site increased.

DISCUSSION

Spotted Owls in our study area were distributed through nearly 2000 m of elevation and three forest types. The vegetation of the study area was very heterogeneous and often included several forms of grassland, shrubland, woodland and forest within close proximity. Extensive areas of forest were rare. This is typical of southern California, which prompted Noon & McKelvey (1992) to report that Spotted Owl distribution in this region has an insular structure at both local and regional scales.

The mean nearest neighbour distance for owl territories in the San Bernardino Mountains (1,496 m) was very similar to that reported by Hunter *et al.* (1995) for northwestern California. However, both were less than nearest neighbour distances reported by Moen & Gutiérrez (2,414 m; 1997) from the Sierra Nevada, California or Peery *et al.* (2,120 m; 1999) from New Mexico. These differences may result from variations in carrying capacities, population dynamics or survey effort among study areas.

All major ridges in the San Bernardino Mountains were oriented east–west and most of the forest and most of the owl territories (~80%) were located on north-facing slopes. Most south-facing slopes, up through 2600 m elevation (maximum known elevation for a Spotted Owl territory centre) were unforested.

Most landscape studies of Spotted Owls found the birds to be concentrated in mature and old forest (Ripple *et al.* 1991, 1997; Lehmkuhl & Raphael 1993; Hunter *et al.* 1995; Moen & Gutiérrez 1997; Peery *et al.* 1999) containing larger, less fragmented patches (Lehmkuhl & Raphael 1993; Hunter *et al.* 1995; Moen & Gutiérrez 1997; Ripple *et al.* 1997). Our results were consistent with these findings.

Owl numbers have fluctuated substantially during the twelve years of this study. Still, our adjusted crude density estimate of 0.15 owls km^{-2} was lower than equivalent estimates from other California Spotted Owl studies (0.67 owls km^{-2} for the central Sierra Nevada, 1.14 owls km^{-2} for the southern Sierra Nevada, 1.21 owls km^{-2} for the San Jacinto Mountains, Noon *et al.* 1992). These figures compare with 0.09 owls km^{-2} in Chihuahua, Mexico (Young *et al.* 1998), ~0.10 owls km^{-2} in Arizona and ~0.20 owls km^{-2} in New Mexico (Seamans *et al.*1999). Low densities of owls may reflect the fragmented nature of forested vegetation in the southern portion of this species' range. Our ecological density (0.58 owls km^{-2}) was comparable to Franklin *et al's.* (1990) estimate from a northern California Spotted Owl population.

In the San Bernardino Mountains, the highest ecological density of owls was found in the lower elevation Canyon Live Oak/Big-cone Fir forests. These forests apparently provided better conditions for roosting, nesting and foraging than forests at higher elevations (Barrows & Barrows 1978; Verner *et al.* 1992b).

Patches of nonforested vegetation do not preclude owls from nesting in adjacent forests in southern California. Additionally, some heterogeneity in cover type may be beneficial to Spotted Owls (see Franklin *et al.* 2000). However, forest fragmentation can lead to the loss of biotic diversity (Harris 1984), predation on dispersing owls (Forsman *et al.* 1984), loss of adequate cover (Forsman *et al.* 1984; Gutiérrez & Carey 1985; Verner *et al.* 1992b), and increased home range sizes (Carey *et al.* 1992). Thus, once a site becomes too fragmented it may not provide the essential components needed for the Spotted Owls to survive and reproduce (Johnson 1992).

Our results clearly indicated that Spotted Owl territories were not randomly distributed across the landscape. They consistently contained more forested vegetation which occurred in fewer, larger patches than found at random sample points. In addition, our models consistently distinguished between owl sites and random sample points. Despite a unique physiographic setting and the fragmented nature of their populations, Spotted Owls in southern California showed numerous similarities in landscape habitat selection in contiguous populations of Spotted Owls observed in other parts of their range.

ACKNOWLEDGMENTS

We thank D.Call, D.Smith, P.Ward, A.Franklin, C.Moen, D.Lutz, S.Rinkevich, M.Neel, J.Stephenson, S.Loe, M.Hamilton, M.Nicholson, R.Lockwood, J.Rechel and the numerous field assistants on this project. L.Fox, D.Kitchen and C.Zabel read earlier drafts of the paper. Funding was provided by: California Fish & Game (Grants FG0271, FG0510); Humboldt State University Foundation; Southern California Edison; U.S. Forest Service, Big Bear Ranger District; Pacific Southwest Forest and Range Experiment Station; and the University of Minnesota Agricultural Experiment Station.

REFERENCES

Barrows, C.W. & Barrows, K. 1978. Roost characteristics and behavioral thermoregulation in the Spotted Owl. *Western Birds* **9**: 1–8.

Burnham, K.P. & Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. In McCullough, D.R. & R.H. Barret (eds.) *Wildlife 2001*: *populations*: 16–30. New York: Elsevier Applied Science.

Carey, A.B., Horton, S.P. & Biswell, B.L. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecol. Monogr*. **62**: 223–250.

Congalton, R. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sens. of the Environ*. **37**: 35–46.

Dillworth, J.R. 1975. *Log scaling and timber cruising*. Corvallis: Oregon State University Bookstore, Inc.

ESRI. 1993. *ARC/INFO Users Manuals*. Redlands, CA: Environmental Systems Research Institute.

ESRI. 1996. *ArcView Users Manuals*. Redlands, CA: Environmental Systems Research Institute.

Forsman, E.D., Meslow, E.C. & Wight, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr*. **87**.

Franklin, A.B., Ward, J.P., Gutiérrez, R.J. & Gould, G.I. 1990. Density of Northern Spotted Owls in northwest California. *J. Wildl. Manage*. **54**: 1–10.

Franklin, A.B., Anderson, D.R., Forsman, E.D., Burnham, K.P. & Wagner, F.W. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Stud. Avian Biol*. **17**: 12–20.

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J. & Burnham, K. P. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* **70**: 539–590.

Fujioka, F.M., Roads, J.O. & Chen, S.-C. 1998. Climatology. In Miller, P. R. & McBride, J. R. (eds.) *Oxidant air pollution impacts in the montane forests of southern California*: *a case study of the San Bernardino Mountains*: 28–43. New York: Springer.

Gutiérrez, R.J. & Carey, A.B. (eds.). 1985. *Ecology and management of the Spotted Owl in the Pacific Northwest*. Gen. Tech. Rep. PNW–185. Portland, OR: USDA-Forest Service.

Gutiérrez, R.J., Verner, J., McKelvey, K.S., Noon, B.R., Steger, G.N., Call, D.R., LaHaye, W.S., Bingham, B.B. & Senser, J.S. 1992. Habitat relations of the California Spotted Owl. In Verner, J., McKelvey, K.S., Noon, B.R., Gutiérrez, R.J., Gould, G.I. & Beck, T.W. (technical coordinators.) *The California Spotted Owl: a technical assessment of its current status*: 79–98. Gen. Tech. Rep. PSW-GTR–133. Albany CA: USDA-Forest Service.

Gutiérrez, R.J., Franklin, A.B. & LaHaye, W.S. 1995. Spotted Owl (*Strix occidentalis*). In Poole, A. & Gill, F. (eds.) *The Birds of North America*, No. **179**. Washington, DC: The Academy of Natural Sciences, Philadelphia, and The American Ornithologists Union.

Hanes, T.L. 1988. Chaparral. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 417–470. Sacramento, CA: California Native Plant Society.

Harris, L.D. 1984. *The Fragmented Forest*. Chicago: University of Chicago Press.

Horton, J.S. & Wright, J.T. 1944. The woodrat as an ecological factor in southern California watersheds. *Ecology* **25**: 341–351.

Hunter, J.E., Gutierrez, R.J. & Franklin, A.B. 1995. Habitat configuration around Spotted Owl sites in northwestern California. *Condor* **97**: 684–693.

Johnson, D.H. 1992. *Spotted Owls, Great Horned owls, and forest fragmentation in the central Oregon Cascades*. Corvallis: Master's thesis, Oregon State University.

Krebs, C.J. 1989. *Ecological Methodology*. New York: Harper and Row.

LaHaye, W.S., Gutiérrez, R.J. & Call, D.R. 1992. Demography of an insular population of Spotted Owls (*Strix occidentalis occidentalis*). In McCullough, D. R. and R. H. Barret (eds.) *Wildlife 2001: populations*: 803–814. New York: Elsevier Applied Science.

LaHaye, W.S., Gutiérrez, R.J. & Akçakaya, H.R. 1994. Spotted Owl metapopulation dynamics in Southern California. *J. Anim. Ecol.* **63**: 775–785.

LaHaye, W.S., Gutierrez, R.J. & Call, D.R. 1997. Nest-site selection and reproductive success of California Spotted Owls. *Wilson Bull.* **109**: 42–51.

Lehmkuhl, J.F. & Raphael, M.G. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. *J. Wildl. Manage.* **57**: 302–315.

Lillesand, T.M. & Kiefer, R.W. 1987. *Remote sensing and image interpretation*, 2nd edn. New York: John Wiley and Sons, Inc.

McGarigal, K. & Marks, B.J. 1995. *FRAGSTATS: spatial pattern analysis program for quantifying landscape structure*. Gen. Tech. Rep. PNW-GTR–351. Portland, OR: USDA-Forest Service.

Minnich, R.A. 1988. *The biogeography of fire in the San Bernardino Mountains of California*. Los Angeles: University of California Press.

Minnich, R.A. 1998. Vegetation, fire regimes, and forest dynamics. In Miller, P.R. & McBride, J.R. (eds.) *Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains*: 44–80. New York: Springer.

Moen, C.A. & Gutiérrez, R.J. 1997. California Spotted Owl habitat selection in the central Sierra Nevada. *J. Wildl. Manage.* **61**: 1281–1287.

Mooney, H.A. 1988. Southern coastal scrub. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 471–490. Sacramento, CA: California Native Plant Society.

Noon, B.R. & McKelvey, K.S. 1992. Stability properties of the Spotted Owl metapopulation in southern California. In Verner, J., McKelvey, K.S., Noon, B.R., Gutiérrez, R.J., Gould, G.I., & Beck, T.W. (technical coordinators) *The California Spotted Owl: a technical assessment of its current status*: 187–206. Gen. Tech. Rep. PSW-GTR–133. Albany CA: USDA-Forest Service.

Noon, B.R., McKelvey, K.S., Lutz, D.W., LaHaye, W.S., Gutiérrez, R.J. & Moen, C.A. 1992. Estimates of demographic parameters and rates of population change. In Verner, J., McKelvey, K.S., Noon, B.R., Gutiérrez, R.J., Gould, G.I. & Beck, T.W. (technical coordinators) *The California Spotted Owl: a technical assessment of its current status*: 175–186. Gen. Tech. Rep. PSW-GTR–133. Albany CA: USDA-Forest Service.

Peery, M.Z., Gutiérrez, R.J. & Seamans, M.E. 1999. Habitat composition and configuration around Mexican Spotted Owl nest and roost sites in the Tularosa Mountains, New Mexico. *J. Wildl. Manage.* **63**: 36–43.

Richards, J.A. 1993. *Remote sensing digital image analysis: an introduction*, 2nd edn. Berlin: Springer-Verlag.

Ripple, W.J., Johnson, D.H., Hershey, K.T. & Meslow, E.C. 1991. Old-growth and mature forests near Spotted Owl nests in western Oregon. *J. Wildl. Manage.* **55**: 316–318.

Ripple, W.J., Lattin, P.D., Hershey, K.T., Wagner, F.F. & Meslow, E.C. 1997. Landscape composition and pattern around Northern Spotted Owl nest sites in southwestern Oregon. *J. Wildl. Manage.* **61**: 151–158.

Sawyer, J.O., Thornburgh, D.A., & Griffin, J.R. 1988. Mixed evergreen forest. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 359–382. Sacramento, CA: California Native Plant Society.

Seamans, M.E. & Gutiérrez, R.J. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. *Condor* **97**: 944–952.

Seamans, M.E., Gutierrez, R.J., May, C.A. & Peery, M.Z. 1999. Demography of two Mexican Spotted Owl populations. *Conserv. Biol.* **13**: 744–754.

Simpson, E.H. 1949. Measurement of diversity. *Nature* **163**: 688.

Tanner, J.T. 1978. *Guide to the study of animal populations*. Knoxville: University of Tennessee Press.

Terra Mar. 1990. *MicroImage Software Users Manuals*. Mountain View, CA: Terra Mar Resource Information Services, Inc.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R. & Verner, J. 1990. *A conservation strategy for the Northern Spotted Owl*. Washington, DC: Government Printing Office.

Thorne, R.F. 1988. Montane and subalpine forests of the transverse peninsular ranges. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 537–557. Sacramento, CA: California Native Plant Society.

Titus, K., Mosher, J.A. & Williams, B.K. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Amer. Midl. Nat.* **111**: 1–7.

USDI. 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Northern Spotted Owl. *Fed. Reg.* **55**: 26114–26194.

USDI. 1992. *Recovery plan for the Northern Spotted Owl*: *draft*. Portland, OR: U. S. Department of Interior.

USDI. 1993. Endangered and threatened wildlife and plants; final rule to list the Mexican Spotted Owl as a threatened species. *Fed. Reg.* **58**: 14248–14271.

USDI. 1995. *Recovery Plan for the Mexican Spotted Owl*: *draft*. Albuquerque, NM: U. S. Fish & Wildlife Service.

Vasek, F.C. & Barbour, M.G. 1988. Mojave desert scrub vegetation. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 835–868. Sacramento, CA: California Native Plant Society.

Vasek, F. C. & Thorne, R. F. 1988. Transmontane coniferous vegetation. In Barbour, M. G. & Major, J. (eds.) *Terrestrial vegetation of California*, 2nd edn.: 797–834. Sacramento, CA: California Native Plant Society.

Verner, J., McKelvey, K.S., Noon, B.R., Gutiérrez, R.J., Gould, G.I. & Beck, T.W. (technical coordinators). 1992a. *The California Spotted Owl*: *a technical assessment of its current status*. Gen. Tech. Rep. PSW-GTR–133. Albany CA: USDA-Forest Service.

Verner, J., Gutiérrez, R.J. & Gould, G.I. 1992b. The California Spotted Owl: general biology and ecological relations. In Verner, J., McKelvey, K.S., Noon, B.R., Gutiérrez, R.J., Gould, G.I., & Beck, T.W. (technical coordinators) *The California Spotted Owl*: *a technical assessment of its current status*: 55–77. Gen. Tech. Rep. PSW-GTR–133. Albany CA: USDA-Forest Service.

Young, K.E., Valdez, R., Zwank, P.J. & Gould, W.R. 1998. Density and roost site characteristics of Spotted Owls in the Sierra Madre Occidental, Chihuahua, Mexico. *Condor* **100**: 732–736.

Zimmerman, G.S., LaHaye, W.S. & Gutiérrez, R.J. 2001. Breeding season home ranges of Spotted Owls (*Strix occidentalis occidentalis*) in the San Bernardino Mountains, California. *Western Birds*: **32**: 83–87.

15

EFFECTS OF HABITAT FRAGMENTATION AND SLOPE ON THE DISTRIBUTION OF THREE OWL SPECIES IN THE MANITOBA ESCARPMENT, CANADA – A PRELIMINARY ANALYSIS

HEATHER L. HINAM[1] *& JAMES R. DUNCAN*[2]

1. Department of Zoology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2 Canada
Currently, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada

2. Biodiversity Conservation Section, Wildlife Branch, Manitoba Conservation, Box 24, 200 Saulteaux Crescent, Winnipeg, Manitoba, R3J 3W3 Canada

The resident owl species in the forested western upland region of Manitoba, known as the Manitoba Escarpment, respond differently to forest fragmentation and slope. The preliminary results of a habitat use versus availability analysis are presented in this paper. Locations for Great Horned Owls *Bubo virginianus*, Great Gray Owls *Strix nebulosa* and Barred Owls *S. varia* were obtained through nocturnal surveys run from 15 March 1999 to 6 June 1999 and from incidental records obtained during the breeding season. Species' locations were overlayed on digital forest resource inventory maps and examined for stand type, age, degree of fragmentation and slope characteristics which were then compared with similar data from random sites. Barred and Great Gray Owl plots contained fewer clearcut/burn areas and associated young open forest than did random plots. In contrast, Great Horned Owl plots did not differ from random in this respect, but they did contain less treed muskeg. Barred Owls were associated with forests with high crown closure values. Owl and random plots did not differ significantly with respect to edge/area, plot elevation or slope aspect. However, Great Gray Owl plots were found significantly more often than expected on northwest-facing slopes, Barred Owl plots were found significantly less often on southeast-facing slopes and Great Horned Owl plots did not differ from random in regards to slope direction.

INTRODUCTION

Despite living sympatrically throughout much of their ranges, three owl species present in the forests of Manitoba, namely the Great Horned Owl *Bubo virginianus*, Great Gray Owl *Strix* *nebulosa* and Barred Owl *S. varia*, respond differently to variations in their environment (Johnsgard 1988). Forest fragmentation, through forestry, agriculture and development, is becoming an increasingly prominent factor influencing the distribution of owl species (Johnson 1993, Mazur *et al.* 1997, Niemi & Hanowski 1997, Stepniski 1997, Takats 1997). Decreases in suitable habitat due to timber harvest and agricultural clearing may be the main factor contributing to observed declines in some raptor populations (Kirk & Hyslop 1998). Forest raptors, because of their position at the top of the food chain and their relatively large home ranges, may be highly sensitive to forest fragmentation (Niemi & Hannowski 1997).

The Manitoba Escarpment comprises the western section of this Canadian province, rising an average of 350m above the surrounding Manitoba lowlands. In this area, the effects of habitat fragmentation from both natural and human causes may be further compounded by variation in the degree and direction of slope. Forest fragmentation in the Manitoba Escarpment is set to proceed at an increasing rate. Tolko industries has proposed a 13-year mangement plan for a 12 million hectare forest management license agreement (FMLA) encompassing Grass River Provincial Park, Porcupine Provincial Forest, Duck Mountain Provincial Park and bordering on Riding Mountain National Park (Jensen & Mausberg 1998). This includes the harvest of an average 3 million cubic meters of trees per year.

How owls in western Manitoba respond spatially to forest fragmentation is not known. The Great Gray Owl and the Barred Owl are considered uncommon or rare in Manitoba (Nero 1980, Duncan 1996) and most other species of Manitoba's forest owls are considered of conservation concern (Duncan 1996).

Our aim in this paper is to assess the effects of habitat fragmentation and slope on the spatial distribution of owls in the Manitoba Escarpment. Our specific objectives are to describe and quantify: (1) Stand characteristics and forest fragmentation at sites occupied by owls compared with random sites in the study area; (2) The relationship between owl occurrences and slope features.

STUDY AREA AND METHODS

Field research for this study was conducted from 15 March to 6 June 1999.The 20,000 km^2 study area encompasses Riding Mountain National Park (RMNP, 2,976 km^2), Duck Mountain Provincial Park and Forest (DMPP, 3,770 km^2) and Porcupine Provincial Forest (PPF, 2,090 km^2) (Fig. 1). The dominant tree species in the area include Trembling Aspen *Populus tremuloides*, Balsam Poplar *P. balsamifera*, White Birch *Betula papyrifera*, Balsam Fir *Abies balsamea*, White Spruce *Picea glauca*, Jack Pine *Pinus banksiana*, Black Spruce *Picea mariana* and Tamarack *Larix laricina* (Baily 1968, McCready *et al.* 1980, Davy 1995). Limited timber extraction has occurred in RMNP since its designation as a protected area in 1930. Timber harvest and agricultural activities have greatly affected the forest vegetation of the provincial parks and forests and the surrounding land.

Owl locations were determined by nocturnal surveys, using playbacks of seven owl species known to occur in the area (Duncan & Duncan 1997). Surveys were conducted along 21 routes, consisting of roads and trails, each with 10–40 sampling stations. To further increase the area surveyed, volunteers with the Manitoba Nocturnal Owl Survey surveyed five previously designated routes (Duncan & Duncan 1997). Locations were also recorded for owls that were detected during the breeding season through incidental encounters and through the Duck Mountain forest bird survey program (R. P. Berger unpublished).

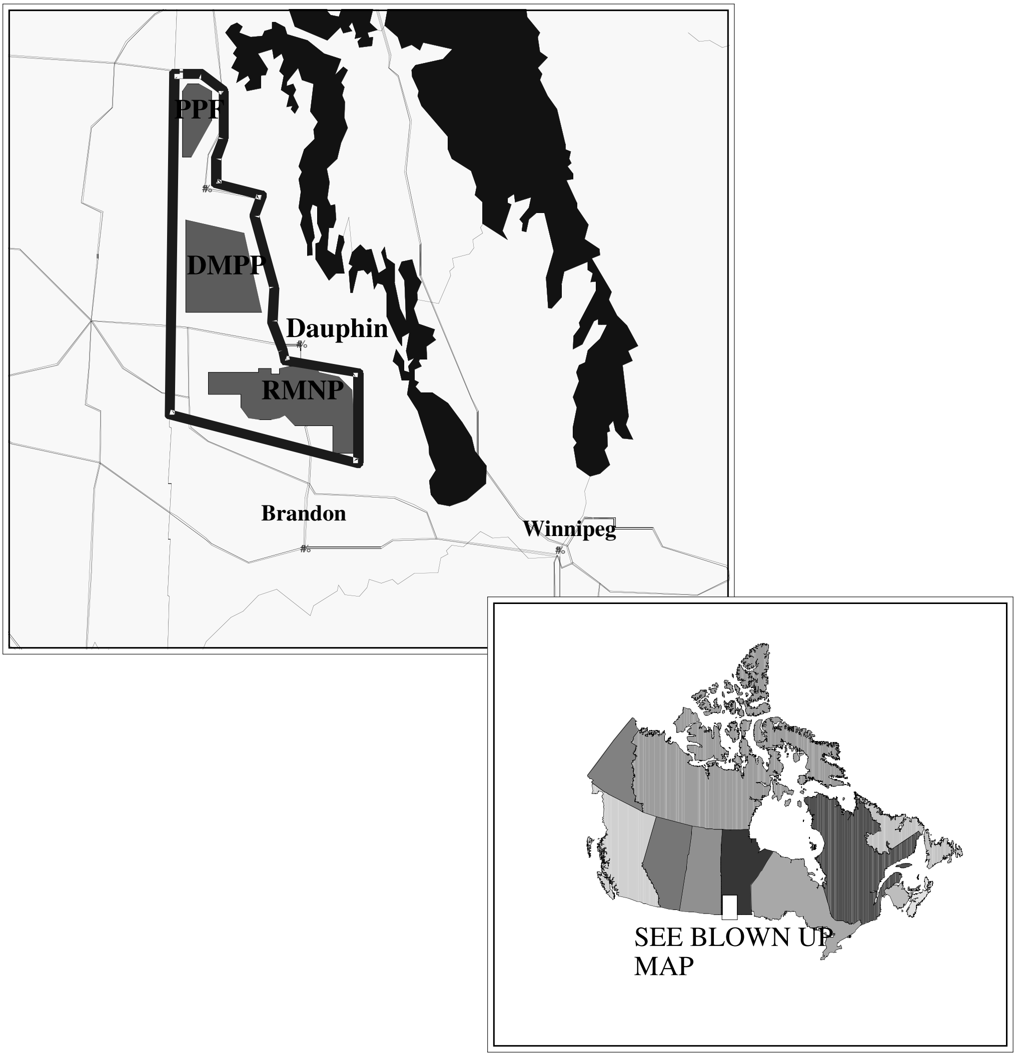


Fig. 1. Approximate delineation of study site in the Manitoba Escarpment, Manitoba, Canada (highlighted). PPF = Porcupine Provincial Forest, DMPP = Duck Mountain Provincial Park, RMNP = Riding Mountain National Park.

We surveyed 17 routes twice at 2–3 week intervals, using broadcasts from different species each time, in order to stimulate responses from the species most vocal at different times of the year. Four other routes were surveyed only once. Listening stops were spaced at 0.8-km intervals. The location of each stop was recorded either as Universal Transverse Mercator (UTM) coordinates, using a Global Positioning System (GPS) or plotted by hand in relation to landmarks on a 1:50,000 topographic map.

Surveys began at one-half hour after sunset and continued until the route was finished, or until one half hour before sunrise, on nights with negligible precipitation and temperatures greater than –20°C (Mosher *et al.* 1990, Johnson 1993, Clark & Anderson 1997, Takats 1997).

Each survey stop began with three minutes of silent listening in order to detect calling owls (Duncan & Duncan 1997, Takats 1997). This period was then followed by 20-second broadcasts of the calls of four of the target species, separated by 1-minute listening periods, followed by a final 3-minute listening period. Broadcasts from 15 March to 23 April 1999 were played in the order of Boreal Owl *Aegolius funereus*, Great Gray Owl, Barred Owl and Great Horned Owl, species found to be most vocal during this period (Johnsgard 1988, Bull & Duncan 1993). The broadcast order from 24 April to 6 June was Northern Saw-whet Owl *Aegolius acadicus*, Eastern Screech-owl *Otus asio*, Long-eared Owl *Asio otus* and Great Horned Owl to target the most vocal species of this period (Johnsgard 1988). Although it is unclear whether playbacks of larger owls inhibit responses in smaller owls (Fuller & Mosher 1981, McGarigal & Fraser 1985, Clark & Anderson 1995), playbacks were broadcast in order from largest to smallest. During surveys both Boreal and Northern Saw-whet Owls frequently called through the Great Horned Owl playbacks and could often be heard at the next survey stop. At stops where owls responded, the time of response, species responding and the apparent distance and direction (estimated to the nearest degree) of the response was recorded. Survey stops were plotted on 1:50,000 topographic maps. Measurements from one or more survey stops were used to estimate owl locations.

Locations for each individual species were computerized as a separate point layer and then overlaid on digital Forest Resource Inventory (FRI) maps (Manitoba Department of Conservation) using the geographic information system (GIS) ArcView GIS Ver.3.1. Circular plots centered on each owl location were used to approximate owl home ranges (Mazur *et al.* 1997). Two plot sizes were selected (314 and 500 ha), based on species' published home range estimates from studies conducted in similar habitats (Duncan 1992, Johnson 1993, Mazur *et al.* 1998).

Analysis of habitat characteristics

The following habitat variables were recorded for each set of species plots and an associated set of random plots: cover type, stand age, crown closure, degree of fragmentation (edge/area ratio), slope direction, aspect and elevation (Bouchart 1991, Johnson 1993, Takats 1997).

Cover type was divided into 13 categories: conifer forest, softwood-dominated mixedwood, hardwood-dominated mixedwood, hardwood forest, treed muskeg, marsh/muskeg, willow/alder, meadow, agricultural land, clearcut/burn, water, roads and other. Cutting class is a measure of the state of growth, size and maturity of the forest stand in relation to its harvest rotation age (Appendix 1). Crown closure is a measure of the density of the forest canopy (Appendix 2, Natural Resources Manitoba 1996).

The degree of fragmentation was measured as the ratio of edge to forested area within each circular plot (Johnson 1993). In this study, edge was defined as the transition between forest and non-forest habitats (cutting classes 0 and 1, treed muskeg and vegetation classes not containing forest cover). Elevation (meters above sea-level), slope aspect and direction were interpolated from contour lines on 1:50,000 topographic maps.

Statistical analyses

One hundred random point locations were chosen by generating UTM coordinates within a 2 km buffer of all survey routes (Mazur *et al.* 1997, Stepnisky 1997). Fifty were used for comparison with 314 ha plots and 50 were compared with 500 ha plots. A chi-square goodness-of-fit test was applied to determine if owls were associated with habitat disproportionately to its availability as determined by the random plots (Neu *et al.* 1974, Byers *et al.* 1984, Bouchart 1991). Bonferroni confidence intervals were then calculated for each variable to infer habitat preferences (Neu *et al.* 1974, Byers *et al.* 1984, Bouchart 1991).

Differences in edge/area ratios, slope aspect and elevation between owl plots and random plots were assessed using a Mann–Whitney U-statistic because the data were not normally distributed. Slope direction was divided into cardinal and sub-cardinal points and differences (owl *v.*random) were analysed using a chi-square and Bonferroni confidence intervals.

RESULTS

A total of 235 individual owls of eight species were recorded at 887 survey stops. An additional 22 individuals were detected within the study area through incidental encounters, giving a total of 257 individual owls detected (Table 1). Habitat and slope data were analyzed for Great Horned Owl (500 ha) plots ($n = 41$) as well as Great Gray Owl ($n = 19$) and Barred Owl ($n = 48$) (314 ha) plots.

Habitat Data

Cover type. The proportional composition of the 12 cover types within owl plots differed significantly from that of the corresponding random plots for all three species ($\chi^2_{\mathrm{GGOW}} = 28.26$, $P = 0.005$, $\chi^2_{\mathrm{BAOW}} = 38.94$, $P < 0.001$, $\chi^2_{\mathrm{GHOW}} = 22.03$, $P = 0.037$, Figs. 2 & 3). In all three species, mixedwood forest made up the greatest proportion of the plot area, with hardwood-dominated mixedwood being more abundant, but this did not differ significantly from random plots (Figs. 2 & 3). Based on Bonferroni confidence intervals, both Great Gray and Barred Owl plots contained significantly less clearcut/burn area than random plots (Fig. 2). In both Great Gray and Barred Owl plots, coniferous forest made up a relatively small proportion (Fig. 2).

Great Horned Owl plots contained significantly less treed muskeg than random 500 ha plots (Fig. 3). Unlike the two *Strix* species, there was no significant difference in the proportion of clearcut/burn areas between owl and random plots (Fig. 3).

Cutting class. Only Great Gray and Barred Owl plots differed significantly from their associated random plots in relation to the proportional composition of cutting classes ($\chi^2_{\mathrm{GHOW}} = 37.4$, $P = 0.000$, $\chi^2_{\mathrm{BAOW}} = 25.92$, $P = 0.000$, $\chi^2_{\mathrm{GHOW}} = 3.83$, $P = 0.574$, Figs. 4 & 5). Mature forests

Table 1. Number of individuals of each owl species detected through surveys in Riding Mountain National Park (RMNP), Duck Mountain Provincial Park and Forest (DMPP) and Porcupine Provincial Forest (PPF), as well as through incidental encounters in each area within the Manitoba Escarpment, Manitoba, Canada (15 March–6 June, 1999).

	Great Horned Owl *Bubo virginianus*	Great Gray Owl *Strix nebulosa*	Barred Owl *Strix varia*	Long-eared Owl *Asio otus*	Short-eared Owl *Asio flammeus*	Boreal Owl *Aegolius funereus*	Northern Saw-whet Owl *Aegolius acadicus*	Eastern Screech-owl *Otus asio*	Northern Hawk Owl *Surnia ulula*	Total
RMNP	37	11	24	2	0	0	18	0	1	93
Incidental	2	2	3	0	0	0	1	0	0	8
DMPP/ PPF	12	12	32	2	0	34	50	0	0	142
Incidental	7	0	1	1	1	0	4	0	0	14
Total	**58**	**25**	**60**	**5**	**1**	**34**	**73**	**0**	**1**	**257**

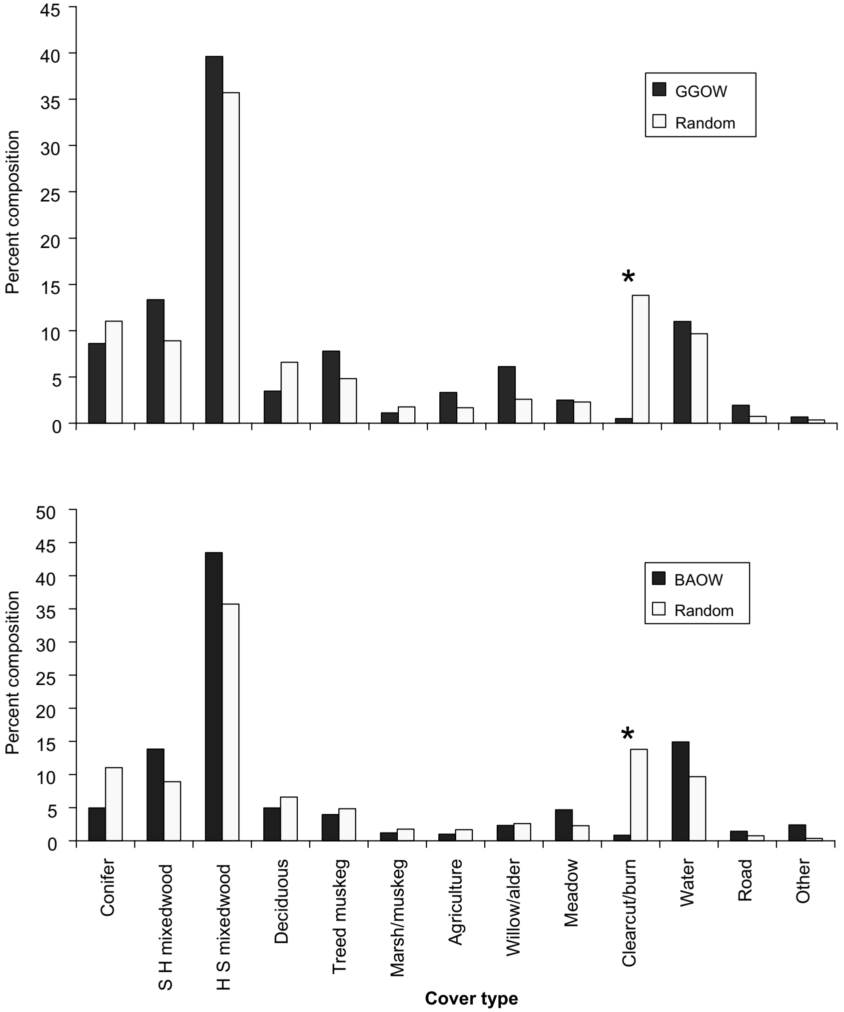


Fig. 2. Comparison of the percent composition of cover types within Great Gray Owl (*n* = 19), Barred Owl (*n* = 48) and random (*n* = 50) 314 ha plots. * indicates significant difference at $\alpha = 0.05$ using Bonferroni confidence intervals.

(cutting class 4) made up the greatest proportion of all three species' plots (Figs. 4 & 5). Both Great Gray and Barred Owl plots contained significantly less of cutting class 0 (non-restocked forested land) than the random plots (Fig. 4). The proportional composition of cutting classes in Great Horned Owl plots almost perfectly matched that of its associated random plots ($\chi^2_{\mathrm{GHOW}} = 3.83$, $P = 0.57$).

Crown Closure. Great Gray and Barred Owl plots differed significantly from their associated random plots with respect to the proportional composition of crown closure classes ($\chi^2_{\mathrm{GGOW}} = 21.96$, $P < 0.001$, $\chi^2_{\mathrm{BAOW}} = 25.61$, $P < 0.001$, Fig. 5). Crown closure class 4 made up the largest proportion of all three species' plots. Great Horned Owl plots differed significantly from random with respect to the frequency distribution of crown closure classes ($\chi^2_{\mathrm{GHOW}} = 13.97$, $P = 0.003$), but based on Bonferroni confidence intervals, no one class differed significantly from random (Fig. 6).

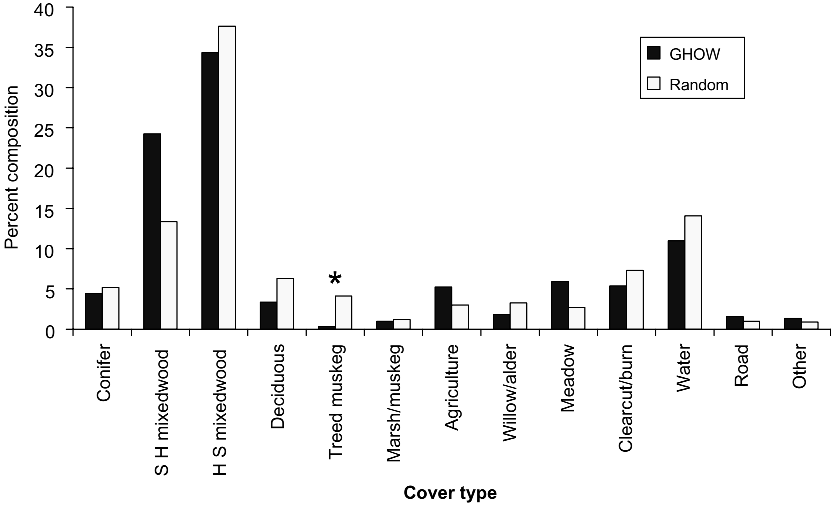


Fig. 3. Comparison of the percent composition of cover types within 500 ha Great Horned Owl ($n = 41$) and random ($n = 50$) 500 ha circular plots. * indicates significant difference at $\alpha = 0.05$ using Bonferroni confidence intervals.

Based on Bonferroni confidence intervals, Great Gray and Barred Owl plots contained significantly less crown closure class 0 than random plots (Fig. 5). Barred Owl plots also contained a significantly higher proportion of crown closure class 4 than the associated random plots (Fig. 5).

Degree of fragmentation

Mean edge to area ratios equalled 80.1 ± 31.0 m/ha for Barred Owl plots, 87.1 ± 44.2 m/ha for Great Gray Owl plots and 87.4 ± 63.3 m/ha for Great Horned Owl plots. Despite relatively small standard deviations, owl plot edge/area ratios did not differ significantly from those of random plots ($U_{GGOW} = 1786$, $P = 0.520$, $U_{BAOW} = 1173$, $P = 0.983$, $U_{GHOW} = 443$, $P = 0.758$).

Elevation and slope characteristics

Great Horned Owl plots were found at a mean elevation of 612.5 ± 81.9 m, while Barred Owl and Great Gray Owl plots were found at 640.4 ± 59.0 m and 647.2 ± 48.3 m respectively. All three species' locations did not differ significantly from their associated random locations in terms of mean elevation ($U_{GHOW} = 1137$, $P = 0.781$; $U_{BAOW} = 1750$ $P = 0.359$; $U_{GGOW} = 453$, $P = 0.864$). Mean slope aspect ranged from 1.23 ± 2.0° for Great Gray Owl locations to 2.18 ± 2.16° and 2.39 ± 3.1° for Barred Owl and Great Horned Owl locations respectively. None of these three sets of owl locations differed significantly from their associated random locations ($U_{GGOW =}$ 457, $P =$ 0.465, $U_{BAOW} = 998$, $P = 0.199$, $U_{GHOW} = 947$, $P = 0.761$).

Great Gray Owl and Barred Owl plots did differ significantly from random plots in terms of the direction of slope (Fig. 7). Great Gray Owl plots were located on northwest facing slopes significantly more often than random and were less frequently found on east, southeast and south facing slopes (Fig. 7). Significantly fewer Barred Owl plots were on southeast facing slopes (Fig. 7). Both species' plots and random plots were rarely found on north facing slopes. The

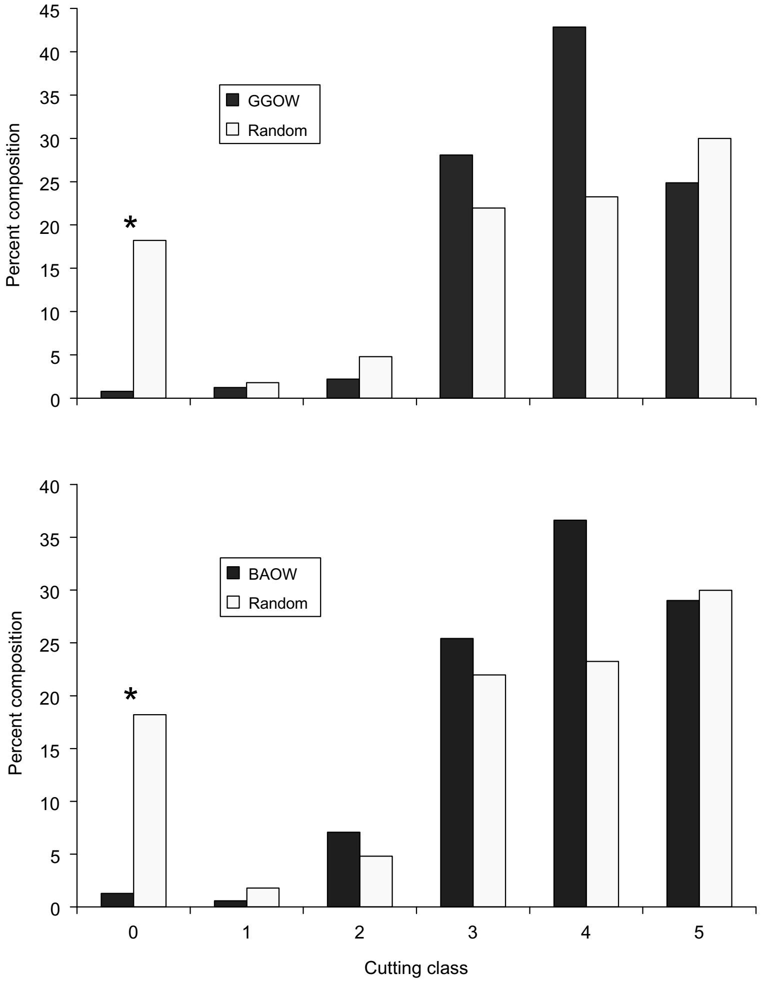


Fig. 4. Comparison of the percent composition of cutting classes within Great Gray Owl (n = 19), Barred Owl (n = 48) and random (n = 50) 314-ha plots. * indicates significant differences from random at α = 0.05 using Bonferroni confidence intervals. For definition of cutting classes, see Appendix 1.

distribution of Great Horned Owl plots among direction categories did not differ significantly from random plots (Fig. 7).

DISCUSSION

Home range composition

The proportional composition of habitat characteristics of all three species' plots differed significantly from random, based on the habitat composition of the overall study area. Both *Strix* species appear to have avoided clearcut/burn areas and associated young forest. Mature and overmature (old-growth) mixedwood forest stands made up the largest proportion of their plots.

The Great Gray Owl's apparent avoidance of young forest, resulting from clearcuts and burns,

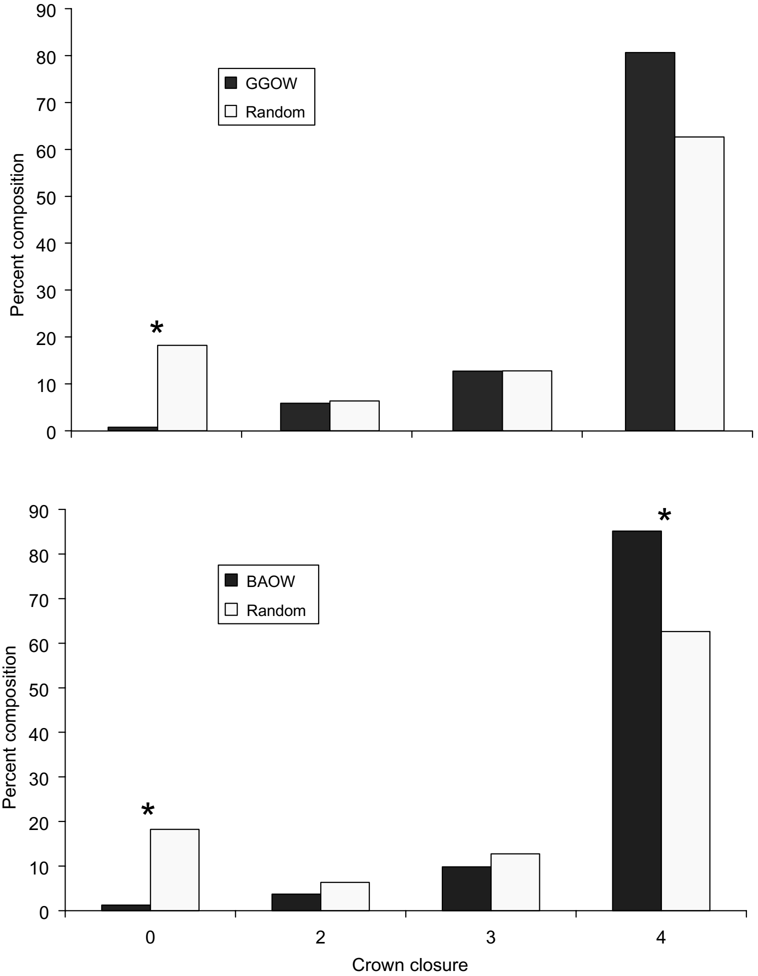


Fig. 5. Comparison of the percent composition of crown closure classes within Great Gray Owl (*n* = 19), Barred Owl (*n* = 48) and random (*n* = 50) 314 ha plots. * indicates significant difference at $\alpha = 0.05$ using Bonferroni confidence intervals. For definition of crown closure classes, see Appendix 2.

differed from what has been found in the southeastern part of the province (Nero 1980, Servos 1986, Bouchart 1991). In that region, summer home ranges contained large proportions of cleared forest (Servos 1986). Servos (1986) suggested that individuals preferred cleared areas for hunting due to large densities of preferred prey. Because owls in our study were located during the breeding season, in early spring, Great Gray Owls may forfeit open hunting areas for the greater security of closed forest, moving to forest edges in the summer. Great Gray Owl plots contained large amounts of hardwood-dominated mixedwood and in this respect more closely matched those found in Alberta than southeastern Manitoba (Stepnisky 1997).

The relatively low occurrence of clearcut/burn areas and the predominance of older mixedwood forests in Barred Owl plots further supports the findings of a number of studies in Canada and northern U.S and validates the Habitat Suitability Index (HSI) model derived for Manitoba

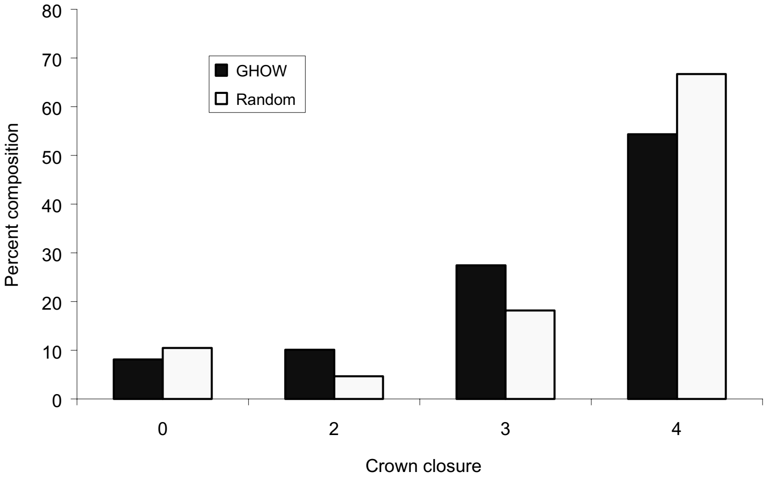


Fig. 6. Percent composition of crown closure classes in Great Horned Owl (*n* = 41) and random 500 ha plots (*n* = 50). Distributions differed significantly (χ^2_{GHOW} = 13.97. *P* = 0.003).

(Bosakowski *et al.* 1987, Duncan & Kearns 1997, Mazur *et al.* 1997, Takats 1997, Mazur *et al.* 1998). Mainly secondary cavity nesters, Barred Owls require large diameter trees that occur mainly in old mixedwood forests (Mazur *et al.* 1997). Older forests are considered more structurally diverse and may contain higher prey densities than younger forests. The relatively open understory of older forests may also allow for easier hunting (McGarigal & Fraser 1984)

Lakes and other water bodies made up a relatively large percentage of Barred Owl plots. Large amounts of water within home ranges have been previously documented for this species (Bosakowski *et al.* 1987, Takats 1997). Forests bordering on water bodies may be protected from fire and thus contain trees large enough to provide cavities suitable for this species (Takats 1997). Barred Owl plots contained significantly greater proportions of the highest crown closure class than did random plots. This relationship was also found in a study in Alberta (Takats 1997). Forests with a high crown density generally have cooler microclimates and selection for these habitats may be based on thermoregulation needs (Mazur *et al.*1998).

Great Horned Owl plots contained significantly lower proportions of treed muskeg than what was available in the area, but showed no differences with respect to clearcut/burn areas and their associated young open forests. This is probably due to the Great Horned Owl's preference to hunt in open areas (Houston *et al.*1998). Mature and overmature forests made up a large percentage of the owl plots. Great Horned Owls have elsewhere been associated with older forests, usually near fields and other open areas (McGarigal & Fraser 1984). However, Johnson (1993) found a decrease in Great Horned Owl encounters with increasing amounts of old forest in the Pacific Northwest.

Degree of fragmentation and slope

No significant differences existed between owl and random plots with respect to degree of fragmentation, elevation and slope aspect. Great Horned Owl locations had a significant tendency to be found near agricultural areas at the base of the escarpment, while the other two species were less frequently encountered outside the parks.

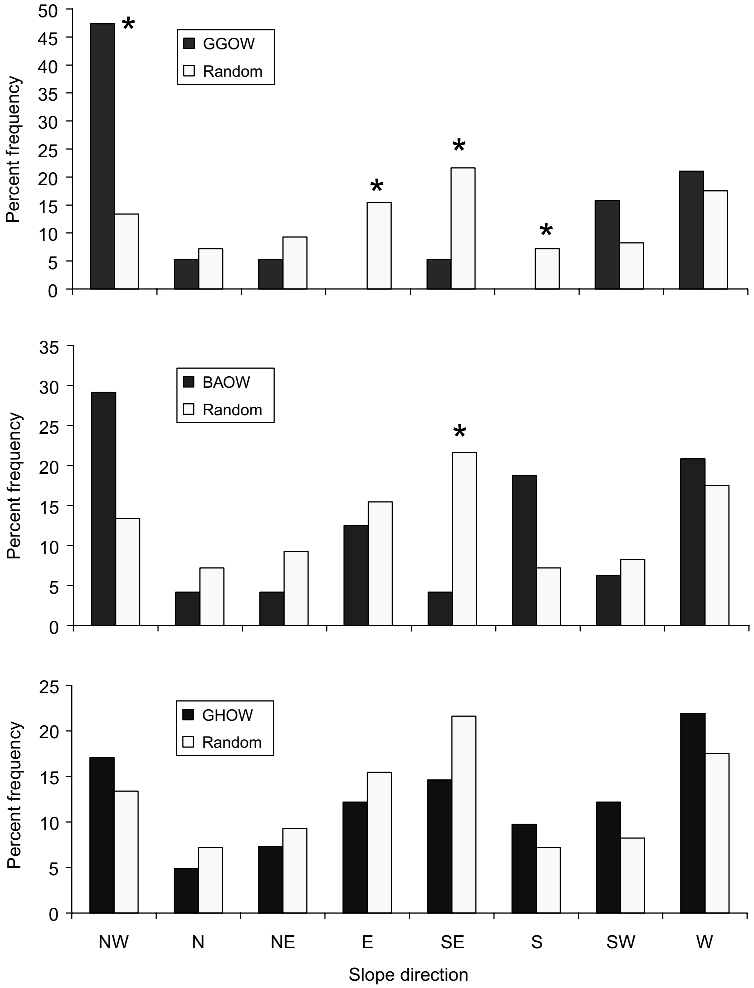


Fig. 7. Comparison of the direction of slope for owl and random plots. Significant differences existed between Great Gray Owl and random and Barred Owl and random plots. * indicates significant difference at $\alpha = 0.05$ using Bonferroni confidence intervals.

Great Gray Owl locations showed the greatest degree of difference from random locations with regards to slope direction, occurring predominantly on northwest facing slopes and less frequently on slopes ranging from east to south. Barred Owls appeared to avoid southeast facing slopes and a relatively large proportion of plots were found on northwest facing slopes. Great Horned Owl plots showed no such preferences. Owls could be choosing certain slope faces based on microclimate conditions. Slopes that do not get direct midday sun may retain greater moisture and thus produce a denser tree cover, and some owls seek out cooler microclimates that facilitate thermoregulation (Bull & Duncan 1993). Slope direction thus appears to influence the distribution of at least Great Gray and Barred Owls.

Limitations and applications of this study

Using circular plots centred on estimated owl locations obtained through auditory surveys is not a precise method of characterizing owl habitat. An owl may be lured off its home range in response to playback calls, or it may be recorded calling from the edge of its home range (Mazur *et al.* 1997). Despite these potential biases, this technique has been proven effective in defining habitat in many studies (Bouchart 1991, Johnson 1993, Mazur *et al.* 1997, Mazur *et al.* 1998).

ACKNOWLEDGMENTS

This study has been conducted with funding through a Natural Sciences and Engineering Research Council of Canada Post Graduate Scholarship, The Cooper Ornithological Society, The Manitoba Owl Symposium Fund, The Manitoba Big Game Trophy Association, The Mixedwood Forest Research and Advisory Committee, and The Manitoba Conservation, Wildlife Branch. We are very grateful for the help of the staff of Riding Mountain National Park, Manitoba Conservation Swan River Branch, Nancy McLennan, Hugh and Phyllis Hornbeck, Dan Soprovich and Shelley Curry in making the first field season run smoothly. Robert W. Nero and Spencer G. Sealy made valuable edits to this paper and provided guidance throughout.

Appendix 1. Cutting class categories defined by the Manitoba Department of Conservation Forestry Branch.

Class	Description
0	Forest land not restocked following fire, cutting, windfall or other major disturbances (hence potentially productive land). Some reproduction or scattered residual trees may be present.
1	Stands which have an average height less than 3 meters. They may have been restocked either naturally or artificially and have scattered residual trees.
2	Advanced young growth of post size, with some merchantable volume. The average height of the stand must be over 3 meters.
3	Immature stands with merchantable volume growing at or near their maximum rate and should definitely not be cut. The average height of the stand should be over 10 meters and average diameter should be over 9.0cm at d.b.h.
4	Mature stands which may be cut as they have reached rotation age.
5	Overmature stands which should be given priority in cutting.

Appendix 2. Crown closure classes defined by the Manitoba Department of Conservation Forestry Branch.

Class	Percentage canopy cover
0	0–20
2	21–50
3	51–70
4	71–100

REFERENCES

Baily, R.H. 1968. Notes on the vegetation of Riding Mountain National Park. National Park Survey Report. No. 2. Department of Forestry and Rural Development, Forest Management Institute, Ottawa.

Bosakowski, T., Speiser, R., & Benzinger, J. 1987. Distribution, density and habitat relationships of the Barred Owl in northern New Jersey. In Nero, R.W., Clark, R.J., Knapton, R.J. & Hamre, R.H. (eds.) *Biology and conservation of northern forest* owls: 135–143.Winnipeg, Manitoba. Gen. Tech. Rep. RM–142. Fort Collins Co: USDA Forest Service Rocky Mountain Forest and Range Experiment Station:.

Bouchart, M.L. 1991. Great Gray Owl habitat use in southeastern Manitoba and the effects of forest resource management. MNRM Practicum, Natural Resources Institute, University of Manitoba.

Bull, E.L. & Duncan, J.R. 1993. Great Gray Owl (*Strix nebulosa*). *The Birds of North America*, No.41. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C.

Byers, C.R., Steinhorst, R.K. & Krausman, P.R.1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* **48**:1050–1053.

Clark, K.A. & Anderson, S.H. 1997. Temporal, climatic and lunar factors affecting owl vocalizations in Wyoming. *J. Raptor Res.* **31**:358–363.

Davy, H.S. 1995. *Porcupine Mountain – Eastern region preliminary 1994 botanical survey*. Ecologically Significant Areas Program. Parks and Natural Areas Branch, Manitoba Department of Natural Resources, Winnipeg.

Duncan, J.R. 1992. Influence of prey abundance and snow cover on Great Gray Owl breeding dispersal. Ph.D. dissertation, University of Manitoba.

Duncan, J.R. 1996. Conservation status ranks of the birds of Manitoba. Manitoba Conservation Data Centre MS Report Number 96–05, Winnipeg, Manitoba.

Duncan, J.R. & Duncan, P.A. 1997. Increase in distribution records of owl species in Manitoba based on a volunteer nocturnal survey using Boreal Owl (*Aegolius funereus*) and Great Gray Owl (*Strix nebulosa*) playback. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and conservation of owls of the Northern Hemisphere*: 519–524. Gen. Tech. Rep. NC–190. St Paul MN USDA Forest Service North Central Research Station.

Duncan, J.R. & Kearns, A.E. 1997. Habitat associated with Barred Owl (*Strix varia*) locations in southeastern Manitoba: A review of a habitat model. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and conservation of owls of the Northern Hemisphere*: 138–145. Gen. Tech. Rep. NC–190. St Paul MN USDA Forest Service North Central Research Station

Fuller, M.R. & J.A. Mosher. 1981. Methods of detecting and counting raptors, a review. *Stud. Avian Biol.* 6: 235–246.

Houston, C.S., Smith, D.G. & Rohner, C. 1998. Great Horned Owl. *The Birds of North America*, No.372. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, Washington D.C.

Jensen, K.L. & Mausberg, B. 1998. The fight to protect Manitoba's forests. Editorial. *Toronto Star*. Oct. 29, 1998: p. A28.

Johnsgard, P.A. 1988. *North American Owls, Biology and Natural History*. Smithsonian Institution Press, Washington, D.C.

Johnson, D.H. 1993. Spotted Owls, Great Horned Owls and forest fragmentation in the central Oregon Cascades. M.Sc. Thesis. Oregon State University.

Kirk, D.A. & Hyslop, C. 1998. Population status and recent trends in Canadian raptors: a review. *Biol. Conserv.* **83**:91–118.

Mazur, K.M., James, P.C., Fitzsimmons, M.J., Langen, G. & Espie, R.H.M. 1997. Habitat associations of the Barred Owl in the boreal forest of Saskatchewan, Canada. *J. Raptor Res.* **31**:253–259.

Mazur, K.M., Frith, S.D., & James, P.C. 1998. Barred Owl home range and habitat selection in the boreal forest of central Saskatchewan. *Auk* **115**:746–745.

McCready, S., Rewcastle, C., Guinan, D. & L'Arrivee, L. 1980. *Duck Mountain Resource Inventory*. Manitoba Parks Branch, Dept. of Natural Resources. Winnipeg.

McGarigal, K. & Fraser, J.D. 1984. Barred Owl responses to recorded vocalizations. *Condor*. **87**:552–553.

Mosher, J.A., Fuller, M.A. & Kopeny, M. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. *J. Field. Ornithol*. **61**: 453–461.

Natural Resources Manitoba. 1996. *Forest inventory field instruction manual*. Winnipeg, Manitoba. Forest Resources Management.

Niemi, G.J. & Hanowski, J.M. 1997. Raptor responses to forest management: a holarctic perspective. *J. Raptor Res*. **31**:93–94.

Nero, R.W. 1980. *The Great Gray Owl. Phantom of the Northern Forest*. Smithsonian Institution Press, Washington D.C.

Neu, C.W., Byers, R.C. & Peek, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage*. **38**:541–545.

Servos, M.C. 1986. Summer habitat use of Great Gray Owls (*Strix nebulosa*) in southeastern Manitoba. MNRM Practicum. Natural Resources Institute, University of Manitoba.

Stepniski, D.P.1997. Landscape features and characteristics of Great Gray Owl (*Strix nebulosa*) nests in fragmented landscapes of central Alberta. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and conservation of owls of the Northern Hemisphere*: 601–607. Gen. Tech. Rep. NC–190. St Paul MN USDA Forest Service North Central Research Station.

Takats, D.L. 1997. Barred Owl habitat use and distribution in the Foothills Model Forest. FMF Final Report. Department of Renewable Resources. University of Alberta, Edmonton.

16

COMPARATIVE HABITAT USE BY OWLS IN A HIGH ALTITUDE (1,700–3,000 M) ROCKY MOUNTAIN FOREST

STANLEY H. ANDERSON & KATHLEEN A. CLARK

Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Box 3166, Bio Sciences Bldg. 419, Laramie, Wyoming 82071 USA

Between 1992 and 1994, we surveyed owls in the Grey's River Watershed on the Bridger Teton National Forest Wyoming, USA. This rugged area, composed primarily of conifers, is inaccessible between November and February due to snow cover. Six species of owls were heard and seen between March and June, namely the Great Horned Owl *Bubo virginianu*, Long-eared Owl *Asio otus*, Great Gray Owl *Strix nebulosa*, Boreal Owl *Aegolius funereus*, Northern Saw-whet Owl *Aegolius acadicus* and Northern Pigmy Owl *Glaucidum gnoma*. By using a geographic information system, and habitat variables collected on site, we were able to identify characteristics at sites used by owls. Boreal Owls were found in structurally complex Engelmann Spruce *Picea engelmannii* /Subalpine Fir *Abies lasiocarpa* habitats; however the mean stand size in which they were found was 538 ha, while for Long-eared Owls the stand size was 111 ha. Additionally, Boreal Owls were never found within 100 m of a road, whereas Long-eared Owls were often heard within the narrow forest stands that paralleled roads and watercourses. Great Gray Owls and Great Horned Owls used Lodgepole Pine *Pinus contorta* habitats. For Great Gray Owls the average stand size was only 75 ha, and vocalizing owls were often in close proximity to large wet meadows. Great Horned Owls were found at the base of slopes in larger Lodgepole stands, but in close proximity to either wet meadow or open sagebrush habitats. Northern Saw-whet Owls preferred stands dominated by Quaking Aspen *Populus tremuloides* and avoided areas near clearcuts. The small number of Northern Pygmy Owls were found in areas with larger and taller trees relative to availability. Our results showed how the six owl species used different habitat types within the study area.

INTRODUCTION

In high altitude forests in North America, little is known of the distribution and habitat preferences of different owl species. Craighead & Craighead (1956) and Craighead & Mindell (1981) reported nesting habitat and population status for owl species within the Jackson Hole and western Wyoming areas. Since that time, most studies in the North American Rocky Mountains have been limited to single species or to areas where timber was not harvested (Hayward *et al.* 1993, Herren *et al.* 1996).

Knowledge of the owl species composition of an area, and which habitat attributes are important for each, are vital steps towards understanding how owls use an area. The purposes of our study were to: (1) locate and identify owl species present within the Greys River drainage of western Wyoming in the Northern Rocky Mountains; (2) determine habitat variables important for each species; and (3) evaluate habitat use by each species in relation to landscape features.

STUDY AREA

The study area was located in western Wyoming, on the Greys River watershed of the Bridger-Teton National Forest. It encompassed approximately 113,700 ha. This area was bordered on the west by the Salt River Mountain Range and on the east by the Wyoming Mountain Range. The landscape was rugged with elevations between 1,768 and 3,350 m.

The Greys River drainage occurs along a vegetative transition zone between the plant species of the Great Basin and the Rocky Mountain Regions (USFS 1990). Dominant stand types are Lodgepole Pine *Pinus contorta*, Engelmann Spruce *Picea engelmannii* /Subalpine fir *Abies lasiocarpa*, and Douglas-Fir *Psuedotsuqa menziesii*. They represent approximately 40%, 20%, and 2% of the study areas' respective habitat types (USFS 1990). Dominant stands of Englemann Spruce exist sporadically along stream terraces (Steele *et al.* 1983). Hardwood stands represent only a small portion (5%), and are usually small stands of Quaking Aspen *Populus tremuloides* on upland mesic sites. Stand size of conifer and aspen varied from a few hectares to hundreds of hectares. These tree stands were usually surrounded by sage or grassland communities, or wet meadows at lower elevations. A sparse number of mature Narrowleaf Cottonwood *Populus angustifolia* stands are scattered along the floodplains.

Approximately 30% of the area is nonforested, consisting of grassland, wet meadow, riparian shrub or upland shrub vegetation. In the lowland riparian areas, predominant shrubs consist of a variety of willow *Salix* species. In the upland shrub communities, Mountain Big Sagebrush *Artemisia tridentata vaseya*) dominates (Steele *et al.* 1983).

METHODS

Owl sampling

Twenty-six transects were randomly placed in accessible areas between 1,768 m and 2,713 m elevation. They were arranged perpendicular to roadways in areas with lower avalanche potential. Because the vegetation of the Greys River study area was patchily distributed, transects could not be contained within homogenous habitat segments. Distances between transects varied, but all were at least 1 km apart and most were >5 km apart. Transect length varied from 3 km to 10 km, and width was also variable. Transects were surveyed using snowmobiles, all-terrain vehicles, snowshoes and skis.

Surveys were conducted in 1992 and 1993, between 1 March and 1 June. This sampling period corresponds to early courtship and the most vocal period for many owl species of the northern temperate zone (Johnsgard 1988). Each transect was surveyed three times during a field season.

We began our nightly surveys at twilight on calm nights with little wind (0 to 10 km/hr) or precipitation. Observers were placed at 250 m intervals along the transects at alternating calling and listening stations. At calling stations, one observer played a series of recorded owl songs while listening and looking for owls. At listening stations, the observer looked and listened for owls while the tape was being played at the adjacent calling station.

Based upon literature review and a preliminary survey in 1991, we concluded that more than one species of owl song must be played to increase the likelihood of soliciting a response from all species potentially present in the immediate area. We played the primary songs of the Northern Saw-whet Owl *Aegolius acadicus*, Boreal Owl *Aegolius funereus* and Great Gray Owl *Strix nebulosa* in that order. The rationale for this sequence was that playing the song of a larger owl first might inhibit the chance of eliciting a response from a smaller species. Each species song was repeated twice for 45 seconds and was followed by 90 seconds of listening.

When an owl responded, we recorded the species and its location. To prevent double sampling of owls that may have followed us along the transect or moved in response to the recording, only the first vocalization was recorded. Owl location was determined either by direct observation or through bi-angulations produced by the two observers. If an owl vocalization could be located to forest stand, slope position or estimated distance, it was eliminated from the data set. We also used records from owls that were already vocalizing when we arrived. We conducted a preliminary test to determine how much owls moved in response to vocalization. Our observations indicated that the initial response of the owl occurred in its perch or roosting site. Second or third responses came from owls that were drawn to the recording.

Habitat data

We collected habitat data at all owl locations using the sampling method proposed by James & Shugart (1970), with modifications by Noon (1981) (Table 1). These data were collected in 0.04 ha plots, and included tree and snag basal areas, snag density, overstory density, tree height, shrub density, percent canopy and herbaceous cover, density of downed logs, and average downed log circumference. Slope and aspect were also recorded. Additionally, we determined canopy density through a point-center quarter method.

In addition, 201 random plots were measured for comparison between available habitat and the habitat used by each owl species. We established these plots by using randomly generated, Universal Transverse Mercator (UTM) coordinates within 1 km of each sampling transect. This distance represented to us the maximum distance for which any owl species could be identified.

Landscape features

Elevation and UTM coordinates for owl locations were identified using a global positioning system (GPS). Owl coordinates were incorporated into a vector-based geographic information system (GIS) and landscape characteristics were obtained for each owl species. ARC/INFO is a vector-based GIS in which GPS data are stored as a sequence of precise x and y coordinates. Vectors are then established that connect these coordinates to form a polygon for each owl location (Shaw & Atkinson, 1990). The vegetation layer was checked with random field location. GPS unit accuracy was evaluated as 3 to 5m. This procedure enabled us to obtain proximity and forest stand measurements for owl locations. The landscape variables measured at owl locations were:

Table 1. Mean stand size and adjacent habitat areas at owl sites for five species of owls in the Grey's River drainage of western Wyoming

Values in brackets indicate standard deviation.

	Great Horned Owl	Long Eared Owl	Great Grey Owl	Boreal Owl	Saw-Whet Owl
Sample Size	91	18	10	14	78
Owl Locations					
Stand Size (ha)	419 (588)	111 (969)	75 (84)	538 (559)	312 (506)
Range (stand size)	1 – 2269	16 – 294	12 – 259	71 – 1418	1 – 2269
Adjacent Habitat Type (%)					
Spruce/Fir	27.9	15.4		4.5	13.0
Douglas Fir			16.7		2.2
Lodgepole	27.7	61.5		66.7	30.4
Clear-cut	4.7			16.7	13.0
Aspen ≥ 50%	2.3	7.7			8.7
Wet Meadow	23.3		83.3	16.7	13.0
Sagebrush Slope	7.0	7.7			17.4
Other	7.7	7.7			2.2

Table 2. Mean values for perimeter: area ratio (P: A), shape index (SI), and fractal dimension (FD) for adjacent stand, nearest opening, and nearest clear-cut versus owl locations.

Values in brackets indicate standard deviation. For definition of S1 and FD see text. Sample size of owls as in Table 1.

	Great Horned Owl	Long Eared Owl	Great Grey Owl	Boreal Owl	Saw-Whet Owl
Occupied stand					
P:A	0.01 (0.01)	0.01 (0.0)	0.01 (0.0)	0.01 (0.0)	0.01 (0.0)
SI	3.74 (2.14)	2.25 (0.97)	2.37 (0.89)	3.39 (1.16)	2.94 (1.51)
FD	1.75 (0.1)	1.84 (0.08)	1.82 (0.07)	1.76 (0.07)	1.8 (0.1)
Nearest stand					
P:A	0.02 (0.02)	0.01 (0.0)	0.02 (0.01)	0.01 (0.0)	0.01 (0.01)
SI	3.21 (2.13)	2.41 (0.93)	2.27 (1.04)	3.39 (1.16)	2.44 (1.15)
FD	1.78 (0.12)	1.82 (0.08)	1.83 (0.08)	1.76 (0.07)	1.82 (0.09)
Nearest opening					
P:A	0.02 (0.03)	0.02 (0.01)	0.02 (0.01)	0.02 (0.0)	0.02 (0.01)
SI	3.58 (3.29)	2.18 (1.10)	2.58 (1.14)	1.80 (0.89)	2.12 (1.14)
FD	1.78 (0.16)	1.86 (0.10)	1.80 (0.09)	1.88 (0.11)	1.87 (0.09)
Closest clear-cut					
P:A	0.02 (0.03)	0.03 (0.04)	0.02 (0.00)	0.01 (0.01)	0.02 (0.01)
SI	1.79 (1.06)	2.41 (1.98)	2.65 (2.40)	1.85 (1.02)	1.65 (0.99)
FD	1.89 (0.13)	1.84 (0.17)	1.86 (0.18)	1.86 (0.11)	1.92 (0.10)

(1) stand type and size; (2) distance of nearest edge and habitat type; (3) distance, type and size of nearest natural opening; (4) distance and size of nearest clear-cut, and (5) distance to nearest road.

Landscape indices

Edge effects were determined by calculating the perimeter: area ratio, shape index and fractal dimension for owl habitat locations, nearest adjacent habitat, nearest natural opening and nearest clear-cut. These indices were used to examine species-specific landscape attributes (Groom & Schumaker 1990).

- Perimeter: area ratio – the relative edge influence on a patch. Low P:A indicates less influence by the edge on the patch (range 0–1).
- Shape index – determines edge effects by quantifying edge in relation to the shape of a patch and its deviation from a circle of equal area. One equals a circle, >1 indicates increasing deviation from a circle (range 1–∞).
- Fractal dimension – quantifies the shape of fragments, closely reflects the patch perimeter and may be more accurate at estimating edge-to-interior ratios (range 1–2). One indicates simple shaped perimeters, 2 indicates complex shapes.

Statistical analysis

Mann–Whitney U tests were used to determine the continuous habitat variables important for each owl species. Not all these variables were normally distributed, so we chose to run nonparametric analysis to maintain consistency in testing procedures. The Mann–Whitney U test is a conservative method even with normally distributed data. A P-value of 0.01 was used to determine significance. This lowered value reduced the chance of a Type 1 error while conducting numerous univariate tests.

Chi-square goodness of fit tests were used to determine use versus availability for habitat categorical variables. Variables analyzed were: (1) habitat type, (2) percent slope, (3) slope aspect, (4) slope position, (5) overstory tree species composition, (6) midstory tree species composition, and (7) understory tree species composition. Bonferroni 95% confidence intervals were constructed for all species using a 0.01 probability level (Neu *et al.* 1974, Byers & Steinhorst 1984).

One-way ANOVAs helped us determine interspecific difference in habitat selection at a 0.01 alpha level. Tukey multiple comparison tests identified which groups were plausibly different at a 0.05 probability level.

RESULTS

General survey

Throughout the survey, we recorded more than 450 owl vocalizations or sightings, but could identify only 216 of these as to species and stand location. Habitat characteristics were established for six species. Great Horned Owl *Bubo virginianus*, Long-eared Owl *Asio otus*, Great Gray Owl, Boreal Owl, Northern Saw-whet Owl, and the Northern Pygmy Owl *Glaucidium gnoma*. For the latter only four locations were obtained.

Great Horned Owl habitat (GHOW)

During the study, we heard 91 GHOW vocalizations. GHOWs used mature, homogenous, Lodgepole Pine stands ($P \leq 0.01$), and avoided both Douglas-Fir and open sagebrush habitats ($P \leq 0.01$) where they were seen. The average stand size at GHOW locations was 419 ha (range 1 – 2,269 ha), with a low fractal dimension and a high shape index (Tables 1 & 2). This species was located most often at the base of a slope, and avoided both the top quarter and midslope positions ($P \leq 0.003$). Habitat attributes were not significantly different (i. e. $P \leq 0.01$) from random sites. However, mean canopy tree density was less at use sites (= 111 canopy trees/ha) than at random sites (= 139 canopy trees/ha) ($P = 0.017$).

The average distance to an opening was 98 m (range 0 – 1,145 m), with 82% of records occurring within 100 m of a natural opening (Table 3). Natural openings included both wet meadow (39% occurrence) and sagebrush slope (29% occurrence). In contrast, the average distance to a clear-cut was 1,356 m (range 0 – 4,141 m).

GHOWs utilized all habitat types, although Lodgepole Pine stands were used significantly more than expected. Additionally, canopy tree density was less at GHOW locations ($P = 0.017$), suggesting that GHOWs used more open forest stands than were randomly available. Additionally we found GHOWs to be in close proximity to natural openings. Although wet meadows occurred 39% of the time, they represented only 4% of the study area.

Long-eared Owl habitat (LEOW)

We found 18 LEOW locations all between 1,982 – 2,380 m ($\bar{x}$ = 2104 m) elevation. Ten of these locations were in mature Spruce/Fir habitat ($P \leq 0.01$). The mean overstory dbh at LEOW sites was 46 cm compared to 35 cm at random sites ($P = 0.003$). Basal area and canopy height were also greater at LEOW locations, although these variables were not statistically significant at $P = 0.01$ from random locations. Additionally, these owls used open sagebrush slopes significantly less than expected ($P \leq 0.01$) and were not heard calling here.

Landscape indices revealed that LEOWs were within or in a close to relatively small stands with low interior: edge characteristics (Tables 1 & 2). Average stand size was 111 ha at LEOW

Table 3. **Mean** values for habitat used, distance to, and size of, natural openings and clearcuts for five owl species found at Grey's River study site.

Values in brackets indicate standard deviation. Sample sizes as in Table 1.

	Great Horned Owl	**Long Eared Owl**	**Great Grey Owl**	**Boreal Owl**	**Saw-Whet Owl**
Habitat type and percent occurrence (%)					
Wet Meadow	39.0	57.1	83.3	42.5	28.2
Sagebrush Slope	29.3	14.3		14.2	45.2
Clear Cut	17.1	21.4		28.7	17.5
Other	14.6	7.2	16.7	14.2	9.1
Natural opening					
Average area	157 (323)	185 (362)	280 (462)	12 (14)	222 (389)
Range (ha)	0.2	956 3.3	956 3.2	956 3.9	39 1.2
Distance (m)	98 (243)	360 (481)	110 (149)	191 (206)	240 (531)
Range	0.0	1445 0.0	1460 7	428 27	586 0.0
Clear-cut					
Average Area	21 (21)	17 (14)	6 (10)	40 (34)	19 (38)
Range	13.7	76 3.6	38 6.6	21 5.9	76 2.2
Distance	1356 (1267)	1104 (1601)	1062 (838)	836 (751)	1285 (1277)
Range	0	4141 26	4951 10	2134 27	2216 0

locations. The average distance to an adjacent habitat was 33 m, and 62% adjacent habitats were Lodgepole Pine stands.

The predominant nearest opening type was wet meadow (Table 3). Average distance to a natural opening was 360 m, with 53% of LEOW sites occurring within 100 m. Average distance to a clear-cut was 1104 m, with 49% of all LEOW observations found within 500 m of a clear-cut (Table 3).

In our study LEOWs utilized dense mature coniferous habitats. The Greys River drainage contained mainly coniferous corridors along the riparian areas, with moderate amounts of willows along the floodplains, but other deciduous tree species were scarce. Sampling along these deciduous areas did not produce any LEOW vocalizations. Most locations occurred in mature spruce/fir forest stands or in open sites along rivers or streams. This suggests that dense coniferous stands were important habitats for LEOWs within the drainage.

Occupied stands were small with low interior: edge characteristics, suggesting that this species occupied 'edge type' habitats with little interior (i.e. the spruce/fir corridors that occurred along the lower elevation streams). Wet meadows were commonly found within 400 m of LEOW locations.

Great Gray Owl habitat (GGOW)

We identified the locations of ten GGOWs between 1,951 – 2,357 m (= 2,166 m) elevations. Great Gray Owls used small, homogenous, Lodgepole Pine stands (= 75 ha) ($P \leq 0.01$), but these stands showed no distinctive structural differences from random sites. Percent slope was not statistically significant at $P = 0.01$; despite eight out of ten GGOW observations occurring in flat areas with <20% slope.

Adjacent habitats were approximately 38 m away (range 7 – 80 m), and eight out of ten GGOW locations were within 100m of wet meadows (Table 3). These wet meadows were large, averaging 110 ha (range 3.2 – 956 ha). Average clear-cut distance was 1,062 m away from GGOW locations. One individual was within 15 m of a clear-cut, but the majority of GGOW locations were >500 m away.

During our study, although slope gradient was not reliably different between GGOW locations and random sites ($P = 0.03$), eight out of ten GGOW observations were on flattish areas within 100 m of a wet meadow (Tables 1 & 3).

Boreal Owl habitat (BOOW)

Boreal Owls were located at altitudes of 2,103 – 2,590 m (= 2,337 m), in spruce/fir habitats ($P \leq 0.001$). Nine of the 14 identified vocalizations occurred in this habitat type. These BOOW sites contained larger and taller trees, with greater basal area and canopy cover than random locations ($P = 0.004$, $P = 0.003$, $P = 0.002$, and $P = 0.011$ respectively). Average overstory diameter at breast height (dbh) was 49.5 cm, compared with 35.0 cm at random sites. Also, mean canopy cover was 50% at BOOW locations and only 32% at random locations.

Boreal Owls were found in areas with moderate to high interior: edge ratios (Table 2). Mean shape index and mean fractal dimension were 3.39 and 1.76 respectively. Average stand size was 538 ha and, on average, Boreal Owls occupied the largest stands of any owl species found within the drainage.

All BOOW locations were found within 500 m of the forest edge (= 93.5 m). Lodgepole Pine was the dominant adjacent habitat type. Forty-three percent of all the nearest openings were wet meadows and 29% were clearcuts. The average distance to a natural opening was 191 m compared to 836 m for clear-cut areas. BOOWs were found as close as 27 m to a clear-cut, but 70% of the closest clearcuts were greater than 500 m away, whereas 83% of the natural openings were within 500 m of a BOOW location. Average size of the nearest natural opening was 12 ha compared to 40 ha for the nearest clear-cut (Table 3). On the study area, BOOWs were never found within 100 m of a road (range 128 – 1,308 m, mean = 414 m).

During our study we found that large, multi-layered stands of Englemann Spruce/Subalpine Fir habitat were used by BOOWs ($P \leq 0.001$). These areas displayed relatively high degrees of structural complexity, with moderate to high interior: edge characteristics. Trees were taller and larger with a higher degree of canopy cover than was available at the random sites.

Northern Saw-whet Owl habitat (SWOW)

We found 78 SWOW locations between 1,777 and 2,602 m (mean = 2,274 m) elevation. SWOWs were either in, or in close proximity to, coniferous areas, with 46% of adjacent habitat types being dominated by conifers. They preferred stands with ≥ 50% Quaking Aspen in the overstory ($P \leq 0.01$). They avoided both clear-cut and open sagebrush habitat types ($P \leq 0.01$). Average stand size was 312 ha (range 1 – 2,269 ha), with a shape index of 2.94 and a fractal dimension of 1.80.

Adjacent habitat types were predominantly Lodgepole Pine (30% occurrence) or open sagebrush habitats (17% occurrence). The average distance from owl sites to adjacent habitat types was 88 m (range 2 – 407 m).

Mean distance from SWOW locations to the closest opening was 240 m with 50% occurring within 100 m. Seventy-three percent of all the nearest openings were natural (i.e. sagebrush or wet meadow areas) and 18% were clearcuts. The average distance to a clear-cut was 1,285 m. Average opening size was 222 ha at natural sites and 19 ha at clear-cut sites (Table 3). Natural openings also exhibited higher interior: edge ratios compared to clearcuts.

We found a strong association ($P \leq 0.01$) between SWOWs and the presence of Quaking Aspen in the overstory. Although 59% of our SWOW locations contained coniferous species, many sites contained quaking aspen as the dominant overstory tree species (= 34%). Nearly half (48%) of these locations were in pure aspen stands.

Though the presence of Quaking Aspen in SWOW breeding territories was important, 59% of SWOW locations were in coniferous stands and 46% of adjacent habitat types were dominated by conifers (Table 1). Additionally, 72% of SWOW locations were within 100 m of an adjacent habitat. These coniferous areas potentially provided roosting cover, whereas aspen snags may have provided optimal nesting sites for SWOWs on the Greys River watershed.

Northern Pygmy Owl habitat (POOW)

We heard only four vocalizations in Douglas Fir ($n = 2$) and spruce/fir ($n = 2$) habitat types at 2,335 – 2,400 m elevations. POOW locations were in areas containing significantly larger and taller trees than were randomly available. We found both overstory dbh ($P = 0.007$) and average canopy height ($P = 0.007$) to be important variables.

Interspecific microhabitat analysis

Tukey tests revealed that GHOWs used areas with lower basal areas (mean = 14.5 m^2/ha) than SWOWs (= 24.7 m^2/ha), BOOWs (= 34.3 m^2/ha), LEOWs (= 28.3 m^2/ha), and POOWS (mean = 41.0 m^2/ha). Both SWOWS (mean = 20.7 m) and GHOWs used areas with shorter canopy trees (mean = 18.9 m) than did BOOWs (mean = 26.1m) or POOWs (mean = 28.8 m). In addition, differences were noted between midstorey tree diameters at GHOW locations (= 18.9 cm) and POOW locations (mean = 31.1 cm).

Interspecific differences of microhabitat

Tukey tests revealed that both GHOWs and SWOWs occurred in stands of lower canopy height than did POOWs and BOOWs. In addition, GHOWs were in stands with less basal area than POOWs and BOOWs. Both POOWs and BOOWs were primarily found in mature stands of spruce/fir or Douglas Fir whereas both GHOWs and SWOWs preferred Lodgepole Pine stand and ≥ 50% aspen, respectively. Mature spruce/fir and Douglas Fir habitat types were the most structurally complex habitats found on the Greys River study area.

DISCUSSION

Great Horned Owl

The GHOW is a large New World species. It can be found throughout North and South America from northern Alaska and Canada to the tip of South America at Tierra del Fuego (Johnsgard 1988). It is considered a common resident in many parts of the Rocky Mountain region. GHOWs are found in a vast array of habitats and elevations ranging from subalpine boreal forest to dry, arid coastal deserts (Johnsgard 1988). Habitat plasticity enables them to be one of the greatest habitat generalists of all Strigiformes. In Wyoming, GHOW nesting territories overlap much of their winter hunting and roosting areas (Craighead & Craighead 1956).

Some studies revealed that habitat diversity around GHOW nesting sites was no different from habitat available within the area, and that no selection was occurring (Johnsgard 1988). Walsh (1989) associated increased densities of GHOW breeding territories with high rabbit densities. He stated that this was the most important factor, but GHOWs utilized areas significantly more than expected when there was high physiographical relief, relatively low mammal densities and high mean foliage height.

During our study, GHOWs utilized all habitat types to some extent. They did tend to utilize Douglas-Fir and open sagebrush habitats less than expected. In general, GHOWs were found within large stands with higher interior: edge than any other owl species in the Greys River drainage, but most GHOW observations were within 100 m of natural openings or habitat edges, especially wet meadows. No structural variables were found to be different from those present at random locations.

Long-eared Owl

The LEOW is a medium-sized, stick-nesting species, distributed throughout the boreal, temperate, Mediterranean, and steppe climatic zones of North America and Eurasia (Mikkola 1983). In northwestern Wyoming, the species is considered a permanent resident (Craighead & Craighead 1956). The latter authors believed coniferous woods to be important winter roost sites for Long-eared Owls, while open areas were used for hunting. In our study area, most nest sites were located along the deciduous riparian floodplain. In one project, Bull *et al.* (1988) identified 20 LEOW nest locations, all in Douglas-Fir trees.

Overall, the LEOWs found within the Greys River drainage utilized patches with a higher degree of ‘edge’ than any other owl species. Although they were found in structurally complex spruce/fir habitats, these stands were relatively small. Often they occurred in stands along watercourses, and wet meadows were the main nearest opening. These results are similar to those of Henrioux (2000), who found Long-eared Owls in Switzerland preferred wooded areas bordering fields. In our study area no conclusions could be drawn in regards to clearcuts, but these areas were within LEOW potential home ranges. In addition, nearby clear-cut areas were small with a high perimeter:area ratio (see Holt 1997).

Great Gray Owl

The GGOW is the largest owl species in North America. It is widely distributed in the boreal climatic zone of Eurasia and North America (Mikkola 1983), occurring throughout the northern Rocky Mountains, south to Montana, Idaho, northern Utah, and northwestern Wyoming, and can also be found in the Cascade Mountains south to the Sierra Nevada Mountains of California (Bull *et al.* 1988).

In mountainous regions, long distance latitudinal migrations are not routine (Bull *et al.* 1988). Craighead & Craighead (1956) described GGOWs as permanent residents in northwestern Wyoming. Franklin (1988) observed that breeding GGOWs in northwestern Wyoming were found as high as 3000 m, but they overwintered in areas with less snow accumulation. The birds show considerable tolerance of habitat modification (Whitfield & Gaffney 1997). Altitudinal migrations allow GGOWs to remain within the general vicinity of breeding sites, but also permit foraging in areas where prey is accessible (Collister 1997).

During our study, we found GGOWs at the lower elevations between 1,951 and 2,357 m. We observed them only during the early breeding season, but this coincided with the period of maximum snow accumulation within the study area. In April, average snow depth above 2,133 m was 1–3 m for the Bridger-Teton National Forest (USFS 1990). This was well beyond the maximum penetration depth (50 cm) described for obtaining prey (Nero 1980). The two individuals we observed above 2,133 m occurred on south or southwestern facing slopes, which were especially more open with less snow accumulation. Snow depth and associated prey availability may have limited GGOW distribution within the Greys River study area.

Boreal Owl

The BOOW is a small, secondary cavity-nesting species with a circumboreal distribution (Johnsgard 1988). In western North America, this species ranges from the boreal forests of Alaska and Canada south to northern New Mexico and southern Colorado (Hayward *et al.* 1993).

Most Rocky Mountain studies suggest that Boreal Owls inhabit forests within the high elevation spruce-fir zone (Hayward & Hayward 1989). Hayward *et al.* (1993) reported that 90% of all BOOW breeding territories found in Idaho, Montana, and northwestern Wyoming were within this zone. Breeding populations have been found as low as 1,525 m throughout the Rocky Mountain region (Holt & Hillis 1987), with the highest densities at above 3,000 m in Colorado.

Holt & Ermatinger (1989) reported BOOWs in mature to ‘climax’ Engelmann Spruce/Subalpine Fir forests with overstorey of trees on an average of 35.6 cm diameter at breast height. Lane *et al.* (1997) also described this species as associated with mature upland type forests. Hayward *et al.* (1993) reported that a high density of large trees (>38 cm dbh), open understorey, and a layered canopy were important characteristics when identifying BOOW breeding territories. They also stated that BOOWs were absent from dense, even-aged forest stands (Hayward *et al.* 1993).

In our study area, BOOWs used mature spruce/fir habitats interspersed with small wet meadows. They preferred a multi-layer canopy with large tall trees dominating the overstorey. They were found in close proximity to clearcuts, but more often close to smaller natural openings. Road systems might have altered the distribution.

Northern Saw-whet Owl

The SWOW is a small cavity- nesting species distributed throughout the transition and montane zones of North America (Gill & Cannings 1977, Johnsgard 1988). Within the Rocky Mountain region, the species is found along a broad elevation gradient ranging from low elevation woodland to high elevation conifer forests (Craighead & Craighead 1958). In Wyoming, SWOW are regarded as common year-round residents and we identified 78 locations in the Greys River study area.

In British Columbia, Cannings (1987) found higher SWOW densities within deciduous riparian areas than in pine-fir habitats. He attributed this pattern to the higher densities of Deer Mice *Peromyscus maniculatus* in hardwood stands.

We found a strong association ($P < 0.01$) between SWOWs and the presence of Quaking Aspen in the overstorey. Although 59% of SWOW locations contained primarily coniferous species, 34% of the sites contained quaking aspen as the dominant overstorey species. Forty-eight percent of the SWOW locations occurring in the 50% aspen category were in pure aspen stands.

SWOWs in our study area tended to avoid clearcuts, probably because they provide no suitable roosting or nesting sites.. However, ten SWOW locations were in close proximity to clearcuts when the surrounding habitat contained some mature aspen.

Northern Pygmy Owl

In the Rocky Mountain region, POOWs are considered permanent residents that exhibit some altitudinal migration (Johnsgard 1988). They range from the lower elevation riparian areas in the winter to the higher montane forests during the breeding season. Webb (1982) reported breeding POOWs at elevations up to 3,657 m for certain areas of Colorado. In the Greys River study area, we found POOWs at moderate elevations between 2,335 and 2,500 m. They may have existed in areas higher than this, but high avalanche potential deterred us from sampling the summit sections.

POOWs utilize a vast array of coniferous habitat types, and thus are considered as habitat generalists (Johnsgard 1988). Although they are present in many habitats, they prefer open forest stands with large diameter conifers (Hayward & Garton 1988). Similarly, we found the four POOWs in our area in Douglas Fir and spruce/fir habitats. These areas had larger, taller trees with higher basal areas than occurred at random sites. However, canopy closure was only 38.8% at POOW sites compared to 31.5% at random sites. This would indicate the presence of large trees, but not a dense forest stand.

CONCLUSIONS

A total of six species of owls were found on the Greys River drainage in western Wyoming. The presence of wet meadows appeared to be an important habitat feature. GHOWs were found in large stands of Lodgepole Pine at the base of slopes, especially near wet meadows. LEOWs were found in mature spruce/fir corridors along the watercourses of the study area. GGOWs were found in Lodgepole Pine stands, with eight of ten locations being within 100m of a wet meadow. Forest stands with >50% Quaking Aspen were used in greater proportion by SWOWs. Clear-cut areas were avoided by SWOWs, but were commonly found in the adjacent stand.

BOOWs selected mature spruce/fir forest stands with large, tall trees and a multi-layered canopy, containing spruce and fir, in close proximity to small wet meadows with complex perimeters and low interior:edge ratios. BOOWs were found close to clearcuts if the surrounding matrix contained mature 'old growth' characteristics. However, the majority of BOOW locations were >100 m from a clear-cut and from the nearest road.

Landscape indices revealed different edge characteristics for nearest natural openings and nearest clear-cut areas between the GGOW and SWOW. Four POOW vocalizations were heard from structurally complex forest stands. Clear-cut areas were commonly near to owl locations, but proximity measurements revealed that natural openings were often closer.

REFERENCES

Bull, E.L., Henjum, M.G. & Rohweder, R.S. 1988. Nesting and foraging habitat of Great Gray Owls. *J. Raptor Res.* **22:** 107–115.

Byers, C.R. & Steinhorst, R.K. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* **48:** 1050–1053.

Cannings, R.J. 1987. *The Breeding Biology of Northern Saw-whet Owls in Southern British Columbia*. USFS Gen. Tech. Rept. RM 142:193–198.

Collister, D.M. 1997. Seasonal distribution of the Great Gray Owl in southwestern Alberta. In Duncan, J.R., Johnson, D.H., & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere*: 119–122. USDA, Forest Service GTR NC–190.

Craighead, F.C. Jr. & Mindell, D.P. 1981. Nesting raptors in western Wyoming, 1947 and 1975. *J. Wildl. Manage.* **45:** 865–872.

Craighead, J.J. & Craighead, F.C. Jr. 1956. *Hawks, owls, and wildlife*. Harrisburg: Stackpole Pub.Co.

Franklin, A.B. 1988. Breeding biology of the Great Gray Owl in southeastern Idaho and northwestern Wyoming. *Condor* **90:** 689–696.

Gill, M. & Cannings, R.J. 1977. Habitat selection of Northern Saw-whet Owls on the Queen Charlotte Islands, British Columbia. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere*: 197–204. USDA, Forest Service GTR NC–190.

Groom, M.J. & Schumaker, N. 1990. Evaluating landscape change: patterns of worldwide deforestation and local fragmentation. In Kareiva, P.M., Kinsolver, J.G. & Huey, R.B. (eds.) *Biotic Interactions and Global Change*: 24–44. Sunderland, MA: Sinauer Assoc. Inc.

Hayward, G.D. & Garton, E.O. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* **75:** 253–265.

Hayward, G.D., Hayward, P.H. & Garton, E.O. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, U.S.A. *Wildl. Monogr.* No. **124.**

Hayward, P.H. & Hayward, G.D. 1989. Boreal owls (*Aegolius funereus*). In Harvey, A.H. (ed.) *Rare, Sensitive, and Threatened Species of the Greater Yellowstone Ecosystem*: 84–86. The Nature Conservancy, Northern Rockies.

Henrioux, F. 2000. Home range and habitat use by Long-eared Owls in Northwestern Switzerland. *J. Raptor Res.* **34:** 93–101.

Herren, V., Anderson, S.H. & Ruggiero, L.F. 1996. Boreal Owl mating habitat in the northwestern United States. *J. Raptor Res.* **30:** 123–129.

Holt, D.W. 1997. The Long-eared Owl (*Asio otus*) and forest management: a review of the literature. *J. Raptor Res.* **31:** 175–186.

Holt, D.W. & Ermatinger, D. 1989. First confirmed nest site of Boreal Owls in Montana. *Northwest Nat.* **70:** 27–31.

Holt, D.W. & Hillis, J.M. 1987. Current status and habitat associations of forest owls in western Montana. In Nero, R.W., Clark, R.J., Knapton, R.J. & Hamre, R.H. (eds.) *Proceedings of Biology and Conservation of Northern Forest Owls*: 281–288. USDA, Forest Service GTR RM–142.

James, F.C. & Shugart, H.H. 1970. A quantitative method of habitat description. *Audubon* **24:** 727–735.

Johnsgard, P.A. 1988. *North American owls*. Washington, D.C: Smithsonian Institution Press.

Lane, W.H., Anderson, D.E. & Nicholls, T.H. 1997. Distribution, abundance, and habitat use of territorial male boreal owls in northeast Minnesota. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere*: 246–247. USDA, Forest Service GTR NC–190.

Mikkola, H. 1983. *Owls of Europe*. Carlton, UK:T. & A.D. Poyser Ltd.

Nero, R.W. 1980. *The Great Gray Owl*: *Phantom of the Northern Forest*. Washington D.C.: Smithsonian Inst. Press.

Neu, C.W., Byers, R.R. & Peek, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* **38:** 541–545.

Noon, B.R. 1981. Techniques for sampling avian habitats. In Capen, D.E. (ed.) *Proceedings of The Use of Multivariate Statistics in Studies of Wildlife Habitat*: 42–52. USDA, Forest Service GTR RM–87.

Shaw, D.M. & Atkinson, S.F. 1990. An introduction to the use of geographical information systems for ornithological research. *Condor* **92:** 564–570.

Steele, R., Cooper S.V., Ondov, D.M., Roberts, D.W. & Pfister, R.D. 1983. *Forest habitat types of eastern Idaho-western Wyoming*. USDA, Forest Service GTR INT–144.

USFS. 1990. *Bridger-Teton National Forest land and resource management plan*: *proposed forest plan*. USFS Bridger-Teton National Forest, Jackson, WY.

Walsh, D.T. 1989. *Population densities and vocal behavior of the Great Horned Owl in central Utah*. Ph.D. Dissertation. Brigham Young University, Provo, UT.

Webb, B. 1982. Distribution and nesting requirements of montane forest owls in Colorado. Part 2. Northern Pygmy-owl. *J. Colo. Field Ornithol.* **16:** 58–65.

Whitfield, N.B. & Gaffney, M. 1997. Great Gray Owl breeding habitat use within altered forest landscape. In Duncan, J.R., D. H. Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere*: 498–505. USDA, Forest Service GTR NC–190.

17

COMPARATIVE DIETS OF THE POWERFUL OWL (*NINOX STRENUA*), SOOTY OWL (*TYTO TENEBRICOSA*) AND MASKED OWL (*TYTO NOVAEHOLLANDIAE*) IN SOUTHEASTERN AUSTRALIA

RODNEY P. KAVANAGH

Forest Research Division, State Forests of New South Wales, P.O. Box 100, Beecroft, NSW,
Australia, 2119. Email: rodk@sf.nsw.gov.au

The three large forest owls of southeastern Australia, the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae*, often occur sympatrically but little is known about how they partition their habitat. The places where owls obtain their food and what they eat may have a crucial bearing on our understanding of their habitat requirements. Totals of 1,672 prey items from 47 Powerful Owl territories, 1,466 items from 28 Sooty Owl territories, and 175 items from six Masked Owl territories (or locations) were analysed. There was virtually no overlap between the diets of the Powerful Owl and Masked Owl. The Powerful Owl preyed almost exclusively on arboreal mammals, most of which weighed 50–100% of adult owl body weight, supplemented by diurnal birds. In contrast, the Masked Owl preyed almost exclusively on small terrestrial and scansorial mammals, most of which weighed 3–20% of adult owl body weight, supplemented by diurnal birds. At any one site, both owls appeared to specialise on just one or two prey species. The diet of the Sooty Owl was strikingly different by its generalist nature, comprising, at any one site, a wide range of arboreal and terrestrial or scansorial mammals, mostly weighing 2–100% of adult owl body weight. The Sooty Owl appeared to take any available small and medium-sized mammals and foraged throughout its more limited habitat (rainforest, tall moist eucalypt forest) from the forest canopy to the ground. Geographical variation in owl diets was related to differences in the availability of potential prey. All three species were found to survive and breed successfully in the coastal and foothill forests of southeastern New South Wales on a diet composed principally of prey species that are not dependent on old-growth forest.

INTRODUCTION

Studies of resource partitioning among owls have generally emphasised the differences in food types between species (Lack 1946, Marti 1974, Herrara & Hiraldo 1976, Jaksic 1983, Korpimaki

1992, Marti *et al.* 1993). Relatively few studies have investigated resource use in terms of multiple niche dimensions, such as habitat use and time of activity in addition to food type (e.g. Korpimaki 1986, Hayward & Garton 1988). However, Lundberg (1980) explained the co-occurrence of the Ural Owl *Strix uralensis* and the Tawny Owl *Strix aluco*, which have a similar diet, by their different habitats. The suggestion from the above studies is that species with high dietary overlap co-exist either by differential habitat selection or by exploitation of super-abundant (non-limiting) food supplies, such as occur during peak vole years in the Northern Hemisphere. Hayward & Garton (1988) found that the largest and smallest sympatric owl species differed most in diet, whereas intermediate or similar-sized owls differed from one another most in habitat selection and use. Similar patterns of resource use have been described among other assemblages of carnivores (Schoener 1974), as well as among other trophic groups of vertebrates (Brown *et al.* 1986, Pianka 1986).

The vast differences in small mammal prey availability in many cool temperate areas of the Northern Hemisphere, which occur annually (often in 3–4 year cycles) and seasonally (in part due to snow cover), are well known and documented (Southern 1970, Krebs & Myers 1974, Hansson & Henttonen 1985, Houston 1987, Korpimaki 1992, Taylor 1992, Newton 2002). These fluctuations in prey abundance have powerful effects on the ecology and life history traits of some northern hemisphere owls (Korpimaki 1992, Newton 2002). Generalist predators tend to be resident while specialist predators tend to be migratory or nomadic. Such marked fluctuations in the abundance of small terrestrial mammals and arboreal marsupials do not occur in Australian temperate forests. However, the degree to which resident predators can switch to alternative prey (functional response) when favoured prey become unavailable is likely to influence the resilience of these species to habitat alteration, such as that caused by logging. Short-term population changes (numerical response) among Australian forest-dwelling predators are likely to occur infrequently unless, for example, habitat alteration results in a general depletion of prey.

The diets of Australian large forest owls are perhaps the best known aspect of their ecology, but most previous studies have been anecdotal, opportunistic, or limited to only one species within a given region. In this paper, I document the diets of the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae* at a range of locations in southern New South Wales (NSW). I conclude that, despite the frequent co-occurrence of these three species, they frequently forage in different places and take different prey.

METHODS

Study animals

The Powerful Owl is Australia's largest owl, with males weighing approximately 1,700 g and females slightly less (approximately 1,600 g); the Sooty Owl is the largest mainland *Tyto*, and differs greatly in size between the sexes, with females up to 1,170 g and males approximately 650 g; and male mainland Masked Owls weigh approximately 670 g and females approximately 835 g (Schodde & Mason 1980, Hollands 1991, Kavanagh personal observations). All three owls are widespread throughout the forests of southeastern Australia, with the Sooty Owl favouring the taller, wetter forest types and the Masked Owl including drier woodlands among its habitat. Sympatry between the Powerful Owl and Sooty Owl, and between the Powerful Owl and Masked Owl, is common, but all three species occasionally co-occur in the same areas. Powerful Owls are regular winter breeders, but the two *Tyto* owls are much less predictable, with Masked Owls possibly breeding mainly in autumn and Sooty Owls in spring.

Study areas

The ecology and behaviour of individual pairs of owls was studied from 1990 to 1996 at eight initially, then many other, locations near Eden, Bega and Bombala in southeastern NSW, and at more than ten locations near Newcastle, Sydney and Wollongong on the central coast of NSW. These study areas were centred on the territories of one or more species of large forest owls: for Powerful Owls, 28 territories in southeastern NSW plus 19 on the Central Coast; for Sooty Owls, 21 territories in southeastern NSW plus seven on the Central Coast; and for the Masked Owl, from one territory and the stomachs of three road-killed owls in southeastern NSW plus one territory and the stomach of one road-killed owl on the Central Coast. The approximate locations of the study territories were determined initially, either by the intensity and frequency of responses to call-playbacks made by owls detected during regional surveys (e.g. Kavanagh & Bamkin 1995), or by the chance discovery of an owl at its diurnal roost. A number of the areas were selected for study because the territories of different species overlapped.

In each study area, systematic searches were made to locate regular roost and nest trees, and to collect regurgitated pellets for analysis. All three owls nest inside large tree hollows; all three commonly roost among foliage, but the two *Tyto* owls also roost frequently inside tree hollows and occasionally in caves. The procedure for locating owl roosts, and subsequently nests, began with regular visits to each study area about one hour before dusk or dawn to listen for calls made by owls as they moved to and from their roosts. Areas where calls were heard were then searched the following day to locate the roost site, as indicated by the presence of the owl or of white-wash and pellets. The owls did not always call at dusk or dawn, and when they did vocalise the calls were often inaudible to an observer greater than 200m away. Thus, dusk/dawn listening was required at many locations before the general roosting areas were found. Furthermore, roost sites within hollow trees took longer to confirm because identification had to be done at night as the owls left or entered the hollows, and pellets deposited inside tree hollows were usually inaccessible. Often it was necessary to search systematically all likely areas in daylight, even at sites where owls were known to occur, because no calls were heard at dusk or dawn. Later, radio-tracking of owls at several locations led to the discovery of many new roost sites at which pellets could be collected.

Owl pellet identification and analysis

Owl diets were determined principally by analysis of regurgitated pellets collected from the ground below foliage roosts or from inside the tree hollows used as roost sites or nest sites. Occasionally, pellets and other prey remains were collected from below nocturnal perches.

If an owl was not present at the time of collection, pellets could usually be allocated to a particular species with confidence from the type of roost site (e.g. tree species and position in the landscape), and from the size, shape and colour of the pellets (Powerful Owl pellets were grey, while Sooty Owl and Masked Owl pellets were usually black and shiny; see König *et al.* 1999), and by the colour of the nearby whitewash (whiter in *Tyto* owls). Powerful Owl pellets were also distinguishable by the presence of broken skulls of prey species; both *Tyto* owls tended to regurgitate the entire, unbroken skulls of their prey. Also, Powerful Owl pellets rarely contained more than one prey item, but two or more items were common in Sooty Owl pellets.

Individual pellets are often used as the basic sampling unit in dietary studies, but this was not always appropriate in my study. Pellets tended to split into fragments when they landed on the ground, and began to degrade after several days owing to beetles (Leiodidae: *Pseudonemadus* sp.) and moth larvae (Tineidae: possibly *Monopis* sp.) consuming the mammalian hair which bound the pellets together, leaving a scattered pile of bones. This was the condition of most pellet material collected from inside caves and tree hollow roosts or nests. Several of the pellet 'samples' collected for the Sooty Owl and Masked Owl formed nest debris representing many pellets. Pellets were separated into different samples, where possible, according to the degree of weathering and decomposition, but there were many instances of multiple pellets bagged as one sample. The data are therefore presented mainly as the relative proportions by frequency of individual prey items. Mean liveweights of each prey species were determined from standard reference books so that contributions to total prey biomass could be calculated.

Pellet contents were identified by analysis of mammalian hair (Brunner & Coman 1974) and by comparison with reference bone material. The pellets were stored in a freezer to kill any moth larvae present, then prepared for analysis by washing in warm water to separate fur from bones followed by drying overnight in a warm oven. Cross-sections of hair samples permitted identification to genus and usually to species. Similarly, identification of animal bones was usually possible to species and counts of jaw bones, skulls, limb bones and pelvic girdles permitted assessment of the minimum number of individuals present in each pellet or pellet sample. Where analysis was based on the identification of hair only, the number of prey items was underestimated because two or more pellets were frequently bagged as one sample.

RESULTS

Powerful Owl

Almost all prey taken by the Powerful Owl were exclusively or primarily arboreal in habit (Strahan 1995), suggesting that this owl hunts only for animals that live in trees (Table 1; Fig. 1). Within the specialised arboreal food niche, the Powerful Owl appeared to be a dietary generalist that preyed opportunistically on the largest available prey, usually mammalian. Fifteen prey species or prey groups (including 'birds' and 'insects') were recorded in Powerful Owl diets across all sites (47), but only three of these were recorded at 23 or more sites, namely Common Ringtail Possum *Pseudocheirus peregrinus* (33 sites), Sugar Glider *Petaurus breviceps* (26 sites) and 'birds'. A regional comparison of Powerful Owl diets showed that birds were taken significantly less often in southeastern NSW compared to the Central Coast of NSW, with relatively minor differences between regions in the contribution of all species of arboreal mammals grouped together, and all insects ($\chi^2 = 44.8$, df. = 2, $P < 0.01$).

The Common Ringtail Possum (900 g; Strahan 1995) comprised 58% of prey items across all sites; however, in many coastal or low (<300 m) elevation forests (37 territories) this species comprised 65–95% of the diet, compared to 0–12% in higher (>300 m) elevation forests (10 territories). The Common Ringtail Possum constituted, numerically, 49% of prey items in southeastern NSW (28 territories), but 62% on the Central Coast (19 territories) (Table 1). The Sugar Glider (125 g; Strahan 1995) comprised only 7% of prey items across all sites, but appeared to be taken more commonly in southeastern NSW (9%) than on the Central Coast (6%). The Greater Glider *Petauroides volans* (1300 g; Strahan 1995) comprised 12% of prey items across all sites, but occasionally predominated at particular sites. For example, two sites (Nunnock Swamp

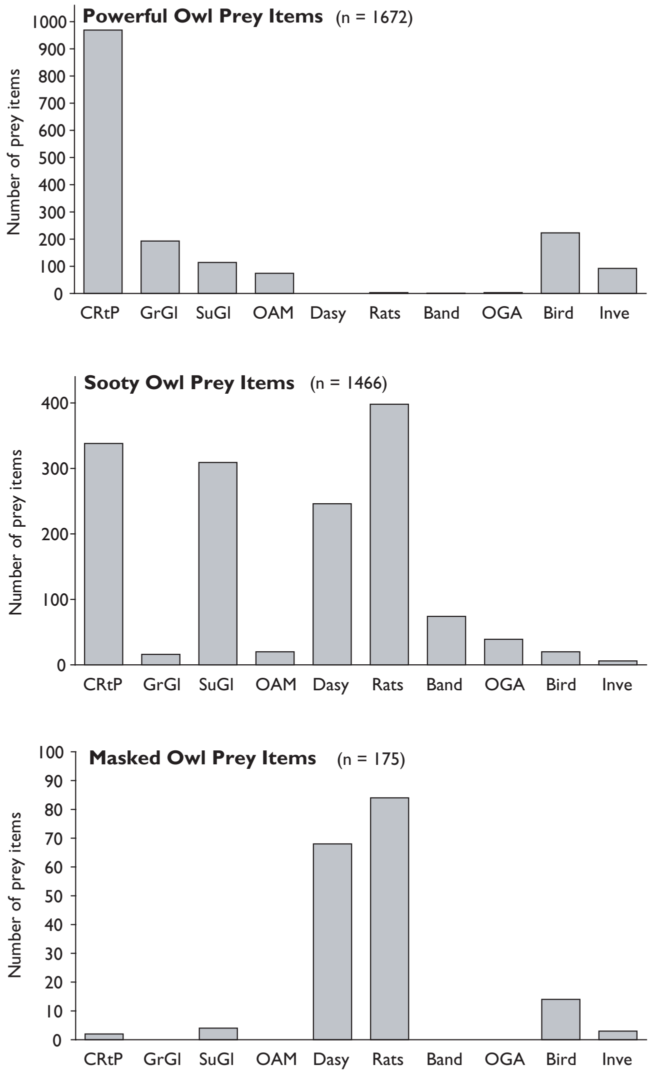
Table 1. Comparative diets of the Powerful Owl, Sooty Owl and Masked Owl in southeastern NSW and on the Central Coast of NSW.

Data are the proportions by number (%) of each prey species taken across all study sites, using owl pellet data only.

Prey item	**Southeastern N.S.W.**			**Central Coast**		
	Powerful Owl	**Sooty Owl**	**Masked Owl**	**Powerful Owl**	**Sooty Owl**	**Masked Owl**
Arboreal mammals	**91.2**	**47.6**	**4.6**	**76.5**	**44.3**	**0**
Common Ringtail Possum	48.6	23.0	1.5	61.6	23.3	0
Greater Glider	29.9	0.4	0	4.3	2.9	0
Yellow-bellied Glider	2.1	0.8	0	0	0	0
Sugar Glider	9.1	22.6	3.1	5.9	17.2	0
Mountain Brushtail Possum	0.2	0	0	0	0	0
Common Brushtail Possum	1.3	0.2	0	1.9	0.2	0
Eastern Pygmy Possum	0	0.6	0	0	0.5	0
Koala	0	0	0	0.3	0	0
Grey-headed Flying Fox	0	0	0	2.5	0	0
Micro-bat (*Nyctophilus*?)	0	0	0	0	0.2	0
Terrestrial mammals	**0**	**51.5**	**89.4**	**0.5**	**48.1**	**79.5**
Red-necked Wallaby	0	0	0	0.1	0	0
Long-nosed Bandicoot	0	4.6	0	0.1	3.9	0
Southern Brown Bandicoot	0	1.0	0	0	0	0
Brown Antechinus	0	10.6	29.0	0	10.9	0
Dusky Antechinus	0	8.2	22.9	0	0.2	0
White-footed Dunnart	0	0.2	0	0	0	0
Bush Rat	0	25.0	35.9	0	18.5	0
Black Rat	0	0	0.8	0.3	12.9	70.5
Swamp Rat	0	0.2	0	0	0	0
Broad-toothed Rat	0	0.1	0	0	0	0
House Mouse	0	0	0.8	0	0.7	9.1
European Rabbit	0	1.6	0	0	1.0	+
Other	**8.7**	**1.2**	**6.1**	**23.0**	**7.5**	**20.5**
Birds	5.5	1.0	3.8	16.4	2.2	20.5
Reptiles	0	0.1	0	0.2	4.1	0
Crustaceans	0	0	0	0.2	0.2	0
Insects	3.2	0.1	2.3	6.2	1.0	0
Total	471	1054	131	1201	412	44

and Blue Gum Swamp Creek) accounted for 86% of all records for this prey item. Both sites, and most other territories where the Greater Glider was recorded in owl diets, occurred in high elevation (>300m) forests where this species was usually abundant and the Common Ringtail Possum was rare or absent. No Greater Gliders were recorded in 17 of the 19 owl territories on the Central Coast of New South Wales, where low fertility soils do not support forests capable of providing habitat for this species (Braithwaite 1984, Kavanagh & Lambert 1990), although the Common Ringtail Possum may be abundant.

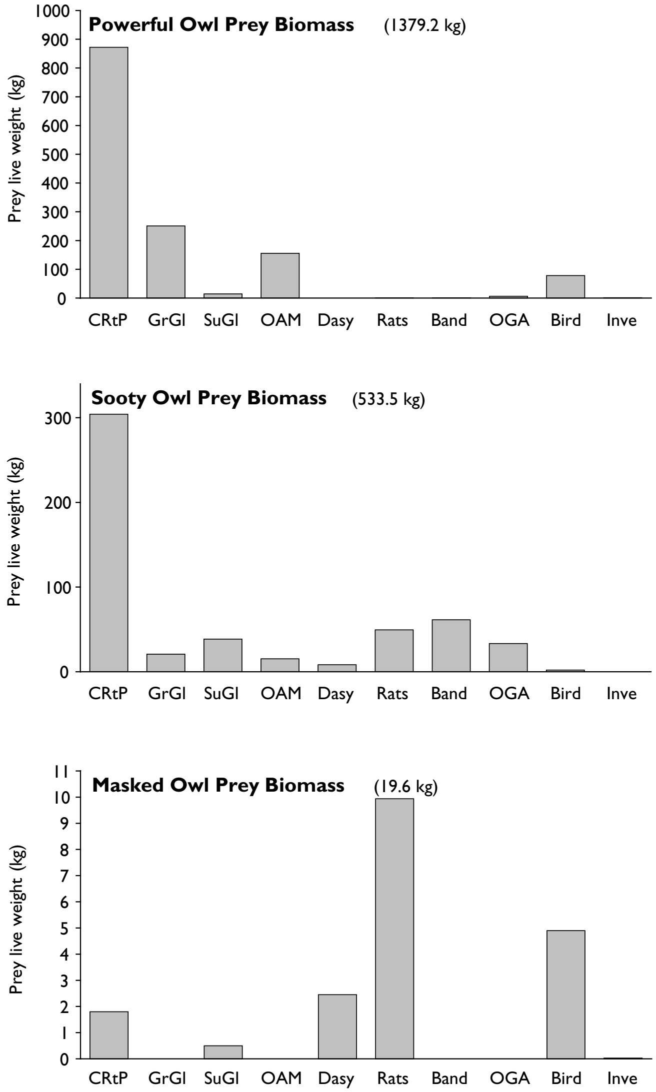
Birds comprised 13% of prey items across all sites but, as indicated above, differences between regions were apparent. In southeastern NSW, birds comprised only 6% of prey items across 28 territories of the Powerful Owl. This contrasts with 16% of prey items across 19 territories on the



Code	Prey Group	Code	Prey Group
CRtP	Common Ringtail Possum	Rats	Rodents
GrGl	Greater Glider	Band	Bandicoots
SuGl	Sugar Glider	OGA	Other Ground Animals
OAM	Other Arboreal Mammals	Bird	Birds
Dasy	Small Dasyurids	Inve	Invertebrates

Fig. 1. Numbers of major prey items in owl diets in southeastern NSW and the Central Coast of NSW; (a) Powerful Owl (*n* = 47 owl territories); (b) Sooty Owl (*n* = 28 owl territories); (c) Masked Owl (*n* = 6 owl territories or locations).

Central Coast of NSW where many sites occurred in close proximity to urban areas and the forest habitat for owls was located on low fertility soils derived from Hawkesbury Sandstone geology. The bird species most commonly taken by the Powerful Owl were the Pied Currawong *Strepera graculina* (350 g; Strahan 1995) and Crimson Rosella *Platycercus elegans* (150 g; Crome & Shields 1992).



Code	Prey Group	Code	Prey Group
CRtP	Common Ringtail Possum	Rats	Rodents
GrGl	Greater Glider	Band	Bandicoots
SuGl	Sugar Glider	OGA	Other Ground Animals
OAM	Other Arboreal Mammals	Bird	Birds
Dasy	Small Dasyurids	Inve	Invertebrates

Fig. 2. Biomass contributions of major prey items in owl diets in southeastern NSW and the Central Coast of NSW; (a) Powerful Owl (*n* = 47 owl territories); (b) Sooty Owl (*n* = 28 owl territories); (c) Masked Owl (*n* = 6 owl territories or locations).

Also recorded were the Galah *Cacatua roseicapilla* (350 g; Crome & Shields 1992), Rainbow Lorrikeet *Trichoglossus haematodus* (130 g; Crome & Shields 1992), King Parrot *Alisterus scapularis* (225 g; Crome & Shields 1992) and Sulphur-crested Cockatoo *Cacatua galerita* (775 g; Crome & Shields 1992). The average prey weight for these birds was taken to be approximately 350 g.

Insects, mainly large arboreal Christmas Beetles (Scarabaeidae) and large Ghost Moths (Hepialidae), made up more than 5% of the diet of Powerful Owls (each pellet sample containing insects was given the value of one), but insects were used by owls at many (15) sites.

The Grey-headed Flying Fox *Pteropus poliocephalus* (mean weight 675 g; Strahan 1995) comprised 2% of the diet of the Powerful Owl across all sites, however, this prey item was recorded only at four territories, all on the Central Coast. One site, Rocky Creek, was responsible for 77% of records for this species. The main roosting area for the Rocky Creek owls was less than two kilometres from a large, traditional maternity camp of these fruit bats and the owls were often heard calling nearby. The Common Brushtail Possum *Trichosurus vulpecula* (3,500 g; Strahan 1995) comprised 2% of Powerful Owl diets but this species was recorded at 10 sites.

The remaining prey species each comprised numerically less than 1% of the overall diet. These were the Yellow-bellied Glider *Petaurus australis* (575 g; Strahan 1995), Mountain Brushtail Possum *Trichosurus caninus* (4,000 g; Strahan 1995) and Koala *Phascolarctos cinereus* (6,000 g; Strahan 1995). Adults of the two latter species are much larger than the Powerful Owl, but some adults were taken even though the majority were juveniles. The paucity of records for the smaller Yellow-bellied Glider is notable given the widespread distribution of this species in southeastern New South Wales (Braithwaite 1983, Davey 1984, Kavanagh 1984, Lunney 1987, Kavanagh & Bamkin 1995).

Only nine (0.5%) prey items were from species which are terrestrial in habit. These included one Long-nosed Bandicoot *Perameles nasuta*, one juvenile Red-necked Wallaby *Macropus rufogriseus*, three unidentified rats (possibly Black Rat *Rattus rattus*), two unidentified reptiles (possibly Eastern Water Dragon *Physignathus lesueuri*), and two unidentified crustaceans (possibly freshwater crayfish). Several of these unusual records may represent errors in pellet sample identification.

The numerical proportions of prey taken by the Powerful Owl across all 47 sites are summarised in Fig. 1. These data were converted, using the approximate liveweight of individual prey items (see above), to indicate the contribution of each species to total prey biomass (Fig. 2). The importance of the Common Ringtail Possum and the Greater Glider to the Powerful Owl is clearly illustrated.

Sooty Owl

The diet of the Sooty Owl across all sites was characterised by a much broader range of prey species or prey groups (22) than that of the Powerful Owl (Table 1; Fig. 1). In addition to all of the common arboreal prey species taken by the Powerful Owl, the Sooty Owl took large numbers of terrestrial mammals, ranging in size from the House Mouse *Mus musculus* (13 g; Strahan 1995) to the Long-nosed Bandicoot *Perameles nasuta* (mean weight 850 g; Strahan 1995) and European Rabbit *Oryctolagus cuniculus* (1,500 g; Strahan 1995).

The Sooty Owl appeared to be a dietary generalist that hunted throughout the vertical strata of its habitat from the tops of trees to the ground, taking mainly the largest available mammalian prey and those other smaller prey that were relatively abundant. Despite the diversity of prey types, four species were taken at almost every site, namely the Common Ringtail Possum, Sugar Glider, Brown Antechinus *Antechinus stuartii* and Bush Rat *Rattus fuscipes*. Relatively few birds or insects were taken, compared to the Powerful Owl. A regional comparison of Sooty Owl diets revealed no significant difference in the numbers of three main prey groups (all arboreal mammals, all terrestrial mammals and birds) in southeastern NSW compared to the Central Coast of NSW ($\chi^2 = 3.31$, df. = 2, $P = 0.19$).

The Common Ringtail Possum comprised 23% of prey items across all sites, with no marked difference between southeastern New South Wales and the Central Coast (Table 1). This species was the most significant component by biomass in the diet of the Sooty Owl (Fig. 2). Only at three sites (where few pellets were collected) was the Common Ringtail Possum unrecorded. The Sugar Glider comprised 21% of prey items across all sites, but appeared to be taken more commonly in southeastern New South Wales (23%) than on the Central Coast (17%). The Sugar Glider formed a greater proportion of the diet of the Sooty Owl than of the Powerful Owl.

The Bush Rat (125 g; Strahan 1995) and the introduced Black Rat *Rattus rattus* (125 g) were occasionally difficult to distinguish in pellets, so the numbers of these two species were lumped in this analysis. The majority of confident identifications were attributed to the Bush Rat, while the Black Rat was reliably recorded in Sooty Owl pellets only near Sydney. Both rats together comprised 27% of prey items across all sites. Sooty Owl diets on the Central Coast appeared to consist of a greater proportion of rats (31%) than those in southeastern New South Wales (25%). Two additional rats (Muridae) were recorded occasionally in Sooty Owl pellets from southeastern New South Wales: the Swamp Rat *Rattus lutreolus* (125 g; Strahan 1995) and the Broad-toothed Rat *Mastacomys fuscus* (125 g).

The Brown Antechinus (25 g; Strahan 1995) and the Dusky Antechinus *Antechinus swainsonii* (50 g) comprised 11% and 6% of Sooty Owl diets across all sites. In southeastern New South Wales, where most records of the Dusky Antechinus were made, these two species together comprised 19% of the Sooty Owl diet. The Long-nosed Bandicoot and the Southern Brown Bandicoot *Isoodon obesulus* (700g; Strahan 1995) together comprised 5% of the recorded prey items but, because of their large size, they formed a substantial part of the overall prey biomass (Fig. 2). Birds were uncommon in Sooty Owl diets (1% of all prey items), and most of those taken were much smaller (approximately 100 g) than those taken by the Powerful Owl. Similarly, only few Greater Gliders (1% of all prey items) were taken by the Sooty Owl.

A wide range of additional prey was taken by the Sooty Owl, most of which were recorded only at a few sites. The European Rabbit comprised more than 1% of all prey items but nearly all records came from one location (Bodalla State Forest). Other species taken occasionally (each comprising less than 1% of the diet) included the Yellow-bellied Glider, Eastern Pygmy Possum *Cercartetus nanus* (25 g; Strahan 1995), Common Brushtail Possum, House Mouse and the White-footed Dunnart *Sminthopsis leucopus* (23 g; Strahan 1995). Insects (beetles) were recorded only in five pellet samples from three sites. Eighteen unidentified reptiles (possibly Eastern Water Dragon), one unidentified crustacean (possibly freshwater crayfish) and one micro-chiropteran bat (possibly *Nyctophilus* sp.) were also recorded.

The numerical and biomass proportions of prey taken by the Sooty Owl across all 28 sites are summarised in Fig. 1 and Fig. 2. The importance of the Common Ringtail Possum and the Bush Rat is clearly illustrated.

Masked Owl

The Masked Owl appeared to be a specialised predator of small terrestrial mammals although samples were limited. Four small terrestrial and scansorial (climbing) mammals numerically comprised 85% of the recorded diet. However, a small number of arboreal prey was also taken.

Arboreal marsupials comprised only 3% (Sugar Glider) and 2% (Common Ringtail Possum) of prey items, while birds comprised 8%. A regional comparison of Masked Owl diets showed that birds were taken significantly more often on the Central Coast of NSW than in southeastern NSW, with relatively minor differences between regions in the contribution of all species of arboreal mammals grouped together, and all terrestrial mammals ($\chi^2 = 13.6$, df. = 2, $P < 0.01$).

No prey species additional to those recorded for the Powerful Owl and Sooty Owl were recorded. The native Bush Rat (29% of prey items) and the introduced Black Rat (13%) together comprised 43% of the diet of the Masked Owl. The scansorial Brown Antechinus (24% of prey items) and the terrestrial Dusky Antechinus (19%) together comprised another 43% of the diet. The introduced House Mouse was also taken occasionally (>1% of prey items). Only trace quantities of beetles were recorded in some Masked Owl pellets.

An interesting contrast occurred between the mammalian prey of a pair of Masked Owls living within an entirely forested environment (Old Hut Creek near Eden in southeastern NSW), which included only native prey species, and the diet of another pair living in a highly fragmented semi-urban environment (Warners Bay near Newcastle on the Central Coast of NSW), which included only introduced species (Table 1). Additional prey remains found below regular nocturnal perches of the Masked Owls at Warners Bay suggested that these owls also consumed European Rabbits and a number of birds, including the Sulphur-crested Cockatoo and Tawny Frogmouth *Podargus strigoides*. The average prey weight for these birds, as for the Powerful Owl, was taken to be approximately 350 g.

The proportions of prey taken by the Masked Owl across all six sites are summarised by numbers and by biomass in Fig. 1 and Fig. 2. The importance in terms of biomass of the Bush Rat or the Black Rat, and also birds, to the Masked Owl is clearly illustrated.

Species comparisons

The diets of the three owls, assessed across all sites and in terms of the total numbers of arboreal mammals, terrestrial mammals, birds and insects recorded, were significantly different ($\chi^2 = 1429.0$, df. = 6, $P < 0.01$). Powerful Owls took more arboreal mammals, birds and insects and fewer terrestrial mammals than expected on the basis of comparisons with the other two species. Both the Sooty Owl and the Masked Owl took more terrestrial mammals and fewer arboreal mammals (less significant for the Sooty Owl) than expected, and the Sooty Owl took fewer birds and insects than expected on the basis of comparisons between all three owl species.

DISCUSSION

There was virtually no overlap between the diets of the Powerful Owl, assessed across all sites, and the Masked Owl. The Powerful Owl preyed almost exclusively on arboreal mammals, most of which weighed approximately 800–1,700 g, or 50–100% of adult owl body weight, supplemented by diurnal birds. In contrast, the Masked Owl preyed almost exclusively on small terrestrial and scansorial mammals, most of which weighed approximately 25–125 g, or 3–20% of adult owl body weight, supplemented by diurnal birds. At any one site, both owls appeared to specialise on just one or two prey species. The diet of the Sooty Owl was more diverse, including a wide range of both arboreal and terrestrial or scansorial mammals at any one site, most of which weighed approximately 25–900 g, or 2% to over 100% of adult owl body weight. The Sooty Owl appeared to take any available small or medium-sized mammal and foraged throughout its more limited habitat (rainforest, tall moist eucalypt forest) from the forest canopy to the ground.

Studies of dietary overlap among raptor assemblages are usually undertaken at a regional scale, and are often taken to indicate the potential for competition (Lack 1946, Marti 1974, Herrera & Hiraldo 1976, Jaksic 1983, Korpimaki 1986, Hayward & Garton 1988). However, to understand whether competition is likely to affect raptor populations and distributions, comparisons need to be done at the local scale of overlapping pairs (Marti *et al.* 1993). According to these latter authors, only two studies (Nilsson 1984, Korpimaki 1987) had attempted to connect the breeding success of raptors with competition for food. Both showed reduced breeding success in the presence of a competitor.

The results of the present study are reported generally at the regional scale, although attempts were made in several localities to compare the diet and breeding success of overlapping species pairs. Only at one site (Bellbird Creek near Eden) was this achieved effectively. Of 12 prey types or prey groups (including 'birds' and 'insects'), only four (Common Ringtail Possum, Sugar Glider, Yellow-bellied Glider and 'birds') were taken by both the resident overlapping pairs of Powerful Owl and Sooty Owl. The Powerful Owl took an additional three prey types (Greater Glider, Common Brushtail Possum and 'insects'), two of which were very large items (>1500 g), while another five species were taken exclusively by the Sooty Owl (Bush Rat, Brown Antechinus, Dusky Antechinus, Eastern Pygmy Possum and Long-nosed Bandicoot). Despite these differences, one species, the Common Ringtail Possum, formed about 66% of the biomass taken by the Sooty Owl and more than 81% of the prey biomass taken by the Powerful Owl. This suggests that, unless the Common Ringtail Possum was in plentiful supply (as appeared to be the case), competition for food might occur between these two species at Bellbird Creek. Unfortunately, breeding could not be confirmed for the Sooty Owl pair during the study, although it may have occurred, while the Powerful Owl pair produced two young (the maximum number) in each of three consecutive years (1992–1994).

The range of prey species taken by the Powerful Owl, Sooty Owl and Masked Owl was generally as reported in the literature (Fleay 1968, Seebeck 1976, Hyem 1979, James 1980, Schodde & Mason 1980, Van Dyck & Gibbons 1980, Tilley 1982, Smith 1984, Loyn *et al.* 1986, Barker & Vestjens 1989, Hollands 1991, Chafer 1992, Debus 1993, 1994, Lundie-Jenkins 1993, Mooney 1993, Peake *et al.* 1993, Debus & Chafer 1994, Debus & Rose 1994, Holmes 1994, Lavazanian *et al.* 1994, Pavey 1994, 1995, Pavey *et al.* 1994, McNabb 1996). Differences in the recorded importance of particular prey species (the Greater Glider and the Common Ringtail Possum) to the Powerful Owl (Kavanagh 1992; Pavey 1992) simply reflect geographical variation.

The present study, like many others (e.g. Donázar 1987), found that geographical variations in owl diets were related to differences in the availability of potential prey. For example, the Greater Glider was abundant in the higher elevation forests of southeastern New South Wales (Kavanagh & Peake 1993, Kavanagh & Bamkin 1995; see also Kavanagh 1984, 1988) and formed more than 97% of total prey biomass for one pair of Powerful Owls (Nunnock Swamp pair). However, the Greater Glider was uncommon or absent in the lower elevation forests of the region where the Common Ringtail Possum formed the main component of Powerful Owl (and Sooty Owl) diets. On the Central Coast of New South Wales, the Greater Glider was absent at most sites, but at one site (Blue Gum Swamp Creek) this species formed nearly 68% of prey biomass and the Common Ringtail Possum, which was also present but not abundant, formed only 9% of prey biomass. Thus, the greater proportion of low elevation (<300 m) sites in this study (79%)

may have underestimated the overall importance of the Greater Glider in the diet of the Powerful Owl. Also, birds were taken more frequently by both Powerful Owls and Masked Owls living in bushland fragmented by urban and rural developments where arboreal marsupials are usually less abundant. Masked Owls preyed extensively on introduced species of small terrestrial mammals in highly disturbed environments but took only native species in less disturbed forests (see also Kavanagh 1996, Kavanagh & Murray 1996).

The general patterns of distribution, habitat and habits of arboreal marsupials and small terrestrial mammals in the forests of eastern Australia are summarised by Strahan (1995). Information about the susceptibility of the main prey species to habitat alteration is crucial for owl conservation. The marsupial gliders have been identified as potentially sensitive to a general reduction in the extent of old-growth forest due to their requirements for large hollows in old trees for shelter and breeding and their habit of foraging in the forest canopy (Tyndale-Biscoe & Calaby 1975, Kavanagh 1991, Scotts 1991). The two largest gliders, the Greater Glider and the Yellow-bellied Glider, are reported to have the closest associations with old-growth forest habitats (Kavanagh 1987, Lunney 1987, Macfarlane 1988, Lindenmayer *et al.*1990, Milledge *et al.*1991, Kavanagh & Bamkin 1995, Kavanagh & Webb 1998, Kavanagh 2000). The Sugar Glider, Feathertail Glider and Mountain Brushtail Possum use large old trees but are less demanding in their requirements, as shown by their varying associations with characteristics of the understorey (Smith 1982, Kavanagh 1984, 1987a, Seebeck *et al.* 1984, Lunney 1987, Lindenmayer *et al.*1990, 1996, Goldingay & Kavanagh 1995). The more adaptable and fecund Common Ringtail Possum and the Common Brushtail Possum use (but do not require) tree hollows for shelter. Both commonly utilise disturbed environments, and the Common Ringtail Possum forages extensively, and builds leaf shelters (dreys), among dense understorey and forest regrowth (Thomson & Owen 1964, Davey 1984, How *et al.* 1984, Kerle 1984, Pahl 1987, Lunney 1987, Macfarlane 1988).

Many species of small ground-dwelling mammals also use trees as nesting or foraging sites (Wood 1970, Dickman 1991), making use of hollows, loose bark on the trunk and upper branches, leaf and bark litter around the base of trees and logs on the ground. However, the composition of the ground-dwelling mammal fauna in southeastern New South Wales is determined principally by the structural complexity of the understorey and ground layer (Catling & Burt 1995a). Logging and prescribed burning result in dynamic changes to understorey conditions that are tracked rapidly by populations of small ground mammals (Recher *et al.* 1980, Lunney *et al.* 1987, Macfarlane 1988, Catling 1991, Kavanagh & Webb 1998). Logging is generally not regarded as having a long-term (>10 years) deleterious effect on populations of most small ground mammals but frequent, low-intensity prescribed burns can simplify forest structure.

Owl prey (arboreal and terrestrial mammals) in southeastern New South Wales tend to be most abundant in gully or riparian forests on lower slope topography and, except for the Greater Glider, at lower elevations in the region (Kavanagh & Peake 1993, Catling & Burt 1995b, Kavanagh & Bamkin 1995, Kavanagh 1997). However, the structural characteristics of the vegetation in many gully forests, and potentially also in forests regenerating after logging, could reduce the availability of prey for the owls (e.g. Southern & Lowe 1968). Thus species such as the Masked Owl, which prey almost exclusively on small terrestrial mammals, may hunt most efficiently in open forests where the ground cover is patchy or sparse, but close to dense cover which provides good habitat for small ground mammals.

The degree of resilience by owls to habitat disturbance may be predicted by their ability to switch to alternative prey (Korpimaki & Norrdahl 1989) and by the population responses of their prey species to disturbance. The Sooty Owl is a dietary generalist compared to the Powerful Owl and the Masked Owl and may therefore be better adapted to habitat alteration. The Powerful Owl and the Masked Owl have more specialised but different diets due to vertical partitioning of the forest as foraging habitat. Owing to its specialisation on arboreal mammal prey, the Powerful Owl is predicted to be more sensitive to habitat disturbance by logging than either the Sooty Owl or the Masked Owl. This sensitivity is likely to be most acute in the higher elevation forests where the Greater Glider forms the main prey of the Powerful Owl.

Despite the overall differences in diet between the three owls, the overlap was considerable. Both Powerful Owl and Sooty Owl took many Common Ringtail Possums, and similarly the Sooty Owl and Masked Owl took many Bush Rats and Antechinuses. In a review of the mechanisms involved in resource partitioning in ecological communities, Schoener (1974) regarded habitat differences to be more frequent than diet differences, which in turn were more frequent than temporal differences in feeding. Clearly, food competition between forest owls is possible, especially where prey abundance is reduced by disturbance. However, differences in habitat may reduce this competition.

The Powerful Owl is widespread throughout most forest environments east of the Great Dividing Range from wet to dry forest types, including some woodlands (e.g. Kavanagh & Peake 1993, Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995). The Sooty Owl, which overlaps in diet most with the Powerful Owl (arboreal marsupials), was almost confined to the wettest forests but occasionally ventured into drier forests where cave-roosting sites were available (Kavanagh & Jackson 1997). The Masked Owl, which overlaps in diet most with the Sooty Owl (small terrestrial mammals), appeared to avoid the wetter forests and to exploit only the drier, more open forests. While the Powerful Owl and Masked Owl may occur together in drier forest types, the diets of these two species were almost mutually exclusive.

ACKNOWLEDGMENTS

All pellet samples collected in southeastern New South Wales were analysed by Barbara Triggs (the acknowledged Australian expert on identification of mammalian hair and bones), as were some of the samples collected from all other study sites. Mark Chidel analysed most of the remaining pellets using reference samples provided by Barbara. Tony (A.B.) Rose and Chris-Anne Urquhart identified the beetles and moth larvae responsible for consuming the mammalian hair within owl pellets. A number of colleagues collected owl pellets within the study sites, including Khia Atkins, David Coombes, Richard Jackson, Michael Murray, Sandy Sansom, Matthew Stanton, Dick Turner and Judy Wiles. I am most grateful to all of the above for their assistance. Very helpful comments on the manuscript were provided by Ian Newton and an anonymous referee.

REFERENCES

Barker, R.D. & Vestjens, W.J.M. 1989. *The Food of Australian Birds. 1. Non-Passerines*. Melbourne: CSIRO.

Braithwaite, L.W. 1983. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, N.S.W. I. The species and distribution of animals. *Aust. Wildl. Res.* **10:** 219–229.

Braithwaite, L.W. 1984. The identification of conservation areas for possums and gliders in the Eden Woodpulp Concession District. In Smith, A.P. & Hume, I. D. (eds.) *Possums and Gliders*: 501–508. Sydney: Australian Mammal Society.

Brown, J.H., Davidson, D.W., Munger, J.C. & Inouye, R.S. 1986. Experimental community ecology: the desert granivore system. In Diamond, J. & Case, T.J. (eds.) *Community Ecology*: 41–61. New York: Harper and Row.

Brunner, H. & Coman, B. 1974. *The Identification of Mammalian Hair*. Melbourne: Inkata Press.

Catling, P.C. 1991. Ecological effects of prescribed burning practices on the mammals of southeastern Australia. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 353–363. Mosman: Royal Zoological Society of New South Wales.

Catling, P.C. & Burt, R.J. 1995a. Studies of the ground-dwelling mammals of eucalypt forests in south-eastern New South Wales: the effect of habitat variables on distribution and abundance. *Wildl. Res.* **22:** 271–288.

Catling, P.C. & Burt, R.J. 1995b. Studies of the ground-dwelling mammals of eucalypt forests in south-eastern New South Wales: the effect of environmental variables on distribution and abundance. *Wildl. Res.* **22:** 669–685.

Chafer, C.J. 1992. Observations of the Powerful Owl *Ninox strenua* in the Illawarra and Shoalhaven Regions of New South Wales. *Aust. Bird Watcher* **14:** 289–300.

Crome, F. & Shields, J. 1992. *Parrots and Pigeons of Australia*. Sydney: Angus and Robertson.

Davey, S.M. 1984. Habitat preferences of arboreal marsupials within a coastal forest in southern New South Wales. In Smith, A.P. & Hume, I. D. (eds.) *Possums and Gliders*: 509–516. Sydney: Australian Mammal Society.

Debus, S.J.S. 1993. The mainland Masked Owl *Tyto novaehollandiae*: a review. *Aust. Bird Watcher* **15:** 168–191.

Debus, S.J.S. 1994. The Sooty Owl *Tyto tenebricosa* in New South Wales. *Aust. Birds* **28** (supplement)**:** 4–19.

Debus, S.J.S. & Chafer, C.J. 1994. The Powerful Owl *Ninox strenua* in New South Wales. *Aust. Birds* (Supplement) **28:** 21–38.

Debus, S.J.S. & Rose, A.B. 1994. The Masked Owl *Tyto novaehollandiae* in New South Wales. *Aust. Birds* (Supplement) **28:** 40–64.

Dickman, C.R. 1991. Use of trees by ground-dwelling mammals: implications for management. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 125–136. Mosman: Royal Zoological Society of New South Wales.

Donázar, J.A. 1987. Geographic variations in the diet of Eagle Owls in Western Mediterranean Europe. In Nero, R.W., Clark, R.J., Knapton R.J. & Hamre, R.H. (eds.) *Biology and Conservation of Northern Forest Owls*: 220–224. USDA Forest Service General Technical Report RMñ142, Fort Collins, Colorado.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. (Reprinted 1979). Brisbane: Jacaranda Press.

Goldingay, R.L. & Kavanagh, R.P. 1995. Foraging behaviour and habitat use of the Feathertail Glider (*Acrobates pygmaeus*) at Waratah Creek, New South Wales. *Wildl. Res.* **22:** 457–470.

Hansson, L. & Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* **67:** 394–402.

Hayward, G.D. & Garton, E.O. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* (*Berlin*) **75:** 253–265.

Herrera, C.M. & Hiraldo, F. 1976. Food-niche and trophic relationships among European owls. *Ornis Scand.* **7:** 29–41.

Hollands, D. 1991. *Birds of the Night. Owls, Frogmouths and Nightjars of Australia*. Sydney: Reed Books.

Holmes, G. 1994. Prey of the Sooty Owl in subtropical Australia. *Sunbird* **24:** 25–27.

Houston, C.S. 1987. Nearly synchronous cycles of the Great Horned Owl and Snowshoe Hare in Saskatchewan. In Nero, R.W., Clark, R.J., Knapton R.J. & Hamre, R.H. (eds.) *Biology and Conservation of Northern Forest Owls*: 56–58. USDA Forest Service General Technical Report RM–142, Fort Collins, Colorado.

How, R.A., Barnett, J.L., Bradley, A.J., Humphreys, W.F. & Martin, R. 1984. The population biology of *Pseudocheirus peregrinus* in a *Leptospermum laevigatum* thicket. In Smith, A.P. & Hume, I. D. (eds.) *Possums and Gliders*: 261–268. Sydney: Australian Mammal Society.

Hyem, E.L. 1979. Observations on owls in the Upper Manning River District, N.S.W. *Corella* **3:** 17–25.

Jaksic, F.M. 1983. The trophic structure of sympatric assemblages of diurnal and nocturnal birds of prey. *Amer. Midl. Nat.* **109:** 152–162.

James, J.W. 1980. Food of the Powerful Owl *Ninox strenua* in south-eastern Queensland. *Emu* **80:** 34–35.

Kavanagh, R.P. 1984. Seasonal changes in habitat use by gliders and possums in southeastern New South Wales. In Smith, A.P. & Hume, I.D. (eds.) *Possums and Gliders*: 527–543. Sydney: Australian Mammal Society.

Kavanagh, R.P. 1987. *Floristic and phenological characteristics of a eucalypt forest in relation to its use by arboreal marsupials*. M.Sc. Thesis, Australian National University, Canberra.

Kavanagh, R.P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Australian Journal of Ecology* **13**, 445–450.

Kavanagh, R.P. 1991. The target species approach to wildlife management: gliders and owls in the forests of south-eastern New South Wales. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 377–383. Mosman: Royal Zoological Society of New South Wales.

Kavanagh, R.P. 1992. Reply: The impact of predation by the Powerful Owl *Ninox strenua* on a population of the Greater Glider *Petauroides volans*. *Aust. J. Ecol.* **17:** 469–472.

Kavanagh, R.P. 1996. The breeding biology and diet of the Masked Owl *Tyto novaehollandiae* near Eden, New South Wales. *Emu* **96:** 158–165.

Kavanagh, R.P. 1997. *Ecology and Management of Large Forest Owls in South-eastern Australia*. Ph.D. Thesis, University of Sydney, Sydney.

Kavanagh, R.P. 2000. Effects of variable-intensity logging and the influence of habitat variables on the distribution of the Greater Glider *Petauroides volans* in montane forest, southeastern New South Wales. *Pac. Cons. Biol.* **6:** 18–30.

Kavanagh, R.P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biol. Conserv*. **71**: 41–53.

Kavanagh, R.P., Debus, S., Tweedie, T. & Webster, R. 1995. Distribution of nocturnal forest birds and mammals in north-eastern New South Wales: Relationships with environmental variables and management history. *Wildl. Res*. **22**: 359–377.

Kavanagh, R.P. & Jackson, R. 1997. Home-range, movements, habitat and diet of the Sooty Owl *Tyto tenebricosa* near Royal National Park, Sydney. In Czechura, G.V. & Debus, S.J.S. (eds.) *Australian Raptor Studies 2*: 2–13. Birds Australia Monograph No. 3. Melbourne: Royal Australasian Ornithologists Union.

Kavanagh, R.P. & Lambert, M.J. 1990. Food selection by the Greater Glider, *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? *Aust. Wildl. Res*. **17**: 285–299.

Kavanagh, R.P. & Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96:** 250–257.

Kavanagh, R.P. & Peake, P. 1993. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In P. Olsen (ed.) *Australian Raptor Studies*: 101–125. Melbourne: Royal Australasian Ornithologists Union.

Kavanagh, R.P. & Webb, G.A. 1998. Effects of variable-intensity logging on mammals, reptiles and amphibians at Waratah Creek, southeastern New South Wales. *Pac. Cons. Biol.* **4:** 326–347.

Kerle, J.A. 1984. Variation in the ecology of *Trichosurus*: its adaptive significance. In Smith, A.P. & Hume, I. D. (eds.) *Possums and Gliders*: 115–128. Sydney: Australian Mammal Society.

König, C., Weick, F. & Becking, J.-H. 1999. *Owls*: *A Guide to the Owls of the World*. New Haven: Yale University Press.

Korpimaki, E. 1986. Niche relationships and life-history tactics of three sympatric *Strix* owl species in Finland. *Ornis Scand.* **17:** 126–132.

Korpimaki, E. 1987. Dietary shifts, niche relationships, and reproductive output of co-existing Kestrels and Long-eared Owls. *Oecologia* (*Berlin*) **74:** 277–285.

Korpimaki, E. 1992. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds.) *The Ecology and Conservation of European Owls*: 1–10. UK Nature Conservation No. 5, Joint Nature Conservation Committee, Peterborough, UK.

Korpimaki, E. & Norrdahl, K. 1989. Predation of Tengmalm's Owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. *Oikos* **54:** 154–164.

Krebs, C.J. & Myers, J.H. 1974. Population cycles in small mammals. *Adv. Ecol. Res.* **8:** 267–399.

Lack, D. 1946. Competition for food by birds of prey. *J. Anim. Ecol.* **15:** 123–129.

Lavazanian, E., Wallis, R. & Webster, A. 1994. Diet of Powerful Owls (*Ninox strenua*) living near Melbourne, Victoria. *Wildl. Res.* **21:** 643–646.

Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. & Nix, H.A. 1990. Habitat requirements of the Mountain Brushtail Possum and the Greater Glider in the montane ash-type eucalypt forests of the Central Highlands of Victoria. *Aust. Wildl. Res.* **17:** 467–478.

Lindenmayer, D.B., Welsh, A., Donnelly, C.F. & Meggs, R.A. 1996. Use of nest trees by the Mountain Brushtail Possum (*Trichosurus caninus*) (Phalangeridae: Marsupialia). I. Number of occupied trees and frequency of tree use. *Wildl. Res.* **23:** 343–361.

Loyn, R.H., Traill, B.J. & Triggs, B.E. 1986. Prey of Sooty Owls in East Gippsland before and after fire. *Victorian Nat.* **103:** 147–149.

Lundberg, A. 1980. Why are the Ural Owl *Strix uralensis* and the Tawny Owl *S. aluco* parapatric in Scandinavia? *Ornis Scand.* **11:**, 116–120.

Lundie-Jenkins, G. 1993. The diet of the Sooty Owl *Tyto tenebricosa* in the Blue Mountains, N.S.W. *Emu* **93:** 124–127.

Lunney, D. 1987. Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, N.S.W. *Aust. Wildl. Res.* **14:** 263–274.

Lunney, D., Cullis, B. & Eby, P. 1987. Effects of logging and fire on small mammals in Mumbulla State Forest, near Bega, New South Wales. *Aust. Wildl. Res.* **14:** 163–181.

Macfarlane, M.A. 1988. Mammal populations in Mountain Ash (*Eucalyptus regnans*) forests of various ages in the Central Highlands of Victoria. *Aust. For.* **51:** 14–27.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. *Condor* **76:** 45–61.

Marti, C.D., Korpimaki, E. & Jaksic, F.M. 1993. Trophic structure of raptor communities: a three-continent comparison and synthesis. In Power, D.M. (ed.) *Current Ornithology* **10**: 47–137. New York: Plenum Press.

McNabb, E.G. 1996. Observations on the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16:** 267–295.

Milledge, D.R., Palmer, C.L. & Nelson, J.L. 1991. 'Barometers of change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 53–65. Mosman: Royal Zoological Society of New South Wales.

Mooney, N. 1993. Diet of the Masked Owl in Tasmania: past and present. In P. Olsen (ed) *Australian Raptor Studies*: 160–174. Melbourne: Royal Australasian Ornithologists Union.

Newton, I. 2002. Population limitation in Holarctic Owls. This volume.

Nilsson, I.N. 1984. Prey weight, food overlap, and reproductive output of potentially competing Long-eared and Tawny Owls. *Ornis Scand.* **15:** 176–182.

Pahl, L.I. 1987. Feeding behaviour and diet of the Common Ringtail Possum, *Pseudocheirus peregrinus*, in *Eucalyptus* woodlands and *Leptospermum* thickets in southern Victoria. *Aust. J. Zool.* **35:** 487–506.

Pavey, C.R. 1992. Comment: Impact of Powerful Owl predation on a population of the Greater Glider: A response to Kavanagh (1988). *Aust. J. Ecol.* **17:** 463–467.

Pavey, C.R. 1994. Records of the food of the Powerful Owl *Ninox strenua* from Queensland. *Sunbird* **24:** 30–39.

Pavey, C.R. 1995. Food of the Powerful Owl *Ninox strenua* in suburban Brisbane, Queensland. *Emu* **95:** 231–232.

Pavey, C.R., Smyth, A.K. & Mathieson, M.T. 1994. The breeding season diet of the Powerful Owl *Ninox strenua* at Brisbane, Queensland. *Emu* **94:** 278–284.

Peake, P., Conole, L.E., Debus, S.J.S., McIntyre, A. & Bramwell, M. 1993. The Masked Owl *Tyto novaehollandiae* in Victoria. *Aust. Bird Watcher* **15:** 124–136.

Pianka, E.R. 1986. *Ecology and Natural History of Desert Lizards*. Princeton, New Jersey: Princeton University Press.

Recher, H.F., Rohan-Jones, W. & Smith, P. 1980. *Effects of the Eden Woodchip Industry on terrestrial vertebrates with recommendations for management*. Research Note No. 42, Forestry Commission of New South Wales, Sydney.

Schodde, R. & Mason, I. 1980. *Nocturnal Birds of Australia*. Melbourne: Landsdowne.

Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* **185:** 27–39.

Scotts, D.J. 1991. Old-growth forests: their ecological characteristics and value to forest-dependent vertebrate fauna of south-east Australia. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 147–159. Mosman: Royal Zoological Society of New South Wales.

Seebeck, J.H. 1976. The diet of the Powerful Owl, *Ninox strenua*, in western Victoria. *Emu* **76:** 167–170.

Seebeck, J.H., Warneke, R.M. & Baxter, B.J. 1984. Diet of the Bobuck, *Trichosurus caninus* (Ogilby) (Marsupialia: Phalangeridae) in a mountain forest in Victoria. In Smith, A.P. & Hume, I. D. (eds.) *Possums and Gliders*: 145–154. Sydney: Australian Mammal Society.

Smith, A.P. 1982. Diet and feeding strategies of the marsupial Sugar Glider in temperate Australia. *J. Anim. Ecol.* **51:** 149–166.

Smith, P. 1984. Prey items of the Sooty Owl and Barn Owl at Bega, New South Wales. *Corella* **8:** 71–72.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool., London* **162:** 197–285.

Southern, H.N. & Lowe, V.P.W. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *J. Anim. Ecol.* **37:** 75–97.

Strahan, R. 1995. *The Mammals of Australia*. (2nd ed.). Sydney: Reed Books.

Taylor, I.R. 1992. An assessment of the significance of annual variations in snow cover in determining short-term population changes in Field Voles *Microtus agrestis* and Barn Owls *Tyto alba* in Britain. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds.) *The Ecology and Conservation of European Owls*: 32–38. UK Nature Conservation No. 5, Joint Nature Conservation Committee, Peterborough, UK.

Thomson, J.A. & Owen, W.H. 1964. A field study of the Australian Ringtail Possum *Pseudocheirus peregrinus* (Marsupialia: Phalangeridae). *Ecol. Monog.* **34:** 27–52.

Tilley, S. 1982. The diet of the Powerful Owl, *Ninox strenua*, in Victoria. *Aust. Wildl. Res.* **9:** 157–175.

Tyndale-Biscoe, C.H. & Calaby, J.H. 1975. Eucalypt forests as refuge for wildlife. *Aust. For.* **38:** 117–133.

Van Dyck, S. & Gibbons, D. 1980. Tuan predation by Powerful Owls. *Victorian Nat.* **97:** 58–63.

Wood, D.H. 1970. An ecological study of *Antechinus stuartii* (Marsupialia) in a south-east Queensland rainforest. *Aust. J. Zool.* **18:** 185–207.

18

NOTES ON THE DIET AND OBSERVATIONS OF THE SOUTHERN BOOBOOK (*NINOX NOVAESEELANDIAE*) IN SOUTHERN VICTORIA

EDWARD G. McNABB

Arthur Rylah Institute for Environmental Research, Department of Natural Resources and Environment, PO Box 137, Heidelberg 3084,Victoria, Australia.

Early studies suggested that the Southern *Boobook* (*Ninox novaeseelandiae*) feeds predominantly on small animals up to the size of House Mouse *Mus musculus*. Recent reports have shown it to take a wide range of prey, including invertebrates, amphibians, reptiles, birds and mammals up to the size of Rock Dove *Columba livia* and juvenile Common Ringtail Possum *Pseudocheirus peregrinus* (Higgins 1999). Despite this, a general perception within ornithological circles is that Boobooks are mainly insectivorous, based on data from New South Wales (e.g. Hollands 1991). This paper briefly reviews these studies and presents new data, based on analysis of regurgitated pellets and field observations in southern Victoria. Results show that the Southern Boobook preys heavily on vertebrates where these prey items are abundant, taking a broad range of small to medium-sized mammals and birds and few invertebrates. Some cryptic species were detected in pellets. Field observations are described of a Southern Boobook taking a sub-adult Common Ringtail Possum, and attempting to take a Leadbeater's Possum *Gymnobelideus leadbeateri*. An incident of conflict with a Barn Owl *Tyto alba* is also described.

INTRODUCTION

Although the Southern Boobook *Ninox novaeseelandiae* is the most common and widespread owl in Australasia (Higgins 1999), little has been published on its diet on the mainland. This paper reviews previous studies and presents new data based on pellet analyses and observations in southern Victoria. Studies of the smaller New Zealand nominate subspecies, *N. n. novaeseelandiae*, show that it eats mainly invertebrates, with small birds, mice and young rats taken infrequently (e.g. Cunningham 1948, Lindsay & Ordish 1964, Imboden 1975). Vertebrates were found only in the gizzards of females (the larger sex) during inspection of 19 individuals (Clarke 1994). The Tasmanian Boobook, subspecies *leucopsis* has been reported by Green *et al.* (1986) to prey on insects, spiders, frogs, mice and to a lesser extent, small birds up to the size of Common Starling *Sturnus vulgaris*.

On mainland Australia, Baker-Gabb (1984) reported high percentages of mice and invertebrates, and few birds, in the diet of Boobooks (subspecies *boobook*) (male 250g, female 315g. Higgins 1999) in Victoria. More recent reports by Hollands (1991), Rose (1996) and Campbell & Rose (1996) have also described high frequencies of invertebrates but low numbers of small mammals, the largest prey being juvenile Rabbit (*Oryctolagus cuniculus*). These studies have reinforced the general impression that the 'Boobook is mainly insectivorous although capable of taking vertebrates up to the size of a rat' (Campbell & Rose 1996). Interestingly, Rose (1996) described the occurrence of a juvenile Common Ringtail Possum among the small vertebrate and invertebrate remains at a roost used by a Barn Owl *Tyto alba* as well as a Southern Boobook; he thought that the possum had most likely been taken by the larger Barn Owl.

METHODS

A total of 113 regurgitated pellets was collected from daytime roosts at sites in and near the Dandenong Ranges, Victoria, between 1980 and 1989, as follows.

Lysterfield Lake Park (37° 58'S, 145° 18'E), March-August 1980, 1981, 1982, 1983: 46 pellets from three different roosts.

Ferntree Gully (37° 53'S, 145° 19'E), September-October 1987: 26 pellets from one roost.

Olinda State Forest (37° 50'S, 145° 23'E), June-July 1989: 41 pellets from one roost.

To avoid unnecessary disturbance, pellets were usually collected when the bird was absent, but the identity of the owl at each site was confirmed by observation at least once at each site. Date and location were recorded with each pellet at the time of collection. Fragments of pellets were matched to enable reassembly into whole pellets. Major bones were identified by comparison with reference specimens, and the minimum number of prey individuals in each collection was estimated by pairing major limb bones and cranial bones, including dentaries. Hairs were identified microscopically, as described by Brunner & Coman (1974). Any prey remains that were not identifiable to species were identified as precisely as possible to genus, family or order. The minimum number of prey individuals and the total biomass of each species estimated from the weights in Appendix 1.

Traces of small insect remains seen on the ground at roosts were not collected because of the impracticality of quantifying them. They may also have been there a long time, after the remaining parts of the pellets had disappeared.

RESULTS

Pellet analyses

All 113 pellets found comprised mainly vertebrate prey and none consisted wholly of insects. At Lysterfield Lake Park, pellets were collected from three roosts: one at Gate 4, in a Cherry Ballart *Exocarpos cupressiformis* in heathland abutting the eastern shore of the lake ($n = 35$); the second on a leafy branch overhanging the Casuarina Track on the boundary of a Spotted Gum *Corymbia maculata* plantation, approximately 100 m west of the lake ($n = 3$); and the third on a dense branch of a Monterey Pine *Pinus radiata* on the west shore of the lake ($n = 8$).

The Lysterfield pellets contained a more diverse range of prey than the other sites, with three small bird species including the cryptic Baillon's Crake *Porzana pusilla*, three rodent species, one dasyurid species, and a small number of invertebrates, including some burrowing crayfish *Engaeus* sp. (Fig. 1). Common Starling (n = 13), Bush Rat *Rattus fuscipes* (n = 6) and unidentified rats (n = 5) made up 79% of the total estimated prey biomass (3170g) (Fig. 1).

At Ferntree Gully, pellets were collected beneath one roost at the base of a large frond in the lower crown of a tall, mature Date Palm *Phoenix canariensis*, in the main picnic area. This site yielded the greatest number of pellets containing insects (n = 21) and House Mouse (n = 11). Only one or two pellets contained remains of Black Rat *Rattus rattus*, Agile Antechinus *Antechinus agilis*, burrowing crayfish, an unidentified rat and an unidentified micro-bat (Fig. 1). The two introduced rodents, House Mouse (n = 11) and Black Rat (n = 2), provided about 78% of the total prey biomass (971g), followed by an unidentified rat, probably Black Rat(16.7%), an Antechinus (2.8%), an unidentified micro-bat, burrowing crayfish and insects. Although more insects were recorded at this site than the other two sites, they still formed only about 2% of the total prey biomass (Fig. 1).

At Olinda State Forest, pellets were collected from beneath one roost amid the dense foliage of an overhanging Messmate *Eucalyptus obliqua* branch, in a forested gully. The contents comprised one introduced and three endemic rat species, including the difficult-to-detect Broad-toothed Rat *Mastacomys fuscus* (n = 10), one Agile Antechinus, one Feather-tailed Glider *Acrobates pymeaus*, one small passerine and small traces of insect (Fig. 1). The four species of rat made up 98% of the total prey biomass (4344g) at this site (Fig. 1).

OBSERVATIONS

Capturing a Common Ringtail Possum

At 20.55 h on 26 October 1983, in the Sherbrooke sector (formerly Sherbrooke Forest Park, 37° 53'S, 145° 22'E) of Dandenong Ranges National Park, a Southern Boobook was seen alighting on a branch of an old, spreading Mountain Ash *Eucalyptus regnans* in which two adult and one sub-adult Common Ringtail Possums *Pseudocheirus peregrinus* were foraging. The sub-adult was approximately 60% of the size of the adults, so estimated to weigh about 420 g (based conservatively on Strahan 1983). The owl appeared to be interested in the possums, so I switched the spotlight off and only used it for a brief check twice during the next two minutes. On hearing a series of high-pitched distress squeals, I switched the spotlight on to find that the owl and the sub-adult possum had disappeared from the tree. On scanning the area I located the owl nearby, approximately 12 m above ground, in the fork of a dead tree. It was 'holding' onto a horizontal branch by gripping it beneath the right wing and grappling with the weakly wriggling possum with both feet. The owl then flew to another nearby tree, still clutching the possum, which was dangling tail-down. It maintained position by thrusting a wing over a horizontal branch, holding the branch between wing and body. The possum was then killed by a bite to the back of the neck. After a brief scramble, the owl perched for a few moments on its feet with the dead possum between its left foot and the branch, and then flew off with the possum in its left foot. The sex of the owl was not determined but, because of the size of the captured possum, it was assumed to be the (larger) female. All this took about five minutes.

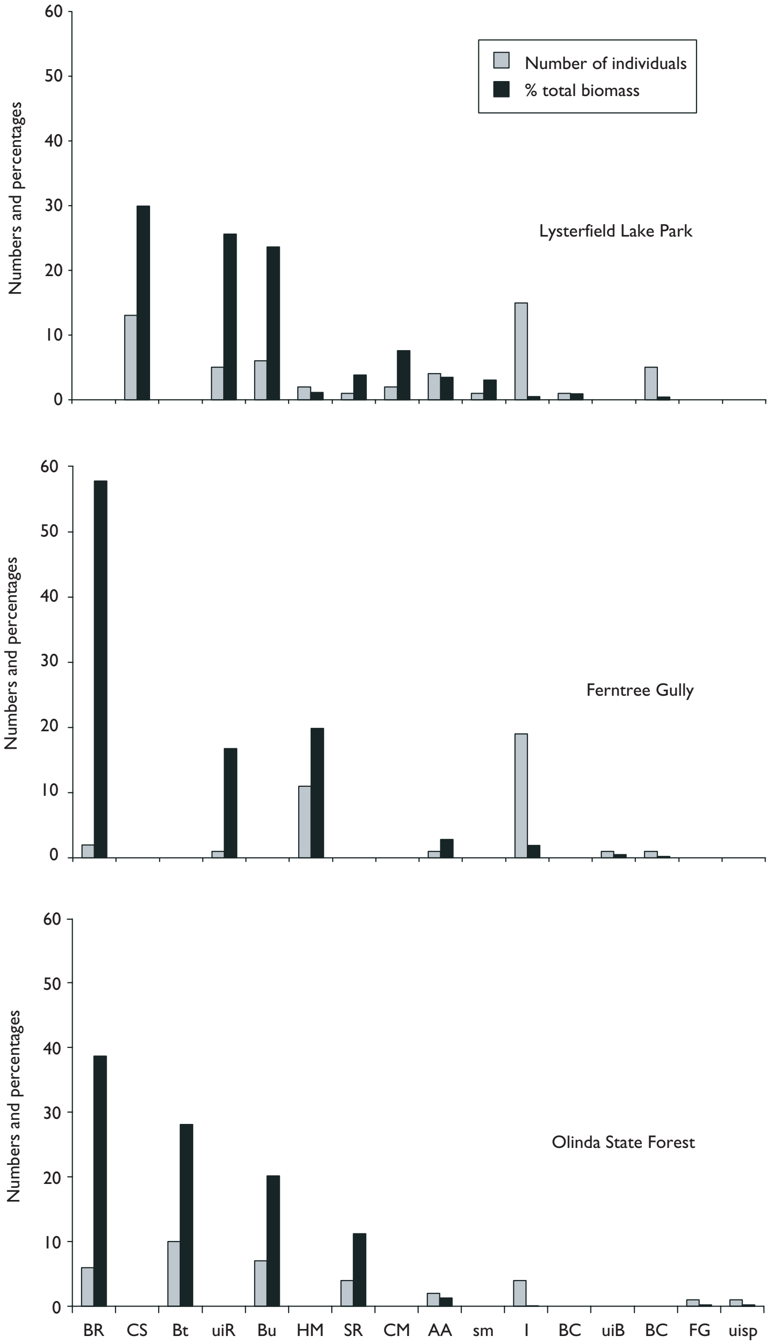


Fig. 1. Number of individuals of each prey species found in Southern Boobook pellets and their percentage of the total prey biomass at each of three sites: Lysterfield Lake Park (total biomass 3,170 g), Ferntree Gully (total biomass 969 g) and Olinda State Forest (total biomass 4,344 g). BR = Black Rat; CS = Common Starling; Bt = Broad-toothed Rat; uiR = unidentified rat; Bu = Bush Rat; HM = House Mouse; SR = Swamp Rat; CM = Common Myna; AA = Agile Antechinus; sm = Starling or Myna; I = insect; BC = Baillon's Crake; uiB = unidentified bat; BC = burrowing crayfish; FG = Feathertail Glider; uisp = unidentified small passerine.

Attacking a Leadbeater's Possum

Surveys of large forest owls, using playback of tape-recorded territorial calls, were conducted by staff from the Arthur Rylah Institute for Environmental Research throughout the Victorian Central Highlands during 1996–97. One survey was conducted at 0152 h on 24 November 1996, on Gaffneys Creek Jeep Track (37° 31'S, 146° 12'E), 7.1 km SSW of Gaffneys Creek. The site was on a ridge 1050 m above sea level, with many Alpine Ash *E. delegatensis* and Snow Gum *E. pauciflora* trees.

During playback of tape-recorded owl calls, including the *boo-book* call, two Southern Boobooks began to call in response from less than 200 m away. A few minutes after the playback ended, the owls stopped calling. I then noticed the *tss tss tss*….. alarm call of a Leadbeater's Possum *Gymnobelideus leadbeateri* near the track. The animal was quickly located in the spotlight beam, and found to be dashing back and forth along a horizontal branch about 5 metres above ground, vocalising repeatedly. On about the third return dash along the branch the possum suddenly dropped from the branch as a Southern Boobook, with open feet thrusting forward, made a silent, shallow gliding swoop, narrowly missing the possum. The owl followed through its glide and landed in another tree a few metres further on. The possum then disappeared and the owl was not seen to attack it again.

Attacking a Barn Owl

A plague of House Mice *Mus musculus* occurred in the Victorian Mallee during winter and spring 1984. A visit was made to Lake Albacutya State Park (35° 45'S, 141° 58'E) to observe and photograph Barn Owls that had been reported nesting in response to the mouse irruption. A Barn Owl roost hollow in a dead tree was monitored at dusk over four evenings, 20–23 August: One or two Barn Owls were seen at the hollow on each occasion. On 23 August, at 1839 h, one Barn Owl appeared from within the hollow spout and sat looking out from the entrance as a Southern Boobook began to call '*Por por por*…….' nearby. A second Barn Owl called nearby, and flew toward the spout, apparently delivering food. As it was approaching the dead tree it was suddenly attacked from above and behind by a Southern Boobook. A brief flurry occurred between the airborne birds and ended when they flew away in separate directions. The Barn Owl in the spout retreated out of view into the hollow, making plaintive squeaking sounds. I have no idea whether this was an attempt at prey capture, at food robbing or territorial defence by the Boobook.

DISCUSSION

This study showed that birds and mammals are important prey items for Southern Boobooks in Victoria, at least during winter when potential insect prey are scarce. If the few loose insect remains ignored at roost sites had been included, they would have shown insects to provide a slightly higher proportion of the prey biomass than revealed by pellet analysis, but this would not have affected the main conclusion. Previous work by Rose (1996) and Campbell & Rose (1996) in northern New South Wales was also undertaken during the non-breeding (colder) season, but insects were found to be a more important prey source. Boobooks certainly do take advantage of insects during periods of abundance, as at the massing of Bogong Moths (*Agrotis infusa*), and throughout summer, when airborne insects are plentiful and the owls have young. However, my study suggests that birds and mammals are needed to provide the bulk of the biomass needs, at least during the colder season.

This study demonstrates further that Southern Boobooks can capture cryptic, difficult-to-detect vertebrates, such as Broad-toothed Rat and Feather-tailed Glider. Starlings were probably captured as flocks gathered noisily at dusk and began to settle in their communal roosts. Barn Owls (310 – 360g) prey mainly on small terrestrial mammals such as rats, mice and Dasyurids and take only juveniles of larger species such as Rabbit (Higgins 1999). My observation of a Southern Boobook taking a sub-adult Ringtail Possum suggests that Rose (1996) may have been incorrect in attributing the ringtail remains he found to a Barn Owl.

McNabb (1996) described Boobooks attacking Powerful Owls during the Boobooks' breeding season. Such attacks were probably in defence of young. Although Barn Owls were nesting at Lake Albacutya, the Boobooks were not observed nesting at that time. However, their por-calling in late August suggests that they were preparing to nest. The attack, therefore, could have been territorial defence rather than an attempt to get food.

In conclusion, this study presents strong evidence concurring with Higgins (1999) that the Southern Boobook (subspecies *boobook*) is a versatile predator, capable of taking large numbers of small birds and mammals and occasionally individuals up to 130% of its own mass. Vertebrates may be a more important source of prey during the cooler season in southern Victoria than found in studies further north in Australia (Hollands 1991, Campbell & Rose 1996, Rose 1996).

ACKNOWLEDGMENTS

Pellet collection and observations were conducted under research permits issued by Parks Victoria. Robert Baird, Barbara Baxter, Belinda Gillies, Lindy Lumsden, Malcolm MacFarlane, Tarmo Raadik and John Seebeck provided assistance with various aspects of the prey identification and weight estimates. Barbara Triggs conducted the bulk of the pellet analysis. Jim McNabb

Appendix 1. Estimated mass of prey species of Southern Boobook in southern Victoria.

Prey species	Mass (g)
Agile Antechinus *Antechinus agilis*	28
Broad-toothed Rat *Mastacomys fuscus*	122
Bush Rat *Rattus fuscipes*	125
Swamp Rat *Rattus lutreolus*	122
Black Rat *Rattus rattus*	280
Unidentified rat	162
House Mouse *Mus musculus*	18
Feathertail Glider *Acrobates pygmaeus*	12
Common Ringtail Possum *Pseudocheirus peregrinus* (sub-adult)	420
Baillon's Crake *Porzana pusilla*	30
Common Blackbird *Turdus merula*	89
European Starling *Sturnus vulgaris*	73
Common Mynah *Acridotheres tristis*	120
Unidentified insect	0.5
Unidentified Sturnidae	96
Unidentified small passerine	10
Unidentified *Engaeus*	3
Unidentified Vespertilionideae	5

Footnote. Estimates for mammals from Strahan (1983), for Baillon's Crake from Higgins (1999), for other birds from Australian Bird and Bat Banding Scheme, for *Engaeus* from T. Raadik and for Vespertilionids from L. Lumsden.

assisted during owl survey fieldwork. The Arthur Rylah Institute for Environmental Research funded the latter stage of pellet analysis. Nick Clemann made valuable comments on an early draft and assisted with editing. Richard Loyn, Rod Kavanagh and Ian Newton provided support throughout the drafting process and comments from two anonymous referees were greatly appreciated.

REFERENCES

Baker-Gabb, D.J. 1984. The feeding ecology and behaviour of seven species of raptor overwintering in coastal Victoria. *Australian Wildlife Research* **11**, 517–532.

Brunner, H. & Coman, B. 1974. *The Identification of Mammalian Hair*. Melbourne: Inkata Press.

Campbell, B & Rose, A.B. 1996. Diet of the Southern Boobook *Ninox novaeseelandiae* on the north coast of New South Wales. *Australian Bird Watcher* **16,** 349–351.

Clarke, J.M. 1992. Food of the Morepork in Taranaki. *Notornis* **39**, 94.

Cunningham, J.M. 1948. Food of a Morepork. *Notornis* **3**, 22–24.

Green, R.H., Rainbird, J.L. and McQuillan, P.B. 1986. Food of the Southern Boobook *Ninox novaeseelandiae*. *Tasmanian Naturalist* **86,** 1–3.

Higgins, P.J. (Ed.)1999. *Handbook of Australian*, *New Zealand and Antarctic Birds*, Vol 4. Melbourne: Oxford University Press.

Hollands, D. 1991. *Birds of the Night*. Sydney: Reed Books.

Imboden, C. 1975. A brief radio-telemetry study on Moreporks. *Notornis* **22**, 221–230.

Lindsay, C.J. & Ordish, R.G. 1964. The food of the Morepork. *Notornis* **11**, 154–158.

McNabb, E.G. 1996. Observations of the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16**, 267–295.

Rose, A.B. 1996. Notes on the diet of the Southern Boobook *Ninox novaeseelandiae* in New South Wales. *Aust. Bird Watcher* **16,** 339–343.

Strahan, R. (Ed.) 1983. *Complete Book of Australian Mammals*. Sydney: Angus and Robertson.

Part 3

Conservation and management

This Page Intentionally Left Blank

19

CONSERVATION AND MANAGEMENT OF LARGE FOREST OWLS IN SOUTHEASTERN AUSTRALIA

RODNEY P. KAVANAGH

Forest Research Division, State Forests of New South Wales, P.O. Box 100, Beecroft, NSW, Australia, 2119. Email: rodk@sf.nsw.gov.au

The three large forest owl species of southeastern Australia, the Powerful Owl (*Ninox strenua*), Sooty Owl (*Tyto tenebricosa*) and Masked Owl (*T. novaehollandiae*), are wide-ranging, naturally uncommon species whose conservation requirements are unlikely to be met wholly within a system of formal nature conservation reserves. Until recently, little was known about the distribution, abundance and habitat requirements of these owls, and the extent to which wood production forestry may be compatible with their conservation. All three species are listed as 'vulnerable' under the New South Wales Threatened Species Conservation Act 1995. Research over the past 10 years has indicated that these owls are more abundant and evenly distributed throughout their ranges in NSW than thought previously. The Sooty Owl has the most restricted distribution, being confined to rainforest and the wetter eucalypt forest types near the coast and adjacent mountain ranges, whereas the Powerful Owl and the Masked Owl also occur among the drier forest types. The Masked Owl is the least common in forested environments. Regional surveys showed little evidence for a decline in owl numbers in a mosaic of logged and unlogged forest. The Powerful Owl and Sooty Owl were recorded commonly in logged landscapes but the home-ranges for these birds were centred upon significant areas of unlogged or less disturbed forest in riparian areas. These areas were used for nesting and roosting by the owls, and also were preferred foraging areas. The Masked Owl appeared to have a closer association with unlogged or selectively-logged forests, particularly those having an open understorey and sparse ground cover. Forests on private land that were highly fragmented and degraded by agricultural practices appeared to make little contribution to regional conservation of large forest owls. The management procedures in place for large forest owls in wood production forests in NSW and Victoria may now be adequate to conserve these species, but their effectiveness needs to be monitored.

INTRODUCTION

Compared to the state of knowledge existing for many owls of the Northern Hemisphere, knowledge of Australian owls is in its infancy. A notable difference is the lack of any studies of the population demography and dynamics of any owl species in Australia. A major contributing factor to this has been the abundance of natural tree hollows for breeding by Australian owls, making nest-box schemes inappropriate in many areas. Only few nests have been found for most species of Australian owls and very few birds have been banded. In contrast, more is known about the general habitats used by Australian owls and the ecology of their main prey species. Until recently (1988), there had been no systematic surveys to determine the distribution and relative abundance of any Australian owl. The survey method developed in 1988 (Kavanagh & Peake 1993) has since been applied widely and is now part of a standard survey procedure used throughout many areas of Australia (e.g. York *et al.* 1991, Anon. 1994, 1999).

Australian owls appear to differ from Northern Hemisphere owls in several important ways. The clutch sizes are generally smaller (Southern 1970, Korpimaki 1986, Saurola 1989, Thomas *et al.* 1990, Olsen & Marples 1993, Hayward & Verner 1994, Taylor 1994), and annual mortality may be lower in Australian temperate regions owing to the absence of severe winters and of pronounced cycles in the abundance of prey (e.g. Korpimaki 1992, Taylor 1994, Newton 2002). A larger proportion of Australian owls is primarily forest-dwelling and most species utilise natural tree hollows for nesting (Hollands 1991, Burton 1992). All Australian owls are exclusively nocturnal. Only two species, the Barn Owl *Tyto alba* and Grass Owl *T. capensis*, specialise upon a limited range of small terrestrial mammal prey (compared to many Northern Hemisphere owls), and all but these two species are thought to be residents with little or no nomadic or migratory behaviour (Schodde & Mason 1980, Baker-Gabb & Fitzherbert 1989). Although few data are available, several Australian species are thought to have very large (>500–1000 ha) home-ranges, which they defend vigorously (Kavanagh and Murray 1996, Kavanagh and Jackson 1997, Kavanagh 1997).

The nine species of Australian owls are the Powerful Owl *Ninox strenua* (Gould, 1838), Rufous Owl *N. rufa* (Gould, 1846), Barking Owl *N. connivens* (Latham, 1801), and Southern Boobook *N. novaeseelandiae* (Gmelin, 1788) from the family Strigidae, and the Sooty Owl *Tyto tenebricosa* (Gould, 1845), Lesser Sooty Owl *T. multipunctata* Mathews, 1912, Masked Owl *T. novaehollandiae* (Stephens, 1826), Barn Owl *T. alba* (Scopoli, 1796) and Grass Owl *T. capensis* (Smith, 1834) from the family Tytonidae (Christidis & Boles 1994, Higgins 1999). The *Ninox* and *Tyto* owls display different behavioural strategies, chief among these being the regular and predictable breeding seasons for *Ninox* owls and the highly irregular and unpredictable breeding patterns for most of the *Tyto* owls (Hollands 1991, Olsen & Marples 1993).

In this paper, I review the available data on the ecology, status and threats to Australian owls, with emphasis on the three large forest species of southeastern Australia. Measures proposed by managers to conserve these species within wood production forests are briefly discussed.

STATUS AND DISTRIBUTION

All nine owl species occur in eastern Australia and most are more widespread throughout the continent (Fig. 1). The Powerful Owl is confined to southeastern Australia, extending north to about Mackay where it overlaps with the more northerly Rufous Owl (Pavey 1993, Eyre & Schulz 1996). The Australian form of the Sooty Owl (a possibly distinct form occurs in New Guinea) is

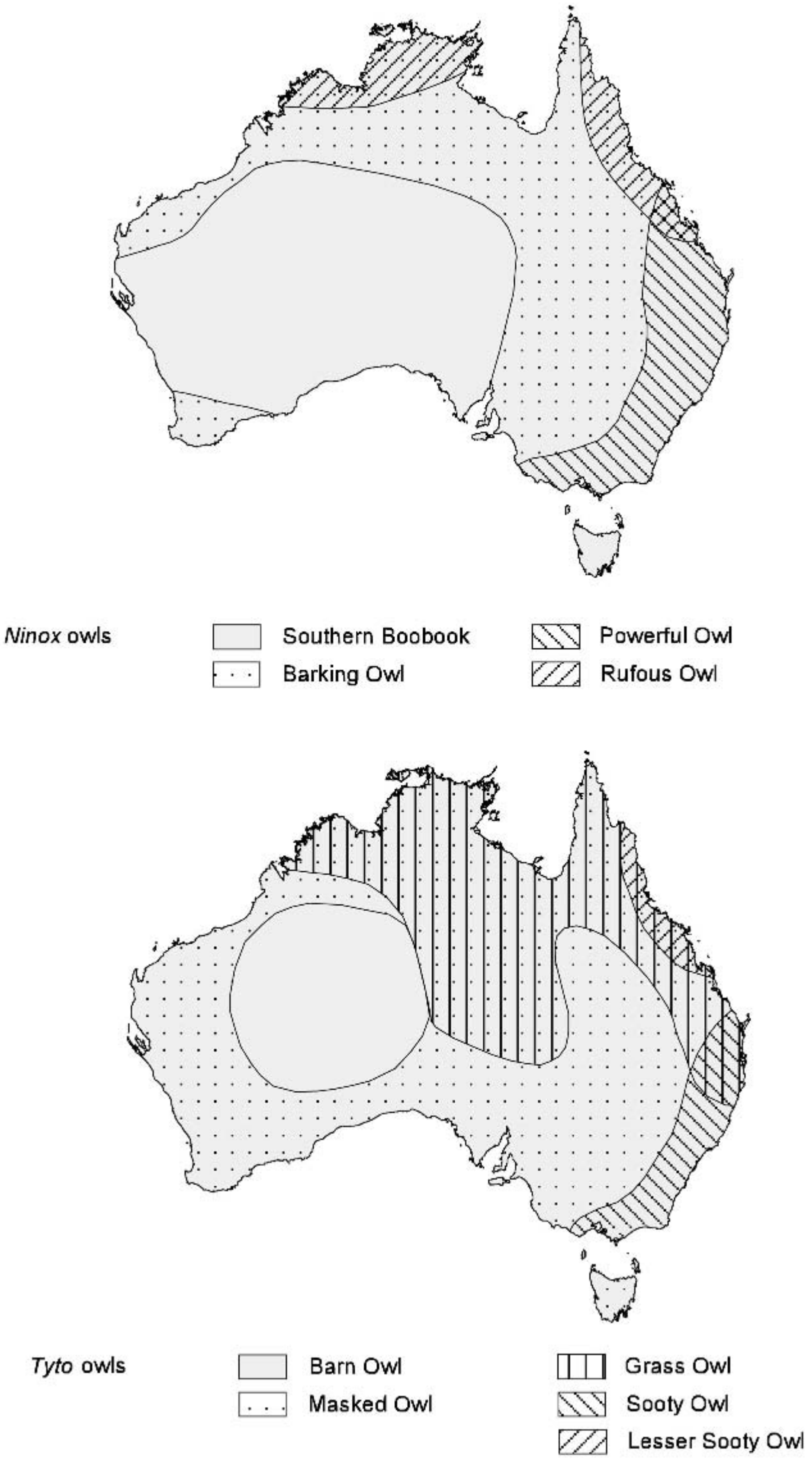


Fig. 1. Generalised distributions of owls in Australia.

also confined to southeastern Australia (Schodde & Mason 1980, Blakers *et al.* 1984). The Masked Owl, which is represented by four subspecies, occurs sparsely throughout the continent and on nearby islands, including Tasmania and southern New Guinea (Schodde & Mason 1980, Blakers *et al.* 1984, Debus 1993, Higgins 1999). The Rufous Owl and the Lesser Sooty Owl are confined to northern Australia (Hollands 1991). The Barking Owl is distributed sparsely throughout the temperate and semi-arid areas of mainland Australia, becoming most abundant in the tropical north (Fleay 1968, Conole 1985, Hollands 1991, Kavanagh *et al.* 1995a). The Grass Owl occurs patchily in northeastern Australia, including coastal and semi-arid environments (Hollands 1991). The Southern Boobook and the Barn Owl are widespread throughout Australia, occurring wherever there are trees with hollows available for nesting (Schodde & Mason 1980, Blakers *et al.* 1984).

The distribution, status and general ecology of the Powerful Owl, Sooty Owl and Masked Owl have recently been reviewed by Debus (1993), Pavey (1993), Peake *et al.* (1993), Debus (1994), Debus and Chafer (1994), Debus and Rose (1994), Kavanagh (1997) and Higgins (1999). The Powerful Owl, Rufous Owl, Sooty Owl and the southern mainland subspecies of the Masked Owl *T. n. novaehollandiae* were each regarded as 'rare' in Australia (Garnett 1992), but recent assessments place them in the categories of 'least concern' (Powerful and Sooty Owls) or 'near threatened' (Rufous and Masked Owls) (Garnett & Crowley 2000). That is, they have small populations that are thinly scattered over an extensive range which are not at present 'endangered' or 'vulnerable' (*sensu* Mace and Lande 1991, IUCN 1994 cited in Garnett & Crowley 2000) nationally. In New South Wales, all three species of large forest owls, together with the Barking Owl and Grass Owl, are listed as 'vulnerable' in the Threatened Species Conservation Act 1995.

The listing of some owls as vulnerable in New South Wales may be a function of the paucity of former records but recent surveys have greatly increased the number of field records for the

Table 1. Increasing numbers of owl survey records from 1982 to 2000.

Field records of large forest owls in Australia prior to 1982, and in New South Wales only for January 1996 and for January 2000. # indicates 'number of'.

Species	Australia RAOU Bird Atlas (Blakers *et al.* 1984)			New South Wales NPWS Wildlife Atlas January 1996		New South Wales NPWS Wildlife Atlas January 2000		
	# records	# 1° blocks	# breeding	**# records**	# 1° blocks	**# records**	# 1° blocks	# breeding
Powerful Owl	**287**	45	8	**740**	27	**1845**	30	12
Sooty Owl	**130***	21*	5*	**552**	20	**1395**	21	8
Masked Owl	**168**	42	2	**285**	33	**754**	34	10
Barking Owl	**724**	172	11	**n.a.**	n.a.	**214**	49	4
Rufous Owl	**77**	18	1					
Southern Boobook	**8344**	537	67					
Barn Owl	**2919**	343	37					
Grass Owl	**49**	22	3					

* includes Lesser Sooty Owl *Tyto multipunctata*

Table 2. Relative abundance of owls in southeastern Australia.

Data represent the frequency of occurrence (% of sites) for each species as determined by listening, call playback and spotlighting surveys.

Region	Vegetation type	No. sites	Powerful Owl	Sooty Owl	Masked Owl	Barking Owl	Southern Boobook	Barn Owl
[1]NE NSW	Forest	291	39	21	11	2	76	0
[2]SE NSW	Forest	706	15	10	4	<1	42	+
[3]SE NSW	Farm-forest landscapes	120	5	3	3	3	29	22
[4]SW NSW	Forest	253	8	0	0	0	36	0
[5]CVH	Forest	130	4	17	0	0	12	0

Sources: [1]Kavanagh, Debus, Tweedie & Webster (1995); [2]Kavanagh & Peake (1993), Kavanagh & Bamkin (1995), Kavanagh (1997); [3]Kavanagh & Stanton (2002); [4]Kavanagh & Stanton (1998); [5]Milledge, Palmer & Nelson (1991)

Powerful Owl and Sooty Owl (Table 1). For example, the national bird atlas survey, which ran for five years during 1977–81 (Blakers *et al.* 1984), reported only 287 records for the Powerful Owl and less than 130 records for the Sooty Owl throughout the range of these two species. However, in New South Wales alone, by early 1996 there were 740 records of the Powerful Owl and 552 records of the Sooty Owl. By early 2000, the NSW NPWS database had increased to 1845 and 1395 records for these two species (Table 1). Records of the Masked Owl also increased substantially in NSW, but this species appears to be less common in forests (where most survey work has been done) than the Powerful Owl and the Sooty Owl. In contrast, records of Barking Owls have not increased rapidly, although this species remains widespread (recorded in 49 1° blocks in NSW) (Table 1). The Southern Boobook and Barn Owl are widespread and abundant throughout Australia.

Standardised surveys in southeastern Australia indicate that the Barking Owl is rarely recorded in tall forests, instead favouring dry forests and woodlands, and numbers of this species appear to be very low east of the Great Dividing Range where most of the surveys were undertaken (Table 2). Barn Owls were also virtually absent from tall forests, but were common in fragmented forest-woodland embedded in agricultural landscapes. Powerful Owls, Sooty Owls and Masked Owls were widespread throughout the forests east of the Great Dividing Range and each attained its greatest relative abundance in northeastern NSW. Sooty Owls were also relatively abundant in the Mountain Ash (*Eucalyptus regnans*) forests of the Victorian Central Highlands. The Southern Boobook was not specifically targeted in these surveys, but it was abundant in all regions sampled (Table 2).

HABITAT MODELLING

The generally larger scale of movements and home-range sizes of owls, compared to many other species, demands an integrated landscape approach to conservation and management. The first step is to build a spatial model of the predicted distribution of habitat for the owls. This task is now relatively straightforward because of the increasing availability of remotely-sensed, digitised map layers for a wide range of forest attributes. Landscape contextural variables can be 'clipped' from these map layers using a geographical information system (GIS), exported to statistical programs for analysis, then imported back to the GIS for plotting as a map of the distribution of predicted habitat. Examples of spatial and conceptual models of habitat for owls in northeastern

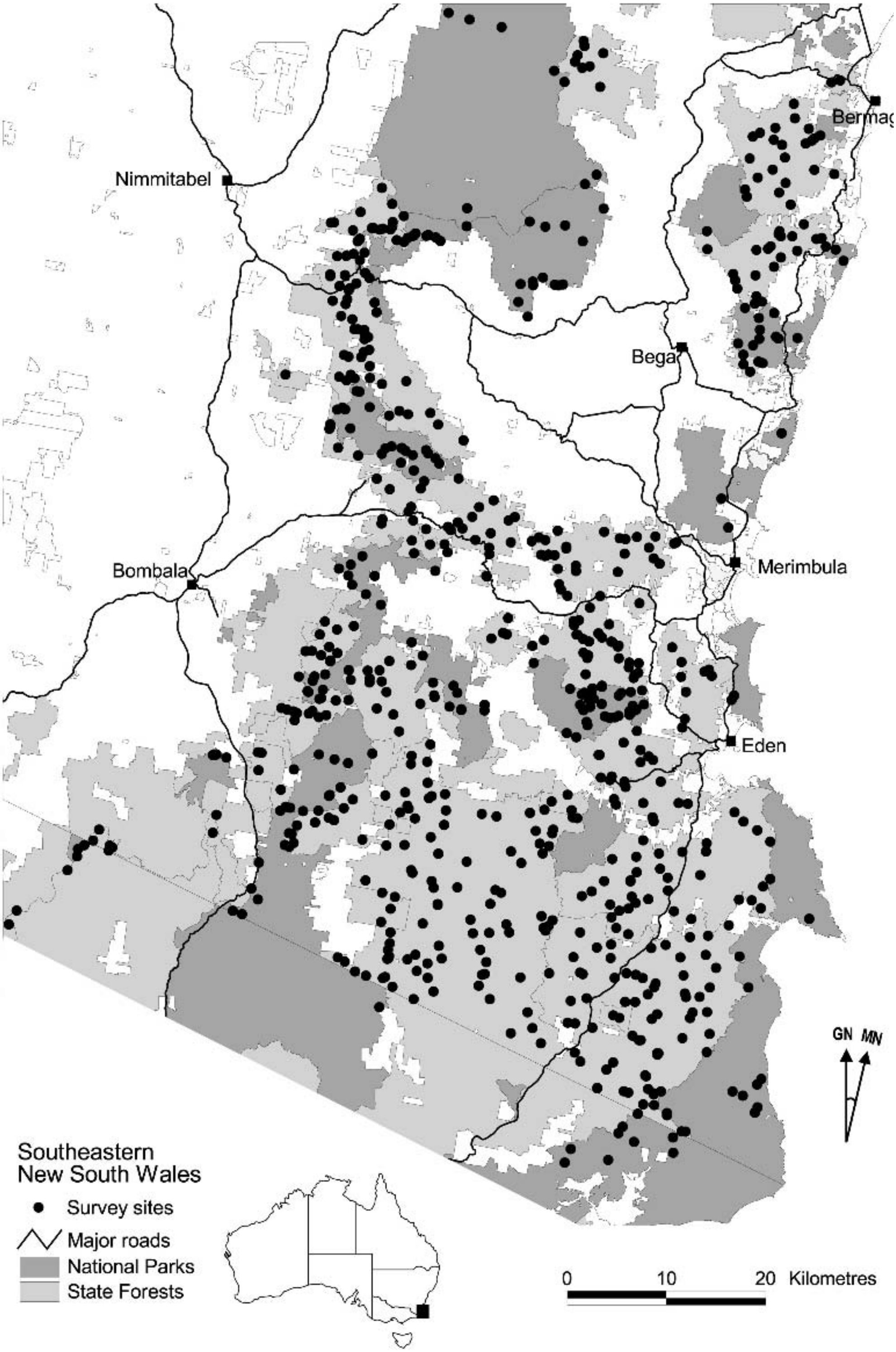


Fig. 2. Distribution of owl survey sites in southeastern New South Wales.

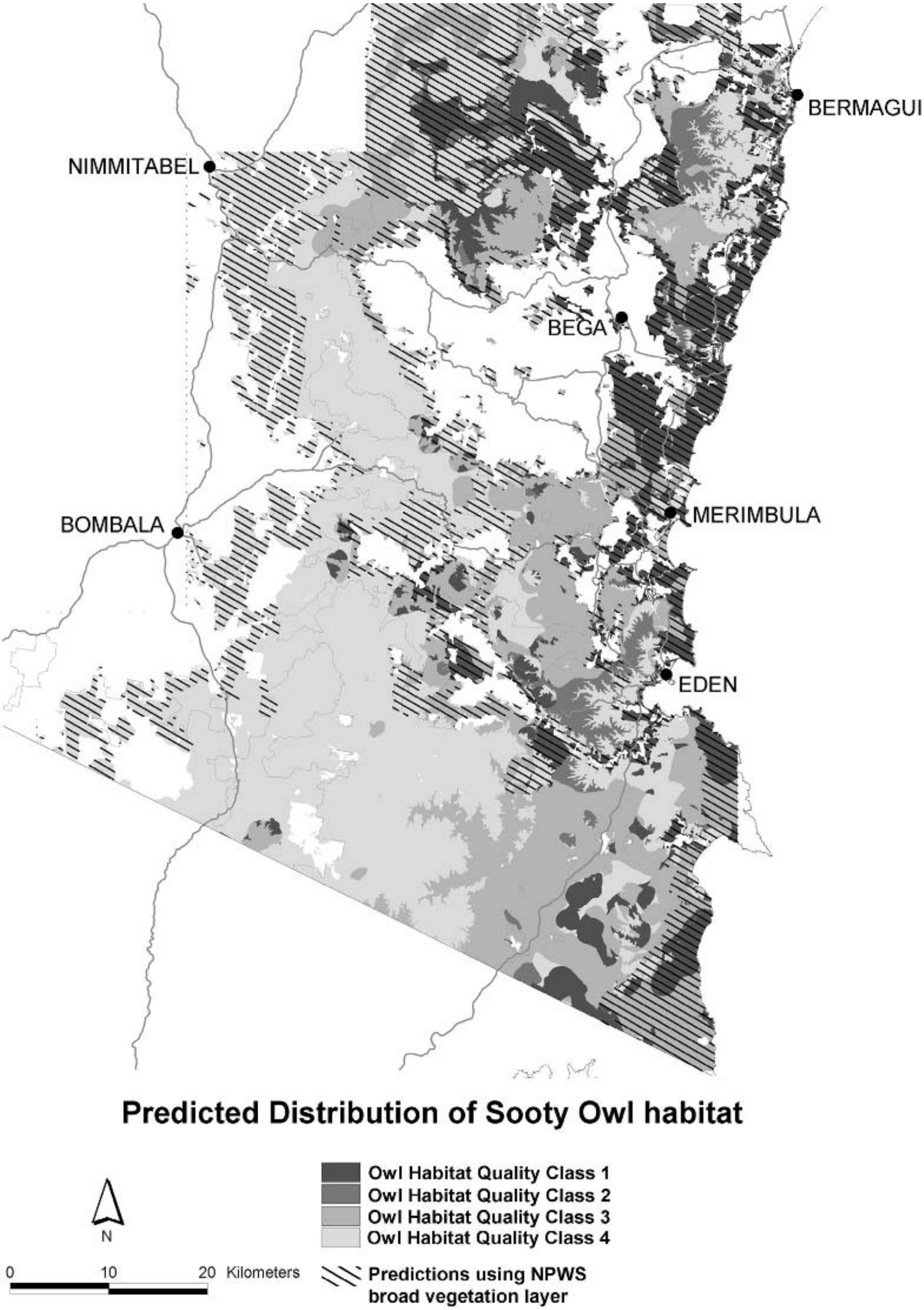


Fig. 3. Predicted distribution of Sooty Owl habitat in southeastern New South Wales.

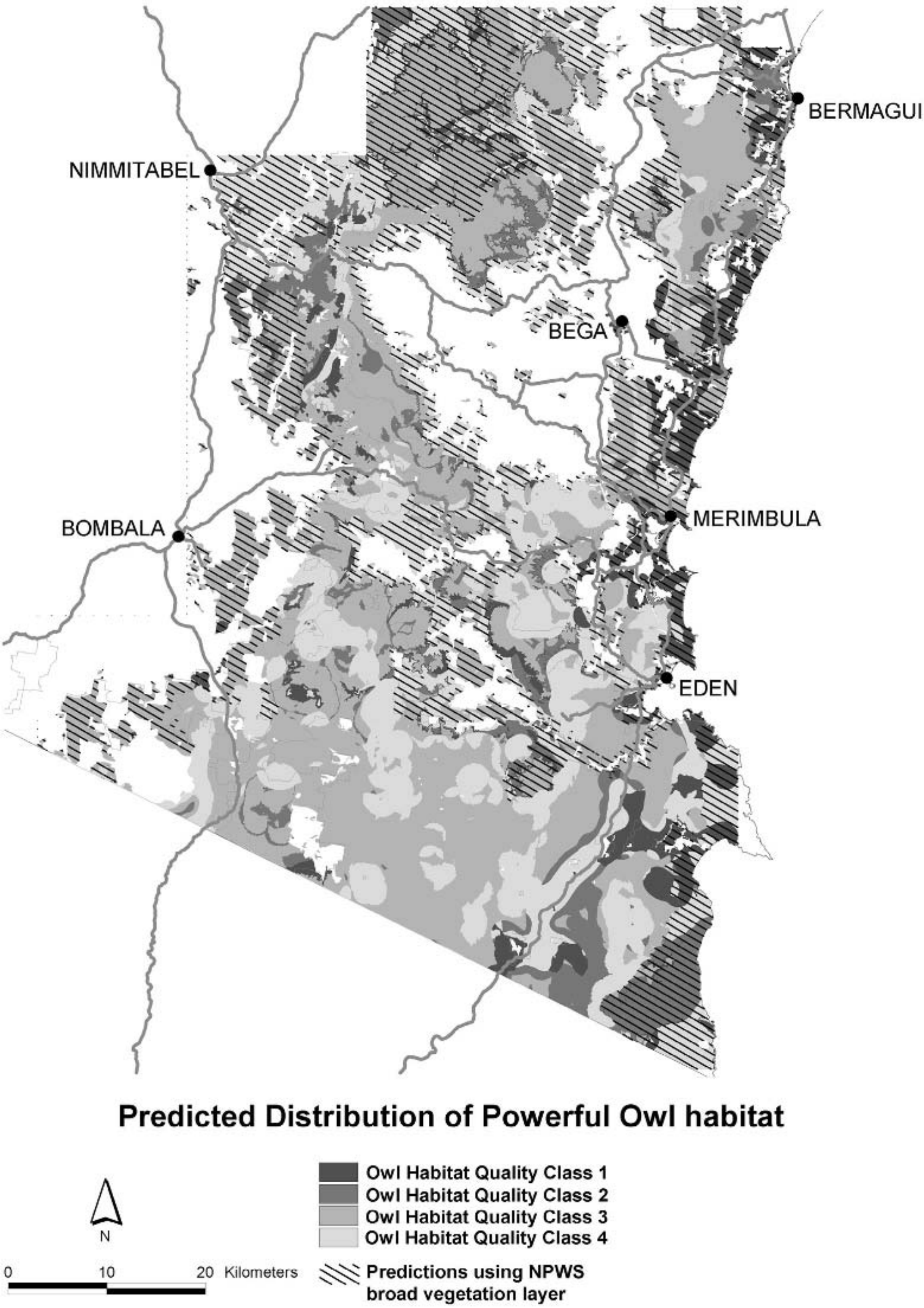


Fig. 4. Predicted distribution of Powerful Owl habitat in southeastern New South Wales.

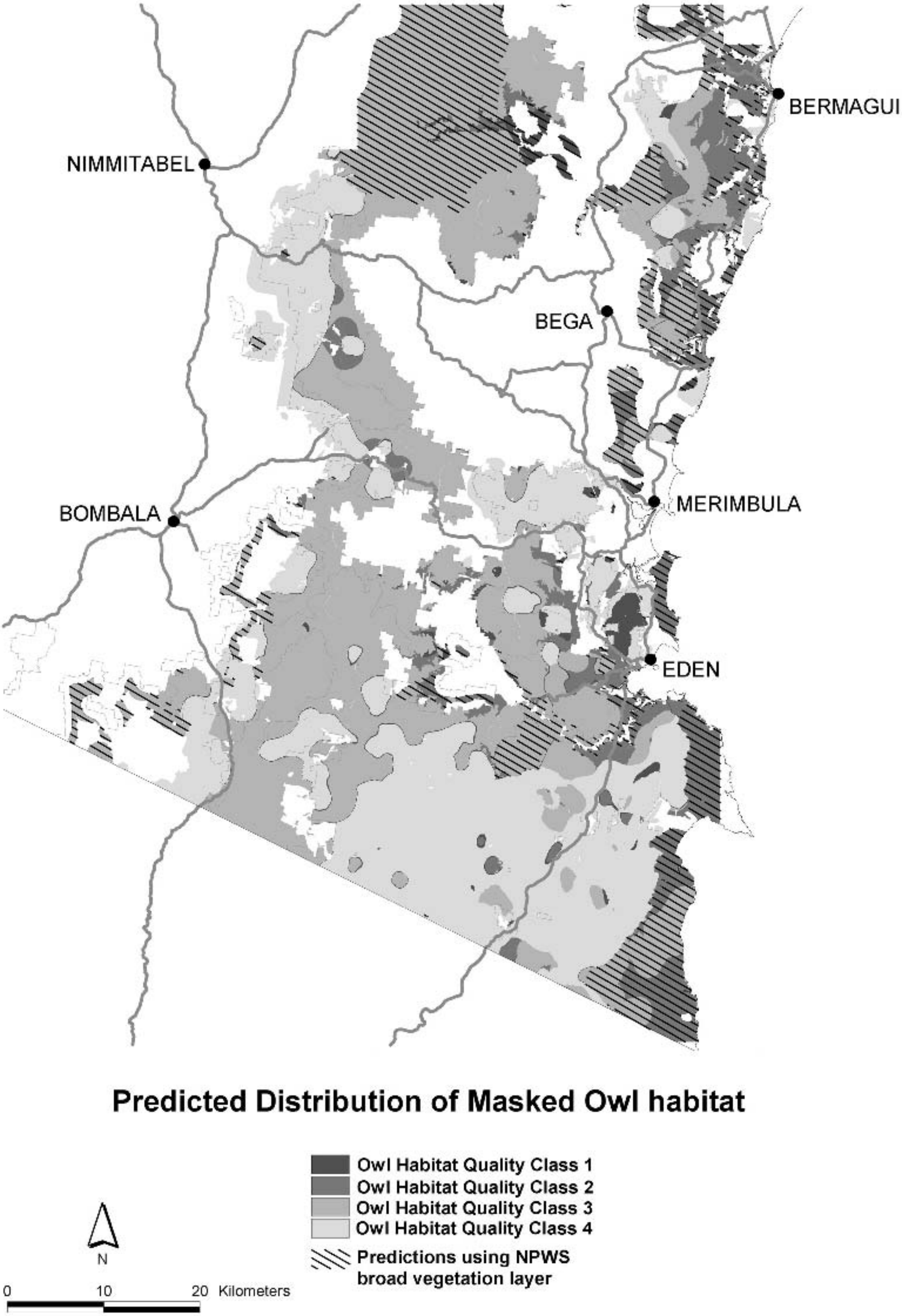


Fig. 5. Predicted distribution of Masked Owl habitat in southeastern New South Wales.

NSW are given by Anon. (1994) and Kavanagh *et al.* (1995b), for southeastern NSW by Kavanagh (1997), and for northeastern Victoria by Loyn *et al.* (2002). Similar, but coarser, wildlife-habitat models and maps were produced for many species during 1997–1999 to assist the CRA ('comprehensive, representative, adequate') negotiations over land-use planning for each of the four Regional Forest Agreements in NSW.

The only owl habitat models that have been field-tested and revised to date include those of Kavanagh (1997) for the Powerful Owl, Sooty Owl and Masked Owl in southeastern NSW (Figs. 2–5). Field-tests showed that two important variables in all three models, elevation and proximity to rainforest, accurately reflected the distribution of owl habitat during the 1990's when the data were collected. The next step, involving the incorporation of a temporal component into the models, is the subject of new work which will establish the response curves of the abundance of the owls, and several of their main prey species, to time since forest disturbance. In parallel with these developments, forest tree growth modellers are working to predict wood yields from forest stands of different ages and structural composition. The third step is to link these models and so predict the likely consequences of different timber harvesting strategies on the supply of habitat for large forest owls and their prey in the long-term. Aside from the technical aspects of modelling, and estimates of animal population density in each 'habitat type', this work needs to be underpinned by a thorough knowledge of the biology and ecology of each species.

BIOLOGY AND ECOLOGY

Wildlife-habitat models are very good for displaying the 'big picture', such as regional distribution, relative abundance, and where to focus conservation efforts, but they are not adequate for explaining how different areas should be managed. In part, this depends on knowledge of the critical resources for owls, including roost and nest sites, foraging habitat and diet, and home-range size.

Roost-site characteristics assessed for the three large forest owls of NSW demonstrate that, across 39 territories, the Powerful Owl (excluding nesting females) roosted entirely among foliage and principally among rainforest trees or tall understorey and sub-canopy trees (Table 3). The Sooty Owl, across 27 territories, also roosted commonly among foliage of rainforest trees, including among vines (unlike the Powerful Owl). In addition, the Sooty Owl commonly roosted by day inside hollows (cavities) of large old trees, and in some territories the owls roosted almost exclusively in caves and rocky overhangs or on sheltered rocky ledges near cliffs (Table 3). The Masked Owl was observed roosting inside tree hollows and among dense foliage of tall sub-canopy trees (Table 3). The frequency of use of tree hollows for roosting by the Sooty Owl and Masked Owl may have been underestimated, because it is easier to locate birds roosting among foliage than inside tree hollows.

Table 3. Roost tree characteristics for owls in southeastern New South Wales.

			Proportion of roost sites in				
	Number of roost sites*	Number of territories	Rainforest trees	Eucalypt trees	Other trees	Caves/ ledges	Hollow trees
Powerful Owl	315	39	51	16	33	0	0
Sooty Owl	82	27	56	>15	0	<29	>15
Masked Owl	11	6	0	73	27	0	73

* Each roost site may have been used on multiple occasions.

Table 4. Nest tree characteristics and nest site fidelity for owls in southeastern New South Wales.

	Number of nest trees*	Number of territories	Nest type	Tree diameter	Hollow inclination	Nest site fidelity
Powerful Owl	13	13	eucalypt	77–180	lateral	high
Sooty Owl	4	4	eucalypt / cave	124–183	lateral / vertical	high?
Masked Owl	5	5	eucalypt	100–191	vertical	high?

* Nest trees may have been used on multiple occasions; most nest trees were located near minor drainage lines (stream order 1, based on 1:25,000 scale maps).

Table 5. Owl diets in southeastern New South Wales.

			Proportion of prey biomass (%)			
	Number of territories	Number of prey items	Arboreal mammals	Ground mammals	Birds	Other
Powerful Owl	47	1672	94	>0?	6	>0
Sooty Owl	28	1466	71	28	>0	>0
Masked Owl	6	175	12	63	25	>0

Nest sites for all three large forest owls are restricted primarily to hollows in large old trees, although at least one pair of Sooty Owls has been recorded breeding inside a cave (Table 4; see also Hollands 1991). The type of tree hollow used for nesting, and its vertical orientation, may differ between species (Table 4). Most nest trees have been found near riparian zone forest, and usually in minor drainage lines (side gullies). Powerful Owls generally display high nest tree fidelity in successive breeding seasons (Kavanagh 1997), but one study (in which the nestlings were banded each year) reported one pair using seven nest trees in 15 years (McNabb 1996).

Basic population demography, including age-sex structure, mortality, fecundity and dispersal, are poorly known in all Australian owls. The only good data collected relate to the breeding success of the Powerful Owl across a small number of territories (approx. 40) that have been closely monitored in Victoria and NSW (McNabb 1996, Kavanagh 1997). Powerful Owls produce only one clutch of eggs per pair per year, with a maximum of two young per clutch. Most pairs nested each year and most produced at least one young.

The diets of Australian owls are well known in a qualitative sense (Schodde & Mason 1980, Barker & Vestjens 1989, Hollands 1991), but few quantitative studies have been made. In New South Wales, the diets of the Powerful Owl, Sooty Owl and Masked Owl were assessed within 47 (1672 prey items), 28 (1466 prey items) and six (175 prey items) territories, respectively (Kavanagh 1997, Kavanagh 2002). The Powerful Owl feeds predominantly on arboreal marsupials, in particular the Common Ringtail Possum *Pseudocheirus peregrinus* (approx. 900 g) and the Greater Glider *Petauroides volans* (approx. 1300 g), supplemented by large (approx. 350 g) diurnal birds (Table 5). It takes few or no ground-dwelling mammals. The Sooty Owl also feeds predominantly on arboreal marsupials, in particular the Common Ringtail Possum, but in addition it preys extensively upon ground dwelling mammals, especially rats (*Rattus* spp.) (approx. 125 g), bandicoots (*Perameles nasuta* and *Isoodon* spp.) (approx. 700 g) and marsupial 'mice' (*Antechinus* spp.) (approx. 30 g) (Table 5). It takes very few birds. The Masked Owl feeds predominantly on ground-dwelling mammals, particularly *Rattus* spp. and *Antechinus* spp., but also

Table 6. Summary of life history traits and habitat characteristics of Australian owls

	Body weight (g)[1,3]		Clutch size[2,3]		Main food	Predominant	Nest site[1,3]	Roost site[1,3]
Species	**male**	**female**	**mean**	**range**	**types[1,3]**	**habitat type[1,3]**		
Powerful Owl *Ninox strenua*	1700	1600	1.9	1–2	arboreal mammals	forest	tree hollow	among foliage
Rufous Owl *Ninox rufa*	1300	1050	2	2	birds, arboreal mammals	dense forest and woodland	tree hollow	among foliage
Barking Owl *Ninox connivens*	510	485	2.2	1–3	birds, insects, terrestrial mammals	woodland	tree hollow	among foliage
Southern Boobook *Ninox novaehollandiae*	298	360	2.5	1–4	insects, terrestrial mammals	forest and woodland	tree hollow	foliage/hollow/cave
Sooty Owl *Tyto tenebricosa*	650*	1170*	1.5	1–2	arboreal and terrestrial mammals	dense forest	tree hollow/cave	foliage/hollow/cave
Lesser Sooty Owl *Tyto multipunctata*	450	540	-	-	terrestrial and arboreal mammals	dense forest	tree hollow	foliage/hollow
Masked Owl *Tyto novaehollandiae*	670	835*	2.6	2–4	terrestrial mammals	forest and woodland	tree hollow/cave	foliage/hollow
Barn Owl *Tyto alba*	418	475	4.0	1–7	terrestrial mammals	open woodland	tree hollow	foliage/hollow
Grass Owl *Tyto capensis*	375	450	6.0	3–8	terrestrial mammals	grassland and heathland	ground	ground

Source: [1]Schodde & Mason (1980); [2]Olsen & Marples (1993); [3]Hollands (1991). * RPK personal observations (Note: female *T. n. castanops* up to 1260g).

takes some arboreal marsupials and birds (Table 5). The Barking Owl has a very broad diet in New South Wales which is dominated by ground-dwelling mammals, birds and insects (Kavanagh *et al.* 1995a).

Radio-tracking studies of Australian owls are few and mostly unpublished (except Kavanagh & Murray 1996, Kavanagh & Jackson 1997) and, to date (January 2000), have been limited to twelve individual Powerful Owls, six Sooty Owls, one adult Masked Owl (and several captive bred juveniles) and one Barking Owl. Home-range sizes for adult, territorial birds appear to be in the order of 800–1000 ha for Powerful Owls, 600–800 ha for Sooty Owls and 800–1200 ha for Masked Owls (Kavanagh 1997, and other unpublished data), but some much larger home-ranges have been recorded (e.g. Kavanagh & Jackson 1997, Soderquist 2002).

A summary of the life history traits and habitat characteristics of Australian owls is presented in Table 6. Among the three large forest owls of NSW, the Powerful Owl and the Masked Owl can both be regarded as diet specialists (taking different prey from one another), and habitat generalists, owing to the range of forest types in which they occur. In contrast, the Sooty Owl can be regarded as a habitat specialist because it is confined to the wetter forest types, and a diet generalist because of the wide range of prey taken within its more limited habitat. Quantitative data are unavailable for most of the remaining species, but an interim classification is proposed as follows. Southern Boobook: habitat generalist-diet generalist; Barn Owl: habitat generalist-diet specialist; Barking Owl, Rufous Owl and Lesser Sooty Owl: habitat specialist-diet generalist; and Grass Owl: habitat specialist-diet specialist.

THREATENING PROCESSES

Large forest owls, and the marsupial gliders that they feed upon, are among the species regarded as having the closest associations with old-growth forest environments in eastern Australia, thus warranting particular attention by forest managers (Tyndale-Biscoe & Calaby 1975, Kavanagh 1991, Scotts 1991). Studies reporting the likely effects of logging on the owls or their prey include those of Lunney (1987), Lunney *et al.* (1987), Macfarlane (1988), Lindenmayer *et al.* (1990), Milledge *et al.* (1991), Kavanagh & Peake (1993), Kavanagh (1997, 2000), Kavanagh & Bamkin (1995), Kavanagh *et al.* (1995b), Kavanagh & Stanton (1995, 1998), Goldingay & Daly (1997) and Kavanagh & Webb (1998). Most of these were retrospective or correlative, the only experimental logging studies being those of Kavanagh & Webb (1998) and Kavanagh (2000), and no studies assessed differences in the survivorship and fecundity of the owls or their prey between logged and unlogged areas. Only Kavanagh & Bamkin (1995) accounted for the proportion of disturbance in the broader landscape around each sampling site; an important parameter for assessing owl responses.

The data available suggest that the three large forest owls occur with similar frequency in unlogged and selectively-logged areas, but at lower frequency in heavily-logged areas (e.g. Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995b). The impact of logging appears to be reduced greatly when unlogged reserves are retained along streams and in minor drainage lines, and where the Common Ringtail Possum, a species generally resilient to heavy logging, forms the principal prey (Kavanagh 1997, Kavanagh & Stanton 2002a). In contrast, the Greater Glider has been found by all studies to be sensitive to heavy logging, so reductions in the abundance of this species could be detrimental to the Powerful Owl where it forms a major component of the owl's diet. The ground-mammal feeding Masked Owl displays the strongest negative association with heavily-logged forests, probably because of reduced hunting opportunities within dense forest regrowth.

A related issue to that of habitat alteration caused by logging is the impact of habitat fragmentation caused by clearing for agriculture and urbanisation. Data concerning species persistence in fragments of native forest and woodland, particularly on privately-owned lands, is important for regional conservation planning. A survey of 120 sites in southeastern NSW revealed that small (<200 ha) fragments of native forest and woodland embedded in an agricultural landscape did not provide adequate habitat for the Powerful Owl, Sooty Owl or Masked Owl (Kavanagh & Stanton 2002b). Virtually all records of these owls were associated with extensively forested areas, or occurred within one km of such areas, which usually occurred on publicly-owned land (vacant crown land, state forest or national park). Surprisingly, resident, territorial Masked Owls (i.e. individuals that responded to call-playback) were unrecorded in the smaller fragments of native forest and woodland, despite the number of roadkills of this species in these environments (Peake *et al.* 1993, Debus & Rose 1994). No assessment has been made of the age and breeding status of these roadkilled birds.

During the past decade, increasing numbers of records have been made of owls (especially Powerful Owls) breeding or occurring near major human population centres (e.g. Pavey *et al.* 1994, Lavazanian *et al.* 1994, Kavanagh & Murray 1996, Kavanagh 1997, Kavanagh & Jackson 1997, Cooke *et al.* 2002), all in association with substantial areas of native forest. Grey-headed Fruit-bat (*Pteropus poliocephalus*) colonies occurring within several km of the central business districts of Brisbane, Sydney and Melbourne each appear to support some pairs of Powerful Owls. The Common Ringtail Possum and the Black Rat (*Rattus rattus*) are common in leafy suburbs and all three large owls have been observed foraging near residential areas. Aside from loss of habitat, the main threats to owls caused by urban developments include increased mortality of adults and young due to motor vehicles (becoming more common) and dogs, and disturbances to roosting areas and nest sites. There have been no recorded instances in Australia of owls killed by contact with high voltage electricity lines.

The impact on owls of wildfire or hazard-reduction burning is poorly known. A radio-tagged Sooty Owl near Sydney foraged almost entirely within that part of its home-range that had escaped a severe wildfire 18–30 months previously (Kavanagh & Jackson 1997). Elsewhere, another Sooty Owl was present three months after its habitat was burnt by wildfire (Loyn *et al.* 1986). A pair of Powerful Owls near Eden was recorded breeding successfully 16 years after a major wildfire burnt out its entire home-range (Kavanagh 1997). This was possible because eucalypt forests possess several adaptations to enable them to survive or regenerate naturally after wildfire (Gill 1981). Hazard reduction burning, which unintentionally burnt some *Allocasuarina littoralis* roost trees used by another two pairs of Powerful Owls near Eden, resulted in no further use of these roost trees for several years by one pair, but continued breeding in the same nest tree nearby by the other pair.

OWL MANAGEMENT PRESCRIPTIONS

New South Wales and Victoria are the only Australian States that have developed management plans on public forest lands (wood production forests and national parks) for large forest owls, and strong legislation in both States requires the protection of these owls across all land tenures. In East Gippsland (Victoria), 100 locations (each 500–800 ha in size) have been designated as special protection zones (primarily as unlogged reserves) for each large owl species (Powerful, Sooty and Masked Owls), based on survey results and the distribution of suitable habitat (Anon. 1995, McIntyre & Henry 2002). Elsewhere, some unlogged forest is retained as linear strips in riparian zones and some old hollow-bearing trees are retained on every hectare. A similar plan involving the designation of 160 locations in total (each 500 ha in size) for all three owls combined has been implemented in Northeast Victoria (Loyn *et al.* 2002).

In wood production forests of NSW between 1990 and 1997, every owl survey record became the centre of a 707 ha reserve (1.5 km radius). Elsewhere, as standard practice, a variable number (depending on forest type, which was used as a surrogate for arboreal mammal habitat suitability) of old hollow-bearing trees was retained within logged areas. Unlogged forest strips were also reserved in most riparian zones. Since 1997, owl management (and management for other species) in wood production forests has been regulated by 'conservation protocols' that form the terms of licence for forestry operations under the NSW Threatened Species Conservation Act 1995 (Anon. 1999). A summary of the main features of these conservation protocols for owls is given in Table 7. Special protection is given to forests occurring in all riparian zones where owl nests, roosts and prey are most likely to be found. In addition, old hollow trees are retained within logged areas to reduce logging impacts on the owls and their prey. These conditions apply throughout wood production forests, regardless of whether owls are known to occur. Additional conditions apply if an owl is recorded or predicted to occur, based on wildlife-habitat models.

Table 7. Conservation protocols used in NSW wood production forests.

1st tier: General prescriptions (applies everywhere)

- exclusion buffers (10–40 m) around: *rainforest*, *wetlands*, *heath*, *rocky outcrops*, *etc*
- habitat tree retention (variable, depending on forest type) : *4 – 12 hollow trees /2 ha*
  + 4 – 12 recruits / 2 ha
  + most dead trees (*stags*)
- stream exclusion zones: *at least 10 m either side of all first order streams*
  at least 20 m either side of all second order streams
  at least 30 m either side of all third order streams
  at least 50 m either side of all fourth and higher order streams
- over-ridge and headwater habitat corridors: *in each 500 ha block*
  retain 2 × 40 m width corridors, or
  retain 1 × 80 m width corridor

2nd tier: Species-specific prescriptions (applies when species is detected during pre-logging surveys, or is predicted to occur)

For owls, there are two optional approaches:

A. Site-based management

- If an owl is detected, *reserve 300 ha habitat within surrounding 2 km radius* (*1257 ha*)
- If nest tree found, *apply 50 m radius buffer*
- If roost tree found, *apply 30 m radius buffer*
- Increase habitat tree retention (*16 per 2 ha*) in high quality habitat for the Greater Glider

B. Landscape approach

- Delineate owl management units of ~ 10,000 ha (may include NP and SF)
- Reserve 25% of owl management unit
- At least 15% must come from wood production forest as exclusion zones
- Increase habitat tree retention (*16 per 2 ha*) in high quality habitat for the Greater Glider

This can take the form of site-specific management, based on individual owl territories, or landscape management in which large (approx. 10,000 ha) blocks of forest are managed to maintain owl populations (Table 7). Preliminary tests of the effectiveness of these prescriptions for large forest owls are underway in NSW (e.g. Cann *et al.* 2002), but regional monitoring programmes need to be implemented.

Management of owls and their habitat on privately-owned lands in NSW ranges from non-existent to application of the principles and practices which apply on public forest lands. Few attempts have been made to co-ordinate owl conservation efforts over multiple holdings of private land. The Barking Owl, which is more likely to occur on private lands than in state forests and national parks, has been listed as 'vulnerable' under the NSW TSC Act, but appropriate management prescriptions for this species have not yet been developed.

CONCLUSIONS

Owls have featured prominently in conservation planning on public forest lands in NSW and Victoria, partly because of their role as top predators and their potential as indicators of biodiversity in forest ecosystems. More than 100 new national parks have been established recently in NSW and Victoria, using criteria that included suitability of habitat for large forest owls and several of their main prey species. In addition, both States have made significant advances to conserve these species in wood production forests. While the effectiveness of these conservation prescriptions remains to be tested experimentally, early indications suggest that these prescriptions may be adequate to conserve large forest owls in wood production forests.

Most owl research in Australia has been concentrated in a few areas where the focus has been on the ecology and conservation needs of large forest owls. Systematic surveys for owls have now been done in several additional regions, but no follow-up work has determined how owls in these regions use different parts of their habitat within the landscape. For example, do owls still nest, roost and forage preferentially in riparian zones if the landscape is comprised of a much higher proportion of tall, moist forest? Specific details of owl nest sites, roost sites and diets in different environments and vegetation types are still unknown.

A much greater effort needs to be made to collect basic demographic data for owl populations in different environments. The establishment of regional owl monitoring programmes is needed. These would provide a focus for collecting long-term demographic data and should also be implemented to track long-term changes in population levels. The role of nest-boxes for use in owl research in Australia needs to be investigated.

ACKNOWLEDGMENTS

I gratefully acknowledge the funding from World Wide Fund for Nature (Australia) which provided the stimulus for me to begin this study and the momentum to keep it going. Fieldwork assistance was provided by a number of colleagues, especially Khia Atkins, David Coombes, Paul Peake, Sandy Sansom, Matthew Stanton and John Young. Harsh Verma assembled the landscape data from the GIS prior to the construction of owl-habitat models. Harsh, Mick Kilby and Alison Towerton produced the maps. Mark Chidel and Barbara Triggs analysed most of the owl pellets. Comments on earlier drafts were provided by Wayne Braithwaite, Chris Dickman and Nick Nicholls. The paper benefited from comments by Brad Law, Ian Newton and Iain Taylor. My sincere thanks to all of the above for their valuable contribution.

REFERENCES

Anon. 1994. Fauna of north-east NSW forests. North East Forests Biodiversity Study Report No. 3, unpublished report, National Parks and Wildlife Service, Sydney.

Anon. 1995. Forest Management Plan for the East Gippsland Forest Management Area. Melbourne: Department of Conservation and Natural Resources.

Anon. 1999. Terms of Licence under the Threatened Species Conservation Act 1995 – Eden. Licence conditions for forestry operations in the Eden Regional Forest Agreement, State Forests of New South Wales, Sydney (see website: www.racac.nsw.gov.au/rfa/pdf/Eden_TSL.pdf).

Baker-Gabb, D.J. & Fitzherbert, K. 1989. An overview of raptor movements and wintering places in Australia and New Zealand. In Meyburg, B.-U. & R.D. Chancellor (eds.) *Raptors in the Modern World*: 159–166. World Working Group on Birds of Prey and Owls, Berlin, London and Paris: International Council for Bird Preservation, IUCN.

Barker, R.D. & Vestjens, W.J.M. 1989. *The Food of Australian Birds. 1. Non-Passerines*. Melbourne: CSIRO.

Blakers, M., Davies, S.J.J.F. & Reilly, P.N. 1984. *The Atlas of Australian Birds*. Melbourne: Royal Australasian Ornithologists Union, Melbourne University Press.

Burton, J.A. (ed.) 1992. *Owls of the World*: *their Evolution*, *Structure and Ecology*. Italy: Peter Lowe, Eurobook Limited.

Cann, B., Williams, J. & Shields, J. 2002. Forest owl management in north-central New South Wales. This volume.

Christidis, L. & Boles, W.E. 1994. The taxonomy and species of birds of Australia and its Territories. Melbourne: Royal Australasian Ornithologists Union, Monograph 2.

Conole, L.E. 1985. The distribution of owls (Aves: Strigidae and Tytonidae) in the Geelong-Otway districts. *Geelong Naturalist* **22**, 3–17.

Cooke, R., Wallis, R. & Webster, A. 2002. Urbanization and the ecology of Powerful Owls (*Ninox strenua*) in outer Melbourne, Victoria. This volume.

Debus, S.J.S. 1993. The mainland Masked Owl *Tyto novaehollandiae*: a review. *Aust. Bird Watcher* **15:** 168–191.

Debus, S.J.S. 1994. The Sooty Owl *Tyto tenebricosa* in New South Wales. *Aust. Birds* **28** (supplement): 4–19.

Debus, S.J.S. & Chafer, C.J. 1994. The Powerful Owl *Ninox strenua* in New South Wales. *Aust. Birds* (Supplement) **28:** 21–38.

Debus, S.J.S. & Rose, A.B. 1994. The Masked Owl *Tyto novaehollandiae* in New South Wales. *Aust. Birds* (Supplement) **28:** 40–64.

Eyre, T.J. & Schulz, M. 1996. Northern range extension of the Powerful Owl *Ninox strenua*. *Aust. Bird Watcher* **16**, 296–298.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. (Reprinted 1979). Brisbane: Jacaranda Press.

Garnett, S. (ed.) 1992. *Threatened and Extinct Birds of Australia*. Melbourne: Royal Australasian Ornithologists Union and Australian National Parks and Wildlife Service, RAOU Report No. 82.

Garnett, S.T. & Crowley, G.M. 2000. *The Action Plan for Australian Birds 2000*. Canberra: Commonwealth of Australia, Environment Australia.

Gill, A.M. 1981. Adaptive responses of Australian vascular plant species to fires. In Gill, A.M, Groves, R.H. & Noble, I.R. (eds) *Fire and the Australian Biota*: 243–272. Canberra: Australian Academy of Science.

Goldingay, R. & Daly, G. 1997. Surveys of arboreal and terrestrial mammals in the montane forests of Queanbeyan, New South Wales. *Aust. Mammal.* **20**: 9–19.

Hayward, G.D. & Verner, J. (eds.) 1994. Flammulated, Boreal, and Great Gray Owls in the United States: A Technical Conservation Assessment. USDA Forest Service General Technical Report RM–253, Fort Collins, Colorado.

Higgins, P.J. (ed.) 1999. Handbook of Australian, New Zealand & Antarctic Birds. Vol. 4 Parrots to Dollarbird. Melbourne: Oxford University Press.

Hollands, D. 1991. *Birds of the Night. Owls, Frogmouths and Nightjars of Australia*. Sydney: Reed Books.

Kavanagh, R.P. 1991. The target species approach to wildlife management: gliders and owls in the forests of south-eastern New South Wales. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 377–383. Mosman: Royal Zoological Society of New South Wales.

Kavanagh, R.P. 1997. *Ecology and Management of Large Forest Owls in South-eastern Australia*. Ph.D. Thesis, University of Sydney, Sydney.

Kavanagh, R.P. 2000. Effects of variable-intensity logging and the influence of habitat variables on the distribution of the Greater Glider *Petauroides volans* in montane forest, southeastern New South Wales. *Pac. Cons. Biol.* **6**, 18–30.

Kavanagh, R.P. 2002. Comparative diets of the Powerful Owl, Sooty Owl and Masked Owl in south-eastern Australia. This volume.

Kavanagh, R.P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biol. Conserv*. **71**: 41–53.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B. & Turner, R.J. 1995a. Diet and habitat of the Barking Owl *Ninox connivens* in New South Wales. *Aust. Bird Watcher* **16**, 137–144.

Kavanagh, R.P., Debus, S., Tweedie, T. & Webster, R. 1995b. Distribution of nocturnal forest birds and mammals in north-eastern New South Wales: Relationships with environmental variables and management history. *Wildl. Res*. **22**: 359–377.

Kavanagh, R.P. & Jackson, R. 1997. Home-range, movements, habitat and diet of the Sooty Owl *Tyto tenebricosa* near Royal National Park, Sydney. In Czechura, G.V. & Debus, S.J.S. (eds) *Australian Raptor Studies 2*: 2–13. Melbourne: Birds Australia Monograph No. 3, Royal Australasian Ornithologists Union.

Kavanagh, R.P. & Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96:** 250–257.

Kavanagh, R.P. & Peake, P. 1993. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In P. Olsen (ed) *Australian Raptor Studies*: 101–125. Melbourne: Royal Australasian Ornithologists Union.

Kavanagh, R.P. & Stanton, M.A. 1995. Nocturnal birds and non-flying mammals of the Dorrigo Three-year Environmental Impact Statement Area, Northern Region, New South Wales. Forest Resources Series No. 26, State Forests of New South Wales, Sydney.

Kavanagh, R.P. & Stanton, M.A. 1998. Nocturnal forest birds and arboreal marsupials of the South-western Slopes, New South Wales. *Aust. Zool.* **30:** 449–466.

Kavanagh, R.P. & Stanton, M.A. 2002a. Early successional changes in habitat quality for large forest owls following intensive logging and wildfire in south-eastern New South Wales. Abstract, this conference.

Kavanagh, R.P. & Stanton, M.A. 2002b. Response to habitat fragmentation by the Powerful Owl, Sooty Owl, Masked Owl and other nocturnal fauna in south-eastern Australia. Abstract, this conference.

Kavanagh, R.P. & Webb, G.A. 1998. Effects of variable-intensity logging on mammals, reptiles and amphibians at Waratah Creek, southeastern New South Wales. *Pac. Cons. Biol.* **4:** 326–347.

Korpimaki, E. 1986. Niche relationships and life-history tactics of three sympatric *Strix* owl species in Finland. *Ornis Scand.* **17:** 126–132.

Korpimaki, E. 1992. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds) *The Ecology and Conservation of European Owls*: 1–10. UK Nature Conservation No. 5, Joint Nature Conservation Committee, Peterborough, UK.

Lavazanian, E., Wallis, R. & Webster, A. 1994. Diet of Powerful Owls (*Ninox strenua*) living near Melbourne, Victoria. *Wildl. Res.* **21:** 643–646.

Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Smith, A.P. & Nix, H.A. 1990. Habitat requirements of the Mountain Brushtail Possum and the Greater Glider in the montane ash-type eucalypt forests of the Central Highlands of Victoria. *Aust. Wildl. Res.* **17:** 467–478.

Loyn, R.H., McNabb, E.G. Volodina, L. & Willig, R. 2002. Modelling distributions of large forest owls as a conservation tool in forest management. This volume.

Loyn, R.H., Traill, B.J. & Triggs, B.E. 1986. Prey of Sooty Owls in East Gippsland before and after fire. *Victorian. Nat.* **103**: 147–149.

Lunney, D. 1987. Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, N.S.W. *Aust. Wildl. Res.* **14:** 263–274.

Lunney, D., Cullis, B. & Eby, P. 1987. Effects of logging and fire on small mammals in Mumbulla State Forest, near Bega, New South Wales. *Aust. Wildl. Res.* **14:** 163–181.

Mace, G.M. & Lande, R. 1991. Assessing extinction threats: towards a re-evaluation of IUCN threatened species categories. *Conserv. Biol.* **5**, 148–157.

Macfarlane, M.A. 1988. Mammal populations in Mountain Ash (*Eucalyptus regnans*) forests of various ages in the Central Highlands of Victoria. *Aust. For.* **51:** 14–27.

McIntyre, A.D. & Henry, S.R. 2002. Large forest owl conservation in the East Gippsland Forest Management Area, Victoria. This volume.

McNabb, E.G. 1996. Observations on the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16:** 267–295.

Milledge, D.R., Palmer, C.L. & Nelson, J.L. 1991. 'Barometers of change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 53–65. Mosman: Royal Zoological Society of New South Wales.

Newton, I. 2002. *Population limitation in Holarctic owls*. This volume.

Olsen, P. & Marples, T.G. 1993. Geographic variation in egg size, clutch size and date of laying of Australian raptors Falconiformes and Strigiformes. *Emu* **93**, 167–179.

Pavey, C.R. 1993. The distribution and conservation status of the Powerful Owl *Ninox strenua* in Queensland. In P. Olsen (ed) *Australian Raptor Studies*: 144–154. Melbourne: Royal Australasian Ornithologists Union.

Pavey, C.R., Smyth, A.K. & Mathieson, M.T. 1994. The breeding season diet of the Powerful Owl *Ninox strenua* at Brisbane, Queensland. *Emu* **94:** 278–284.

Peake, P., Conole, L.E., Debus, S.J.S., McIntyre, A. & Bramwell, M. 1993. The Masked Owl *Tyto novaehollandiae* in Victoria. *Aust. Bird Watcher* **15:** 124–136.

Saurola, P. 1989. Ural Owl. In Newton, I. (ed) *Lifetime reproduction in birds*: 327–345. London: Academic Press.

Schodde, R. & Mason, I. 1980. *Nocturnal Birds of Australia*. Melbourne: Landsdowne.

Scotts, D.J. 1991. Old-growth forests: their ecological characteristics and value to forest-dependent vertebrate fauna of south-east Australia. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 147–159. Mosman: Royal Zoological Society of New South Wales.

Soderquist, T. 2002. Home range and habitat quality of the Powerful Owl (*Ninox strenua*) in Box-Ironbark forest of central Victoria, Australia. This volume.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool., London* **162:** 197–285.

Taylor, I. 1994. *Barn Owls: predator-prey relationships and conservation*. Cambridge U.K.: Cambridge University Press.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R. & Verner, J. 1990. A Conservation Strategy for the Northern Spotted Owl. Report of the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. USDA Forest Service, USDI Bureau of Land Management, USDI Fish and Wildlife Service, USDI National Park Service, Portland, Oregon.

Tyndale-Biscoe, C.H. & Calaby, J.H. 1975. Eucalypt forests as refuge for wildlife. *Aust. For.* **38:** 117–133.

York, A., Binns, D. & Shields, J. 1991. Flora and fauna assessment in N.S.W. State Forests: Survey Guidelines, Version 1.1. Unpublished report, Forestry Commission of N.S.W., Sydney.

20

LARGE FOREST OWL CONSERVATION IN THE EAST GIPPSLAND FOREST MANAGEMENT AREA, VICTORIA

ANDREW D. McINTYRE[1,2] *& STEPHEN R. HENRY*[1*]

[1]Department of Natural Resources and Environment, PO Box 260, Orbost, Victoria, 3888.

([2]Currently, National Parks and Wildlife Service of New South Wales, Coffs Harbour, NSW, 2450)

*Corresponding author email: Stephen.Henry@nre.vic.gov.au

The East Gippsland Forest Management Area, situated in the far east of Victoria, supports substantial populations of Powerful, Sooty and Masked Owls. All are threatened and perceived to be sensitive to timber harvesting. A forest management plan has been produced for East Gippsland, which aims to balance timber production and biodiversity conservation. The planning process included development of conservation guidelines for the owls. Development of the guidelines involved estimating the distribution and preferred habitat of Powerful, Sooty and Masked Owls, allocating target numbers of pairs to be specifically protected across the region, devising protection guidelines for each species and delineating areas of suitable habitat to be included in a protected area network. Habitat was protected for 120 pairs of Powerful Owls, 131 pairs of Sooty Owls and 103 pairs of Masked Owls. This included 100,000 ha of State Forest.

INTRODUCTION

The conservation of large owls in forests used for timber production is a major issue in Australia (Kavanagh 1991, Milledge *et al.* 1991, Scotts 1991) and elsewhere. The most notable overseas example is the Spotted Owl *Strix occidentalis* in the northwestern United States (Dickson & Juelson 1987, Simberloff 1987). This species has now been well studied and sophisticated conservation strategies have been developed (Murphy & Noon 1992).

The forests of East Gippsland support populations of three species of large forest owls, the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae*

(Atlas of Victorian Wildlife database). Powerful and Masked Owls are classed as endangered in Victoria, the Sooty Owl as vulnerable (NRE 1999a), and all are listed under Victoria's threatened species legislation, the *Flora and Fauna Guarantee Act* 1988.

In the mid 1980's, the Victorian Government initiated a comprehensive program to develop management plans for each of the 15 Forest Management Areas in the state. These plans were required to provide for a sustainable supply of forest products and enhanced biodiversity conservation. The East Gippsland Forest Management Area planning process commenced in 1988 and the plan was published in 1995 (CNR 1995). The plan, with some amendments, served as the basis for the first Regional Forest Agreement in Australia (Commonwealth of Australia 1996). Its preparation presented us with a powerful opportunity to implement a systematic biodiversity conservation strategy in State Forest.

As part of that strategy, we developed systematic guidelines for owl conservation which had not previously existed in Victoria. A key objective was to establish a simple and predictable process for owl conservation, based on the ecological information available at the time, and within the context of the wider forest management planning process. In this paper, we place the owl guidelines in the context of the East Gippsland Forest Management Plan, give a brief account of large forest owl populations in East Gippsland, and provide a description of the guidelines and their application.

THE EAST GIPPSLAND FOREST MANAGEMENT AREA AND PLANNING PROCESS

The East Gippsland Forest Management Area (hereafter called East Gippsland) is about 1.2 million hectares and comprises 159,000 ha (13%) of private land, 640,000 ha (53%) of State Forest and 413,000 ha (34%) of National Parks and other statutory reserves (referred to hereafter as Parks) (Fig. 1). The region is a major reservoir of biodiversity in southeastern Australia and the only place in Australia where largely natural landscapes are continuous from the alps to the ocean. East Gippsland also supports a large timber industry, which produces a quarter of the State's sawn hardwood timber (Bartlett & Lugg 1993). The vascular flora and vertebrate fauna of the forest are reasonably well documented (Davies & Thompson 1993, Henry & Murray 1993). The floristic and structural characteristics of the forests have been mapped and used to identify 44 vegetation types known as Ecological Vegetation Classes (EVCs), and the principal age-classes including old growth forest (Woodgate *et al.* 1994). These data sets form the basis upon which the biodiversity conservation elements of the plan were built.

The plan produced a three tiered State Forest zoning system (Fig. 1). This comprised a General Management Zone (41% of the 1,053,000 ha of public land), where timber production is a high priority; a Special Management Zone (4% of public land), which will be managed to conserve specific features including wildlife sensitive to timber harvesting, while catering for timber production under modified prescriptions; and a Special Protection Zone (16% of public land), which will be managed for conservation alone and from which timber harvesting will be excluded. The balance of public land is Park (39%) in which no timber harvesting occurs.

The biodiversity conservation objective of the plan is to conserve all species and vegetation communities across their range and to provide special protection for threatened species and vegetation communities, and species sensitive to intensive logging. A key component of the plan is the application of conservation objectives across all public land (State Forest and Park). The

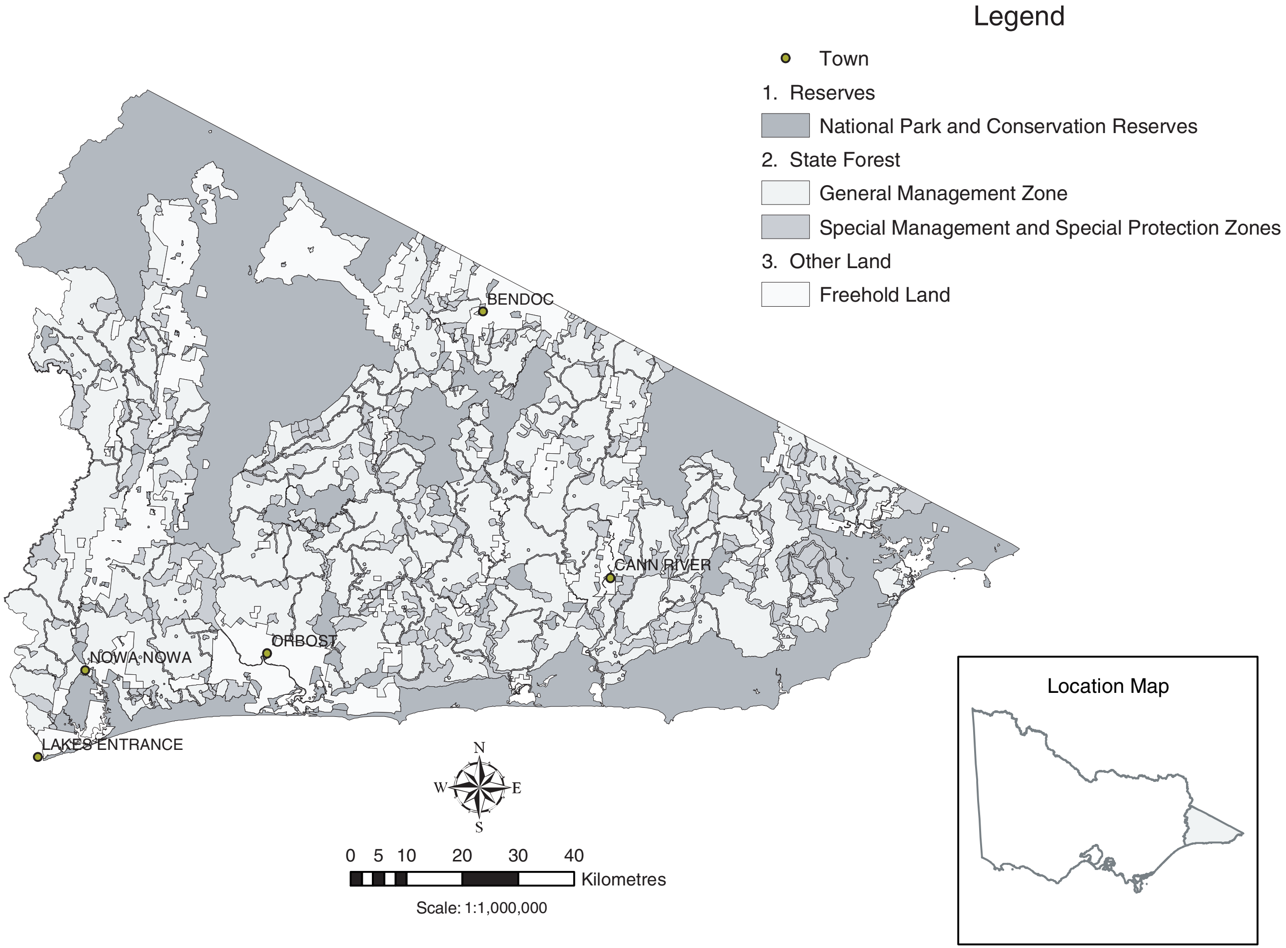


Fig. 1. East Gippsland Forest Management Area, showing land tenure.

Forest Management Plan, although not specifically concerned with the management of Parks, builds upon the considerable contribution the Parks make to biodiversity conservation in East Gippsland.

Fundamental to the biodiversity strategy was the conservation of representative areas of each of the 44 Ecological Vegetation Classes in the region. The EVCs were conserved according to status. The target for rare EVCs (occurring on less than 1,000 ha in East Gippsland) was at least 90% of their extent; uncommon EVCs (1,000 to 10,000 ha) between 30% and 90%; and common EVCs (>10,000 ha) at least 30%. The strategy also required the protection of all patches of heathland and rainforest, and the creation of a linear reserve network, so that no part of the conservation system remains isolated. Prescriptions for the protection of all threatened plant and animal species in State Forest were also developed. Large forest owls fell into this group and made a substantial contribution to the area reserved.

To facilitate representative conservation across the forest management area, East Gippsland was divided into eleven sections known as Geographic Representation Units (GRUs). Each unit is about 100,000 ha and is characterised by a consistent set of landscape features or patterns of features. The units are described in CNR (1995).

LARGE FOREST OWLS IN EAST GIPPSLAND

Four species of large forest owls occur in East Gippsland: the Powerful Owl, Masked Owl, Sooty Owl and Barking Owl *Ninox connivens*. The Barking Owl occurs primarily in open woodland and has not been confirmed as present in State Forest in the region. Although the plan makes provision for the species, it will not be discussed further in this paper.

The Powerful Owl is widespread in Victoria (Emison *et al.* 1987, Atlas of Victorian Wildlife database) through a range of forest types, but is nowhere common. The East Gippsland population is of particular significance because it appears to be relatively large and occupies an extensive area of forest which is continuous from the coast to subalpine environments.

The Sooty Owl occurs through the wetter parts of the Eastern Highlands of Victoria (Atlas of Victorian Wildlife database), from the Dandenong Ranges near Melbourne to East Gippsland, where it is generally associated with rainforest and wet forest. The East Gippsland population appears to be relatively large in the southeast Australian context.

The Masked Owl is also widespread in Victoria but appears in much lower numbers than either the Powerful or Sooty Owl (Peake *et al.* 1993). East Gippsland supports the largest known population in Victoria (Atlas of Victorian Wildlife database). The preferred habitat of the species in East Gippsland is lowland and coastal forest (McIntyre & Bramwell, in prep). The region is the only area in southeastern Australia that still contains large intact tracts of these forest types.

Powerful, Sooty and Masked Owls are considered to be sensitive to timber harvesting and largely dependent upon older forest (Kavanagh 1991, Milledge *et al.* 1991, Scotts 1991, Peake *et al.* 1993, Debus 1993, Debus & Chafer 1994, Debus & Rose 1994). All three species are thought to live as monogamous, sedentary pairs and are known to nest in large tree hollows. They also prey extensively on arboreal mammals, many of which also require large hollows and are themselves sensitive to logging. In addition, the owls occupy large home ranges thought to cover hundreds to thousands of hectares (Schodde & Mason 1980, Davey 1993, Kavanagh 1997). Consequently, conserving these species in State Forest has the potential to have a significant impact on forest management as protection of large areas of older forest is required.

OWL CONSERVATION GUIDELINES

The development of the owl conservation guidelines has involved: (1) Surveying for each species of large forest owl in East Gippsland; (2) developing a model of the preferred habitat of each species; (3) estimating the size of a population that is likely to be secure and using this as the target; (4) negotiating conservation guidelines for each species; and (5) applying the prescriptions to conserve the target population. These points are addressed in turn below.

Surveying for large forest owls

Censuses for Powerful, Sooty and Masked Owls were performed at 440 sites across the public land in East Gippsland between 1991 and 1993 (McIntyre & Bramwell, in prep). The censuses were stratified so that all the Ecological Vegetation Classes covering more than 1,000 ha in the region were included, approximately in proportion to their extent, and to give a reasonably even geographic coverage of the region. For analysis, the 44 Ecological Vegetation Classes were lumped into 16 groups, based on structural and floristic similarities and natural associations (see below).

The censuses were conducted during the first four hours of still nights and each site was censused once. Sampling occurred throughout the year, with most between November and March, as part of comprehensive flora and fauna surveys of forest areas. The census employed a standard call broadcast-and-search protocol. Taped calls of each species were broadcast using a walkman and megaphone. The call of the Powerful Owl was broadcast for four minutes, followed by a quiet listening period of five minutes, followed by similar call and listening periods for Sooty and Masked Owls. This was followed by an active spotlight search and listening period of 30 minutes in the vicinity of the census site. Each census was deemed to sample a circle of 1000 m radius, equal to 315 ha. This was the distance over which a human listener could readily detect the broadcast calls on a still night. The estimated location of each responding owl was noted. Responses from owls that were clearly more than 1,000m from the census point were noted, but not used in further analysis.

The surveys yielded 53 locations for Powerful Owls (12% of sites sampled), 67 locations for Masked Owls (15% of sites) and 76 locations for Sooty Owls (17% of sites), where the birds were estimated to be within the census circles. The census method clearly tends to underestimate the actual number of owls present, as sites were censused only once and not all owls present would be expected to respond to playback, especially in the non-breeding season.

Preferred habitat for each species

The results of the systematic census program were used to generate a model of preferred owl habitat (McIntyre & Bramwell, in prep). The following variables were measured within 1,000m of each census site using a geographic information system (ARC/INFO):

Area of each of 16 Ecological Vegetation Class (EVC) Groups (coastal vegetation, heathland, wetland, banksia woodland, lowland forest, riparian forest, shrubby dry forest, grassy dry forest, box-ironbark forest, limestone grassy forest, woodland, rocky outcrop scrub, damp forest, wet forest, rainforest and montane forest).

Area of each of four age-classes of forest (senescent dominant, mature dominant, mixed age-classes and regrowth, from Woodgate *et al.* 1994).

Index of steepness (calculated as the difference between the minimum and maximum altitude within the census area, so that high values indicate steep terrain).

Distance from the broadcast site to the nearest patch of heathland.
Distance from the broadcast site to the nearest patch of rainforest.
Distance from the broadcast site to the nearest patch of old-growth forest.

Statistical analysis compared the mapped habitat variables at the detection and non-detection sites for the three species of large forest owl. Three analyses were undertaken: multiple t-tests, discriminant function analysis and logistic regression. This procedure generated a profile of preferred habitat characteristics, summarised as follows:

Powerful Owl – not significantly associated with any particular EVC group, but significantly less heathland and wetland vegetation in detection sites than in non-detection sites.

Sooty Owl – significantly associated with lower elevation damp forest EVC group in close proximity to rainforest gullies.

Masked Owl – significantly associated with banksia woodland EVC group at low elevation and in flat terrain, and proximity to patches of heathland. There was significantly less of the shrubby dry, damp and wet forest and rainforest EVC groups in detection sites than in non-detection sites.

None of the species were significantly associated with any particular age-class of forest.

We estimated the area of preferred habitat in the region for each species (from Ecological Vegetation Class data in Woodgate *et al.* 1994) as those EVC groups significantly linked to detection sites, plus similar vegetation types closely associated with them in the landscape. On this basis, the preferred habitat for the Powerful Owl is all forest and woodland Ecological Vegetation Classes in the region, totalling 999,276 ha. The preferred habitat of the Sooty Owl is considered to be the EVC's Limestone Box Forest, Riparian Forest, Lowland Forest, Damp Forest and Warm Temperate Rainforest, totalling 507,778 ha. The preferred habitat of the Masked Owl is considered to be the EVC's Coast Banksia Woodland, Coastal Grassy Forest, Coastal Sand Heathland, Sand Heathland, Clay Heathland, Wet Heathland, Banksia Woodland, Limestone Box Forest, Riparian Forest and Lowland Forest, which totals 314,932 ha.

Estimating secure populations and deriving targets for conservation

We aimed to provide a high level of security for the regional populations of Powerful, Sooty and Masked Owls for at least the life of the management plan (ten years). Our census had yielded 53, 67 and 76 locations for the three species respectively. These were deemed to represent pairs, on the basis that owls responding to call playback were likely to be resident birds defending territories, though we acknowledge that the evidence for this view is inconclusive (Higgins 1999). Across the region (and without discriminating between preferred and non-preferred habitat), this is equivalent to one pair every 2,615 ha for the Powerful Owl, one pair every 2,068 ha for the Masked Owl and one pair every 1,823 ha for the Sooty Owl. Given the limitations of our survey, we did not attempt to derive regional population estimates. However, given the extent of the preferred habitat of each species in the region, we could be reasonably confident that there were at least 100 pairs of each species in the region. After a process of consultation with owl ecologists and forest managers, we settled on 100 pairs of each species as a pragmatic minimum target for secure conservation to be met in the planning process. A model of the metapopulation dynamics of the Powerful Owl was subsequently developed by McCarthy *et al.* (1999), which suggested that local populations of 100 pairs or more, as part of the larger continuous southeastern Australian population, should have a low risk of extinction.

Conservation guidelines for each species

For the purposes of application in the forest management plan, we developed a pragmatic, generic and easily applied conservation guideline for each species, based on broad concepts of ecological needs as a first step in an adaptive approach which may be modified in future versions of the plan. The guideline aims to conserve sufficient habitat to comfortably support a pair of owls, within a larger area that is likely to encompass their home range, based on current home range estimates for the species (Schodde & Mason 1980; Davey 1993, Kavanagh 1997). Species guidelines for each pair (from CNR 1995) are:

Powerful Owl

Approximately 800 ha of forest which is dominated by old trees is to be reserved within a circle of 1,500 ha. Forest types with high populations of possums and gliders are to be favoured for reservation (especially wet, damp and riparian forest). This recognises that Powerful Owls prey mainly on arboreal mammals (Kavanagh 1988, Debus & Chafer 1994), which are themselves most abundant in older forests of these types in East Gippsland (Henry and Murray 1993), and that the owls nest in old trees with large hollows.

Sooty Owl

Approximately 500 ha of forest which is dominated by old trees is to be reserved within a circle of 1,000 ha. Reserved areas are generally to be lowland, damp and riparian forest types, and warm temperate rainforest. This prescription recognises that Sooty Owls use large hollows for breeding and prey extensively on both small arboreal and terrestrial mammals (Loyn *et al.* 1986, Kavanagh & Jackson 1997).

Masked Owl

Approximately 500 ha to be reserved within a circle of 1,000 ha. Reserved areas are to be predominantly older age classes of lowland forest and coastal woodland, and the associated riparian forest on flat terrain. They should also include heathland-forest ecotones and areas of banksia woodland. This prescription recognises that Masked Owls prey on a variety of small terrestrial mammals and relatively fewer arboreal mammals than Powerful and Sooty Owls (Debus 1993, Peake *et al.* 1993, Debus and Rose 1994, Kavanagh 1996). They appear to hunt in open forest and woodlands or along forest edges. Large hollows are required for breeding.

For operational application, the home range area took the form of a circle, which, when the area was based on an owl record, was oriented so that the record was in the circle but not necessarily at its centre and the circle encompassed the best potential habitat in the vicinity. Thus logging regrowth and non-preferred vegetation types were to be avoided. As first preference, existing reserves with suitable habitat were placed within the circles. Where a number of pairs of the same species occurred close together, their circles were placed with no overlap, but circles of different species could overlap. The reserved area was then delineated within that circle according to the above prescriptions.

Applying the prescriptions to conserve the target populations

As of 1995, there were 221 records of the three species of owls in East Gippsland, from 181 sites (Atlas of Victorian Wildlife database). These comprised 66 records of Powerful Owls from 62 sites, 92 records of Sooty Owls from 79 sites and 63 records of Masked Owls from 40 sites. These records include those gathered by our survey. The majority (90%) of records were post–1983 and reflected the substantial survey effort associated with ecological surveys in that period.

All records obtained after 1983, which were accurate to within one minute of latitude and longitude, were plotted on both 1:100 000 and 1:25 000 maps. Mapping allowed clusters of records of the same species to be identified. In many instances, these clusters were interpreted as multiple records of the same individual or pair. In cases where multiple records could be reliably interpreted as more than one pair of the same species, sufficient area to support more than one pair of owls was delineated.

The number of sites to be conserved in each geographic representation unit (GRU) was based on the proportion of the total preferred EVC groups and growth stages which occurred in the unit. For example 13% of Powerful Owl habitat was predicted to occur in the Far East Foothills GRU, so 13% of the target (13 pairs) had to be catered for in that unit. Setting targets for each of the geographic representation units allowed us to apportion the conservation effort across East Gippsland and across land tenures, specifically between State Forest and Parks.

We then selected sites to be used as the basis for meeting the reservation target. The order of preference for selection of sites in each GRU was: (1) known or suspected breeding sites in Park; (2) known or suspected breeding sites in State Forest; (3) other confirmed sites in preferred habitat in Park; and (4) other confirmed sites in preferred habitat in State Forest. Known records in clearly non-preferred habitat (eg farmland) were not used as the basis for reserves.

Where the target in the GRU was not met by actual records, we assessed the ability of the balance of the Park and State Forest conservation reserve system (which had been created to meet conservation targets for other values) to provide suitable owl habitat (predicted sites). Areas of predicted suitable owl habitat (based on older age-classes of the preferred EVC groups for each species) which met the size criteria were used to make up any shortfall between the known sites and the targets for each GRU. Additional predicted sites in State Forest were then added if a shortfall still existed.

Owl sites in State Forest where there were multiple conservation values (such as rainforest, other threatened species or representative samples of Ecological Vegetation Classes or old growth forest) were usually Special Protection Zones, while sites where owls were the only special feature were generally Special Management Zones.

THE OUTCOME

There appears to be suitable habitat in Parks and State Forest conservation reserves in East Gippsland for at least one hundred and twenty pairs of Powerful Owls, 52 in Park and 68 in State Forest. All 53 confirmed Powerful Owl sites in good habitat in the region were covered by reserves of one form or another, with the balance being predicted habitat. Forty-eight (73%) of the sites in State Forest are zoned Special Protection, whilst 17 (26%) are zoned Special Management (see below).

There appears to be suitable habitat in Parks and State Forest conservation reserves in East

Gippsland for at least 103 pairs of Masked Owls, 44 in Park and 59 in State Forest. All 67 confirmed owl sites in good habitat are covered. Of the sites in State Forest, 29 (66%) are zoned Special Protection and 15 (34%) are zoned Special Management.

There appears to be suitable habitat in Parks and State Forest conservation reserves in East Gippsland for at least 131 pairs of Sooty Owl, 52 pairs in Park and 79 sites in State Forest. These sites embrace 76 recorded locations. Forty-eight (66%) of the sites are zoned Special Protection and 23 (32%) are zoned Special Management.

Overall, the application of the large forest owl prescriptions contributed to about 100,000 ha of the 200,000 ha of additional reserves created in State Forest by the Forest Management Plan process.

For those owl sites in the Special Management Zone, timber harvesting will be permitted, but modified to maintain sufficient habitat for the owls (CNR 1995). The prescriptions will vary according to site characteristics but will include increased buffering of gullies (from the normal 20m to 40–50m depending on forest type), reservation of patches of unlogged forest within the harvested areas and avoidance of hot silvicultural burning after harvest. These areas constitute an informal experimental zone, where the impacts of harvesting can be monitored, and the results used to inform owl conservation across the region. Harvesting in a number of these zones, and the associated owl monitoring program, have already commenced (Kambouris 2000), but insufficient time has elapsed to detect trends.

DISCUSSION

The approach to large forest owl conservation outlined in this paper is an important part of a comprehensive strategy for biodiversity conservation developed for the East Gippsland Forest Management Area. The strategy integrates conservation measures for a range of biological values into a system of protected habitat across the State Forest and Parks. In catering for large forest owls, a suite of other biological features have been protected, including old growth forest, samples of vegetation communities and a range of other faunal groups. Similarly, areas protected primarily for other biological features are likely to provide further secure habitat for owls. This approach to the conservation of large forest owls and other biodiversity values represents a substantial improvement on the previous *ad hoc* conservation system in State Forest in Victoria and attempts to balance the Victorian Government's biodiversity conservation objectives with its commitment to supply raw materials to the timber industry.

Setting targets for the number of owls to be specifically catered for in the reserve system was a key element of the strategy. These targets were critical in gaining acceptance of the owl conservation guidelines within the Department of Natural Resources and Environment because they created a level of planning certainty. The principle was first developed and applied to the management strategy for the Long-footed Potoroo *Potorous longipes* (Saxon *et al.* 1994). The rationale is to set minimum conservation objectives to be achieved while at the same time setting a limit to the area that is to be reserved. The use of targets provides a degree of predictability in the planning system and avoids a process of *ad hoc* modifications to the forest zoning system.

Modelling of the metapopulation dynamics of at least the Powerful Owl (McCarthy *et al.* 1999) suggests that one hundred pairs of that species should be reasonably secure for the medium term, but this estimate may be incorrect. The owl population might then decline if current timber harvesting practices reduce the area of suitable habitat in State Forest. However, assessing the risks associated with different management strategies has become an important aspect of conservation biology (Burgman *et al.* 1993). The two main risks to owl populations posed by the application of this strategy are: (1) reductions in the populations below levels sufficient to ensure their long term viability, and (2) fragmentation of populations into a number of smaller units that become vulnerable to extinction because of their small size and isolation (Saunders *et al.* 1991).

With regard to total population size, the targets set probably underestimate the actual populations of large forest owls that will persist in East Gippsland. Some owls will persist in those parts of the General Management Zone of State Forest which are not logged because they are close to rivers and streams, are too steep, are non-forest communities or are forest types not economically harvestable. These exclusions are estimated to comprise 119,000 ha (or 19%) of State Forest (CNR 1995). Even if these rather fragmented areas offer only non-breeding habitat, they should contribute to population security. Furthermore, work in southeastern New South Wales and East Gippsland suggests that some Powerful and Sooty Owls will persist in, or re-colonise, landscapes that have been extensively harvested, provided that some areas, such as gullies and streamsides, are reserved (Kavanagh & Bamkin 1995, Kambouris 2000).

Regarding the fragmentation of owl populations in East Gippsland, we need to assess the landscape pattern created by timber harvesting and the ability of large forest owls to move through that landscape. The region has five National Parks each containing tens of thousands of hectares of forest suitable for owls (Croajingolong: 87,000 ha, Coopracambra: 38,800 ha, Errinundra: 25,100 ha, Snowy River: 98,700 ha and part of the Alpine: 107,000 ha). There are seven smaller Parks containing between 1000 and 10 000 hectares of suitable owl habitat (Land Conservation Council 1986). Also contributing to the formal reserve network are the Special Protection and Special Management Zones in State Forest. These areas cover tens to a few thousand hectares, many parts of which were selected because they include higher quality owl habitat. Completing the reserve matrix are the smaller components of the conservation system such as linear reserves, special management sites and forest protected by harvesting prescriptions such as streamside buffers and steep slopes. The linear reserves are designed to link the large and small habitat patches. A consequence of this network is that no point on public land in East Gippsland is more than 5 km from a substantial reserve of at least several hundred hectares and no point is more than a few hundred metres from at least a smaller reserved area. The net result of the various exclusions is that about 600,000 ha (60%) of the East Gippsland Forest Management Area is not available for timber harvesting.

There will be no fragmentation of the public forest by permanent clearing so the continuity of forest cover will be maintained. While the numbers of owls may decline in the general management zone, it is unlikely that the populations will suffer major fragmentation within the forest management area.

It is also important to view East Gippsland in the broader context of the forests of southeastern Australia. The populations of all three owls in East Gippsland are continuous with other populations occupying extensive forested landscapes to the north in New South Wales and to the west in the eastern highlands of Victoria. Similar reserve networks now exist throughout the public lands in these regions (New South Wales Government 1999, NRE 1999b, Commonwealth of Australia 2000). Thus forest owl populations (and the populations of other forest dependent species) should remain continuous over the public lands of southeastern Australia.

We believe that this strategy provides a soundly based and easily applied set of measures for large forest owl conservation. Clearly, it is built on a number of guesses and untested assumptions, but at the very least it is a substantial improvement over previous arrangements for owl conservation in East Gippsland. It is precautionary in the sense that it will retain options until the end of the life of the forest management plan (ten years), by which time current research on owl ecology is likely to have generated further information to enable refinement of conservation measures. This approach has been adopted as the basis for forest owl conservation throughout the State Forests of Victoria (eg Webster *et al.* 1999).

ACKNOWLEDGMENTS

Many people were involved in the development of these conservation guidelines. The East Gippsland Forest Management Planning Team, particularly Brian Thompson and Mick Bramwell, made significant contributions over an extended period. Rod Kavanagh of State Forests of NSW provided much valuable information on owl ecology and forest management. Mark Burgman of Melbourne University, Stephen Debus of the University of New England, Richard Loyn and Keith Cherry both of the Arthur Rylah Institute of NRE, Kim Lowe and Mal McKinty of NRE Melbourne and two anonymous referees made many useful comments on drafts of the paper. Tony Rule of NRE prepared the figure. Mark Burgmann also provided valuable direction with respect to risk analysis. We thank them all.

REFERENCES

Atlas of Victorian Wildlife. Database maintained by the Arthur Rylah Institute, Department of Natural Resources and Environment, Victoria.

Bartlett, A. & Lugg, A. 1993. Timber. In Lugg, A., Marsh, P., Bartlett, A., and King, F. (eds) *Statement of Resources, Uses and Values for the East Gippsland Forest Management Area*: 126–149. Melbourne: Department of Conservation and Natural Resources, Victoria.

Burgmann, M. A., Ferson, S. & Akcakaya, H. R. 1993. *Risk Assessment in Conservation Biology*. London: Chapman & Hall.

CNR 1995. *Forest Management Plan for the East Gippsland Forest Management Area*. Melbourne: Department of Conservation and Natural Resources, Victoria.

Commonwealth of Australia 1996. *East Gippsland Regional Forest Agreement*. Canberra: Australian Government.

Commonwealth of Australia 2000. *Gippsland Regional Forest Agreement*. Canberra: Australian Government.

Davey S. M. 1993. Notes on the habitat of four Australian owl species. In Olsen, P. (ed) *Austr. Raptor Studies*: 126–142. Moonee Ponds: Australian Raptor Studies Association.

Davies, R. & Thompson, B. 1993. Native Flora. In Lugg, A., Marsh, P., Bartlett, A., and King, F. (eds) *Statement of Resources, Uses and Values for the East Gippsland Forest Management Area*: 50–76. Melbourne: Department of Conservation and Natural Resources, Victoria.

Debus, S. J. S. 1993. The Mainland Masked Owl (*Tyto novaehollandiae*): A review. *Aust. Birdwatcher* **15**: 168–191.

Debus, S. J. S. & Chafer, C. J. 1994. The Powerful Owl (*Ninox strenua*) in New South Wales. *Aust. Birds* (*supplement*) **28**:21–39.

Debus, S. J. S. & Rose, A. B. 1994. The Masked Owl *Tyto novaehollandiae* in New South Wales. *Aust.. Birds* **28**: 40–64.

Dickson, K. R. & Juelson, T. C. 1987. The Political Economy of the Spotted Owl. *Ecology* **68**: 772–776.

Emison, W. B., Bearsell, C. M., Norman, F. I., Loyn, R. H. & Bennett, S. C. 1987. *Atlas of Victorian Birds*.

Melbourne: Department of Conservation, Forests and Lands and the Royal Australasian Ornithologists' Union.

Henry S. R. & Murray, A. J. 1993. Fauna. In Lugg, A., Marsh, P., Bartlett, A., and King, F. (eds) *Statement of Resources, Uses and Values for the East Gippsland Forest Management Area*: 77–102. Melbourne: Department of Conservation and Natural Resources, Victoria.

Higgins, P. J. 1999. *Handbook of Australian, New Zealand and Antartic Birds. Volume 4: Parrots to Dollarbird*. Melbourne: Oxford University Press.

Kambouris, P. 2000. *Large Forest Owls in Special Management Zones, East Gippsland Forest Management Area 2000*. East Gippsland Flora and Fauna Group Report No 8. Orbost: Unpublished Report for the Department of Natural Resources and Environment, Victoria.

Kavanagh, R. P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Aust. J. Ecol.* **13**: 445–450.

Kavanagh, R. P. 1991. The target species approach to wildlife management: gliders and owls in the forests of south-eastern New South Wales. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 377–383. Mosman: Royal Zoological Society of New South Wales.

Kavanagh, R. P. 1996. The breeding biology and diet of the Masked Owl *Tyto novaehollandiae* near Eden, New South Wales. *Emu* **96**: 158–165.

Kavanagh, R. P. 1997. *Ecology and management of large forest owls in south-eastern Australia*. Ph. D. Thesis, University of Sydney.

Kavanagh, R. P. & Bamkin, K. L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales. *Biol. Conserv.* **71**: 41–53.

Kavanagh,R. P. & Jackson, R. 1997. Home-range, movements, habitat and diet of the Sooty Owl *Tyto tenebricosa* near Royal National park, Sydney. In Czechura, G. V. & Debus, S. J. S. (eds) *Australian Raptor Studies II. Birds Australia Monograph 3*. Melbourne: Birds Australia.

Land Conservation Council (1986) *East Gippsland Area Review: Final Recommendations*. Melbourne: Land Conservation Council.

Loyn, R. H., Traill, B. J. & Triggs, B. 1986. Prey of Sooty Owls in East Gippsland before and after fire. *Victorian Naturalist* **103**: 147–149.

McCarthy, M. A., Webster, A., Loyn, R. H. and Lowe, K. W. 1999. Uncertainty in assessing the viability of the Powerful Owl *Ninox strenua* in Victoria, Australia. *Pac. Conserv. Biol.* **5**: 144–154.

McIntyre, A. D. & Bramwell, M. D. In prep. Large Forest Owls of the East Gippsland Forest Management Area, Victoria. Orbost: Department of Natural Resources and Environment, Victoria.

Milledge, D. R., Palmer, C. L. & Nelson, J. L. 1991. 'Barometers of change': The distribution of large forest owls and gliders in Mountain Ash Forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 53–65. Mosman: Royal Zoological Society of New South Wales.

Murphy, D. D. & Noon, B. R. 1992. Integrating scientific methods with habitat conservation planning: reserve design for the Northern Spotted Owls. *Ecol. Applic.* **2**: 3–17.

New South Wales Government 1999. *Forest Agreement for the Eden Region*. Sydney: New South Wales Government.

NRE 1999a. *Threatened Fauna of Victoria*. Melbourne: Department of Natural Resources and Environment, Victoria.

NRE 1999b. *Proposed Forest Management Plan for the North East*. Melbourne: Department of Natural Resources and Environment, Victoria.

Peake, P., Conole, L. E., Debus, S. J. S., McIntyre, A. D. and Bramwell, M. D. 1993. The Masked Owl *Tyto novaehollandiae* in Victoria. *Aust. Birdwatcher* **15**: 124–136.

Saunders, D. A., Hobbs, R. J. and Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**: 18–32.

Saxon M. J., Henry, S. R. & Seebeck, J. H. 1994. *Management Strategy for the Conservation of the Long-*

footed Potoroo Potorous longipes, *in Victoria*. Arthur Rylah Institute Technical Report Series No. 127. Melbourne: Department of Conservation and Natural Resources, Victoria.

Schodde, R. & Mason, I. J. 1980. *Nocturnal Birds of Australia*. Melbourne: Lansdowne Editions.

Scotts, D. J. 1991. Old-growth Forests: their ecological characteristics and value to forest-dependant vertebrate fauna of south-east Australia.. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 147–159. Mosman: Royal Zoological Society of New South Wales.

Simberloff, D. 1987. The Spotted Owl fracas: mixing academic, applied and political ecology. *Ecology* **68**: 766–772.

Webster, A., Humphries, R. and Lowe, K. 1999. Powerful Owl *Ninox strenua*. Action Statement No 92. Melbourne: Department of Natural Resources and Environment, Victoria.

Woodgate, P.W., Peel, W. D., Ritman, K. T., Coram, J. E., Brady, A., Rule, A. J. & Banks, J. C. G. 1994. *A Study of the Old-growth Forests of East Gippsland*. Melbourne: Department of Conservation and Natural Resources, Victoria.

21

OWLS IN THE SOUTHWEST FORESTS OF WESTERN AUSTRALIA

G. L. LIDDELOW [1], I. B. WHEELER [1] & RODNEY P. KAVANAGH [2]

[1] Conservation and Land Management, CALMScience Division, Brain Street, Manjimup,
WA 6258.

[2] State Forests of New South Wales, Forest Research Division, PO Box 100, Beecroft, NSW 2119

The first systematic survey of owls in the southwest of Western Australia was conducted during spring 1999 and autumn 2000. This focused on the Masked Owl (*Tyto novaehollandiae*) and the Barking Owl (*Ninox connivens*) and covered an area from Toodyay (near Perth) in the north to Augusta in the southwest and York/Narrogin in the east and Stirling Range National Park and Two Peoples Bay (near Albany) in the southeast.

Seventy sites, stratified by major forest type (Jarrah, Karri, Wandoo) and logging history (up to three categories), were surveyed using taped playback, once in each season, and all nocturnal birds and mammals seen or heard were recorded. A further 30 sites were surveyed to sample transitional vegetation communities (e.g. Jarrah/Wandoo woodland), forest fragments (e.g. Tuart woodland), and forests at a number of outlying locations (e.g. Boranup, Dryandra, Boyagin and the Stirling Ranges).

A total of 196 Southern Boobooks (*Ninox novaeseelandiae*) and 15 Masked Owls were recorded at 67% of sites. Seventy-six Australian Owlet-nightjars (*Aegotheles cristatus*) and 21 Tawny Frogmouths (*Podargus strigoides*) were also recorded. One hundred and fifty-six owls were recorded within the main forest belt and 55 from the outlying forest sites. No Barking Owls were recorded, although the species was reported from privately-owned land outside or adjacent to the main forest belt.

A range of mammals, including 18 Western Ringtail Possums (*Pseudocheirus occidentalis*) and 15 Common Brushtail Possums (*Trichosurus vulpecula*), was also recorded at the survey sites.

INTRODUCTION

Owls are an important component of Australian forest ecosystems, but their cryptic habits often result in them being overlooked in land management planning decisions. To remedy this situation, the first step is to describe their patterns of distribution and associations with different

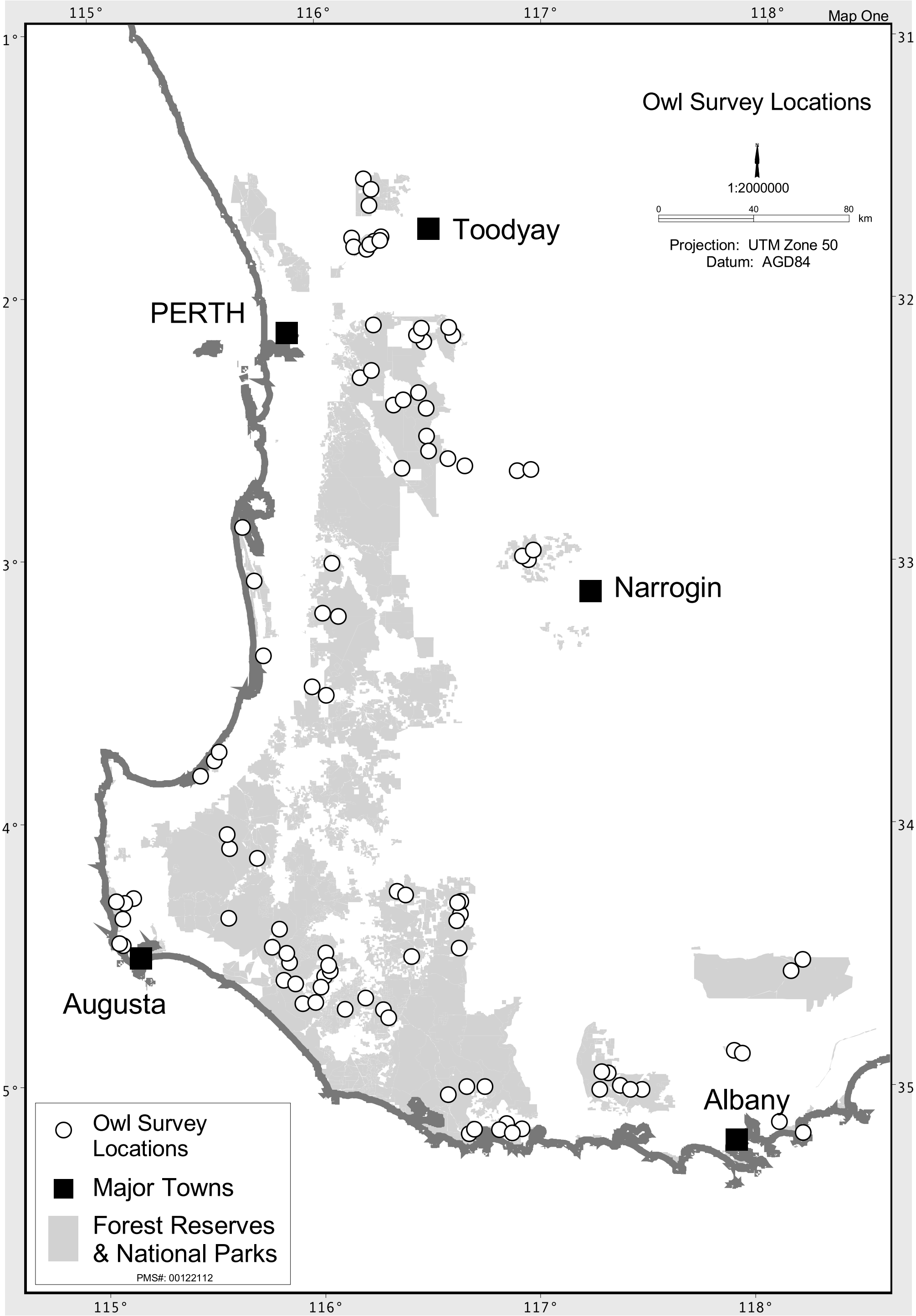


Fig. 1. Location of survey sites in the southwest forests.

forest types and disturbance classes in the forest. Appropriate surveys have now been conducted over the past 12 years in New South Wales and Victorian forests (e.g. Milledge *et al.* 1991, Kavanagh & Peake 1993, Kavanagh *et al.* 1995b, Kavanagh & Stanton 1998, Loyn *et al.* 2002). These surveys focus on the status of each species and their broad habitat requirements, and formed the basis for owl-habitat models that assisted land-use decisions in several Commonwealth-State Regional Forest Agreements.

In this study, we report the results of the first such survey in Western Australia. Nocturnal fauna were sampled using a standard procedure during two seasons at 100 widely-distributed sites throughout the southwest forests. We found that, while the nocturnal fauna was comprised of fewer species than that in the east coast forests, several species displayed similar patterns of abundance between east and west coast forests and the four owl species encountered showed similar associations with forest habitat types.

METHODS

Study area and site stratification

The study area included all public forest lands (state forest and national park) within the southwest forests, extending from Toodyay (near Perth) in the north to Augusta in the southwest and York/Narrogin in the east, and Stirling Range National Park and Two Peoples Bay (near Albany) in the southeast (Fig. 1). Survey sites were selected with the assistance of GIS maps (produced by CALM's Information Management Branch, Perth), but with sampling restricted to forest areas of at least 600ha (for the first 70 sites) and preferably outside areas zoned to quarantine the spread of the root-rot fungus *Phytophthora cinnamomi*. The minimum distance between survey sites was set at 3 km.

Seventy sites were selected within the three major forest and woodland types of the region: Jarrah *Eucalyptus marginata*, Karri *E. diversicolor* and Wandoo *E. wandoo* (Fig. 1). Ten sites were located in each forest type in areas with no record of logging (based on CALM logging history maps of the region). A further ten sites within each forest type were allocated to areas that had been logged on one or two occasions. In the case of Karri, the ten sites represented 15–70 year-old forest regrowth following clearfelling. In Jarrah and Wandoo, the sites had been selectively logged. Finally, ten sites were chosen in Jarrah forests that had been selectively logged on three or more occasions.

A further thirty sites (mainly outliers from the main forest belt) were also surveyed to sample transitional vegetation communities (Jarrah/Wandoo woodland; eight unlogged sites), forest fragments (Tuart *E. gomphocephala* woodland; seven unlogged sites), and forests at outlying locations (Boranup, four logged Karri sites; Porongorup Range National Park, two unlogged Karri sites; Dryandra, three unlogged Wandoo sites; Boyagin Rock Reserve, two unlogged Wandoo sites; Stirling Range National Park, two unlogged Wandoo sites; and Two Peoples Bay Nature Reserve, two unlogged coastal woodland sites) (Fig. 1).

Survey method

A total of two surveys were conducted, spring (13–25 September 1999) and autumn (6–24 March 2000) and all nocturnal birds and mammals seen or heard were noted. At each site, 15 minutes was spent listening for unelicited vocalisations, followed by 10 min (5 min for each species) of intermittently broadcasting pre-recorded calls of Masked Owl (*Tyto novaehollandiae*) and Barking Owl (*Ninox connivens*) and listening for a response. Finally, ten minutes was spent searching a 1ha plot (56.5 m radius) with a hand-held 12V 100W spotlight for animals present at the site that did not call. The numbers of indiviuals of each species were recorded and the closest distance for each species to the plot centre was estimated. This technique was similar to that described and used by Kavanagh & Bamkin (1995). The maximum number of each species recorded at each site during either the spring or the autumn survey comprised the data used in analysis. Arboreal mammals were recorded as an indication of likely prey abundance for owls.

Surveys began after dark, usually 1900 hours, and extended until about 0300 hours. Owl vocalisations were broadcast using a Toa ER–2015 megaphone coupled to a Sony TCM–333 cassette recorder. A rapid habitat assessment was also conducted at each site to record the predominant tree species, the numbers of trees with visible large hollows, and understorey height and density.

During the survey period, a number of requests were made through local media (radio, newspaper) inviting members of the public to supply records of the Masked Owl and Barking Owl in the southwest region.

RESULTS

A total of one hundred and fourteen Southern Boobooks (*Ninox novaeseelandiae*), five Masked Owls, thirty Australian Owlet-nightjars (*Aegotheles cristatus*) and eleven Tawny Frogmouths (*Podargus strigo*ides) were recorded in spring 1999, while in autumn 2000, eighty-two Boobooks, ten Masked Owls, forty-six Owlet-nightjars and nine Frogmouths were recorded from the same sites (Table 1). The Southern Boobook and the Masked Owl appeared to be more common among the forest outlier sites than among the sites within the main forest belt (Table 1). However, detectability of the Southern Boobook declined among these outlying sites during autumn, while it increased for the Masked Owl. Counts of the Australian Owlet-nightjar also increased during autumn, but only within the main forest belt (Table 1). Overall the Jarrah and Woodland sites held 21% of the owls recorded in spring and 28% of those in autumn, the Karri had 26% in spring and 25% in autumn, and the Wandoo had 23% in spring and 26% in autumn, with the Outliers having 30% in spring and 21% in autumn.

Within the main forest belt, the Southern Boobook was recorded at 97.5% of sites with the Western Australian smooth-barked tree species (Karri and Wandoo), but at only at 56.6% of sites dominated by Jarrah (a rough-barked species). Proportion of sites at which Boobooks were detected in the main forest belt was compared with the Outliers using Chi Square analysis; no significant difference was found ($\chi^2 = 0.527$, d$F = 1$, $P = 0.468$). Over the period of the survey, in both spring and autumn, recording rates for the Southern Boobook in the Karri were 90% in the unlogged and 100% in logged forest sites, and 100% in both logged and unlogged Wandoo woodland sites. However, in Jarrah forest, these owls were recorded at 70% of the unlogged sites, at 60% of sites logged once or twice and at 40% of sites logged three or more times (Table 1). A comparison of the frequency of detection of Southern Boobooks in relation to logging history within the main forest belt was conducted using Chi Square analysis; a significant difference was found ($\chi^2 = 20.9$, d$F = 7$, $P = 0.004$). Thus the Southern Boobook was more likely to be recorded in relatively undisturbed forests, but due to the small sample size, some caution is required with this finding.

Table 1. Distribution of nocturnal forest birds and mammals in each forest type.

Figures show the number of sites where each species was detected, using records from both spring and autumn, and the number of individual night birds and mammals recorded during spring and autumn.

	No. Sites Surveyed	**Southern Boobook** *Ninox novaeseelandiae*			**Masked Owl** *Tyto novaehollandiae*			**Tawny Frogmouth** *Podargus strigoides*			**Australian Owlet Nightjar** *Aegotheles cristatus*			**Common Brush Tail Possum** *Trichosurus vulpecula*			**Western Ringtail Possum** *Pseudocheirus occidentalis*			Total
Forest Type		**Spr**	**Aut**	**Sites Occ.**	**Spr**	**Aut**	**Sites Occ.**	**Spr**	**Aut**	**Sites Occ.**	**Spr**	**Aut**	**Sites Occ.**	**Spr**	**Aut**	**Sites Occ.**	**Spr**	**Aut**	**Sites Occ.**	
Main Forest																				
Jarrah unlogged	10	5	7	7	1		1		2	2	1	5	5		2	1	1	1	1	**10**
Jarrah logged one or twice	10	3	4	6					1	1	2	2	3	1		1	3		2	**9**
Jarrah logged 3 times or more	10	3	2	4					1	1		3	3	1		1	3		1	**5**
Karri unlogged	10	7	9	9				1	1	1	5	5	6							**10**
Karri logged once or twice	10	10	6	10				1	1	2	5	6	8							**10**
Wandoo unlogged	10	8	9	10		1	1		1	1	2	3	5							**10**
Wandoo logged one or twice	10	8	8	10				3		3		5	5							**10**
Woodland	8	4	5	6		1	1	2	1	2	3	3	4	2		2	2		2	**8**
sub total -Sites	**78**	**48**	**50**	**62**	**1**	**2**	**3**	**7**	**8**	**13**	**18**	**32**	**39**	**4**	**2**	**5**	**6**	**1**	**6**	**72**
sub total – Individuals		***82***	***71***		***1***	***2***		***10***	***9***		***22***	***40***		***4***	***0***		***9***	***1***		***252***
Outliers																				
Tuart	7	5	4	6	1	3	3	1		1	1		1	4		2	2		2	**6**
Boranup	4	4		4	1	1	1				3		3							**4**
Dryandra	3	3	1	3	2	2	3					1	1	2		1				**3**
Boyagin	2	2			2								1	1	1		1			**2**
Stirlings	2	2		2							2				1	1				**2**
Porongurups	2	1		1							1	2	2	1		1				**2**
T-P-Bay	2		1	1								2	2				5	1		**2**
sub total – Sites	**22**	**17**	**6**	19	**4**	**6**	7	**1**	**0**	1	**7**	**6**	10	**5**	**1**	6	**4**	**1**	2	**21**
sub total – Individuals		***32***	***11***		***4***	***8***		***2***	***0***		***8***	***6***		***8***	***1***		***7***	***1***		***87***
TOTAL SITES	**100**	**65**	**56**	**81**	**5**	**8**	**10**	**8**	**8**	**14**	**25**	**38**	**49**	**9**	**2**	**11**	**10**	**2**	**8**	**93**
TOTAL INDIVIDUALS		***144***	***82***		***5***	***10***		***12***	***9***		***30***	***46***		***12***	***3***		***16***	***2***		***339***

Arboreal mammals were generally uncommon in the southwest forests, and the Karri forest appeared to be the most depauperate (Table1).

DISCUSSION

No Barking Owls were found during this survey at any of the sites in either spring or autumn. As this species breeds in spring, it should have been readily detectable if present (Fleay 1968, Calaby 1990, Hollands 1991, Kavanagh *et al.* 1995a). There were recent reports of Barking Owls (since 1999) from Forest Grove near Margaret River, Deepdene near Augusta, farmland to the east of Balingup, South Coast Highway near the Valley of The Giants at Walpole, Congelin near Narrogin, Mulyinning near Wickepin, Fitzgerald National Park and Torndirrup National Park near Albany. These recent records are taken from the Department of Conservation and Land Management Fauna File and came from a variety of sources. All of these sites are outside the main forest belt and, in this regard, the habitat of the Barking Owl appears to be similar to that in the eastern States where it is not regarded as a bird of tall, continuous forests (Kavanagh *et al.* 1995a). Abbott (1999) also lists a number of sites outside the main forest belt where this species has been either heard or seen. Records from the WA Museum over the past forty-five years indicate occurrences of Barking Owls from Margaret River (1986), Manjimup (1995), Pemberton (1955), Mundaring (1984) and Toodyay (1979) (Fig. 2). All previous records are from 1842 through to 1931. This species was rarely reported in the southwest during the national Bird Atlas surveys during 1977–1981 (Blakers *et al.* 1984). The Barking Owl is clearly uncommon in the southwest and in need of further attention.

Masked Owl records in the southwest of WA were also sparse. The sites where they were recorded by us range from Boranup and the Tuart forest in the west, the proposed Milyeannup Nature Reserve on the Blackwood Plateau, Dryandra Forest, the Avon Valley and Woodland at Walpole. Most of the Masked Owl records came from the Tuart forests and Dryandra. Masked Owls comprised 4.2% of the counts in spring and 11% of those in autumn. The Masked Owl occurs in open forest and woodland, and appears to be associated with ecotones for hunting, either as clearings or natural openings within the forest or forest edges with another vegetation type, but it roosts among dense foliage in gullies, or in caves or tree hollows (Blakers *et al.* 1984, Kavanagh & Murray 1996, Abbott 1999). Apart from the Milyeannup record, all the other records were in woodland with open understorey and forest edges nearby. Two road-killed Masked Owls were recently handed into the CALMScience office (Manjimup) from Palgarup, north of Manjimup (August 1999) and Benger, between Harvey and Brunswick Junction (July 1999). Another Masked Owl was seen between survey points at Lake Muir east of Manjimup and two further individuals were seen at a CALMScience study site in Kingston northeast of Manjimup by Graeme Liddelow and Ian Wheeler of CALMScience, Manjimup. All of these records were in woodland or open forest with cleared agricultural land nearby. There have also been recent reliable records from Bridgetown and Manjimup (Liddelow and Wheeler).

The Barn Owl occurs in even more open, sparsely wooded country, and its numbers can fluctuate greatly from year to year depending on food supply (Calaby 1990b). No Barn Owls were recorded during the survey and only three birds were seen while travelling between sites (between Dryandra and Boyagin). One other bird was seen while travelling between Mumballup and Boyup Brook on the night of 13 September just before the spring survey.

The Southern Boobook was recorded in all of the forest types in this survey. It is clearly widespread throughout the southwest of Western Australia.

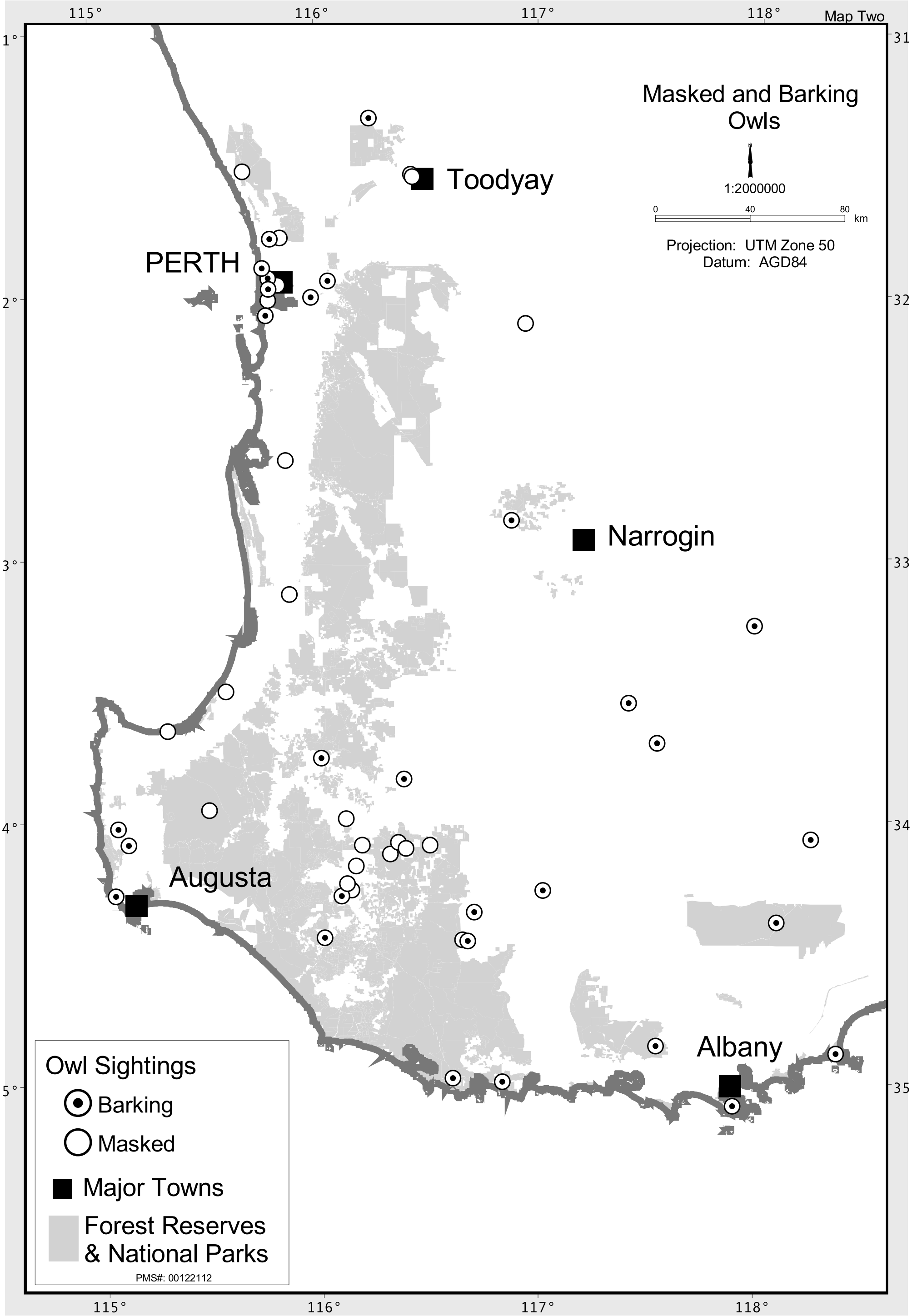


Fig. 2. Distribution of records for Masked Owl and Barking Owl from this survey, from the WA Museum, and from information from the general public on Barking Owls.

Few arboreal mammals were detected, particularly in the Karri forest. However, ground dwelling mammals (*Rattus fuscipes* and *Antechinus flavipes*) are usually abundant in Karri forest (Per Christensen, pers. comm., CALM unpublished data), and these species could be expected to form prey for the Masked Owl and possibly also the Barking Owl (Kavanagh *et al.* 1995, Kavanagh 1996). The tall dense nature of the understorey in the Karri forest may preclude effective hunting by large owls.

CONCLUSIONS

This survey was a preliminary study of the occurrence of owl species in the forests and woodlands of southwest Western Australia. The Southern Boobook Owl is common and widespread throughout this region and the Masked Owl occurs mainly in the woodland region or where agricultural land intrudes into the heavier forest. Barking and Barn Owls do not appear to be forest species in Western Australia, a pattern that is similar to New South Wales and Victoria. The conservation status of the Barking Owl is uncertain and of concern because the species appears to be confined mainly to private land in the southwest. In its open-forest habitat, this species may be more sensitive to continuing fragmentation than is the Barn Owl, which is commonly associated with agriculturally-dominated landscapes.

The sites used in this study should form part of future long-term monitoring of owls in Western Australia. Surveys should also be conducted on private lands, particularly around farmland edges and along the main river systems, to determine the importance of these areas for the conservation of the Masked Owl and the Barking Owl in the southwest. Studies of the ecology of these owls in WA are needed to determine the importance of various habitat components to the conservation of these species.

ACKNOWLEDGMENTS

We thank Dr Ian Abbott and Dr Neil Burrows of CALMScience for inviting RPK to visit WA to design and supervise the running of this project, for providing funding for the study, and for providing GIS maps to assist with site selection. We also thank Matthew Williams from CALMScience for assistance with statistical analysis, and Barry Flett from CALMradio, Manjimup, who modified the megaphones to accept cassette recorder inputs. Trevor Smailes and Shane French from Information Management Branch, Como produced the original field maps and those used in this report. The District Staff at Walpole, Mundaring and Narrogin provided maps and local knowledge to assist site selections within their management areas. Finally, thanks to those members of the public (Kim Williams, Witchcliffe; Per Christensen, Balingup; Chris Goodsell, Walpole; Jo Fowler, Congelin; Geoff Burrows, Mulyinning; Brenda Newbey, Fitzgerald National Park; Vic Smith, Torndirrup National Park) who responded to our request for information about Barking Owls.

REFERENCES

Abbott, I. 1999. The avifauna of the forests of southwest Western Australia: changes in species composition, distribution, and abundance following anthropogenic disturbance. *CALMScience* Supplement 5: 1–175.

Blakers, M. Davies, S.J.J.F. & Reilly, P.N. 1984. *The Atlas of Australian Birds*. Melbourne: Melbourne University Press.

Calaby, J.H. 1990a. Barking Owl (*Ninox connivens*). In *The Readers Digest Complete Book of Australian Birds*: 330, 2nd Edition. Readers Digest (Aust) Pty Ltd.

Calaby, J.H. 1990b. Barn Owl (*Tyto alba*). In *The Readers Digest Complete Book of Australian Birds*: 332, 2nd Edition. Readers Digest (Aust) Pty Ltd.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Brisbane: Jacaranda Press.

Hollands, D. 1991. *Birds of the Night*: *Owls*, *Frogmouths and Nightjars of Australia*. Sydney: Reed Press.

Kavanagh, R.P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in southeastern New South Wales, Australia. *Biol. Conserv*. **71**: 41–53.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B. & Turner, R.J. 1995a. Diet and habitat of the Barking Owl *Ninox connivens* in New South Wales. *Aust. Bird Watcher* **16**: 137–144.

Kavanagh, R.P., Debus, S., Tweedie, T. & Webster, R. 1995b. Distribution of nocturnal forest birds and mammals in northeastern New South Wales: relationships with environmental variables and management history. *Wildl. Res*. **22**: 359–377.

Kavanagh, R.P. & Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96:** 250–257.

Kavanagh, R.P. & Peake, P. 1993. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In P. Olsen (ed.) *Australian Raptor Studies*: 101–125. Melbourne. Australian Raptor Association, Royal Australasian Ornithologists' Union.

Kavanagh, R.P. & Stanton, M.A. 1998. Nocturnal forest birds and arboreal marsupials of the Southwestern Slopes, New South Wales. *Aust.. Zoologist* **30**: 449–466.

Loyn, R.H., McNabb, E.G., Volodina, L., & Willig, R. 2002. Modelling distributions of large forest owls as a conservation tool in forest management. This volume.

Milledge, D.R., Palmer, C.L. & Nelson, J.L. 1991. 'Barometers of change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 53–65. Mosman: Royal Zoological Society of New South Wales.

22

MODELLING DISTRIBUTIONS OF LARGE FOREST OWLS AS A CONSERVATION TOOL IN FOREST MANAGEMENT: A CASE STUDY FROM VICTORIA, SOUTHEASTERN AUSTRALIA

RICHARD H. LOYN[1], EDWARD G. MCNABB[1], LIOUDMILA VOLODINA[2] & ROLF WILLIG[3]

[1]Arthur Rylah Institute for Environmental Research, Department of Natural Resources & Environment, PO Box 137, Heidelberg, Victoria 3084, Australia.

[2]Dept. Statistics and Operations Research, Royal Melbourne Institute of Technology University, GPO Box 2476V, Melbourne, Victoria 3001, Australia.

[3]Forests Service, Dept. Natural Resources & Environment, 14/8 Nicholson St, East Melbourne, Victoria 3002, Australia.

Large owls are top predators in Australian forests, and have large home ranges. They and some of their prey need old hollow-bearing trees. Hence, selected forest stands need to be retained to conserve large owls in managed forests, using a landscape approach. To help select such stands, owls were surveyed at 1,306 sites in eastern Victoria, using call playback and spotlighting. Results were modelled by logistic regression with respect to habitat and landscape variables. Mapped variables explained more variation than habitat variables assessed at survey sites. Powerful Owls *Ninox strenua* favoured drier forest types with many live hollow-bearing trees, Blackwood Wattle trees *Acacia melanoxylon*, diverse habitats and extensive mature forest within 2 to 5 km. Sooty Owls *Tyto tenebricosa* favoured wetter senescent forest, with abundant tree-ferns, Blanket-leaf *Bedfordia arborescens* and Silver Wattle *Acacia dealbata*, diverse habitats and extensive mature forest within 0.5 to 2 km. Barking Owls *Ninox connivens* and Masked Owls *Tyto novaehollandiae* were rare. The models were field-tested and found to discriminate well between high and low probability sites. Actual records and then models were used to help select and conserve 487 protected areas for large owls, each of approximately 500 ha.

INTRODUCTION

Large forest owls pose special challenges to forest managers because they are top predators with large home ranges and complex, demanding habitat requirements. They may be considered to act as 'umbrella species' (Simberloff 1998), in the sense that, if large owls are conserved, many other species will also be well conserved. In Australia, all large forest owls need tree hollows for nesting and some species also need them for roosting (Schodde & Mason 1980; Hollands 1991; Higgins 1999). Arboreal mammals form a high percentage of their prey (Fleay 1968; Seebeck 1976; Tilley 1982; McNabb 1996; Higgins 1999), and most of these mammals depend on tree hollows for daytime shelter (Strahan 1983; Menkhorst 1995). Large hollows suitable for these species may not form until trees are hundreds of years old (Ambrose 1982; Mawson & Long 1994) and large trees tend to contain many more hollows than small trees (Bennett *et al.* 1991; Soderquist 1999a).

Commercially attractive rotations for timber production are usually shorter than the time needed to develop hollows. Three primary strategies are available to conserve hollow-dependent fauna in forests used for wood production (Loyn 1985a), of which selected stand retention is the most popular and generally the most effective. The other primary strategies are extended rotations or tree retention on coupes. The two retention strategies need to include provision to regrow further old stands or trees to replace those that are lost over time to stochastic events such as wildfire. The stand retention strategy is particularly effective if stands are selected on the basis of their value for hollow-dependent fauna such as large forest owls. To this end, a program was initiated in Victoria, southeastern Australia, to help select and conserve valuable habitat for large forest owls. This was done as part of forest planning processes and establishment of Regional Forest Agreements between state and commonwealth governments (Victorian RFA Steering Committee 1998), following a national forest policy initiative (Commonwealth of Australia 1992).

Surveys in northeast Victoria (Loyn *et al.* 2001) have now been extended throughout the forested parts of southern and eastern Victoria. Data have been analysed for 3.5 million ha of forest along the Great Dividing Range in eastern Victoria (from the Gippsland coast to the upper catchment of the Murray River), and form the basis for the case study discussed in this paper. Altitudes range from 0 to 1986 m above sea level. Rainfall varies from about 500 mm in the lowlands to over 1500 mm in the mountains. Climate is generally temperate and strongly seasonal, with warm to hot summers and cool to cold winters. The lowlands have been extensively cleared for agriculture. Forests form a continuous belt between the high Alps and mainly cleared valleys below, including much remote and rugged country. Timber production is economically important, especially from tall forests in high rainfall areas. The forests provide essential habitat for wildlife including owls. Four large forest owls occur in Victoria where all are listed as threatened (Department of Natural Resources and Environment 1999a), and all are endemic to Australia and New Guinea (Higgins 1999).

METHODS

Site selection

Sites were chosen by stratified random sampling based on geographical areas, Ecological Vegetation Classes (EVCs) and climatic and lithographic information, all available on GIS. EVCs are groupings of vegetation communities based on floristic quadrats (vascular species in understorey and overstorey) and extrapolated using combinations of ground survey and aerial photo interpretation. Sites were selected with no regard to land tenure (State Forest or National Park). All sites were chosen to be on mapped tracks, and extra sites were selected to allow some redundancy for sites where access proved impractical. Additional sites were selected at random in the field (using dice), mainly to make sensible use of field time when long distances had to be travelled between pre-selected sites. Each site was at least 2 km from any other site, as broadcast tapes were audible to human observers for up to 2 km. Trials with captive owls showed no response when tapes were played at distances of 1 km.

Field methods

Field teams were assembled with the skills to focus on nocturnal fieldwork. Surveys were conducted at 1,306 sites (472 sites in northeast Victoria and 834 sites in Gippsland and the Central Highlands) from April 1996 to June 1998, using call playback and standard spotlighting as the main methods. Observers worked independently (each with a 4WD vehicle), but pairs of observers worked in the same general area and maintained regular radio contact for safety purposes.

A standard call playback tape was constructed with calls of all four large forest owl species and the smaller Southern Boobook *Ninox novaeseelandiae*, each followed by a 2-minute listening period. The tape ran for 25 minutes and began with repeated calls from Powerful Owl *Ninox strenua* (2 minutes), Southern Boobook (2 minutes) and Barking Owl *Ninox connivens* (2 minutes). It continued with four screams from Sooty Owl *Tyto tenebricosa* over 2 minutes and then a minute of its trilling calls after a minute's wait, and five shrieks from Masked Owl *Tyto novaehollandiae* over 2 minutes, followed by its chattering call after a minute's wait. The tape was broadcast at selected sites using a 10 watt megaphone, at a volume of about 120% of the owls' natural level. Playback surveys were only conducted on calm nights with little or no rain, because wind and rain noise reduce the effectiveness of this survey method (Kavanagh & Peake 1993; Debus 1995). While tapes were running, the observer remained several metres away to avoid distraction from tape noise. All owls and other wildlife seen or heard were recorded, along with details of wind, temperature and other weather conditions.

At the completion of playback, a 10 minute spotlighting session was conducted to search for any owls which may have flown in silently, and any arboreal mammals or other nocturnal wildlife. During this session, the observer walked for about 100m along the track, listening and using a hand-held spotlight. All animals seen or heard were recorded. Incidental observations of birds nearby were recorded separately. Notes were made at each site on landform, topography and aspect, as well as on a range of vegetation and habitat features. The notes referred to forest within 100 m of a central point.

Analysis

Occurrence of owls was considered as a categorical dependent variable (each species either recorded or not recorded at a site). Geographical Information Systems (GIS) were used to assign characteristics to each site, from mapped information held in the NRE corporate database. The principal characteristics considered were EVC and forest growth-stage (Department of Natural Resources & Environment 1999b). These characteristics were also considered within radii of 500m, 2 km and 5 km of each site, representing areas of about 80 ha, 1,250 ha and 7,850 ha respectively (Table 1). The 2 km radius corresponds most closely with current views of home range areas for large forest owls (Hollands 1991; Traill 1993; McNabb 1996; Kavanagh & Murray

Table 1. Variables used for modelling distributions of Powerful and Sooty Owls in northeast Victoria (NE), Gippsland (G) and the Central Highlands (CH), Victoria, Australia, 1996–99

C = categorical, *N* = numerical, M = mapped, O = on-site

Variable	Type of variable	Unit or number of categories
Ecological Vegetation Class (EVC)	C, M	25 in NE (6 groups), 35 in G&CH (10 groups)
Area of EVC group in radius of 0.5 km, 2 km or 5 km	N, M	ha (considered as 4 groups in NE, 10 groups in G&CH)
Number of EVCs in radii as above	N, M	number (reflecting local diversity of vegetation types)
Forest growth-stage	C, M	6 (mainly senescent/mature, mixed senescent/mature/regrowth, mainly mature, mixed mature/regrowth, regrowth with scattered older trees, pure regrowth)
Area of forest dominated by each group of forest growth-stages in radii as above	N, M	ha (considered as 4 groups: mainly senescent, mainly mature, regrowth with scattered older trees, pure regrowth)
Arboreal mammals	N, O	Numbers of each species observed in 10 minute transect and during playback
Wind velocity	C, O	3 (scale 0–3)
Landform	C, O	4 (gully, ridge, slope or saddle)
Topography	C, O	3 (flat, moderate, steep)
Presence of particular plant species	C, O	2 (present/absent) for each of 6 eucalypt groups, 2 wattle species, Blanket-leaf (*Bedfordia arborescens*) or tree-ferns
Mean tree diameter	C, O	3 (low, medium or high, estimated from proportions of size-classes)
Live hollow-bearing trees	C, O	3 (none, few or many within 50 m)
Dead hollow-bearing trees	C, O	3 (none, few or many within 50 m)
Middle storey height	N, O	m
Density of low shrubs	C, O	4 (absent, sparse, medium, dense)

1996; Kavanagh & Jackson 1997; Higgins 1999), and also with the usual range of playback broadcast. Larger home ranges may be used in fragmented dry forests such as Box-Ironbark (Soderquist 1999b). The number of EVCs within each of the radii was calculated as a measure of habitat diversity at each of these landscape scales. Classifications of EVCs and growth-stages at each of these scales were condensed into groups (e.g. wet, riparian, damp or dry forest) to avoid excessive numbers of variables for analysis.

Field data on presence of key plant species (e.g. Silver Wattle *Acacia dealbata*, Blackwood *Acacia melanoxylon* or tree-ferns), densities of hollow-bearing trees (many, few or none), landform (gully, mid-slope, saddle or ridge) and steepness of terrain (flat, moderate or steep) were considered as categorical variables (Table 1). Data on numbers of arboreal mammals of each species (observed during playback and standard spotlighting surveys) were considered as numerical variables. A variable was also calculated for 'preferred prey' of Powerful Owls, as the combined number of three arboreal mammal species (Common Ringtail *Pseudocheirus peregrinus*, Greater Glider *Petauroides volans* and Sugar Glider *Petaurus breviceps*).

Bivariate correlation coefficients were calculated for the matrix of dependent and independent variables as a guide to further analysis. Linear models were developed for Powerful and Sooty Owl (the two most widespread large owl species) for each region (northeast Victoria; Gippsland and the Central Highlands, i.e. eastern Victoria north and south of the Great Divide respectively). Their probability of occurrence was modelled by logistic regression using only mapped variables, only field habitat data, and a combination of both. Pairs of independent variables correlated with r values greater than 0.70 were not included together in any model, and nor were variables that were logically related to each other. For Gippsland and the Central Highlands, models have only been developed using mapped variables at this stage.

Following experience in northeast Victoria, two additional constraints were applied in modelling data for Gippsland and the Central Highlands. Firstly, GIS landscape variables (over radii of 500+ m) were used in preference to site-based GIS data, as the playback site formed only a small part of the expected home range of each owl. Secondly, when several landscape variables were included in one model, they were considered over the same radius when possible (i.e. 500 m, 2 km or 5 km, but not a mixture).

Maps of predicted probabilities of occurrence

GIS maps were produced for predicted distributions of Powerful Owl and Sooty Owl, using models based solely on mapped variables. The maps also showed survey records for each species, and previous records from the Atlas of Victorian Wildlife. Patterns of predicted probabilities were examined in relation to these records and other information about the land in question. If unrealistic patterns arose (e.g. unnatural circles of high or low probability), causes were identified and alternative models generated to overcome the problem. The process was repeated until a plausible model was found. This model was then fed back onto GIS maps and used in forest planning as described below.

Field testing

Using the models, test sites were selected from GIS on mapped tracks and surveyed as above. The sites were selected to include equal numbers of 'PO sites' (where probability of recording Powerful Owl was predicted to be high, >~25%, and probability of recording Sooty Owl was predicted to be low, <~10%) and 'SO sites' (vice versa). Field teams were given map coordinates but no details of test design or expectations at a site, so that the procedure was run as a blind test. An alternative design for the test was considered initially, including sites where both Powerful and Sooty Owls were likely to occur, but few such sites proved to be available. In Gippsland, a good geographic spread of SO sites could be obtained only by relaxing the requirement that the probability of recording Powerful Owl should be low. Hence, little difference was expected in occurrence of Powerful Owls between SO sites and random sites in Gippsland. Altogether 76 PO sites (33 in northeast Victoria and 43 in Gippsland and the Central Highlands) and 71 SO sites (31 and 40) were surveyed in field testing.

Use in forest planning

Results from the field surveys and models were used to establish agreed numbers of reserved areas or Special Protection Zones (SPS) for large forest owls, as part of the Regional Forest

Agreement and Forest Management Planning processes. Those that fell in Parks or reserves were assumed to be adequately protected, and those in State Forest were formally designated as Special Protection Zones (SPZs). Actual records of owls were given first priority in this process, including previous records and new records from the survey and field tests. However, there were not enough actual records to satisfy agreed targets for conservation, and models were used to select additional areas to be protected, where predicted probability of occurrence was high.

Each SPZ covered at least 500 ha, bounded by recognisable features such as ridgelines or roads. Each SPZ was designed to include as much quality habitat as possible and as little poor habitat as possible, based partly on the models, but also on mapped EVCs and growth stages or other habitats likely to be used. Creek headwaters were routinely included as they are known from radio-tracking studies in NSW (Kavanagh 1997) to provide important feeding and nesting habitat. Local knowledge was used on the rare occasions when it was available. Each zone was confined within a radius of 3.5 km so that it included a diversity of habitats and conformed to a plausible foraging range for owls (i.e. it was not a long narrow strip along a creek).

RESULTS

Six owl species and 21 nocturnal mammal species were recorded during the field survey. Owls and some arboreal mammals (e.g. Yellow-bellied Glider *Petaurus australis*) were much more often observed during or after playback than during initial quiet listening periods.

Powerful Owls and Sooty Owls were recorded at 65 and 18 sites respectively in northeast Victoria, and at 115 and 90 sites in Gippsland and the Central Highlands. They ranged from the coast across the Great Dividing Range, but Sooty Owls were not recorded from the lower slopes on the dry inland side of the range. Barking Owls and Masked Owls were rare and confined to distinct parts of the region (Barking Owls at twelve sites in dry forest or woodland in the northern lowlands; Masked Owls at eleven sites mainly in the southern lowlands). Southern Boobooks were common (743 sites), and Barn Owls *Tyto alba* were found only in cleared land outside the forest (three records).

Few large owls were observed when wind strength was listed as moderate (category 2), but there was little difference between categories 0 and 1 (calm or light breeze). No surveys were done when wind was strong (category 3). Other weather variables such as temperature and night-light appeared to have little effect on response to playback calls. Powerful and Sooty Owls were slightly more likely to be observed at the few sites selected because they looked good for owls than at other sites.

Linear models, field testing and habitat relationships

Modelling focused on two large owl species that proved to be widely though sparsely distributed in the region. Preferred significant models for Powerful and Sooty Owls in each region are shown in Table 2, based only on mapped variables. They indicated that Powerful Owls favoured mature forest mainly of the drier types best represented in lowlands and foothills, although the species occurred sparsely at most altitudes. A significant negative term for wet forest was dropped from the model for northeast Victoria because it exaggerated the known aversion of this species for wet forest and produced unrealistically large circles of low probability of occurrence when fed back onto GIS maps. This problem did not arise with the equivalent term for Gippsland and the Central Highlands. A negative term for Riparian Forest was retained although the species is

Table 2. Logistic regression models for Powerful Owl and Sooty Owl in Victoria, Australia, 1996–99, using only mapped variables.

To assist comparison between the two regions, terms for similar groups of habitats are arranged horizontally.

Northeast Victoria	**Gippsland & Central Highlands**
Powerful Owl (*65/472 sites*)	*Powerful Owl* (*115/834 sites*)
logit *P* = – 4.779	logit *P* = 1.775
+0.287 number of EVCs in 2 km	
+1.226 if EVC = Shrubby Dry Forest	+0.00119 ha Lowland Forest in 2 km
	+0.00191 ha Shrubby Damp Forest or Tableland Damp Forest in 2 km
	+0.00044 ha Grassy Forest in 2 km
+0.00027 ha mature forest in 5 km	
-0.0016 ha senescent forest in 5 km	
-0.0249 ha pure regrowth in 5 km	
	-0.00049 ha Wet or Montane Forest in 2 km
-0.0128 ha Riparian Forest in 2 km	-0.00104 ha Damp Forest in 2 km
Sooty Owl (18/472 sites)	*Sooty Owl (90/834 sites)*
logit *P* = –12.96	logit *P* = –3.480
+ 0.426 number of EVCs in 500 m	
+ 1.31 if EVC is Herbrich Foothill Forest	+ 0.00139 ha Damp Forest in 2 km
	+ 0.00428 ha Rainforest or Riparian Forest in 2 km
+ 0.00180 ha senescent forest in 5 km	+ 0.00086 ha senescent forest in 2 km
+ 0.167 ha mature forest in 500 m	+ 0.00118 ha mature forest in 2 km
+ 3.76 if growth-stage = SM [mixed senescent/ mature]	
- 1.44 if growth-stage = MR [mixed regrowth/ mature]	
- 1.56 if EVC is Montane Dry Woodland	-0.00204 ha Subalpine Forest in 2 km
- 2.37 if EVC is Grassy or Heathy Dry Forest	- 0.00182 ha Grassy Forest in 2 km
- 0.0772 ha Drier Forest in 500 m	

known to use this habitat: the relationship probably arose because Riparian Forest in northeast Victoria is often surrounded by unsuitable cleared land.

Sooty Owls favoured wet forest and gullies, although some were recorded in drier environments. They tended to be associated with senescent forest (i.e. forest with many dead-topped trees visible from aerial photographs). In selecting models for northeast Victoria, Powerful Owls responded best to different variables at radii of 2 or 5 km, whereas Sooty Owls responded best at radii of 0.5 or 2 km. For Gippsland and the Central Highlands, landscape variables were most useful for both species at the 2 km radius, according well with current views of home range size in forest environments. Both owl species responded to similar sets of variables in each region (Table 2), although terms for habitat diversity and forest growth-stage were more prominent in models for northeast Victoria than for Gippsland and the Central Highlands.

Field tests showed that both owl species were more likely to be found at high probability sites for that species than at low probability sites or random sites on the original survey. Sooty Owls were found at 15.5% of SO sites (11/71) compared with 3.9% of PO sites (3/76) and 8.3% of random sites on the original survey (108/1306). Powerful Owls were found at 27.6% of PO sites

(21/76) compared with 15.5% of SO sites (11/71) and 13.8% of random sites on the original survey (180/1306). For northeast Victoria alone (where SO sites were expected to have low probabilities for Powerful Owl), Powerful Owls were found at 21.2% of PO sites (7/472) compared with 3.2% of SO sites (1/31) and 13.8% of random sites on the original survey (65/472).

Models based on on-site habitat variables (assessed near the playback site) were much weaker than the landscape models presented in Table 2, and residual variances were only ~10% less than null models. Bivariate correlations for northeast Victoria showed that both species responded positively to numbers of hollow-bearing trees, with Powerful Owls apparently responding to live hollow-bearing trees and Sooty Owls to dead hollow-bearing trees (consistent with their observed associations with mature and senescent forest respectively, Table 2). Powerful Owls also showed positive associations with the presence of 'box' eucalypts (e.g. Red Box *Eucalyptus polyanthemos* and But-but *E.bridgesiana*, although such species were only present at a few sites) and Blackwood Wattles that are known to be favoured as roost trees (McNabb 1996). Sooty Owls were associated with Silver Wattles, Blanket-leaf and tree-ferns, which commonly grow together in wet forest gullies favoured by this owl. Sooty Owls roost mainly in hollows but sometimes in tree-ferns (Hollands 1991).

Use of models

The models were used along with other information to select 125 areas to be protected for Powerful Owls and 100 areas for Sooty Owls in State Forest and National or State Parks in northeast Victoria. In Gippsland and the Central Highlands, 132 areas were selected for Powerful Owls and 130 for Sooty Owls, with emphasis on State Forests and sites where there were actual records of owls. These targets were reached as part of a strategy to protect areas for 500 pairs of each species in the State.

DISCUSSION

Limitations and strengths of the study

Selection of habitat by owls is likely to depend on a more complex set of subtle cues than indicated by the models: the model variables may be surrogates for such cues (Starfield 1997). Nevertheless, the models have been useful in identifying areas likely to be of value for large owls, in a way that has not been possible previously. It is planned to revise the models using a larger data-set and refine management strategies when forest plans are reviewed. The models are based on single visits to each site (deliberately, to maximise numbers of sites covered), with no seasonal replication. Although Powerful Owls make more unelicited calls in autumn than at other times (R. Kavanagh, pers. comm.), we observed no major seasonal pattern in response rates for large owls (in contrast to Southern Boobooks, which responded most strongly in spring). Kavanagh and his co-workers also found that playback was similarly effective at all seasons.

At the start of the study, Sooty Owls were considered rare in northeast Victoria and central Gippsland (Emison *et al.* 1987), and little was known about the detailed distribution of any large owl species. The study highlights the rarity of Barking and Masked Owls in forests of eastern Victoria, as in southeastern New South Wales (Kavanagh *et al.* 1995b; Kavanagh & Bamkin 1995; Kavanagh & Stanton 1998). Further work is needed to develop conservation strategies for these two rare species.

A modelling approach was also used to predict habitat for large forest owls in New South Wales (Kavanagh 1997) and for Masked Owls in Tasmania (Bell *et al.* 1996). These studies provided valuable insights into some of the factors that may determine use of habitat by owls, and the present study drew on the New South Wales experience. An important decision was to generate discrete models using only mapped data (EVCs and forest growth-stages) that were available on a State-wide basis on GIS. This allowed production of GIS maps showing predicted probabilities of occurrence, for use in forest planning. The work was done in co-operation with forest managers, who have used the data and models as described (Department of Natural Resources & Environment 1999b). A co-operative approach to conservation and forest management was developed in Victoria through its integrated Department of Natural Resources & Environment, and encouraged through strategic forest planning projects and by the process of developing Regional Forest Agreements between State and Commonwealth governments (Victorian RFA Steering Committee 1998).

GIS technology played an essential role in the study for two reasons. Firstly, it provided information at appropriate scales for wide-ranging owls. Secondly, it allowed models to be fed back onto maps, tested visually for realism and used to predict areas of high or low value for owls. This sort of application is relatively new but promises to be a valuable tool for managing wildlife in many parts of the world (e.g. Perera & Tateishi 1995; Fuller *et al.* 1998).

Habitat requirements

Models including field habitat data suggest that Powerful and Sooty Owls have quite different requirements, despite a broad overlap in distribution. Sooty Owls favour the wetter sites with understorey and middle storey plants such as Silver Wattle, Blanket-leaf and tree-ferns. Powerful Owls favour the more open forest sites and broad gullies, with plants such as Blackwood Wattle (which they often use as day-time roosts, McNabb 1996). This accords with previous descriptions of their habitats (Emison *et al.* 1987; Hollands 1991; Kavanagh 1997; Higgins 1999), and the known aversion of Powerful Owls for the wettest forest types (Loyn 1985b; Milledge *et al.* 1991). Sooty Owls are known to favour wet gullies and rainforest in much of their range. However, Sooty Owls are clearly not confined to the wettest forests or deep gullies. Both Powerful and Sooty Owls showed positive associations with a range of forest types associated with damp lower slopes (e.g. Herbrich Foothill Forest). Further refinements to the models could provide new insights about their habitat needs. Similar results were found in New South Wales by Kavanagh (1997), using a decision-tree modelling approach. He found that Sooty Owls were most likely to be found at lowland sites on sedimentary shales with rough terrain and high proportions of rainforest, wet forest and logged forest in the landscape. Powerful Owls favoured lowland or upland sites with sedimentary geology and more gentle topography, and were more sensitive to logging than Sooty Owls and less strongly associated with rainforest (Kavanagh 1997). The two approaches appear to be opening different windows on a common set of habitat responses in each State, with Sooty Owls favouring the wetter forests and a degree of overlap that varies between regions.

Kavanagh (1988) showed that Powerful Owls may select areas with abundant arboreal mammals, but then serially reduce populations of prey species within different parts of their large home range. Many arboreal mammals respond positively to densities of old hollow-bearing trees (e.g. Smith & Lindenmayer 1988, 1992; Lindenmayer *et al.* 1990; Nelson *et al.* 1996), as well as to stand age (Macfarlane 1988) and foliar nutrient levels (Braithwaite *et al.* 1984; Kavanagh & Lambert 1990). This relationship may help drive the observed association of owls with old forest and numerous hollow-bearing trees.

Large owls have large home ranges and it is not surprising that they respond to landscape variables and show less association with field habitat data collected close to the point of call playback (Kavanagh & Peake 1993; Kavanagh & Bamkin 1995; Loyn *et al.* 2001). The positive associations with mature or senescent forest support the view that Powerful and Sooty Owls need patches of old forest, and deserve special management in forests where logging occurs. Data from mosaics of logged and unlogged forest (Kavanagh & Bamkin 1995; Kavanagh *et al.* 1995a; present data) show that large owls can survive at reasonable population density in such mosaics, and radio-tracking data show that they include regrowth and cores of mature forest in their home ranges (Kavanagh 1997). The SPZs selected from this study (500 ha each) were smaller than the likely home ranges of large owls, but should provide valuable cores of good habitat from which the birds can range as they need.

In our work, the distribution of SPZs was determined mainly by the distribution of existing habitat, as indicated by records of owls and model predictions. Over 200,000 ha of forest has been selected for special protection on this basis, with about half in State Forest and the remainder in existing reserves. Most of the forest in eastern Victoria is contiguous and isolation of small populations is unlikely to be an issue: population viability analysis suggests that connected populations of over 100 pairs are likely to persist (Kavanagh 1997; McCarthy *et al.* 1999). This contrasts with the situation in North America where fragmentation of mature forest is a controversial issue with respect to the Northern Spotted Owl *Strix occidentalis caurina* (Wilcove & Murphy 1991; Bart & Forsman 1992; Murphy & Noon 1992; Marcot & Thomas 1997; Miller *et al.* 1997). Some of our protected areas were clumped and others more widely dispersed in the forest matrix. Further work is needed to examine the population responses of owls, and the success of these measures in the broader context of managing forests over time.

ACKNOWLEDGMENTS

We would like to thank all who contributed to this work in various ways, and especially the field teams who spent long hours at night in difficult country. Fieldwork was conducted mainly by Ed McNabb, Maria Belvedere, Dale Gibbons, Phil Maher, Chris Tzaros, Rick Webster, Richard Hill, Jim McNabb and Lucy Clausen. Charles Silveira helped field test the models. Kylie White and other forest planners made expert use of the information in the course of their forest planning work. Regional staff from NRE and Parks Victoria provided logistic support. Funds were provided by the Forests Service of NRE and the Commonwealth Department of Environment, Sport & Territories as part of the Regional Forest Agreement process. Lucy Clausen and Phoebe Macak helped with data processing and editing. Many people contributed to the project or its development, including Jerry Alexander, Rod Anderson, Andrew Corrick, Andrew Maclean, Ian Miles, Ross Penny, Brian Thompson and Neil Wilson. We would also like to thank Rod Kavanagh, Andrew McIntyre, Stephen Henry, Mick Bramwell, Stephen Debus, David Hollands and David Milledge for useful discussions and ideas about methods, and Graeme Newell, Todd Soderquist, Andrew Maclean and Kylie White for commenting usefully on drafts of a related paper. This paper benefitted from comments by Rod Kavanagh, Ian Newton and an anonymous referee.

REFERENCES

Ambrose, G.J. 1982. An ecological and behavioural study of vertebrates using hollows in eucalypt branches. PhD thesis, La Trobe University, Melbourne.

Bart, J. and Forsman, E.D. 1992. Dependence of Northern Spotted Owls *Strix occidentalis caurina* on old growth forests in the western USA. *Biol. Conserv*. **62:** 95–100.

Bell, P., Mooney, N., Wiersma, J. & Australaian Raptor Association 1996. Predicting essential habitat for forest owls in Tasmania. Report to the Tasmanian Environment and Heritage Technical Committee. Commonwealth of Australia and the State of Tasmania.

Bennett, A.F., Lumsden, L.F., Alexander, J.S.A., Duncan, P.E., Johnson, P.G. & Silveira, C.E. 1991. Habitat use by arboreal mammals along an environmental gradient in North Eastern Victoria. *Wildlife Research* **18:** 125–146.

Braithwaite, L.W., Turner, J. & Kelly, J. 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, NSW. 3. Relationships between faunal densities, eucalypt occurrence and foliage nutrients, and soil parent materials. *Aust. WildL. Res*. **11:** 41–48.

Debus, S.J.S. 1995. Surveys of large forest owls in northern New South Wales: methodology, calling behaviour and owl responses. *Corella* **19:** 38–50.

Department of Natural Resources & Environment. 1996. Code of Forest Practices for Timber Production. Revision No. 2. Melbourne: Department of Natural Resources & Environment.

Department of Natural Resources & Environment. 1999a. Threatened vertebrate fauna in Victoria 1999. Melbourne: Department of Natural Resources & Environment.

Department of Natural Resources & Environment. 1999b. Proposed Forest Management Plan for the North East. Melbourne: Department of Natural Resources & Environment.

Emison, W.B., Beardsell, C.M., Norman, F.I., Loyn, R.H. & Bennett, S.C. 1987. *Atlas of Victorian Birds*. Melbourne: Department of Conservation, Forests and Lands/ Royal Australasian Ornithologists' Union.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Brisbane: Jacaranda Press.

Fuller, R.M., Groom, G.B., Mugisha, S., Ipulet, P., Pomeroy, D., Katende, A., Bailey, R. & Ogutu-Ohwayo, R. 1998. The integration of field survey and remote sensing for biodiversity assessment: a case study in the tropical forests and wetlands of Sango Bay, Uganda. *Biol. Conserv*. **86:** 379–391.

Higgins, P. (ed.), 1999. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 4. Parrots to Dollarbird*. Melbourne: Oxford University Press.

Hollands, D. 1991. *Birds of the Night*. Balgowlah, New South Wales: Reed Books Pty Ltd

Kavanagh, R.P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Aust. J. Ecol*. **13:** 445–450.

Kavanagh, R.P. 1997. Ecology and management of large forest owls in south-eastern Australia. PhD Thesis, University of Sydney, Sydney.

Kavanagh, R.P., & Peake, P. 1993. Survey procedures for nocturnal forest birds: an evaluation of variability in census results due to temporal factors, weather and technique. In Olsen, P.(ed) *Australian Raptor Studies*: 101–125, Melbourne: Australasian Raptor Association/ Royal Australasian Ornithologists Union.

Kavanagh, R. P., & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in South-Eastern New South Wales, Australia. *Biol. Conserv*. **71:** 41–53.

Kavanagh, R.P. &Jackson, R. 1997. Home-range, movements, habitat and diet of the Sooty Owl *Tyto tenebricosa* near Royal National Park, Sydney. In Czechura, G.V. and Debus, S.J.S. (eds) *Australian Raptor Studies* **2**:2–13, Melbourne: Birds Australia Monograph No. 3, Royal Australasian Ornithologists Union.

Kavanagh, R.P. & Lambert, M.J. 1990. Food selection by the Greater Glider *Petauroides volans*: Is foliar nitrogen a determinant of habitat quality? *Aust. Wildl. Res*. **17:** 285–299.

Kavanagh, R.P. & Peake, P. 1993. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In Olsen, P.(ed) *Australian Raptor Studies* 101–125, Melbourne: Royal Australasian Ornithologists Union.

Kavanagh, R.P., & Stanton, M.A. 1998. Nocturnal forest birds and arboreal marsupials of the southwestern Slopes, New South Wales. *Aust. Zool.* **30**, 449–466.

Kavanagh, R.P., Debus, S., Tweedie, T., & Webster, R. 1995a. Distribution of nocturnal forest birds and mammals in North-eastern New South Wales: relationships with environmental variables and management history. *Wildlife Research* **22:** 359–77.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B., & Turner, R.J. 1995b. Diet and habitat of the Barking Owl *Ninox connivens* in New South Wales. *Aust. Bird Watcher* **16:** 137–144.

Kavanagh, R.P. & Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96:** 250–257.

Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T. & Smith, A.P. 1990. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. 1. Factors affecting the occupancy of trees with hollows. *Biol. Conserv*. **54:** 111–131.

Loyn, R.H. 1985a. Strategies for conserving wildlife in commercially productive eucalypt forest. *Aust. For.* **48:** 95–101.

Loyn, R.H. 1985b. Bird populations in successional forests of Mountain Ash *Eucalyptus regnans*. *Emu* **85:** 213–230.

Loyn, R.H., McNabb, E.G. Volodina, L. & Willig, R. 2001. Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. *Biol. Conserv*. **97:** 361–376.

McCarthy, M.A., Webster, A., Loyn, R.H. & Lowe, K.W. 1999. Uncertainty in assessing the viability of the Powerful Owl *Ninox strenua* in Victoria, Australia. *Pac. Conserv. Biol.* **5:** 144–154.

Macfarlane, M.A. 1988. Mammal populations in Mountain Ash (*Eucalyptus regnans*) forest of various ages in the Central Highlands of Victoria. *Aust. For*. **51:** 14–27.

McNabb, E. G. 1996. Observations on the biology of the Powerful Owl *Ninox strenua* in southern Victoria. *Aust. Bird Watcher* **16:** 267–295.

Marcot, B.G. & Thomas, J.W. 1997. Of Spotted Owls, old growth and new policies: a history since the Interagency Scientific Committee report. *General Technical Report* PNW-GTRñ408. Portland, Oregon: Pacific Northwest Research Station, Forest Service, US Dept. Agriculture,

Mawson, P.R. & Long, J.L. 1994. Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia. *Emu* **94:** 149–155.

Menkhorst, P.W. (ed.) 1995. Mammals of Victoria: distribution, ecology and conservation. Melbourne: Oxford University Press and Department of Conservation & Natural Resources (now NRE).

Milledge, D., Palmer, C.L. & Nelson, J.L. 1991. 'Barometers of change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 53–65. Sydney: Royal Zoological Society of NSW and Surrey Beatty & Sons.

Miller, G.S., Small, R.J. & Meslow, E.C. 1997. Habitat selection by Spotted Owls during natal dispersal in western Oregon. *J. Wildl. Manage*. **61**: 140–150.

Murphy, D.D. & Noon, B.R. 1992. Integrating scientific methods with habitat conservation planning: reserve design for northern Spotted Owls. *Ecological Applications* **2:** 3–17.

Nelson, J.L., Cherry, K.A. & Porter, K.W. 1996. The effect of edges on the distribution of arboreal marsupials in the ash forests of the Victorian Central Highlands. *Aust. For*. **59:** 189–198.

Perera, L.K. & Tateishi, R. 1995. Do remote sensing and GIS have a practical applicability in developing countries (including some Sri Lankan experiences)*? Int. J. Remote Sensing* **16:** 35–51.

Schodde, R. & Mason, I.J. 1980. *Nocturnal birds of Australia*. Melbourne: Lansdowne.

Seebeck, J. H. 1976. Diet of the Powerful Owl *Ninox strenua* in western Victoria. *Emu* **76:** 167–170.

Simberloff, D. 1998. Flagships, umbrellas and keystones: is single species management passe in the landscape era? *Biol. Conserv.* **83:** 247–257.

Smith, A.P. & Lindenmayer, D.B. 1988. Tree hollow requirements of Leadbeater's Possum and other possums and gliders in timber production ash forests of the Victorian Central Highlands. *Aust. Wildl. Res.* **15:** 347–362.

Smith, A.P. & Lindenmayer, D.B. 1992. Forest succession, timber production and conservation of Leadbeater's Possum (*Gymnobelideus leadbeateri* Marsupialia: Petauridae). *For. Ecol. & Manag.* **49:** 311–332.

Soderquist, T. 1999a. Tree hollows in the Box-Ironbark forest. Forests Service Technical Report 99–3, Melbourne: Department of Natural Resources and Environment

Soderquist, T. 1999b. Home range and habitat quality of the Powerful Owl *Ninox strenua* in the Box-Ironbark Forest. Melbourne: Department of Natural Resources and Environment

Starfield, A.M. 1997. A pragmatic approach to modelling for wildlife management. *J. Wildl. Manag.* **61:** 261–270.

Strahan, R. (ed.) 1983. *The Australian Museum Complete Book of Australian Mammals*. Sydney: Angus & Robertson.

Tilley, S. 1982. The diet of the Powerful Owl, *Ninox strenua*, in Victoria. *Aust. Wildl. Res.* **9:** 157–175.

Traill, B. J. 1993. The diet and movements of a pair of Powerful Owls *Ninox strenua* in dry eucalypt forest. In Olsen, P. (ed) *Australian Raptor Studies*: 155–159. Melbourne: Australasian Raptor Association/Royal Australasian Ornithologists Union.

Victorian RFA Steering Committee, 1998. North East Victoria Comprehensive Regional Assessment report. Commonwealth of Australia: Joint Commonwealth and Victorian Regional Forest Agreement Steering Committee

Wilcove, D. & Murphy, D. 1991. The Spotted Owl controversy and conservation biology. *Conserv. Biol.* **5:** 261–262.

23

MONITORING LARGE FOREST OWLS AND GLIDERS AFTER RECENT LOGGING IN PRODUCTION REGROWTH FORESTS OF THE MID-NORTH COASTAL REGION OF NEW SOUTH WALES

BRETT CANN[1]*, JUSTIN WILLIAMS*[2] *& JAMES M. SHIELDS*[3]

[1]SFNSW, PO Box 692, Taree NSW 2430, [2] SFNSW, PO Box 168, Wauchope NSW 2446,
[3]SFNSW, PO Box 273, Eden NSW 2551

Large forest owls were surveyed before and after logging in a standard manner across a large forest management region where two different approaches to owl management in production regrowth forests were taken. This paper reports on the preliminary results of those monitoring surveys and management actions. Owls were detected across the forested landscape in the region. Management prescriptions based on reservation of a standard area (300 ha) per detection were implemented in some sites. In other areas, where it was apparent or assumed that owls were widespread, standard reservation of owl habitat was implemented across the landscape. In the latter approach, 25% of the area in the landscape (in patches of 5,000 to 15,000 ha) was retained for owl management. Monitoring revealed that owl populations persisted at detectable levels under both management regimes for at least 2–4 years after logging. Strengths and weaknesses of the two approaches are discussed, and additional post-harvest monitoring to identify the success or otherwise of current owl management approaches in production forests of New South Wales is recommended.

INTRODUCTION

In recent years concerns have been raised over the potential impacts of forest management activities upon a range of species in Australia, particularly hollow-nesting birds and mammals (Tyndale-Biscoe & Calaby 1975; Milledge *et al.* 1991; Kavanagh 1991). Attention has focussed on hollow-nesting species, because they are most likely to suffer deleterious effects from logging in the short and long terms. It has been suggested that the potential for impact is greatest if silvicultural strategies do not provide sufficient time for hollows to develop between cutting cycles or if insufficient hollow-bearing trees are retained across the landscape (Lindenmayer *et al.* 1990). Consequently, much of the initial research conducted on large forest owls and arboreal gliders has concentrated on the impacts of harvesting old growth forests (eg Milledge *et al.* 1991) or on comparison of owl and arboreal marsupial presence in unlogged, lightly logged or heavily logged forests (Kavanagh & Bamkin 1995; Kavanagh *et al.* 1995). All studies examined medium to long-term trends of the impacts of harvesting activities and their effects on forest structure. They suggested management strategies to mitigate the impacts of harvesting, but did not examine the immediate post-harvesting responses to current management strategies.

Milledge *et al.* (1991) found that the number of Yellow-bellied Gliders *Petaurus australis* declined after clearfelling in Mountain Ash *Eucalyptus regnans* forest in Victoria, and suggested that clearfelling also had adverse affects on Sooty Owls *Tyto tenebricosa*. In New South Wales no significant differences were identified between unlogged, selectively logged and heavily logged sites for Powerful Owls *Ninox strenua*, Sooty Owls and Yellow-bellied Gliders (Kavanagh & Bamkin 1995; Kavanagh *et al.* 1995). Both studies identified significantly fewer Masked Owls *Tyto novaehollandiae* and Greater Gliders *Petauroides volans* on heavily logged sites than on old growth sites. Kavanagh *et al.* (1995) and Kavanagh & Murray (1996) suggested that frequent fire, and the presence of an open understorey, were the most significant environmental correlates of Masked Owl presence, and suggested that the owls were often not associated with young regrowth forests.

In 1990, State Forests of NSW began preparing environmental impact statements (EISs) for harvesting operations in northern NSW (Forestry Commission of NSW 1991 a, b, Forestry Commission of NSW 1993, Truyard Pty. Ltd. 1995, for example). These EISs mainly targeted areas where old growth logging was proposed. The survey and ameliorative strategies developed in the EIS process were designed to reduce potential negative effects of harvesting old growth forests and monitor the longer-term impacts. Harvesting prescriptions developed during, or as a result of, the EIS process were based on establishing undisturbed exclusion areas around sites where large forest owls were detected. In recent years, further development of these approaches is designed to cater for areas with numerous owl records and allow habitat to be protected at a landscape rather than a site-based scale (SFNSW & NPWS 1996).

Given that little emphasis had been placed on monitoring the short-term response of large owls to harvesting in regrowth forests or the efficacy of managing owls in multiple-use forests, SFNSW commenced a program of monitoring large forest owl and Yellow-bellied Glider populations after harvesting.

Recent land-use and forest policy decisions have meant that harvesting of all known high conservation value old-growth forests is prohibited on State Forests, and much of the remaining forest with significant late growth-stage elements has been reserved or excluded from logging. Most harvesting is now based in regrowth or forests that were selectively logged in the past. For future management decisions regarding owls in NSW, the information gained from previous research on the effects of harvesting old growth is less relevant than it was before these changes. Identifying the potential impacts of harvesting, and the efficacy of prescriptions in maintaining populations of large forest owls and arboreal gliders in regrowth and other previously logged forests has become more relevant. This paper reports on the relationship between the presence or absence of the Masked Owl, Sooty Owl, Powerful Owl and Yellow-bellied Glider generally within regrowth forests before and after logging on the Mid North Coast of NSW. The study examined compartments harvested between 1992 and 1999 under a variety of silvicultural regimes.

STUDY AREA

Nineteen monitoring sites were located in nine State Forests on the North Coast of New South Wales between Taree and Macksville and west to Nundle. The sites ranged in altitude from 10 to 1,300 m a.s.l. and occurred over a range of parent materials including metasediments, mudstones and lithic sandstones, serpentine and leucogranite (Truyard Pty Ltd 1993). Topography ranged from coastal flats to steep, deeply incised mountain forests. Rainfall ranged between 1,100 and 1,700 mm per year with a slight peak during summer (Truyard Pty Ltd 1993).

State forests in the area are managed by Mid North Coast Region. The Region covers a geographic area of 2,800 000 ha. Within this area there are 484, 093 ha (17.3%) of National Park and Nature Reserve and 278,000 ha (9.9%) of State Forests. Both areas are predominantly forested. Of the State Forest area, approximately 52% (144,002 ha) is available for harvesting, with the remainder protected in informal reserves. Overall, approximately 19% of the publicly owned forests are available for timber harvest activities.

Vegetation and management

The vegetation varied among sites, but at most was a complex mosaic of moist and dry sclerophyll forests with pockets of rainforest in gullies. For simplicity, each site was categorised into one of the following four groups that characterised the majority of the vegetation in the area and the silvicultural system applied to it during logging.

Dry Hardwood forest (Forestry Commission of New South Wales 1989; types 62 and 74) typically selectively logged in the past, contained mixed age-classes of trees with moderate numbers of old hollow trees and an open grassy understorey.

Moist Hardwood forest (types 47, 53 and 60) was generally previously unlogged, with a dominant overstorey of large old hollow trees and a dense understorey of shrubs and vines.

Blackbutt forest (types 36 and 37) had typically been frequently logged in the past and contained a high density of young regrowth trees with scattered large old hollow-bearing trees and stags. The understorey varied from open grassy to dense shrubs and vines.

Dry Tablelands forest (types 150, 163 and168) had been selectively logged in the past but still contained a high proportion of large old hollow-bearing trees. The understorey was open and grassy with few large shrubs or understorey trees.

Silvicultural practices at the 19 study sites varied from thinning or selective logging of young or mixed-aged regrowth stands to high-intensity single tree selection of old-growth stands. Four major stand conditions occurred: predominantly young regrowth forests; mature single-aged stands from previous high intensity harvesting (may have been clearfell with seed trees); mature mixed-aged stands resulting from previous selective logging; and unlogged old-growth forest. Each of these stand conditions had different silvicultural systems applied to them that reflected their relative maturity, merchantability and timber value. The young regrowth forest sites were Blackbutt *Eucalyptus pilularis* stands, in which harvesting by thinning was carried out. Thinning was used to redistribute growth to a lesser number of desirable stems, without appreciable loss of overall stand growth, by giving greater individual access to growing space and soil. At the same time most of the mature/overmature growing stock was removed but constrained by the retention of some strata for habitat and other environmental purposes (State Forests of NSW 2000). Anticipated basal area removal from the thinned sites was 40%.

Single tree selection (STS) logging of mixed-age regrowth stands occurred at the Dry Hardwood forest sites and aimed to remove all the currently merchantable trees that were not required to meet prescribed wildlife needs and encourage regeneration of a new age class. Expected basal area removal from STS operations in Dry Hardwood types was less than 25%.

The mature predominantly even-aged stands occurred in Blackbutt forest and were harvested using Australian Group Selection (AGS) silvicultural techniques that involved harvesting small groups of trees over areas of less than 0.25 ha with 100% basal area removal in the groups and 20% basal area removal averaged across the stand.

Old growth harvest of moist hardwood forests at two sites involved intensive single tree selection in which almost all trees were removed except those required to meet wildlife management prescriptions. Basal area removal was 70%, and aimed to regenerate a new forest age-class.

Owl management approaches

Techniques used to manage owls varied between sites depending on the forest and owl management guidelines at the time of harvesting and results of pre-harvesting surveys of owls across the landscape. Management approaches can be categorised into general, roost and nest site protection, the option of site-based or landscape level habitat protection and prey management.

In all harvest areas, general guidelines to protect streamside habitat and hollow-bearing trees were implemented. Initially, streamside habitat protection related to the Standard Erosion Mitigation Guidelines for Logging (SEMGLs) and Environmental Impact Statement (EIS) prescriptions (Truyard Pty Ltd 1993). These guidelines required 20–40 m wide streamside protection strips on either side of riparian zones and 4–6 hollow-bearing trees per ha to be retained over a harvesting area. Since 1996, however, conservation protocols developed for forest management have been applied in all logging operations on State Forests (SFNSW & NPWS 1996). These protocols included prescriptions for protection of riparian zones, retention of ridge and headwater habitat, protection of all identified rainforest and old-growth forest and the retention 10 hollow-bearing trees and 10 mature trees to recruit into future hollow-bearing trees per 2 ha.

Protection of nest sites initially required 100 m radius exclusions around owl roost sites and 200 m radius exclusions around nest sites (Truyard Pty Ltd 1993). After 1996 these conditions were reduced to 30 m and 50 m radius exclusions around roost and nest sites respectively. None of the sites in this study had recorded nest sites.

Site-based habitat protection initially required 1–1.5 km radius exclusions around large forest owl records. Since 1996, site based exclusions of 300 ha (within a 2 km radius) of Masked Owl or Powerful Owl records are applied. This approach gave more flexibility as to where owl habitat must be protected than the previous radius exclusion zones, enabled targeting of predicted best habitat for protection and generally allowed greater access to timber resources.

Landscape-based habitat protection for owls requires the development of areas of 10 000 to 15 000 ha, in which at least 25% of the overall area and 10% of the production State Forest area suitable as owl habitat must be excluded from logging (SFNSW & NPWS 1996). Landscape exclusion areas are best suited to large areas of contiguous forest with numerous records of large forest owls and boundaries that are typically based on logical catchment or management boundaries. They may include all forms of publicly owned forests including national parks and other statutory reserves.

A simple approach to managing prey for the Powerful Owl was developed as part of the conservation protocols. It requires protection of additional hollow-bearing trees in areas where Greater Gliders exist at high densities (SFNSW & NPWS 1996). Greater Gliders have been identified as an important dietary component of Powerful Owls, particularly in mountain forests (Kavanagh 1988) and are also known to be sensitive to heavy logging (Tyndale-Biscoe & Calaby 1975). Protection of sufficient habitat trees is an important factor in maintaining Greater Glider abundance and hence in providing food for Powerful Owls.

Yellow-bellied Gliders are also dependent on hollow-bearing trees for nesting and denning and often rely on sap from eucalypts in their diet (Goldingay & Kavanagh 1991). On lands managed by State Forests, they are managed through protection of 15 suitable sap feed trees within 100–200 m of detection sites and harvesting is excluded from within 50 m of known den trees.

METHODS

Monitoring sites were non-randomly selected from a small pool of sites that were surveyed for owls and gliders before harvest. They were chosen to achieve a wide regional coverage of a number of vegetation types and silvicultural practices and to allow efficient sampling of two or three sites per night.

Surveys were based on broadcasting owl calls from a tape player, amplified through a megaphone or from a high-powered portable compact disc player, and listening for call response, twice per site on separate nights (Shields *et al.* 1991). Sessions commenced with a 10 minute listening period followed by five minutes of call broadcast and two minutes of listening for each species, in order of Powerful Owl, Masked Owl, Sooty Owl, Barking Owl *Ninox connivens* and Yellow-bellied Glider. Surveys ended with a 15 minute listening period and 10 minutes of spotlighting around the site. At most sites Barking Owls were not surveyed pre-harvest because the species had not then been listed as vulnerable under the Threatened Species Conservation Act (1995).

Pre-harvesting surveys were carried out between 1991 and 1998 in nine different calendar months. Harvest treatments were carried out in 1993–1999. The period between completion of harvesting and post-logging monitoring ranged between three years and three weeks. Post-harvest surveys at all but three sites were carried out in November-December 1999.

The area of different forest growth stages within a 1500 m radius from each site (703 ha) was identified using data from the CRA Forest Type Inventory project undertaken for the Regional Forest Agreement for North East New South Wales. Growth stages where identified based on the proportions of regrowth, mature and senescent crowns within a stand. A simple classification was developed which placed these growth stages into either a low or high habitat structural value for owls. Stands of rainforest with eucalypt emergents, forest with a high proportion of senescent trees (old growth) and mature forest with a moderate level of senescent trees were considered to have high structural value for owls. The amount of visible disturbance, proportion of trees removed and floristic data were ignored for this simple classification. It was not feasible to utilise the existing data to assess change in those structural elements from the logging events sampled in this study.

A description of the area, vegetation, silvicultural system, owl management approach, proportion of high quality habitat and survey results are provided in Table 1. Presence/absence of large forest owls and Yellow-bellied Glider were tabulated by site producing tables with zero or one values which were compared using the Sign Test, a non-parametric alternative to the Paired T-test (Zarr 1984).

Table 1. Results of post-logging monitoring for large forest owls and Yellow-bellied Gliders from 19 sites on the North Coast of New South Wales.

Site	SF	Cpt No.	Area (ha)	Year of Logging	Major forest type	Silviculture	Owl Protection Type	% High quality structural habitat	Pre-harvest results	Post-harvest results
1	Tuggolo	282	180	98/99	Tablelands	STS	Site	78%	PO	PO
2	Coopernook	198	180	96/99	Blackbutt	Thin	Nil	5%	Nil	SO, MO
3	Lansdowne	195	70	96/99	Blackbutt	Thin	Site	8%	PO	SO
4	Lansdowne	195	70	96/99	Blackbutt	Thin	Site	11%	PO	SO
5	Coopernook	211	70	96/99	Blackbutt	Thin	Nil	15%	Nil	SO
6	Yarratt	79	60	97/99	Dry Hardwood	STS	Nil	13%	Nil	Nil
7	Yarratt	79	60	97/99	Dry Hardwood	STS	Nil	3%	Nil	Nil
8	Yarratt	76	225	97/99	Dry Hardwood	STS	Nil	0%	Nil	MO
9	Yarratt	77	177	97/99	Dry Hardwood	STS	Nil	21%	Nil	Nil
10	Yarratt	76	225	97/99	Dry Hardwood	STS	Nil	0%	Nil	Nil
11	Bril Bril	5			Blackbutt	Thin	Site	58%	PO, YBG	MO, YBG
12	Bellangry	14/20	450	98/99	Blackbutt	Thin	Landscape	46%	SO, YBG	SO
13	Bellangry	13	250		Blackbutt	Thin	Nil	37%	SO	MO, YBG
14	Mt Boss	45	300	93/95	Blackbutt	Thin	Nil	44%	SO	PO, YBG
15	Mt Boss	47	200	98	Blackbutt	Thin	Site	42%	YBG	MO, YBG
16	Mt Boss	175/176	300	93/95	Moist Hardwood	Old Growth	Nil	75%	PO, SO, YBG	PO, SO, MO
17	Mt Boss	195	250	93/95	Moist Hardwood	Old Growth	Nil	79%	YBG	PO, MO, YBG
18	Tamban	67	300	98/99	Blackbutt	AGS	Site	0%	PO, MO, YBG	Nil
19	Tamban	72	250	99	Blackbutt	AGS	Landscape	4%	PO, YBG	BKOW

Notes: Pre-harvest and post-harvest results: PO – Powerful Owl, MO – Masked Owl, SO – Sooty Owl, BKOW – Barking Owl, YBG – Yellow-bellied Glider.

Silviculture: Thin – Thinning of small stems from even-aged regrowth forest, STS – Single Tree Selection in mixed-age regrowth forest, AGS – Australian Group Selection in even-aged mature regrowth forest, Old Growth – intensive single tree selection in old growth forest.

Owl Protection Type: Site – Site based approach to owl management, Nil – No species-specific owl management, Landscape – Landscape approach to owl management.

RESULTS

Pre-logging and post-logging surveys recorded seven species of nocturnal forest birds, including Powerful Owl, Sooty Owl and Masked Owl. The frequencies of detection of these three large

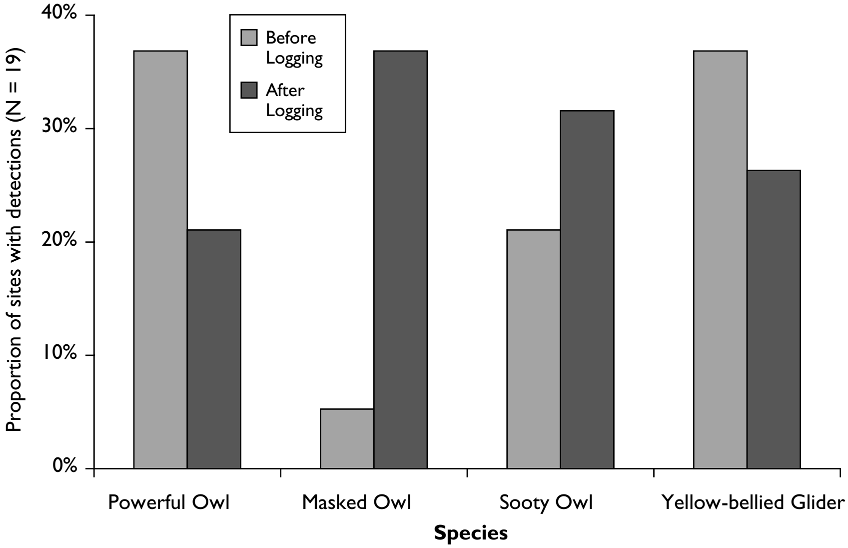


Fig. 1. Proportion of sites with a detection of three species of large forest owls or Yellow-bellied Glider before and after logging.

forest owls and the Yellow-bellied Glider before and after logging are presented in Fig. 1. No signficant differences were detected in the presence of Powerful or Sooty Owls or Yellow-bellied Gliders before and after logging (Table 2). Masked Owls were detected more frequently at sites after logging than before logging ($P < 0.05$).

Over all sites, the three large forest owls and Yellow-bellied Glider were detected frequently, indicating that all species were widespread and present at detectable levels. Each of the species was detected more frequently at sites that supported a large proportion of senescent trees in the canopy than at sites with a low proportion (Table 3). In addition, 17 of the 23 presence records of the three large forest owls and Yellow-bellied Glider recorded after logging were from the eight sites that had a high proportion of forest with senescent elements nearby.

Table 2. Comparison of large forest owl and Yellow-bellied Glider presence at sites before and after logging using the Sign Test.

Negative differences (number of sites with greater presence after logging), positive differences (number of sites with less presence after logging), zero differences (number of sites with same result before and after logging) and P-values are included; n.s = not significant.

Species	Negative Differences	Positive Differences	Zero Differences	P-value
Powerful Owl	2	5	12	n.s.
Masked Owl	7	1	11	0.04
Sooty Owl	4	2	13	n.s.
Yellow-bellied Glider	2	4	13	n.s.
All large owls	7	1	11	0.04

Table 3. Influence on presence of large forest owls and Yellow-bellied Gliders of low and high quality structural habitat within 1500 m radius of sites.

Total number of sites = 19.

Species	Powerful Owl	Sooty Owl	Masked Owl	Yellow-bellied Glider
Number of sites with detections	9	8	8	9
Average proportion of mapped high quality structural habitat at all sites.	28%	28%	28%	28%
Average proportion of mapped high quality structural habitat at sites with detections.	40%	30%	37%	43%
Average proportion of mapped high quality structural habitat at sites without detections.	18%	27%	22%	20%

DISCUSSION

These surveys did not detect any significant differences in the presence of Powerful Owls, Sooty Owls or Yellow-bellied Gliders between pre-logging or three to six years after logging. This result is consistent with that found by Kavanagh & Bamkin (1995) and Kavanagh *et al.* (1995) in NSW. Potential for differences in detection rates between pre-harvesting and post-harvesting surveys existed, because of the varying survey season and time since logging for the post-harvest surveys. Pre-harvest surveys occurred during nine different calendar months, while most post-harvest surveys were done in a four-week period in November-December 1999, some three weeks to three years post-logging. However, given that the proportions of sites with detections both before and after harvesting were of a similar order of magnitude as those previously recorded in northern NSW (Kavanagh *et al.* 1995), seasonality and time since logging were unlikely to have greatly influenced the results. The effects of the application of conservation protocols, along with the relatively low intensity silvicultural practices in northern NSW, will continue to be tested through future monitoring.

The findings suggested a slight decrease in Yellow-bellied Gliders and Powerful Owls post-logging and a slight increase in Sooty Owls. In contrast, Masked Owls appeared to respond favourably to regrowth harvesting. Previous studies in NSW, that have compared owl presence from sites with different harvesting intensities, suggest that Masked Owls may be detrimentally effected by harvesting, possibly from the dense regrowth that follows (Kavanagh *et al.* 1995). This species mainly feeds on terrestrial mammals (Debus and Rose 1994), so probably has a lower dependence on forest with large numbers of hollow trees and arboreal mammals. Most of the sites at which Masked Owls were detected after logging but not before were thinned regrowth blackbutt stands where harvesting activities opened up the understorey. Hollands (1991) reported that Masked Owls colonise areas soon after logging, and the radio tracking results of Kavanagh & Murray (1996) in highly disturbed suburban and agricultural areas confirm the use of altered habitat. The recent cessation of harvesting within most sites has not yet resulted in the dense understorey that is considered to be unsuitable for Masked Owl hunting (Kavanagh *et al.* 1995).

Large forest owls and Yellow-bellied Gliders were more frequently recorded at sites with a high proportion of senescent trees within 1,500 m. Harvest practices at the sites were frequently targeted within the component of the stands with few senescent trees (regrowth thinning) or aimed to retain a substantial proportion of those trees (selective logging to encourage regeneration). Given the silvicultural practices and owl management approaches utilised in northern NSW, we predict that in areas where high proportions of senescent trees exist in the landscape, management practices will maintain that mix. Further, we predict that sites with little old-growth nearby (previously intensively managed coastal Blackbutt forests) will develop old-growth characteristics over time through application of general exclusion prescriptions (stream exclusions, steep slopes, rainforest, ridge and headwater habitat corridors, and the like) and owl landscape prescriptions. Modelling the likely change in stand structure over time within a production forest landscape through application of various management approaches is needed to quantify the nature and scale of those changes and to estimate the likely response of large forest owl and Yellow-bellied Glider populations.

It was impossible to compare the effects of site-based management against landscape management from the results of this study, mainly because all the compartments where the site-based approach was applied had pre-logging records of large forest owls or Yellow-bellied gliders, whereas on numerous sites where the landscape or no approach had been applied no owls or Yellow-bellied Gliders had been detected in the pre-harvest survey. However, all of the 13 sites where a landscape or no approach was applied had at least one species of forest owl or the Yellow-bellied glider after harvesting.

In conclusion, the management approaches to large forest owls and Yellow-bellied Glider in northern NSW have so far maintained populations of these species across production regrowth forest landscapes. Further post-harvest monitoring in regrowth forests to identify the suitability of the current management prescriptions in maintaining populations of large forest owls is desirable. Targeted research into the response of open forest hunters, such as the Masked Owl, to regrowth thinning is needed to see whether the upward trend suggested by our data holds in other areas.

REFERENCES

Debus S.J.S & A. B. Rose. 1994. The Masked Owl in New South Wales. In Roberts P (ed.) *Large forest Owls in NSW*. Volume 28, Supplement Australian Birds.

Forestry Commission of New South Wales 1989. Research Note no. 17, Forest types in New South Wales. Sydney: Govt. Printer.

Forestry Commission of New South Wales 1991. Proposed forestry operations in Mistake State Forest – Environmental Impact Statement. Sydney: Forestry Commission of New South Wales.

Forestry Commission of New South Wales 1993. Fauna impact statement June-July 1993 – Proposed forestry operations in hardwood forests of the Walcha area. Unpublished report. Sydney: Forestry Commission of New South Wales.

Ganey, J.L. & Balda, R.P. 1989. Home-range characteristics of Spotted Owls in northern Arizona, *J. Wildl. Manage* **54**: 1159–1165.

Goldingay, R.L. and Kavanagh, R.P. 1991. The Yellow-bellied Glider: a review of its ecology and management considerations. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 365–375. Sydney: Roy. Zool. Soc. NSW.

Hollands, D. 1991. *Birds of the Night*. Sydney: Reed.

Kavanagh, R. P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Aust. J. Ecol.* **13**:445–450.

Kavanagh, R. P. 1991. The target species approach to wildlife management: gliders and owls in the forests of southeastern New South Wales. In Lunney, D. (ed) *Conservation of Australia's Forest Fauna*: 377–383. Sydney: Roy. Zool. Soc. NSW.

Kavanagh, R.P., & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in north-eastern New South Wales, Australia. *Biol. Conserv*. **71**: 41–53.

Kavanagh, R.P., Debus, S., Tweedie, T. and Webster, R. 1995. Distribution of nocturnal forest birds and mammals in north-eastern New South Wales: relationships with environmental variables and management history. *Wildl. Res*. **22**: 359–77.

Kavanagh, R.P. and Murray, M. 1996. Home-range, habitat and behaviour of the Masked Owl *Tyto novaehollandiae* near Newcastle, New South Wales. *Emu* **96**. 250–257.

Lindenmayer, D.B., Norton, T.W. and Tanton, M.T. 1990. Differences between wildfire and clearfelling on the structure of montane ash forests of Victoria and implications for fauna dependant on tree hollows. *Aust. For*. **53**:61–68.

Milledge, D.R., Palmer, C.L. and Nelson, J.L. 1991. 'Barometers of Change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands. In Lunney, D. (ed.) *Conservation of Australia's Forest Fauna*: 53–65. Sydney: Roy. Zool. Soc. NSW.

Olsen, P.D. (ed.) 1993. *Australian Raptor Studies*. Melbourne: Australasian Raptor Assoc. RAOU.

Shields, J.M., York, A. & Binns, D. 1991. Flora and Fauna Survey, Mt Royal Management Area, New South Wales, Forest Resources Ser. 16, Sydney: NSW Forestry Commission.

State Forests of NSW and National Parks & Wildlife Service 1996. Conservation protocols (unpublished). Hurstville: New South Wales Government.

State Forests of NSW. 2000. Native forests silviculture manual (unpublished). Sydney: State Forests of NSW.

Truyard Pty.Ltd. 1993. Environmental Impact Statement: Kempsey/Wauchope Management Areas, Proposed Forest Management. Sydney: Forestry Commission of N.S.W.

Tyndale-Biscoe. C.H and Calaby, J.H. 1975. Eucalypt forests as refuge for wildlife. *Aust. For*.**38**: 117–33.

Zarr, J. H. 1984. *Biostatistical Analysis*. Second Edition. Englewood Cliffs, NJ. USA: Prentice-Hall, Inc.

24

RESPONSE TO HABITAT FRAGMENTATION BY THE POWERFUL OWL (*NINOX STRENUA*), SOOTY OWL (*TYTO TENEBRICOSA*), MASKED OWL (*TYTO NOVAEHOLLANDIAE*) AND OTHER NOCTURNAL FAUNA IN SOUTHEASTERN AUSTRALIA

RODNEY P. KAVANAGH & MATTHEW A. STANTON

Forest Research Division, State Forests of New South Wales, P.O. Box 100, Beecroft, NSW,
Australia, 2119. Email: RodK@sf.nsw.gov.au

Fragmentation of native forest and woodland by clearing for agriculture and urban development has had a greater effect than logging on large forest owls and their arboreal marsupial prey. In this study, assessments were made of the contribution of forest and woodland fragments on privately-owned and unprotected lands towards the regional conservation of these species in southeastern New South Wales. Small (<200 ha) fragments did not provide a significant reservoir for populations of the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae*. Virtually all records of these owls in the region were associated with extensively forested areas or occurred within one km of the boundary of these areas (mainly state forests, national parks and nature reserves). The Barking Owl *N. connivens*, a 'non-forest' species, was also rarely recorded in forest/woodland fragments, raising concerns about the conservation status of this species in the region. Several important prey species for the three large forest owls, in particular the Common Ringtail Possum *Pseudocheirus peregrinus*, Greater Glider *Petauroides volans* and the Sugar Glider *Petaurus breviceps*, were either absent or less abundant in small forest fragments. The Barn Owl *Tyto alba*, a woodland species, and two other nocturnal 'forest' birds, the Southern Boobook *Ninox novaeseelandiae* and Australian Owlet-nightjar *Aegotheles cristatus*, were common and widespread in small forest and woodland fragments.

INTRODUCTION

Recent studies of Australian nocturnal forest birds and arboreal marsupials suggest that logging may disadvantage some species temporarily through habitat alteration, but that these effects can be reduced by retaining some unlogged areas or old trees among regrowth forests within the landscape (Milledge *et al.* 1991, Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995b, Kavanagh 1997, Kavanagh & Webb 1998). A different but related issue is the effect on these species of habitat fragmentation caused by permanent clearing of parts of the landscape for agriculture and other purposes. Little is known about the persistence of Australian large forest owls within fragments of native forest and woodland, particularly within those areas occurring on privately-owned lands, yet this information is important for regional conservation planning.

The equilibrium theory of island biogeography (MacArthur & Wilson 1967) predicts that large oceanic islands contain more species than small islands and, furthermore, that the distance of an island from the mainland (or larger island) directly influences species numbers due to the potential for recolonisation following local extinctions. The analogy between oceanic islands and native forest/woodland fragments surrounded by a 'sea' of agricultural land or plantations of exotic pine forest is imperfect (see, for example, reviews by Whitcomb *et al.* 1981, Verner 1986 and Usher 1987), but the island concept has been extended to include 'islands' of old growth forest embedded within a landscape of younger forests regenerating after logging (Harris 1984). Nonetheless, numerous studies have demonstrated that the species-area relationship accounts for at least part of the variation in species numbers in terrestrial mainland environments (for example, Suckling 1982, Bennett 1987, Loyn 1987), although the composition of faunal assemblages cannot be predicted by the theory. Other important factors include habitat quality, degree of patch isolation, time since fragmenting processes began and, especially, the population and behavioural characteristics of the individual species involved, including their ability to utilise the surrounding matrix of disturbed environments (Whitcomb *et al.* 1981, Rosenberg & Raphael 1986, Verner 1986, Usher 1987, Laurance 1991, 1997, Saunders *et al.* 1991).

A common approach in studies of the effects of forest/woodland fragmentation on fauna has involved finding the minimum areas of forest required by each species for survival. The greatest advances have been made where island biogeographical approaches have been combined with autecological studies to determine the resource requirements and population dynamics of individual species (e.g. Smith 1982, Suckling 1982, 1984 and Bennett 1987). Redpath (1995) showed for Tawny Owls *Strix aluco* occupying continuous and fragmented woodland in the United Kingdom that measures of breeding success and population turnover were essential in assessing the effects of habitat fragmentation. In addition, this study demonstrated that behavioural flexibility, particularly in terms of habitat selection and hunting behaviour, may account largely for the sensitivity of species to habitat fragmentation. Thus for species displaying a degree of behavioural flexibility, such as the Barking Owl *Ninox connivens* (Kavanagh *et al.* 1995a), it may be more appropriate to consider their environments as 'variegated' rather than 'fragmented' (McIntyre & Barrett 1992). Nonetheless, these and other landscapes are under threat of degradation by continued clearing, and they may require management to maintain local species richness (Barrett *et al.* 1994).

In this paper, we consider the contribution of forest and woodland fragments on privately-owned and unprotected lands towards the regional conservation of large forest owls and their arboreal marsupial prey in southeastern New South Wales. We conclude that small (<200 ha) fragments provide little benefit to these species and that the publicly-owned, continuously forested lands of the region (i.e. state forests, national parks and nature reserves) represent the major areas of habitat remaining for the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* and Masked Owl *T. novaehollandiae*.

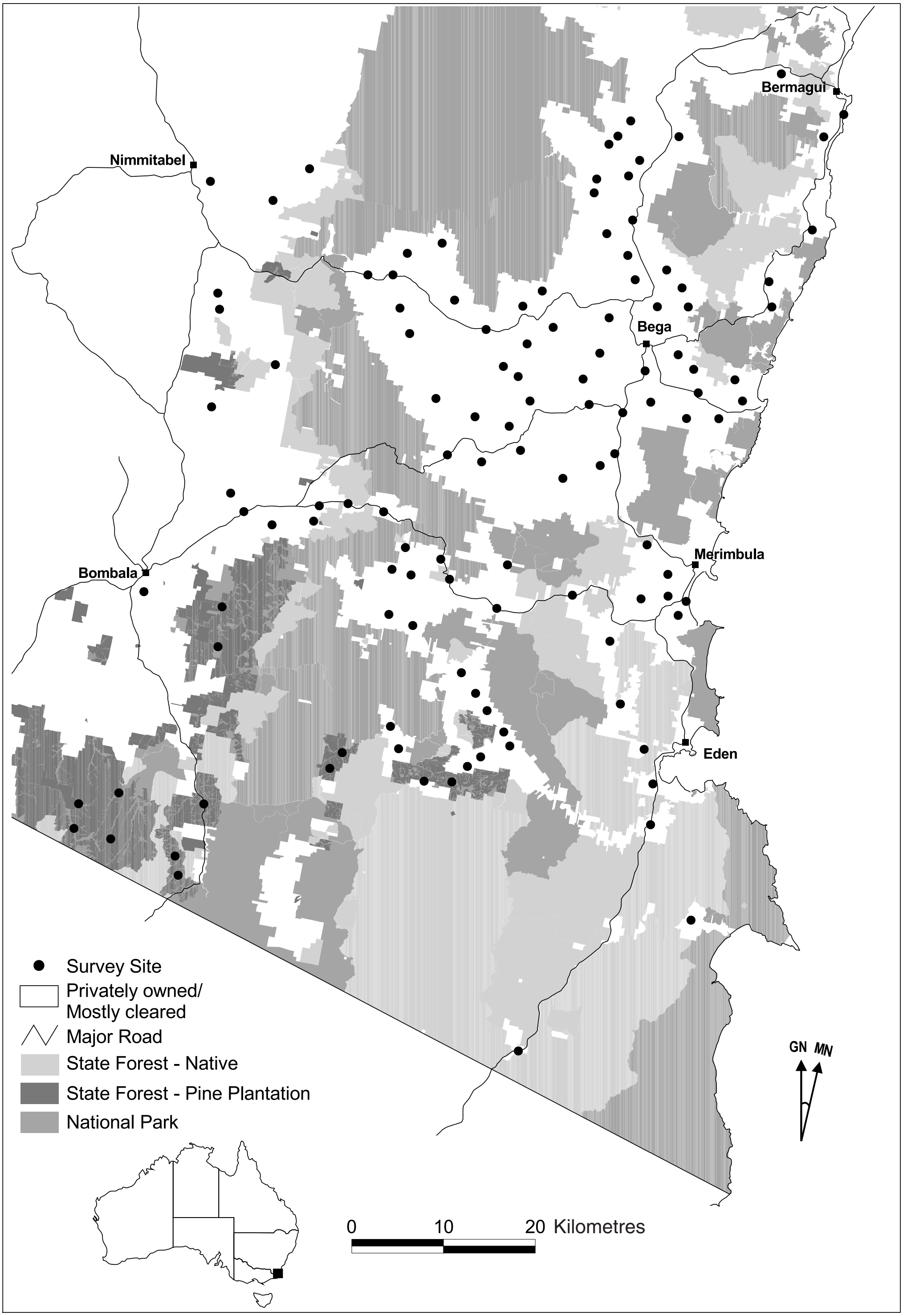


Fig. 1. Location of survey sites among fragmented forest on private lands in southeastern New South Wales.

METHODS

Study area

Southeastern New South Wales is an extensively forested region broken only by two river valleys, each of which has been substantially cleared for agriculture (dairying) (Fig. 1). The Bega River valley in the north of the region, by far the larger of the two valleys, was mainly cleared by 1900. A description of the widespread changes that have occurred since European settlement and subsequent changes in the abundance of native fauna were reported by Lunney & Leary (1988). The Towamba River valley in the south of the region, west of Eden, is much narrower, but was probably cleared about the same time as the Bega River valley. Westwards, beyond the heavily forested parts of the region, lie the Tablelands between Nimmitabel and Bombala. The Tablelands are all above 600 m and have been extensively cleared for grazing by sheep and cattle.

The vegetation of the Bega River valley consists of fragments of the original dry forest-woodland formation that was dominated by Forest Red Gum *Eucalyptus tereticornis* and Rough-barked Apple *Angophora floribunda*. The Towamba River Valley also contains remnants of this formation, as well as patches of Manna Gum *E. viminalis*. Forest/woodland remnants on the Tablelands are comprised mainly of Candlebark *E. rubida*, Mountain Gum *E. dalrympleana*, Narrow-leaved Peppermint *E. radiata* and Snow Gum *E. pauciflora*.

Stratification and sampling

A total of 120 sites was located evenly throughout the privately-owned or otherwise unprotected lands, including vacant crown land and leasehold land, in southeastern New South Wales (Fig. 1). Constraints to sampling included the need for all sites to be accessible by public roads (to avoid the need to contact hundreds of landowners), and the need for sites to be at least 500 m from houses (to minimise disturbance to the occupants during surveys). Given these constraints, sites were located on roads in or near fragments of native forest or woodland. In some parts of the Bega valley, the only fragments remaining were those near farmhouses. These fragments were not sampled. The mean distance between sampling sites was 3,506 m (range 1,314–23,584 m).

Sixty-four sites (53.3%) were located on farmland on predominantly private land well away (>1 km) from state forest or national park boundaries. Another 44 sites (36.7%) sampled farmland or other predominantly privately-owned land, but these sites occurred within about 1 km of state forest, national park or other areas of extensive forest, including vacant crown land. Twelve sites (10%) were remnant patches of eucalypt forest that were either adjacent to, or surrounded by, plantations of Radiata Pine *Pinus radiata*.

The main objective of this study was to determine whether privately-owned or otherwise unprotected lands contribute significantly to conservation of the region's populations of the three large forest owls and their arboreal marsupial prey. However, attempts were also made to assess the relationships between the sizes of native forest/woodland fragments and species occupancy. This was done by classifying at each survey site the degree of fragmentation in the landscape. Subjective classification was necessary because only coarse-scale mapping of remnant vegetation has been undertaken for private lands in the region, and because topographic features (best recognised on site) can limit the area which is sampled effectively during surveys.

A habitat fragmentation score (HFS), ranging from 1 to 6, was estimated within a circle of approximately 1km radius (314 ha) around each site, as follows:

HFS 1	Mostly cleared, scattered trees.
HFS 2	Roadside trees and/or a narrow strip of trees in a gully.
HFS 3	Patches of native forest/woodland ~10–50 ha in size.
HFS 4	Patches of native forest/woodland ~50–200 ha in size.
HFS 5	Patches of native forest/woodland >200 ha in size.
HFS 6	Mostly forested (but some cleared land present in the landscape).

The number of sites sampled were: 6 (5.0%), 13 (10.8%), 26 (21.7%), 30 (25.0%), 33 (27.5%) and 12 (10.0%) for habitat fragmentation scores 1–6, respectively. No assessments were made of the condition of remnant stands or the tree species composition of the vegetation.

Bird and mammal surveys

Numbers of nocturnal forest birds and arboreal mammals were estimated on variable-radius plots using a combination of methods. The procedure at each site was in three stages. Firstly, 15 minutes were spent listening for unelicited vocalisations and non-vocal cues indicating the presence of animals. Secondly, 20 minutes were spent playing the pre-recorded vocalisations of the Sooty Owl, Powerful Owl, Masked Owl and Barking Owl (five minutes for each species, including periods of silence interspersed among calls) and waiting for a response. A Toa ER–66 megaphone, with power output rated at 10W, was used to broadcast owl vocalisations. These call playbacks were audible to the human ear for a distance of at least one kilometre. Finally, ten minutes were spent searching a one ha plot with a 100W spotlight for any animals present at the site (either on or off the plot). Sampling was conducted during autumn (7 March–16 March 1995), and each site was visited once only. Surveys began shortly after dark and continued until about 3 a.m. The number of individuals of each species detected and their closest distances to the plot centre were estimated. Positions of all large owls detected were plotted on 1:25 000 scale maps. Details of weather and moon phase were recorded.

The survey procedure was designed to detect the presence of the large forest owls, but the combination of methods used also proved to be effective in detecting a wide range of nocturnal fauna (e.g. Kavanagh & Rohan-Jones 1982, Kavanagh 1984, Kavanagh & Peake 1993a, Kavanagh & Stanton, 1998). Almost identical methods were used in fauna surveys within continuous forest areas on public land (state forest and national park) elsewhere in the region (Kavanagh & Bamkin 1995), thus enabling comparisons to be made. The only difference was that, in this study, Barking Owl calls were broadcast in addition to the calls of the other three owls.

RESULTS

Species abundance

The nocturnal species most commonly encountered were the Australian Owlet-nightjar *Aegotheles cristatus*, the Sugar Glider *Petaurus breviceps*, and the microchiropteran bats (all species combined; an index of bat activity) (Table 1). The Southern Boobook *Ninox novaeseelandiae*, Barn Owl *Tyto alba*, Common Brushtail Possum *Trichosurus vulpecula* and the European Rabbit *Oryctolagus cuniculus* (22 sites) were also widespread. The species least commonly detected were the Mountain Brushtail Possum *T. caninus* (one site) and the Platypus *Ornithorynchus anatinus* (one site). Other uncommon species included the Long-nosed Bandicoot *Perameles nasuta* (five sites) and Common Wombat *Vombatus ursinus* (nine sites), and

Table 1. Distribution by habitat fragmentation score (HFS) classes (see text) of nocturnal birds and mammals on privately-owned and other unprotected lands (vacant crown land, leasehold land) in southeastern New South Wales; autumn 1995.

Figures show the percentage of sites where each species was recorded and total numbers of animals detected. Probability values are those resulting from a test of association using Fishers Exact Test. NS, not significant; n.a. testing not appropriate, or test results may not be valid.

Species	HFS 1–3	HFS 4–6	Total no. of sites	Total no. individuals	χ^2 value	P value
Powerful Owl	0	8.0	6	9	3.79	n.a.
Sooty Owl	0	5.3	4	4	2.48	n.a.
Masked Owl	0	5.3	4	4	2.48	n.a.
Barn Owl	35.6	13.3	26	31	8.18	<0.01
Barking Owl	4.4	2.7	4	5	0.28	n.a.
Southern Boobook	24.4	32.0	35	40	0.78	NS
Australian Owlet-nightjar	33.3	44.0	48	56	1.33	NS
White-throated Nightjar	0	6.7	5	6	3.13	n.a.
Tawny Frogmouth	6.7	4.0	6	7	0.42	n.a.
Greater Glider	0	0	0	0	n.a.	n.a.
Yellow-bellied Glider	2.2	16.0	13	28	5.53	<0.05
Sugar Glider	22.2	49.3	47	93	8.68	<0.01
Common Ringtail Possum	4.4	21.3	18	30	6.29	<0.05
Common Brushtail Possum	20.0	18.7	23	39	0.03	NS
Mountain Brushtail Possum	0	1.3	1	1	n.a.	n.a.
Koala	0	0	0	0	n.a.	n.a.
Bandicoots (both species)	0	6.7	5	7	n.a.	n.a.
Bats (Microchiroptera)	62.2	66.7	78	129	0.24	NS
Fruit Bats (Megachiroptera)	6.7	9.3	10	55	0.26	NS
European Rabbit	24.4	14.7	22	39	1.80	NS
Total number of sites	45	75	120			

two nocturnal birds the White-throated Nightjar *Eurostopodus mystacalis* (five sites) and Tawny Frogmouth *Podargus strigoides* (six sites). Species expected but not detected were the Greater Glider *Petauroides volans*, the Feathertail Glider *Acrobates pygmaeus* and the Koala *Phascolarctos cinereus*.

The Barn Owl was abundant on farmland and among the fragments of native forest and woodland on private land. It was recorded on 26 (21.7%) sites, which contrasts markedly with its low occurrence in continuously forested areas on state forest and national park in the region (<0.5% sites over all surveys; e.g. Kavanagh & Peake 1993b, Kavanagh & Bamkin 1995). The Barn Owl was particularly common among remnants of the original Forest Red Gum and Rough-barked Apple woodland in the substantially cleared Bega River Valley. Barn Owls were recorded at 20 (33.3%) of 60 sites surveyed in the Bega River valley. This contrasts with four (11.4%) of 35 sites in the Towamba and Pambula River valleys and two (8.7%) of 23 sites on the Tablelands. Some sites among the latter areas were adjacent to, or surrounded by, pine plantations. A further two sites, without Barn Owls, lay within other valley systems.

The Barking Owl was recorded at four (3.3%) sites (near Bega and Bemboka in the Bega valley, near Pericoe in Towamba valley, and near Cathcart on the edge of the Tablelands). This species had been detected only rarely (<0.5% sites) during surveys in state forest and national park in the region (Kavanagh & Peake 1993b, Kavanagh & Bamkin 1995; for other regions see also Kavanagh *et al.* 1995b and Kavanagh & Stanton 1998).

The Powerful Owl and the Sooty Owl were each recorded at lower frequency on privately-owned or otherwise unprotected lands in the region (5.0% and 3.3% of sites, respectively) than in the continuously-forested areas found in state forests and national parks (17.5% and 8.0% of sites, respectively) (Kavanagh & Bamkin 1995). Comparative data for the Masked Owl were 3.3% and 5.0% of sites, respectively.

Pattern in relation to forest fragmentation

Species varied in their responses to forest fragmentation (Fig. 2, Table 1). The Barn Owl inhabited the most fragmented environments ($P < 0.01$). These data support the results of regional surveys in continuously forested areas (Kavanagh & Peake 1993b, Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995b, Kavanagh & Stanton 1998, Milledge *et al.* 1991), and general knowledge among ornithologists, that the Barn Owl is absent from tall, moist forests. No differences were found for the Southern Boobook, Australian Owlet-nightjar, Common Brushtail Possum, and the microchiropteran bats (all species combined; an index of bat activity) and the megachiropteran bats (probably only *Pteropus poliocephalus*) in their frequency of occupation of highly fragmented and less fragmented forests and woodlands. Species associated with less fragmented forests included the Yellow-bellied Glider *Petaurus australis* ($P < 0.05$), Common Ringtail Possum *Pseudocheirus peregrinus* ($P < 0.05$) and the Sugar Glider ($P < 0.01$). Data for the remaining species were insufficient for analysis. However, the Powerful Owl, Sooty Owl and Masked Owl were not detected in the small and often degraded fragments of the original native forest and woodland on private land in the region (Fig. 2, Table 1), being restricted to the larger forest areas.

DISCUSSION

Proximity to larger forest areas

An important qualification needs to be made concerning the survey results for the Powerful Owl, Sooty Owl and the Masked Owl. All but two sites where any of these owls were recorded were situated less than one km from the boundary of state forest, national park or other area of continuous forest. Furthermore, the owls usually responded to call playback from positions more than several hundred metres away from the survey sites. This needs to be kept in mind when interpreting the results presented in Fig. 2. At one site located among farmland, a Powerful Owl was heard calling (in response to call playback) from a distance of at least 1.5 km away where it remained at the edge of continuous forest. Thus, virtually all records of the three large forest owls in this study were associated with the boundaries of extensively forested areas and they were not generally present among the native forest/woodland fragments occurring on private land (see also Law *et al.* 2001). These results were expected for the Powerful Owl and the Sooty Owl, but it appears that resident, territorial Masked Owls may be much less common in fragmented forest and woodland environments than suggested by the number of roadkills of this species. For example, 20% of all records for the Masked Owl in NSW until December 1992, excluding the present surveys, were road-killed birds (Peake *et al.* 1993, Debus & Rose 1994).

All records of the Yellow-bellied Glider were made from sites situated less than one km from

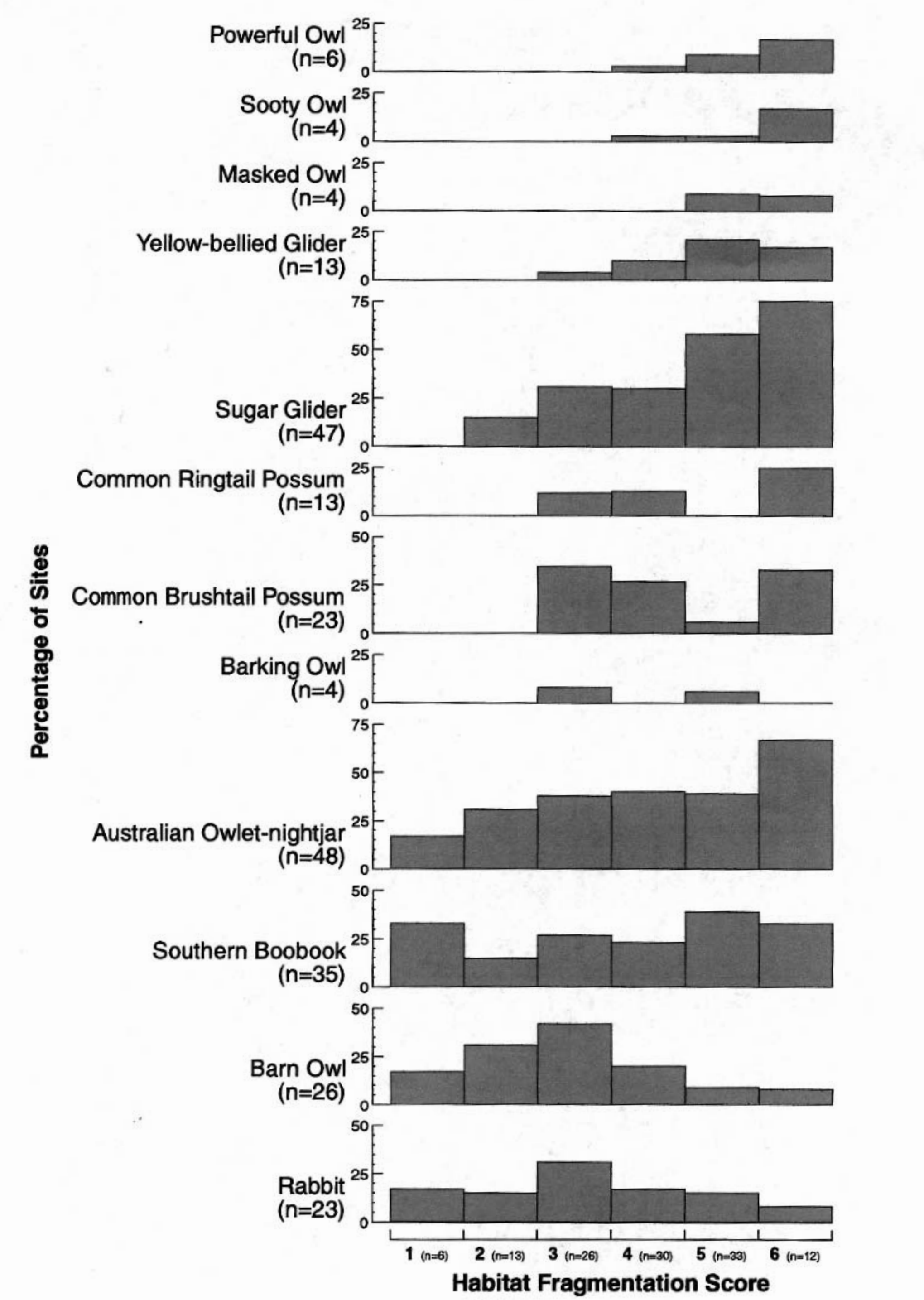


Fig. 2. Frequency of occurrence of nocturnal fauna on private land in southeastern New South Wales in relation to the degree of fragmentation of forest and woodland (see text for explanation of habitat fragmentation scores and Table 1 for data sources). Y-axis indicates proportion of sites in each category.

the boundary of state forest, national park or other area of continuous forest. The Common Ringtail Possum was recorded at several sites situated more than one km from the boundary of continuous forest, but all sites were in forested or riparian locations. In contrast, however, the Sugar Glider, Common Brushtail Possum, Southern Boobook, Australian Owlet-nightjar and the Barn Owl were widespread throughout private land in the region. Similar results for these species were found among small forest remnants on cleared land in northeastern N.S.W. (Law *et al.* 2001).

Fragmentation v. logging

Broad-scale surveys in southeastern and northeastern New South Wales revealed that logging has not caused any major changes to the distribution and abundance of most species of nocturnal forest birds and arboreal marsupials (Kavanagh & Bamkin 1995, Kavanagh *et al.* 1995b). This is partly because logged areas are allowed to regenerate and because modern logging operations ensure that some unlogged forest is retained throughout all logged areas (see Kavanagh 2002a). In contrast, this study suggests that clearing of native forest and woodland for agriculture and urban development, and the resulting fragmentation of habitat, appears to have had a much greater effect on nocturnal forest fauna than logging. However, comparisons between the effects of logging and fragmentation on species must necessarily be circumspect because of potential differences in forest type, geology and rainfall occurring on state forest and partially-cleared private land. Also, clearing took place nearly a century ago, thus allowing more time for adverse impacts to occur, whereas logging has been more recent. Furthermore, fragments of native forest and woodland on private land are likely to have been degraded in a number of ways, including grazing, the introduction of weeds and feral animals, and regular cutting for fenceposts and firewood. Nonetheless, it can be concluded that small (<200 ha) fragments of native forest and woodland on private land do not provide significant habitat for Powerful Owl, Sooty Owl and Masked Owl. The Rufous Owl *Ninox rufa* of tropical north Australia and New Guinea has been recorded in two large (400 ha) rainforest fragments on the Atherton Tablelands of north Queensland (Kanowski 1998).

Virtually all records of large forest owls in this study were associated with extensively forested areas, or occurred within one km of the boundary of these areas, which usually occurred on publicly-owned land (vacant crown land, state forest or national park). Of greatest significance was the apparent absence of resident, territorial Masked Owls (i.e. individuals that responded to call-playback) among the smaller fragments of native forest and woodland. This was despite the number of roadkills of this species in these environments (possibly dispersing immatures) and the reported occurrences of the Masked Owl in semi-arid, western New South Wales (Debus 1993, Peake *et al.* 1993, Debus & Rose 1994).

Arboreal marsupials, in particular the Common Ringtail Possum and Sugar Glider, form a major component of the diet of the Powerful Owl and the Sooty Owl, and are also eaten occasionally by the Masked Owl (Kavanagh 1997, Kavanagh 2002b). The Greater Glider was not recorded in fragmented forest, possibly because the forest types present were unsuitable. Similarly, the Mountain Brushtail Possum was recorded at only one site. Species apparently not disadvantaged by logging (Kavanagh & Bamkin 1995), but affected adversely by fragmentation (this study), included the Yellow-bellied Glider, Sugar Glider and the Common Ringtail Possum. Nonetheless, the Sugar Glider was recorded in some narrow (<20 m) linear remnants of forest along roadsides and in gullies among substantially cleared farmland (see also Suckling 1984). Other species not greatly disadvantaged by logging or fragmentation included the Southern Boobook, Australian Owlet-nightjar and Common Brushtail Possum. The index of bat activity (microchiropteran bats, all species combined) was similar in large and small fragments, although different species are likely to have been involved (Law *et al.* 1999). The Barn Owl, a non-forest species, was surprisingly common in small forest and woodland fragments. These general findings are supported by the studies of fauna occupying small (<2000 ha) forest isolates and remnant forest patches on the southwestern slopes of New South Wales (Kavanagh & Stanton 1998).

This study was not designed specifically to address questions about the size, shape, dispersion, connectivity and composition of habitat required to minimise the effects of fragmentation on nocturnal fauna. These issues are difficult to resolve, not least because patch history (time since isolation and other events) and vegetation composition may vary greatly between patches. However, our studies do not suffer through differential sampling effort in relation to patch size, which has been a problem in some other studies of fragmentation effects (Verner 1986). In general, the species most likely to survive habitat fragmentation are small, abundant, habitat and dietary generalists of low trophic status (see also Redpath 1995).

ACKNOWLEDGMENTS

Alison Towerton is thanked for preparing Fig. 1, and Brad Law, Ian Newton and Steve Petty are thanked for providing comments on the manuscript.

REFERENCES

Barrett, G.W., Ford, H.A. & Recher, H.F. 1994. Conservation of woodland birds in a fragmented rural landscape. *Pac. Conserv. Biol.* **1**: 145–156.

Bennett, A.F. 1987. Conservation of mammals within a fragmented forest environment: the contributions of insular biogeography and autecology. In Saunders, D.A., Arnold, G.W., Burbidge, A.A. & Hopkins, A.J.M. (eds) *Nature conservation*: *the role of remnants of native vegetation*: 41–52. Chipping Norton, Sydney: Surrey Beatty and Sons.

Debus, S.J.S. 1993. The mainland Masked Owl *Tyto novaehollandiae*: a review. *Aust. Bird Watcher* **15:** 168–191.

Debus, S.J.S. & Rose, A.B. 1994. The Masked Owl *Tyto novaehollandiae* in New South Wales. *Aust. Birds* (Supplement) **28:** 40–64.

Harris, L.D. 1984. *The fragmented forest*: *island biogeographic theory and the preservation of biotic diversity*. Chicago: University of Chicago Press.

Kanowski, J. 1998. The abundance of the Rufous Owl *Ninox rufa* in upland and highland rainforests of north-east Queensland. *Emu* **98**: 58–61.

Kavanagh, R.P. 1984. Seasonal changes in habitat use by gliders and possums in southeastern New South Wales. In Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*: 527–543. Sydney: Australian Mammal Society.

Kavanagh, R.P. 1997. *Ecology and management of large forest owls in south-eastern Australia*. Ph.D. Thesis, University of Sydney, Sydney.

Kavanagh, R.P. 2002a. Conservation and management of large forest owls in south-eastern Australia. This volume.

Kavanagh, R.P. 2002b. Comparative diets of the Powerful Owl, Sooty Owl and Masked Owl in south-eastern Australia. This volume.

Kavanagh, R.P. & Bamkin, K.L. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biol. Conserv.* **71**: 41–53.

Kavanagh, R.P., Debus, S.J.S., Rose, A.B. & Turner, R.J. 1995a. Diet and habitat of the Barking Owl *Ninox connivens* in New South Wales. *Aust. Bird Watcher* **16**: 137–144.

Kavanagh, R.P., Debus, S., Tweedie, T. & Webster, R. 1995b. Distribution of nocturnal forest birds and mammals in north-eastern New South Wales: Relationships with environmental variables and management history. *Wildl. Res.* **22**: 359–377.

Kavanagh, R.P. & Peake, P. 1993a. Survey procedures for nocturnal forest birds: an evaluation of variability in census results due to temporal factors, weather and technique. In P. Olsen (ed) *Australian Raptor Studies*: 86–100. Melbourne: Australian Raptor Association and Royal Australasian Ornithologists' Union.

Kavanagh, R.P. & Peake, P. 1993b. Distribution and habitats of nocturnal forest birds in south-eastern New South Wales. In P. Olsen (ed) *Australian Raptor Studies*: 101–125. Melbourne: Australian Raptor Association and Royal Australasian Ornithologists' Union.

Kavanagh, R.P. & Rohan-Jones, W.G. 1982. Calling behaviour of the Yellow-bellied Glider, *Petaurus australis* Shaw (Marsupialia: Petauridae). *Aust. Mammal.* **5**: 95–111.

Kavanagh, R.P. & Stanton, M.A. 1998. Nocturnal forest birds and arboreal marsupials of the South-western Slopes, New South Wales. *Aust. Zoologist* **30**: 449–466.

Kavanagh, R.P. & Webb, G.A. 1998. Effects of variable-intensity logging on mammals, reptiles and amphibians at Waratah Creek, southeastern New South Wales. *Pac. Cons. Biol.* **4**: 326–347.

Laurance, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.* **5**: 79–89.

Laurance, W.F. 1997. Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. *Wildl. Res.* **24**: 603–612.

Law, B.S., Anderson, J. & Chidel, M. 1999. Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. *Biol. Conserv.* **88**: 333–345.

Law, B.S., Chidel, M. & Turner, G. 2001. The use of paddock trees in farmland by wildlife. *Pac. Cons. Biol.* (in press).

Loyn, R.H. 1987. Effects of patch area and habitat on bird abundances, species numbers and tree health in fragmented Victorian forests. In Saunders, D.A., Arnold, G.W., Burbidge, A.A. & Hopkins, A.J.M. (eds) *Nature conservation: the role of remnants of native vegetation*: 65–77. Chipping Norton, Sydney: Surrey Beatty and Sons.

Lunney, D. & Leary, T. 1988. The impact on native mammals of land-use changes and exotic species in the Bega district, New South Wales. *Aust. J. Ecol.* **13**: 67–92.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton, New Jersey: Princeton University Press.

McIntyre, S. & Barrett, G.W. 1992. Habitat variation, an alternative to fragmentation. *Conserv. Biol.* **6**: 146–147.

Milledge, D.R., Palmer, C.L. & Nelson, J.L. 1991. 'Barometers of change': the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. In Lunney, D. (ed) *Conservation of Australia's forest fauna*: 53–65. Mosman: Royal Zoological Society of New South Wales.

Peake, P., Conole, L.E., Debus, S.J.S., McIntyre, A. & Bramwell, M. 1993. The Masked Owl *Tyto novaehollandiae* in Victoria. *Aust. Bird Watcher* **15**: 124–136.

Redpath, S.M. 1995. Habitat fragmentation and the individual: Tawny Owls *Strix aluco* in woodland patches. *J. Anim. Ecol.* **64**: 652–661.

Rosenberg, K.V. & Raphael, M.G. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. In Verner, J., Morrison, M.L. & Ralph, C.J. (eds) *Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates*: 263–272. Madison: University of Wisconsin Press.

Saunders, D.S., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**: 18–32.

Smith, A.P. 1982. Diet and feeding strategies of the marsupial Sugar Glider in temperate Australia. *J. Anim. Ecol.* **51**: 149–166.

Suckling, G.C. 1982. Value of reserved habitat for mammal conservation in plantations. *Aust. Forestry* **45**: 19–27.

Suckling, G.C. 1984. Population ecology of the Sugar Glider, *Petaurus breviceps*, in a system of fragmented habitats. *Aust. Wildl. Res.* **11**: 49–75.

Usher, M.B. 1987. Effects of fragmentation on communities and populations: A review with applications to wildlife conservation. In Saunders, D.A., Arnold, G.W., Burbidge, A.A. & Hopkins, A.J.M. (eds) *Nature conservation: the role of remnants of native vegetation*: 103–121. Chipping Norton, Sydney: Surrey Beatty and Sons.

Verner, J. 1986. Summary: Predicting effects of habitat patchiness and fragmentation – the researcher's viewpoint. In Verner, J., Morrison, M.L. & Ralph, C.J. (eds) *Wildlife 2000. Modelling habitat relationships of terrestrial vertebrates*: 327–329. Madison: University of Wisconson Press.

Whitcomb, R.F., Robbins, C.S., Lynch J.F., Whitcomb, B.L., Klimkiewicz, M.K. & Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the Eastern Deciduous Forest. In Burgess, R.L. & Sharpe, D.M. (eds.). *Forest island dynamics in man-dominated landscapes*: 125–205. New York: Springer-Verlag.

25

LESSONS LEARNED IN 30 YEARS OF RESEARCH AND MANAGEMENT ON THE NORTHERN SPOTTED OWL (*STRIX OCCIDENTALIS*)

ERIC D. FORSMAN

USDA Forest Service, Pacific Northwest Research Station,

Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97332.
email: e.forsman@fs.fed.gov

Extensive areas of forest land in the western United States are owned and managed by the federal government. These lands are home to a diverse array of native plants and animals and are also an important source of lumber for domestic use. In this paper, I describe the long and bitter war that has been waged over control of these forest lands. As a result of this controversy, the management emphasis on federal forest lands has gradually changed from a primary focus on timber production to a primary emphasis on species conservation and forest health. Research on the Northern Spotted Owl played an important role in bringing about these changes.

INTRODUCTION

In the years after 1960, forest management in the western United States underwent profound changes. Public and scientific concerns about Spotted Owls and other forest wildlife had a lot to do with bringing about these changes. The public and scientific debate that took place during this process was often difficult and contentious, and many issues were settled only after lengthy court battles.

There are numerous parallels between the long and often acrimonious conflict over Spotted Owls and forest management in the U.S., and similar conflicts that are taking place in Australia and many other parts of the world. In this paper I present a brief review of the debate over the Spotted Owl, and describe how scientists, laws, federal agencies, environmentalists and the media influenced the process.

EARLY RESEARCH AND THE SEEDS OF CONTROVERSY

The recorded history of the Spotted Owl began rather inauspiciously in 1858, when one of the early American naturalists collected a specimen near Fort Tejon in the Sierra Nevada Mountains of southern California (Xantus 1859). Fourteen years passed before another specimen was collected, this time in Arizona in 1872 (Bendire 1892). During the next 80 years, occasional sightings and nest records led ornithologists to believe that the Spotted Owl was an uncommon resident of forest areas in the western U.S. and Mexico. Based on morphology, they divided the species into three subspecies: the Northern Spotted Owl *Strix occidentalis caurina* in the temperate coniferous forests of southwestern British Columbia, western Washington, western Oregon and northwestern California; the California Spotted Owl *S. o. occidentalis* in the Sierra Nevada Mountains and coastal mountains of central and southern California; and the Mexican Spotted Owl *S. o. lucida* in the mountains of the southwestern U.S. and Mexico.

Most of the early ornithologists who encountered Spotted Owls commented on their lack of fear of humans, which made them easy to collect (Bent 1938). However, because Spotted Owls lived in dense forests in mountainous areas and were active primarily at night, they were rarely encountered and gained a reputation for being mysterious and rare (Gabrielson & Jewett 1940). This perception began to change in the early 1970's, when systematic surveys of Spotted Owls and other forest birds were initiated in the western U. S. The first such surveys for Spotted Owls were initiated in Oregon in 1972 by myself and Howard Wight (Forsman 1976, Forsman *et al.* 1980). The objective of these surveys was to learn as much as possible about the distribution, abundance and life history of the owl. We used acoustic-lure surveys to locate owls, and if we got responses at night we returned during the day to search for roosts and nests.

In the first two years of our survey it became apparent that Spotted Owls were not nearly as rare as originally thought, as we found them in many of the forests surveyed. It also became obvious that the majority of Spotted Owls on federal lands in Oregon were located in old forests or in mixed-age forests that included remnants of old forest that had survived wildfires, windstorms and logging. Many of the locations where we found owls were scheduled for logging. In the early 1970's, commercial logging was in full swing on federal lands in the Pacific Northwest and both the U.S. Forest Service and U. S. Bureau of Land Management (BLM) were rapidly harvesting old forests and replacing them with young, managed forests. The result was a rapidly changing forest landscape in which sites occupied by Spotted Owls were often logged without anyone knowing that the owls were there. By 1976, I estimated that timber sales were either conducted or planned in approximately 50% of the locations where we found Spotted Owls in 1970–1974 (Forsman 1976).

Another finding from our early surveys was that land managers were largely oblivious to the fact that they were harvesting Spotted Owl habitat. Most of them had never seen a Spotted Owl and did not know that the species existed. Regardless, the imperative to produce lumber from federal lands left little room for retention of old forests occupied by Spotted Owls. The prevailing wisdom in the late 1960's and early 1970's was that old forests were stagnant biological deserts and that the greatest good would come from cutting them down and replacing them with young, fast growing forests (Parry *et al.* 1983). The objective was to develop a 'regulated' forest in which fast-growing young trees would be thinned, harvested and replanted at regular intervals, thus ensuring a constant supply of high volumes of wood. This was supposed to take place within the framework of 'multiple use', which meant, in theory, that managers of national forests would carefully manage for all of the different roles of forests, including wildlife and plant conservation, fisheries, water quality, recreation and minerals, as well as lumber production.

In 1973, Gordon Gould with the Department of Fish and Game in California initiated the first surveys of Spotted Owls in California (Gould 1977). His surveys produced results similar to ours. He found Spotted Owls in many different forest types, but the majority were in old forests. He concluded that 'Logging and other forest cutting practices appear to be the major causes making forest habitat unsuitable for Spotted Owls' (Gould 1977:139).

After our initial surveys we began to discuss our findings with other biologists, land managers and conservation groups. Our primary message was that (1) the Spotted Owl was a widespread but relatively uncommon species that seemed more-or-less dependent on old forests, and (2) that a single-minded focus on replacing old forests with intensively managed young forests was unlikely to ensure the long-term persistence of the species. We recommended that the best way to manage for Spotted Owls was to provide them with substantial areas of old forest habitat (Forsman 1976, Forsman *et al.* 1984). At about this same time, other biologists began to emphasize that the elimination of old forests and dead trees might have negative effects on bird species diversity and abundance of cavity nesting birds and mammals (Wight 1974, Bull & Meslow 1977, Thomas 1979, Mannan *et al.* 1980). Forest ecologists also began to emphasize the unique structural and functional attributes of old forests (Franklin *et al.* 1981).

In light of these findings, the Forest Service and Bureau of Land Management were increasingly criticized for their emphasis on conversion of old forests to young forests. This created consternation within these agencies, which had always viewed themselves as occupying the moral high ground in matters of resource management. Concepts like 'multiple use' and 'sustained yield' were deeply ingrained in the institutional psyche of both agencies, and most federal land managers honestly believed that they were doing a good job of meeting the needs and the wishes of the American public. Many of these managers, trained in classical methods of European silviculture, found it difficult to believe that the goal of producing vast areas of fast-growing young forest might actually be detrimental to some types of wildlife, particularly something as charismatic as a Spotted Owl.

CONFLICT IN THE WOODS – THE RISE OF THE ENVIRONMENTAL MOVEMENT

During the early 1900's, the timber industry in the western U. S. cut most of the old forest on private lands. By the 1970's many of the mill owners and woodsworkers of the region had become dependent on the Forest Service and BLM for timber (Parry *et al.* 1983). These groups did not respond warmly to those who suggested that cutting of old forests should be reduced on federal lands to protect wildlife. They viewed reductions in harvest rates as a real threat to a lucrative industry and a way of life.

At the same time that studies of Spotted Owls and other birds and mammals were raising the public consciousness about old forests, the late 1960's and 1970's were a period of growing environmental unrest in the U.S. Mainstream environmental groups like the Sierra Club and Audubon Society were becoming more interested in the management of federal lands, and a number of more radical environmental groups were springing up around the country, heeding the earlier call of outspoken advocates and conservationists like Aldo Leopold, Edward Abbey and John Muir (Arnold 1982, Zakin 1993). Membership in these organizations tended to be dominated by recreational users of federal lands, but also included professional ecologists, biologists and other scientists who were concerned about environmental issues. As these groups gradually gained power and access to the media, they began to question many of the management practices that were in vogue on federal lands. In casting about for examples of what was wrong with forest management as practiced by the federal agencies, they quickly adopted the Spotted Owl as the poster child of what would prove to be a long and brutal fight over control of federal forests in the western U.S. (Dietrich 1992, Durbin 1996).

In the early stages of this rising tide of environmental activism, the professional land managers, engineers and foresters who were in charge of managing federal lands tended to respond rather coolly towards what they perceived to be environmental extremists who did not know what they were talking about and who were concerned only about turning federal forests into wilderness areas. In hindsight, I think some of this cynicism was warranted, but I will get to that later. The main point I want to make here is that the interaction between environmental groups and the federal land management agencies quickly escalated into an us-versus-them game, where neither side trusted the motives of the other. As the battle escalated, the media became more interested and the debate became front page news. As a result, what started out as a regional debate in the western U. S. eventually escalated into a national debate over management of old forests on federal lands. The Spotted Owl became an important player in this debate, at least partly because it was so tame and photogenic. Several environmental groups made television documentaries about the plight of the owl, and Spotted Owls regularly made headlines in newspapers, magazines and television news.

DISSENSION IN THE RANKS

Another major change that occurred in the late 1960's and early 1970's was that the Forest Service and Bureau of Land Management began to hire wildlife biologists to assist their timber sale planners and range managers with evaluation of proposed harvest areas and management programs. This was largely in response to new environmental laws, such as the National Environmental Protection Act of 1970 and the National Forest Management Act of 1976. These federal laws required the agencies to do detailed environmental assessments of their actions and to manage for viable populations of native species. True to their calling, the biologists hired by the federal agencies tended to be advocates for wildlife conservation, which was not always easy in organizations where the dominant paradigm was wood production. This had a profound influence on the agencies, because now they had their own experts telling them that they needed to pay more attention to wildlife and fisheries issues.

FACT AND FICTION ABOUT SPOTTED OWLS

As the debate heated up, the public in the U. S. was bombarded with a tremendous amount of information about Spotted Owls in research papers, government reports, books, magazines, newspapers, court documents, documentaries, and television news. Sorting fact from fiction in these many different sources was daunting. However, a few basic facts were difficult to refute. First, although Spotted Owl populations seemed to be declining (Burnham and Anderson 1996, Franklin *et al.* 1999), they were not rare in most areas and they were very widespread, occurring over a large region from southern British Columbia to central Mexico. No one knew how many there were, but there were a lot of them. For example, during the 13-yr period from 1985 to 1997, 12,389 Northern Spotted Owls were banded in the region covered by the three states of Washington, Oregon and California (Forsman, unpubl. data). Second, no one questioned that Spotted Owls were forest owls, at least in the Pacific Northwest and California. Numerous studies showed that they lived in forests and fed on small mammals that occurred in forests. Their diets were dominated by arboreal or semi-arboreal forest mammals, such as Flying Squirrels *Glaucomys sabrinus*, Woodrats *Neotoma* spp. and Red Tree Voles *Arborimus longicaudus* (Barrows 1980, Forsman *et al.* 1984). Third, Spotted Owls really did seem to prefer old forests. The vast majority of Spotted Owls on federal lands occurred in areas dominated by old forests. However, some occurred in areas dominated by young forests that included remnants of old forest that had survived fires, windstorms or logging (Forsman 1976, Forsman *et al.* 1984). In northern California, densities of Spotted Owls in predominantly young forests sometimes approached densities recorded in old forests (Diller & Thome 1999). In addition, radio-telemetry studies of Spotted Owls generally showed that, while they preferred old forests for foraging, they also hunted in young forests (Forsman *et al.* 1984, Carey *et al.* 1990, 1992).

The use of young forests by Spotted Owls led to much uncertainty about the habitat needs of the species. The protagonists in the debate over old forests tended to interpret this uncertainty along party lines. Environmental groups, many academics, and a fair number of agency scientists like myself have generally argued that, because the owl population is declining, emphasis should be on protection of old forests (preferred habitat). This group has tended to downplay the importance of young forests because they are less suitable for Spotted Owls than are old forests. In contrast, industry advocates, and some scientists representing industry clients, have suggested that use of young forest is evidence that the owl is relatively flexible in the amount of old forest it needs, and that protection of large areas of old forest may be unnecessary. In reality, both sides in this debate are probably at least partially correct. Fueled by the plethora of conflicting evidence and opposing views, the courts, media and lay public are often left wondering who to believe.

PHILOSOPHICAL DIFFERENCES AND LEGAL ACTIONS

The considerable uncertainty in our understanding of the habitat needs of Spotted Owls has not stopped people from taking strong positions. Some of the more ardent environmental groups are adamantly opposed to any commercial harvest of trees on federal lands. They are so cynical of land managers that they generally oppose any suggestion that some kinds of commercial harvest may actually maintain the kinds of structurally diverse forests that are utilized by spotted owls and other species that occur in old forests.

The conflict over old forests is probably inevitable in an increasingly affluent society in which the majority of people live in cities and no longer relate to the hunter-gatherer-agrarian lifestyle that was the norm during all but the last 100 years of human existence. However, all of the parties in this debate are probably to blame for making it worse than it needs to be. The problem is that, regardless of which faction you belong to, the opposition will attack at the first sign of weakness. To avoid looking weak, extreme environmental and industry groups consistently emphasize the facts that best support their views, and ignore or dismiss contrary information. On the other hand, scientists tend to emphasize the uncertainty in their findings and argue that when you are uncertain about something you should proceed cautiously. While this sounds reasonable, it can also be a prescription for management gridlock because all land management decisions involve considerable uncertainty.

Battles over Spotted Owls and old-growth forests have increasingly been fought in the courts, where environmental groups have been successful at using federal rules and regulations to delay or stop management activities on federal lands. The U. S. has some very strong environmental laws, including the Environmental Protection Act, Endangered Species Act and the National Forest Management Act. The Endangered Species Act tends to get a lot of media attention, but in many ways the National Forest Management Act is a much stronger law. It requires the Forest Service to maintain viable populations of native vertebrates on Forest Service lands. The spirit behind these laws is good, but they also present land managers with an unenviable job. There is no way to simultaneously manage a forest for viable populations of all species without taking risks that some species will do poorly. Thus, decisions about which species or forest types should be subjected to the greatest risks are as much social decisions as they are scientific ones. In the case of the Spotted Owl, the Forest Service and BLM were repeatedly sued by environmental groups on the grounds that they were not protecting enough old forests for Spotted Owls or other species that thrived in such forests. The Forest Service and BLM lost many of these cases because of the wealth of circumstantial and empirical evidence that Spotted Owls were not doing well. By 1989 these lawsuits brought the cutting of old forests on Forest Service and BLM lands in the Pacific Northwest to a standstill. Counter lawsuits by representatives of the timber industry were largely unsuccessful in reversing this trend. This impasse eventually forced the Forest Service and BLM to adopt a management plan that greatly restricted harvest of old forest, and that changed management objectives on federal lands from a primary emphasis on wood production to a primary emphasis on species conservation and 'ecosystem health'. This management plan was called the 'Northwest Forest Plan'.

THE NORTHWEST FOREST PLAN

The Northwest Forest Plan, which was adopted in 1994, includes an extensive network of 'Late Successional Reserves', within which the primary objective is to maintain and develop old forest habitats for Spotted Owls and other species associated with old forests (FEMAT 1993, USDA Forest Service and USDI Bureau of Land Management 1994a, b). Late Successional Reserves (LSRs) are typically 16,000 to 50,000 ha in size, and are spaced at 10–20 km intervals across federal forest lands within the range of the Northern Spotted Owl (western Washington, western Oregon, and northwestern California). Of the 9.9 million hectares of federal land within the region covered by the Northwest Forest Plan, 3.1 million ha (30.8%) are in LSRs, 3.0 million ha (29.9%) are in Wilderness Areas or National Parks, 1.1 million ha (10.7%) are in Riparian Reserves and 1.0 million ha (12.3%) are classified as 'Administratively Withdrawn' or 'Adaptive Management' areas where harvest is somewhat restricted. The remaining 1.6 million ha (16.3%) is classified as 'Matrix', which is the area that, at least in theory, will be managed for a variety of uses, including production of wood for commercial markets. Inside LSRs and Riparian Reserves the primary management focus is maintenance and development of old forest habitat, cutting of which is generally not allowed.

Because it is a compromise plan that still allows some commercial harvest of old forests on federal lands, the Northwest Forest Plan is unpopular with many environmentalists who want old forests left alone. It also is not popular with timber industry groups, who argue that it does not provide enough wood for commercial use. However, because the Northwest Forest Plan was a sincere attempt to develop a compromise that was biologically defensible and that still allowed some wood production for commercial use, it has thus far withstood attempts to overthrow it in the courts. This has not stopped the various political factions from continuing to try to find ways to circumvent the intent of the plan. For example, environmental groups frequently protest against proposed timber harvest in areas that were designated as available for harvest in the Northwest Forest Plan. This was why I said earlier that I think people in the Forest Service and BLM were somewhat justified in their early cynicism about demands made by environmental groups. The list of demands started out small, and has gradually grown over the years, from protecting management areas for Spotted Owls to a complete cessation of commercial logging on federal lands. The more extreme groups are opposed to almost any kind of commercial use of forest products from federal lands.

SOME MAJOR LESSONS

Several lessons can be gleaned from the controversy over Spotted Owls and forest management, as follows:

(1) The decades of the 1970's and 1980's saw a huge awakening of environmental activism in the U.S. At the same time, passage of the Environmental Protection Act (1970), Endangered Species Act (1973) and National Forest Management Act (1976) provided environmental groups with legal avenues for challenging management decisions on federal lands. Federal agencies, including the Forest Service and BLM, were at first unresponsive to these groups, which led to cynicism within the environmental movement regarding the motives of these agencies. This cynicism could probably have been somewhat reduced had the agencies been more receptive to new ideas and more cognizant of changing values in an increasingly urban society.

(2) Despite my criticisms of the more extreme environmentalists, the changes that have taken place in management philosophy on federal forests in the U. S. would not have happened without the lawsuits, protests and public involvement of environmental groups. These groups were instrumental in forcing federal land managers to move away from European methods of forestry that focused on production of wood, to a more holistic approach that includes production of lumber as only one objective within the larger context of 'ecosystem health' and conservation of biodiversity (Durbin 1996, Dietrich 1992).

(3) Scientists and wildlife biologists played an important role in the changes that have taken place in management philosophy. They provided the data that showed that a diverse array of habitats was needed in order to maintain the diverse array of species that was present in the forests of the western U. S. This information was then used by conservation organizations to pressure the management agencies into gradually changing the focus of their management philosophies.

(4) Despite the emphasis on science and data in management planning, manipulation of any system reflects value judgements about what we think is important. These judgements are flavored by all kinds of moral, practical, biological and social issues, and typically represent compromises between different interest groups. There is thus a limit to how much a management plan can be 'scientifically based'. Science may provide insights about how different species might respond to certain habitat conditions, but how much habitat to maintain for each species inevitably involves guesswork and compromises with conflicting objectives.

(5) Focusing on a single species without looking at the big picture is a mistake. Scientists and managers spent many years trying to develop a management plan for the Spotted Owl (Thomas *et al.* 1990). That plan was soon rejected by a federal court because it did not adequately address the needs of the other native species that the Forest Service was supposed to manage. Only after the Forest Service and Bureau of Land Management developed a more holistic plan that explicitly addressed the needs of a broad range of species were they able to prevail in the courts. In retrospect, we should have started with the big picture and worked down, rather then starting with a single species and working up.

(6) Natural systems are notoriously unpredictable and may not respond as expected. For many years it was thought that Spotted Owls would flourish if their habitat was protected. This is now less certain, because a closely related species, the Barred Owl *Strix varia*, has recently invaded the entire range of the Northern Spotted Owl from British Columbia to northern California and appears to be displacing Spotted Owls in some areas (Hamer *et al.* 1994, Dark *et al.* 1998, Leskiw & Gutiérrez 1998).

Lastly, although recent management plans have attempted to integrate the needs of many different species, we still know very little about many of the species we are trying to manage. A great deal more research is needed on these species before we can hope to understand how they interact within a larger system.

REFERENCES

Arnold, R. 1982. *At the eye of the storm: James Watt and the environmentalists*. Chicago, IL: Regnery Gateway.

Barrows, C. 1980. Feeding ecology of the Northern Spotted Owl. *J. Raptor Res.* **14**: 73–78.

Bendire, C.E. 1892. Life histories of North American birds. *U. S. Natl. Mus. Spec. Bull.* No. **1**.

Bent, A.C. 1938. Life histories of North American birds of prey. Part 2. Smithsonian Inst. *U.S. Natl. Mus. Spec. Bull.* No. **170**.

Bull, E.L. & Meslow, E.C. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. *J. Forestry* **75**: 335–337.

Burnham, K.P., Anderson, D.R. & White, G.C. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. In Forsman, E.D., DeStefano, S., Raphael, M.G. & Gutiérrez, R.J. (eds) Demography of the Northern Spotted Owl. *Stud. in Avian Biol.* **17**: 92–101.

Carey, A.B., Reid, J.A. & Horton, S.P. 1990. Spotted Owl home range and habitat use in southern Oregon Coast Ranges. *J. Wildl. Manage.* **54**: 11–17.

Carey, A.B., Horton, S.P. & Biswell, B.L. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecol. Monogr.* **62**.

Dark, S.J., Gutiérrez, R.J. & Gould, G.I., Jr. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* **115**: 50–56.

Dietrich, W. 1992. *The final forest: the battle for the last great trees of the Pacific Northwest*. New York: Simon and Schuster.

Diller, L.V. & Thome, D.M. 1999. Population density of Northern Spotted Owls in managed young-growth forests in coastal north California. *J. Raptor Res.* **33**: 275–286.

Durbin, K. 1996. *Tree huggers: victory, defeat and renewal*. Seattle, WA: The Mountaineers.

FEMAT. 1993. Forest ecosystem management: an ecological economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. USDA Forest Service, USDI Bureau of Land Management, USDI Fish and Wildlife Service, Portland OR.

Forsman, E.D. 1976. A preliminary investigation of the Spotted Owl in Oregon. M. Sc. Thesis, Oregon State University, Corvallis.

Forsman, E.D., Meslow, E.C. & Wight, H.M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monogr*. **87**.

Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW–118.

Franklin, A.B., Burnham, K.P., White, G.C., Anthony, R.J., Forsman, E.D., Schwarz, C., Nichols, J.D. & Hines, J. 1999. Range-wide status and trends in Northern Spotted Owl populations. Draft Rept., Colorado Cooperative Fish and Wildlife Research Unit, Dept. of Fishery and Wildlife Biology, Colorado State Univ., Fort Collins.

Gabrielson, I.N. & Jewett, S.G. 1940. *Birds of Oregon*. Oregon State College, Corvallis.

Gould, G. 1977. Distribution of the Spotted Owl in California. *Western Birds* **8**: 131–146.

Hamer, T.E., Forsman, E.D., Fuchs, A.D. & Walters, M.L. 1994. Hybridization between Barred and Spotted Owls. *Auk* **111**: 487–492.

Heinrichs, J. 1983. The winged snail darter. *J. Forestry* **81**: 212–215, 262.

Leskiw, T. & Gutiérrez, R.J. 1998. Possible predation of a Spotted Owl by a Barred Owl. *Western Birds* **29**: 225–226.

Mannan, W.R., Meslow, E.C. & Wight, H.M. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. *J. Wildl. Manage*. **44**: 787–797.

Parry, B.T., Vaux, H.J. & Dennis, N. 1983. Changing conceptions of sustained-yield policy on the National Forests. *J. Forestry* **81**:150–154.

Thomas, J.W. (ed). 1979. Wildlife habitats in managed forests of the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook 553. Washington, DC.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R., & Verner, J. 1990. A conservation strategy for the Northern Spotted Owl: report of the Interagency Scientific Committee to address the conservation of the Northern Spotted Owl. USDA Forest Service and USDI Bureau of Land Management, Portland, OR.

USDA Forest Service and USDI Bureau of Land Management. 1994a. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. U.S.D.A. Forest Service, Portland, OR. 2 Vols.

USDA Forest Service and USDI Bureau of Land Management. 1994b. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl. U.S.D.A. Forest Service, Portland, OR.

Wight, H.M. 1974. Nongame wildlife and forest management. In Black, C. (ed.) *Wildlife and forest management in the Pacific Northwest*: 27–28. Oregon State Univ. School of Forestry, Forest Research Laboratory.

Xantus, J. 1959. Catalogue of birds collected in the vicinity of Fort Tejon, California with a description of a new species of *Syrnium*. *Proc. Phil. Acad. Nat. Sci*. 1859.

Zakin, S. 1993. *Coyotes and town dogs: Earth First! and the environmental movement*. New York, NY: Viking.

26

RODENTICIDES IN BRITISH BARN OWLS (*TYTO ALBA*)

IAN NEWTON & IAN WYLLIE

Centre for Ecology & Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire
PE28 2LS, United Kingdom.

During 1983–98, 836 Barn Owl *Tyto alba* carcasses from Britain were received for autopsy and chemical analysis. Some 48% of recorded deaths were attributed to collisions with road traffic, 31% to starvation and the rest to various minor causes. The proportion of carcasses that contained residues of second-generation rodenticides (in liver) was 28% overall, but increased over the years, from 5% in 1983–84 to 40% in 1997–98. This finding was taken to indicate increasing exposure, as the use of these rodenticides increased over the years. The relative frequency of detection of different rodenticides (difenacoum, bromadiolone, brodifacoum and flocoumafen) in Barn Owl carcasses matched fairly closely the usage patterns on farms. However, only 7% of contaminated owls (forming 2% of all owls examined) were judged to have died of rodenticide poisoning, based on post-mortem symptoms (notably haemorrhaging) and residue levels in liver $>0.1\ \mu g\ g^{-1}$.

INTRODUCTION

In various parts of the world, many different chemicals have been used in rodent control, some of which have caused secondary poisoning in rodent predators, including owls. In this paper, we discuss only one group of commonly-used rodenticides, namely the anticoagulants based on the naturally-occurring plant compound, coumarin. These chemicals act by blocking the vitamin K_1 cycle in the liver, which in turn prevents blood-clotting, so that some days after ingestion of the chemical, the animal dies of internal bleeding. The first such chemicals to be developed, the best known of which was warfarin, required multiple doses to cause death.

In some regions, after exposure of populations over many years to these ‘first generation’ rodenticides, rats and mice became genetically resistant to them. This led to the development of new chemicals for use in rodent control, the so-called ‘second generation’ rodenticides, which have come into increasing use since the 1970s. Although these new chemicals act in a broadly similar way to the first generation anticoagulants, they are more toxic and more persistent, so they have much greater potential to cause secondary poisoning of rodent predators. Typically, rodents die several days after consuming a single dose (a few grams) of poisoned bait, during which time (as well as after death), with much of the poison still in their bodies, they could be caught and eaten by a predator. Animals containing sub-lethal doses could also act as a source of residues for their predators, for up to several months after exposure. Hence, as the use of second-generation rodenticides has increased, concerns about the primary and secondary poisoning of non-target species have grown (e.g. Eason *et al.* 1999, Stone *et al.* 1999). In Britain, four such chemicals are in common use, namely difenacoum (introduced 1975), bromadiolone (1980), brodifacoum (1982) and flocoumafen (1986), each of which is marketed under various trade-names.

In both Europe and North America, second generation rodenticides used on baits have sometimes been broadcast in the open countryside in attempts to reduce local rodent damage to farm crops or young trees. But the largest quantities are used in cities and in farm buildings to control Brown Rats *Rattus norvegicus* and House Mice *Mus musculus*. In Britain, the main bird species at risk is assumed to be the Barn Owl *Tyto alba*, because it nests in farm buildings and hunts nearby, taking both rats and mice (among other prey). The species has declined in Britain in recent decades, so it is important to assess any role that rodenticides might have had as direct mortality agents. The main aims of our work were to therefore assess the contribution of second generation rodenticides to mortality in Barn Owls, based on chemical analyses of specimens found dead. Several aspects of this work have been described in earlier papers (Newton *et al.* 1990, 1994, 1999, Newton & Wyllie 1992), and our aim here is to update the findings by the inclusion of more recent analytical results.

METHODS

To obtain carcasses for examination, we placed regular advertisements in ornithological magazines and journals, asking for bodies of Barn Owls found dead. All carcasses were requested, whatever the cause of death, and from anywhere in Britain. On receipt, each carcass was catalogued, weighed and marked and then stored at –20°C until it could be examined, up to several months later. For post-mortem examination, each unfrozen carcass was opened up and checked for any obvious parasites, lesions or other abnormalities. The findings were used, along with information from the sender, to diagnose the cause of death. Typically, collision victims had extensive bruising and broken bones, and many were found at roadsides, indicating that they were traffic victims. Starved birds were low in weight, with wasted breast muscles, no body fat, and empty blackened or greenish intestines. Diseased birds showed obvious lesions, particularly on the liver, kidneys or lungs, or contained parasites; and many were also thin. Shot birds contained lead pellets or pellet wounds. Diagnosis of other mortality causes, such as drowning and electrocution, was dependent primarily on information from the sender, together with the lack of any conflicting evidence from autopsy. Identification of rodenticide or other poison victims was dependent mainly on chemical analysis, together with the lack of any other obvious mortality cause. For certain birds (7.5% of the total), in the absence of any evidence, the cause of death was classed as ‘unknown’.

Many of the birds examined showed signs of haemorrhaging, which differed according to cause of death. Accident victims typically bled heavily around the site of impact, which also showed extensive bruising, while rodenticide victims typically showed faint subcutaneous bleeding along the keel and on the skull, and external bleeding around the leg joints, mouth and nostrils (Newton *et al.* 1990). However, not all rodenticide victims showed obvious bleeding. Haemorrhaging was therefore not used as the sole diagnosis of any poison victim, only along with other evidence, including chemical analysis.

About 1–2g of liver tissue was removed from each bird and analysed for residues of second generation rodenticides, using the method of Hunter (1985), modified in minor respects (the rest of the liver was re-frozen and kept in case it was needed to confirm the findings or to check for other chemicals). Liver samples were extracted with chloroform-acetone, and the extracts were cleared of fat using Bond-Elut NH_2 columns. The concentrated samples from the columns were then analysed against a standard for each compound by High Pressure Liquid Chromatography, using a 5 µm Hypersil ODS column and a Varian spectrofluorometer (to 1990) or a Shimadzu spectrofluorophotometer (from 1991). When an apparent rodenticide was detected, a recovery test was done from a spiked sample of solvent to validate the identification and to correct the estimate of mass present. Recoveries from most batches in later years were in the range 75–95% and typical detection limits were estimated as 0.0025 µg for difenacoum, 0.004 µg for brodifacoum, 0.005 µg for flocoumafen and 0.01 µg for bromadiolone. From a liver sample weighing 1g, these values were the same as the concentration expressed as µg g^{-1} or mg kg^{-1}. However, because liver weights varied greatly between individuals, some liver samples that were analysed weighed around 2 g. This would have halved the residue concentration levels that could have been detected to around 0.0012 µg g^{-1} for difenacoum, 0.002 µg g^{-1} for brodifacoum, 0.0025 µg g^{-1} for flocoumafen, and 0.005 µg g^{-1} for bromadiolone. In practice, detection limits also varied slightly between batches, as did the water-content of liver samples, and in some specimens residue concentrations were detected as low as 0.001 µg g^{-1} for difenacoum, 0.002 µg g^{-1} for brodifacoum, 0.003 µg g^{-1} for flocoumafen and 0.004 µg g^{-1} for bromadiolone.

The toxicities of the various second generation rodenticides to rats and mice, compared with warfarin, are given in Table 1. In terms of LD_{50} values (lethal dose for 50% of a sample, expressed as mg kg^{-1} body weight), the new chemicals are roughly 100–1000 times more toxic than warfarin. Birds and mammals that have been poisoned by second generation rodenticides are typically found to contain 0.1–1.5 µg g^{-1} wet weight of residue in liver tissue, although some have higher levels (see Table and later results).

RESULTS

In the period 1983–98, a total of 836 Barn Owls was received for analysis. They came from all major regions of Britain, and from all months of the year, with more from outside the main breeding season (September-March) than within it (April-August) (Newton *et al.* 1991). The numbers of owls in different mortality categories are given in Table 2, along with the numbers in which rodenticides were detected. The main recorded causes of death were road accidents (48%) and starvation (31%), with various other causes accounting for the remainder. Surprisingly, little seasonal variation was evident in the relative frequencies of different mortality causes (Newton *et al.* 1997). Road and other accidents were the main form of loss throughout the year, and starved birds were found in every month, even in the main part of the breeding season, May-July.

Of the 836 birds analysed during 1983–98, 235 (28%) contained detectable residues of second generation rodenticides in the liver. Most specimens (163) had residues of only one chemical, but 48 birds had residues of two different chemicals, 23 birds had residues of three chemicals and one had residues of all four. Leaving aside the obvious poison victims, in each of the other main

Table 1. Summary details of four second generation rodenticides and warfarin.

Chemical	Year of introduction	LD_{50} (mg kg^{-1})		Time (days) taken to kill laboratory mice after one-day dose	Poisoned non-target species	Liver levels (mg g^{-1})
		Rat	Mouse			
Warfarin	1952	185	375	Not recorded	None reported	
Difenacoum	1975	1.80	0.80	2–11	Tawny Owl[1] *Strix aluco*	<0.20
					Barn Owl[2] *Tyto alba*	0.25
					Red Kite[4] *Milvus milvus*	0.20
					Weasel[1] *Mustela nivalis*	0.40–4.00
Bromadiolone	1980	0.55	0.99	2–9	Barn Owl[3] *Tyto alba*	0.33–1.72
					Red Kite[4] *Milvus milvus*	0.10–0.14
Brodifacoum	1982	0.26	0.40	3–8	Barn Owl[5] *Tyto alba*	0.63–1.25
					Barn Owl[5] *Tyto alba*	0.52
					Barn Owl[2] *Tyto alba*	1.67
					Barn Owl[6] *Tyto alba*	0.29–0.61
					Screech Owl[7] *Otus asio*	0.40–0.80
					Paradise Shelduck[8] *Tadorna variegata*	0.24–0.80
					Mallard[8] *Anas platyrhynchos*	0.90–1.23
					Grey Duck[8] *Anas superciliosa*	0.91
					Australian Harrier[8]*Circus approximans*	0.61–0.66
					Pukeko[8] *Porphyrio porphyrio*	0.52–1.35
					Southern Black-backed Gull[8] *Larus dominicanus*	0.58
					Eurasian Blackbird[8] *Turdus merula*	0.56–0.78
					Chaffinch[8] *Fringilla coelebs*	0.12–2.31
					Common Myna[8] *Acridotheres tristis*	0.54–1.27
					Australian Magpie[8] *Gymnorhina tibicen*	0.40–0.99
					Morepork (owl)[8] *Ninox novaeseelandiae*	0.97
					Red Kite[4] *Milvus milvus*	0.30–0.98
					Weasel[1]*Mustela nivalis*	0.20–0.80
					Rabbit[10] *Oryctolagus cuniculus*	0.30
					Brushtail Possum[11] *Trichosurus vulpecula*	0.20–1.20
					Brushtail Possum[12] *Trichosurus vulpecula*	0.52–1.20
					Feral Pig[11] *Sus scrofa*	0.72–1.38
Floucoumafen	1986	0.25	1.13	2–12	Barn Owl[10] *Tyto alba*	0.93
					Barn Owl[2] *Tyto alba*	0.57–0.70

1. Anon 1982; 2. Gray *et al.*1994.; 3.Newton & Wyllie, unpublished; 4. Carter & Burn 2000; 5.Newton *et al.* 1990; 6. Greig-Smith *et al.* 1989; 7. Hegdal & Colvin 1988; 8. Dowding *et al.* 1999; 9. Stephenson *et al.* 1999; 10. Newton *et al.* 1994; 11. Meenken *et al.* 1999; 12. Eason *et al.* 1999.

Table 2. Causes of deaths in 836 Barn Owls found dead in Britain during 1983–98

	Number (%) of birds examined	Number (%) in which rodenticide residue was detected
Natural causes	*291 (34.5)*	*78 (26.8)*
Starvation	258 (30.9)	72 (27.9)
Disease	15 (1.8)	3 (20.0)
Predation	18 (2.2)	3 (16.7)
Accidents	*460 (55.0)*	*124 (27.0)*
Road casualties	399 (47.7)	110 (27.6)
Other trauma	50 (6.0)	12 (24.0)
Drowned	8 (1.0)	2 (25.0)
Electrocuted	3 (0.4)	0 (0)
Other human-related causes	*22 (2.6)*	*16 (72.7)*
Poisoned	16 (1.9)	16(100)
Shot	5 (0.6)	0 (0)
Trapped	1 (0.1)	0 (0)
Unknown causes	*63 (7.5)*	*17 (27)*

Table 3. Percentage of Barn Owls whose livers contained rodenticide residues in different periods.

	Number of owls analysed	Number (%) in which rodenticide residues were detected
1983	3	0 (0%)
1984	17	1 (5.9%)
1985	34	4 (11.8%)
1986	42	5 (11.9%)
1987	30	2 (6.7%)
1988	34	9 (26.5%)
1989	69	7 (10.1%)
1990	72	24 (33.3%)
1991	94	34 (36.2%)
1992	68	18 (26.5%)
1993	73	19 (26.0%)
1994	66	23 (34.9%)
1995	59	22 (37.3%)
1996	56	19 (33.9%)
1997	65	19 (29.2%)
1998	54	29 (53.7%)

mortality categories (natural, accidental and unknown) around 27% of carcasses also had detectable rodenticide residues in the liver (Table 2).

No ecological significance could be attached to the rise in numbers received per year over the study period (Table 3), as this could have been due to greater publicity given to the species in more recent years. Over the whole period, however, a marked increase was apparent in the proportion of owls in which residues were detected, from 5% in 1983–84 to 40% in 1997–98 (Table 3). However, this percentage seemed to level off during the 1990s: the estimated asymptote in a fitted regression model was 36%.

The different chemicals appeared in Barn Owl livers over the period 1988–94 roughly in proportion to their usage (Table 4). Questionnaire surveys of farmers in England and Wales, conducted in 1988–89, 1990–92 and 1993–94 (by the Ministry of Agriculture, Fisheries and Food), gave information on the frequency with which the different chemicals were used in those years (Olney *et al.* 1991a, 1991b, 1994, Olney & Garthwaite 1992, 1993, Thomas & Wild 1996). In general, the figures matched fairly closely the relative frequencies with which the same chemicals were detected in Barn Owl livers in those same years (Table 4). Difenacoum was the commonest chemical in use and also the commonest residue found in Barn Owls, while flocumafen was the chemical in least use and also the residue least often found in Barn Owls. It seemed, therefore, that Barn Owls picked up a more or less representative cross-section of the second generation rodenticides in use.

Although rodenticide residues were detected in a total of 235 owls over the years, only 16 (7%) were diagnosed as having died directly of rodenticide poisoning. In the twelve that showed typical haemorrhage symptoms, the following residues (μg g^{-1}) were detected in liver: (1) 0.11 difenacoum, (2) 0.17 difenacoum, (3) 0.16 difenacoum, (4) 0.33 bromadiolone, (5) 1.07 bromadiolone, (6) 0.44 brodifacoum, (7) 0.22 difenacoum plus 0.09 brodifacoum, (8) 0.16 bromadiolone plus 0.02 difenacoum, (9) 1.72 bromadiolone plus 0.07 brodifacoum, (10) 0.25

Table 4. Rodenticide use and Barn Owls contamination in Britain.

	Arable Farms[1]	Livestock Farms[1]	Barn Owls
(a) 1988–89			
Number examined	565	459	103
Number with rodenticide	431	404	16
Difenacoum	62%	54%	75%
Bromadiolone	32%	37%	25%
Brodifacoum	5%	7%	31%
Flocoumafen	0.5%	1.5%	0.0%
(b) 1990–92, arable farms only			
Number examined	1696	–	234
Number with rodenticide	1387	–	76
Difenacoum	52%	–	64%
Bromadiolone	40%	–	37%
Brodifacoum	7%	–	15%
Flocoumafen	0.6%	–	8.0%
(c) 1993–94			
Number examined	1062	709	139
Number with rodenticide	904	606	42
Difenacoum	55%	59%	60%
Bromadialone	37%	36%	50%
Brodifacoum	7%	5%	7%
Flocoumafen	0.9%	–	0.0%

[1] Based on questionnaire surveys of randomly selected farms, 1988–94 (Olney *et al.* 1991a, 1991b, 1994, Olney & Garthwaite 1992, 1993, Thomas & Wild 1996).

brodifacoum plus 0.14 bromadiolone (11) 0.09 brodifacoum plus 0.04 difenacoum, and (12) 0.05 bromadiolone plus 0.002 brodifacoum plus 0.003 flocoumafen. All these birds showed extensive haemorrhaging which was not associated with any impact, and no other cause of death was apparent. Four other birds that showed no haemorrhage symptoms, contained 0.12, 0.20 and 0.42 $\mu g\ g^{-1}$ brodifacoum and 0.12 $\mu g\ g^{-1}$ flocoumafen respectively. They were classed as rodenticide victims because of the relatively high residue level present (consistent with lethal levels found in other owls, Table 1 and above), and because they showed no other obvious cause of death. It seems, then, that despite the increasing occurrence of rodenticide residues in British Barn Owls, only about 2% of our total sample for 1983–98 are likely to have died directly of rodenticide poisoning. Another 66 (8%) contained what were potentially lethal levels (taken as total residues of all chemicals $>0.1\ \mu g\ g^{-1}$), but the birds concerned had died of some other cause.

To judge from these findings, therefore, Barn Owls in Britain have become increasingly exposed to second generation rodenticides over the past two decades, but as yet these chemicals seem to have caused a relatively small proportion of recorded deaths.

DISCUSSION

About 28% of the 836 dead Barn Owls examined in 1983–98 had residues of one or more second-generation rodenticides in their bodies, but only about 2% were diagnosed as having died of rodenticide poisoning, with another 8% having residues in the lethal range. For several reasons, however, these figures may not have reflected the true exposure of owls to those chemicals in the regions concerned, or the actual level of mortality caused. Firstly, the birds in our sample were unlikely to have formed a representative cross-section of Barn Owl deaths, but were instead probably biased towards those forms of mortality associated with people, thus accounting for the high proportion of accident victims. Secondly, our carcass samples may have under-estimated the proportion of mortality due to rodenticides because, some hours before death, affected animals become lethargic. Any affected owls were perhaps most likely to have died at their roost sites, in tree holes or roof cavities, where they were less likely to have been found by the casual observer than were birds that died in the open. Thirdly, as well as causing some deaths directly, rodenticides may also have had sublethal effects which predisposed deaths from other causes.

Despite possible bias in the sampling procedure, carcasses were obtained in a consistent manner throughout, so any temporal change in the recorded causes of death should have been valid. Also, the frequencies with which the different chemicals were recorded in Barn Owls matched the relative frequencies with which those chemicals were used, which gave some confidence in this aspect of the sampling procedure. It is clear, therefore, that contamination of British Barn Owls with second generation rodenticides has been widespread, and that it increased through the 1980s, reaching around 36% in the 1990s. Contaminated specimens came from all major regions of Britain, and were not restricted to the warfarin-resistance areas, as depicted by Shawyer (1987). The increasing contamination of Barn Owls with second generation rodenticides over the study period was expected from the expanding use of these chemicals, which increasingly replaced warfarin and other first generation rodenticides. With yet further increases in usage, these chemicals could become a more important cause of contamination and mortality in future.

Recent work on mammals and birds has shown that sub-lethal residues of second generation rodenticides may persist in liver for up to several months after a single oral dose (Parmar *et al.* 1987, Huckle *et al.* 1989a, b). It is unlikely that contaminated rodent prey species would remain available so long, because in these animals a single oral dose would normally be lethal. Trials have shown that mice and rats die some 2–14 (mostly 3–8) days after a single feed of any of the chemicals involved (Bajomi 1984, Hoppe & Krambias 1984, Newton *et al.* 1990 & unpublished). On the other hand, species such as Barn Owls, which are likely to be exposed chronically to rodenticides, may retain their rodenticide burdens for some time. This means that owls in which residues were detected could have been exposed up to several months previously or on more than one occasion, thereby explaining the presence of more than one rodenticide in the livers of some birds. The long biological half-lives of second-generation rodenticides, and their common mode of toxicity, means that repeated exposure may result in both accumulation of residues and additive toxicity, thereby enhancing the potential for secondary poisoning.

Effects on populations

Of 66 owls containing residues of rodenticide above 0.1 $\mu g\ g^{-1}$ (and hence within the potentially lethal range), 50 had apparently died of accidents or starvation. Rodenticides may have predisposed these birds to die from these other causes, as mentioned above, or they may have reduced the chance of recovery from accidents. Moreover, if they had not died from the recorded causes, they might later have succumbed to rodenticide poisoning. In this case, the maximum likely proportion of recorded deaths by rodenticides would amount to 10% of all birds examined. As yet, however, we have no evidence that second generation rodenticides have contributed appreciably to the overall mortality in British Barn Owls, and hence no evidence that the use of these chemicals is seriously affecting population levels.

The main prey of Barn Owls in Britain is the Field Vole *Microtus agrestis* (Glue 1974, Taylor 1994), which has not yet been subject to extensive control operations. Clearly, if the use of new rodenticides away from buildings increased, the potential for secondary poisoning of owls would also increase. A study of the foraging behaviour of Barn Owls on farmland in the United States (Hegdal & Blaskewicz 1984, Hegdal & Colvin 1988) showed that owls seldom hunted close to buildings and would therefore be unlikely to ingest high rodenticide levels when usage is restricted to those sites. In our sample, three out of four birds from the Isle of Man were contaminated, as were seven out of ten from the Channel Islands. On these islands, Field Voles are absent, and Barn Owls feed much more heavily on commensal Brown Rats and House Mice, together with Wood Mice *Apodemus sylvaticus*. It would not be surprising, therefore, if a high proportion of owls on these islands were contaminated. The different diet of Barn Owls on the Isle of Man also led them, in the 1960s and 1970s, to be more affected by dieldrin than mainland birds (Newton *et al.* 1991).

Surveys of Barn Owl pellets collected in southeast England has revealed that the proportion of Field Voles in the diet has declined over recent years, while the proportion of Wood Mice in the diet has increased. This change in diet (itself resulting ultimately from the conversion of agricultural grassland to arable) could also put Barn Owls at greater risk, because Wood Mice are the most likely non-target rodents to eat the bait. Meanwhile, rats and mice in some parts of Britain are developing resistance to difenacoum and bromadiolone. This could increase the number of live rodents with residues in their bodies, and hence further increase the secondary poisoning risks to Barn Owls.

The Barn Owl is not the only species to have died from rodenticide use in Britain in recent years. No detailed surveys of other species have been made, but occasional suspect specimens have been analysed, and found to contain residues at lethal levels. They include one Kestrel *Falco tinnunculus*, several Tawny Owls *Strix aluco* and several Red Kites *Milvus milvus* (Table 1). The latter came from small reintroduced populations, and their loss may have slowed the rate of population growth.

ACKNOWLEDGMENTS

We are grateful to all the observers, too numerous to mention individually, who contributed carcasses to this programme, to the Joint Nature Conservation Committee for funding part of this work, and the referees Richard Shore and Iain Taylor for helpful comments on the manuscript. The paper was written while Ian Newton was in receipt of a Leverhulme Fellowship.

REFERENCES

Anon. 1982. Secondary toxicity hazard to owls from difenacoum. London, HMSO, Ministry of Agriculture, Fisheries and Food, reference book 252 (81).

Bajomi, D. 1984. Hungarian experience with 'Talon-B' containing brodifacoum. In Dubock A.C. (ed.) *The organisation and practice of vertebrate pest control*: 163–179. Haslemere, England: Imperial Chemical Industries.

Carter, I. & Burn, A. 2000. Problems with rodenticides: the threat to Red Kites and other wildlife. *British Wildlife* **11**: 192–197.

Dowding, J.E., Murphy, E.C. & Veitch, C.R. 1999. Brodifacoum residues in target and non-target species following an aerial poisoning operation on Motuibe Island, Hauraki Gulf, New Zealand. *N.Z. J. Ecol.* **23**: 207–214.

Eason, C.T., Milne, L., Potts, M., Morriss, G., Wright, G.R.G. & Sutherland, O.R.W. 1999. Secondary and tertiary poisoning risks associated with brodifacoum. *N.Z. J. Ecol.* **23**: 219–224.

Glue, D.E. 1974. Food of the Barn Owl in Britain and Ireland. *Bird Study* **21**: 200–210.

Gray, A., Eadsforth, C.V., Dutton, A.J. & Vaughan, J.A. 1994. The toxicity of three second-generation rodenticides to Barn Owls. *Pestic. Sci.* **42**: 179–184.

Greig-Smith, P.W., Fletcher, M.R., Hunter, K., Quick, M.P., Ruthven, A.D. & Shaw, I.C. 1989. Pesticide poisoning of animals 1988: investigations of suspicious incidents in Great Britain. Report of the Environmental Panel of the Advisory Committee on Pesticides. London: Ministry of Agriculture, Fisheries & Food.

Hoppe, A.H. & Krambias, A. 1984. Efficacy of three new anticoagulants against *Rattus rattus frugivorus*. In Dubock A.C. (ed.) *The organisation and practice of vertebrate pest control*: 335–339. Haslemere, England: Imperial Chemical Industries.

Hegdal, P.L. & Blaskiewicz, R.W. 1984. Evaluation of the potential hazard to Barn Owls of talon (brodifacoum bait) used to control rats and house mice. *Environ. Toxicol. & Chem.* **3**: 167–179.

Hegdal, P.L. & Colvin, B.A. 1988. Potential hazard to Eastern Screech-owls and other raptors of brodifacoum bait used for vole control in orchards. *Environ. Toxicol. & Chem.* **7**: 245–260.

Huckle, K.R., Hutson, D.H., Logan, C.J., Morrison, B.J. & Warburton, P.A. 1989a. The fate of flocoumafen in the rat: retention and elimination of a single oral dose. *Pestic. Sci.* **25**: 297–312.

Huckle, K.R., Warburton, P.A., Forbes, S. & Logan, C.J. 1989b,. Studies on the fate of flocoumafen in the Japanese Quail (*Coturnix coturnix japonica*). *Xenobiotica* **19**: 51–62.

Hunter, K. 1985. High-performance liquid chromatographic strategies for the determination and confirmation of anticoagulant rodenticide residues in animal tissues. *J. Chromatography* **321**: 255–272.

Meenken, D., Wright, K. & Couchman, A. 1999. Brodifacoum residues in Possums (*Trichosurus vulpecula*) after baiting with brodifacoum cereal bait. *N.Z. J. Ecol.* **23**: 215–217.

Newton, I., Shore, R.F., Wyllie, I., Birks, J.D.S. & Dale, L. 1999. Empirical evidence of side-effects of rodenticides on some predatory birds and mammals. In Cowand, D.P. & Fear, C.J. (ed.) *Advances in vertebrate pest management*: 347–367. Fürth: Filander Verlang.

Newton, I. & Wyllie, I. 1992. Effects of new rodenticides on owls. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds.). *The ecology and conservation of European Owls* : 49–54. Peterborough: Joint Nature Conservation Committee.

Newton, I., Wyllie, I. & Asher, A. 1991. Mortality causes in British Barn Owls *Tyto alba*, with a discussion of aldrin-dieldrin poisoning. *Ibis* **133**: 162–169.

Newton, I., Wyllie, I. & Dale, L. 1997. Mortality causes in British Barn Owls (*Tyto alba*) based on 1,101 carcasses examined during 1963–1996. In Duncan, J.R., Johnson, D.H. & Nichols, T.H. (eds.). *Biology and Conservation of Owls of the Northern Hemisphere. Second International Symposium, February 5–9, 1997, Winnipeg, Manitoba, Canada*: 299–307. USDA Forest Service Gen. Tech. Rep. NCñ190.

Newton, I., Wyllie, I., Gray, A. & Eadsforth, C.V. 1994. The toxicity of the rodenticide flocoumafen to Barn Owls and its elimination via pellets. *Pestic. Sci.* **41**: 187–193.

Newton, I., Wyllie, I. & Freestone, P. 1990. Rodenticides in British Barn Owls. *Environ. Pollut.* **68**: 101–117

Olney, N.J., Davis, R.P., Thomas, M.R. & Garthwaite, D.G. 1991a. Rodenticide usage on farms in England and Wales growing arable crops 1988. Pesticide Usage Survey Report **89**. London: Ministry of Agriculture, Fisheries & Food.

Olney, N.J., Davis, R.P., Thomas, M.R. & Garthwaite, D.G. 1991b. Rodenticide usage on farms in England and Wales growing grassland and fodder crops 1989. Pesticide Usage Survey Report **90**. London: Ministry of Agriculture, Fisheries & Food.

Olney, N.J., Thomas, M.R. & Garthwaite, D.G. 1994. Rodenticide usage on farms in Great Britain growing grassland and fodder crops 1993. Pesticide Usage Survey Report **122**. London: Ministry of Agriculture, Fisheries & Food.

Olney, N.J. & Garthwaite, D.G. 1992. Rodenticide usage on farms in England growing arable crops 1990. Pesticide Usage Survey Report 95. London: Ministry of Agriculture, Fisheries & Food.

Olney, N.J. & Garthwaite, D.G. 1993. Rodenticide usage in Great Britain on farms growing arable crops 1992. Pesticide Usage Provisional Survey Report **113**. London: Ministry of Agriculture, Fisheries & Food.

Parmar, G., Bratt, H., Moore, R. & Batten, P.L. 1987. Evidence for a common binding site *in vivo* for the retention of anticoagulants in rat liver. *Human Toxicol.* **6**: 431.

Shawyer, C.R. 1987. *The Barn Owl in the British Isles. Its past, present and future*. London: The Hawk Trust.

Stephenson, B.M., Minot, E.O. & Armstrong, D.P. 1999. Fate of Moreporks (*Ninox novaeseelandiae*) during a pest control operation on Mokoia Island, Lake Rotorua, North Island, New Zealand. *N.Z. J. Ecol.* 23: 233–240.

Stone, W.B., Okoniewski, J.C. & Stedlin, J.R. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. *J. Wildl. Dis.* **35**: 187–193.

Taylor, I. 1994. *Barn Owls*. Cambridge: University Press.

Thomas, M.R. & Wild, S. 1996. Rodenticide usage on farms in Great Britain growing arable crops 1994. Pesticide Usage Survey Report **130**. London: Ministry of Agriculture, Fisheries & Food.

27

RACUMIN RODENTICIDE – POTENTIAL ENVIRONMENTAL IMPACT ON BIRDS

WARWICK MADDEN

Research & Development, Bayer Australia Limited, PO Box 903 Pymble NSW 2073.

Email: warwick.madden.wm@bayer-ag.de

Anticoagulants are the principal type of slow-acting rodenticides world wide. In the rodent body, they compete with Vitamin K_1, reducing the blood's clotting ability. If the rodent has eaten sufficient bait, it will die from internal bleeding 3–8 days after the initial feed.

Over the past 40 years, first generation, multiple dose rodenticides have been used to successfully control rats and mice. In that time few, if any, incidents were reported of secondary poisoning of wildlife. Such secondary poisoning has become an issue more recently, following the development of the second generation, single dose rodenticides.

Racumin, containing coumatetralyl, is a first generation, multiple dose bait. The rodent must consume small amounts of bait at least three times to ingest a lethal dose. Single-dose baits require only one feed, but in practice rodents consume bait over several days. The use of Racumin has increased in recent years owing to the lack of secondary poisoning incidents associated with its use. Studies reviewed in this paper indicate that coumatetralyl does indeed carry a low secondary poisoning risk. It is now being used for rat control in sensitive areas, such as the Galapagos Islands and Norfolk Island, and its effects are being monitored.

INTRODUCTION

Anticoagulant rodenticides were first introduced in the 1950s for the control of rodents. In many vertebrates, these chemicals interfere with the mechanism of blood coagulation by competing with Vitamin K_1, an essential compound in the synthesis of the blood-clotting precursor, prothrombin. There is no visible effect on the animal until the existing prothrombin levels in the blood have been depleted, and typically rodents die from internal bleeding 3–8 days after the initial exposure.

This delayed action is important for the effective control of rodent populations, because individuals do not associate symptoms with bait ingestion. They do not therefore develop a conditioned taste aversion, manifest as bait shyness. It is therefore possible to eradicate local populations. Another advantage of anticoagulant rodenticides is their relative safety to people and pets: because they only compete with vitamin K_1 for the active site, an effective antidote is available through the administration of additional vitamin K_1.

The *first generation* of anticoagulants (e.g. warfarin and coumatetralyl) are characterised by a comparatively rapid metabolism, so that the rodent is unlikely to consume sufficient active ingredient at the first feed to be killed. Several feeds over consecutive days are needed to ensure sufficient active ingredient in the animal for long enough to cause death.

From the 1970s onwards, the *second generation* of more potent anticoagulants came into use, including bromadiolone, brodifacoum and difethialone. They bind more strongly to the active sites and are more slowly metabolised. They often prove capable of killing rodents after just a single feed, and are effective against populations that have become resistant to warfarin.

Accidental *primary poisoning* of pets, farm animals and wildlife can occur with any anticoagulant. The greatest number of incidents reported in the United Kingdom were due to intentional or accidental misuse of rodenticides (Hunter 1995). Similarly, most mammal poisonings in New York State were due to direct consumption of bait (Stone *et al.* 1999). Such accidental losses can be reduced by ensuring that non-target animals and birds cannot easily gain access to baits. *Secondary poisoning* occurs when non-target animals (including reptiles and birds) eat rodents that have previously consumed poisoned bait. It is theoretically more likely to happen with second generation compounds, because of their greater toxicity and persistence in animal bodies (Newton & Wyllie 2002).

The possibility of secondary poisoning by anticoagulant rodenticides was raised within a few years after the introduction of warfarin, based on occasional suspicious incidents involving pigs, dogs and cats. In most cases it was not possible to exclude the possibility that these animals had gained access to baits (accidental primary poisoning) or that death was not due to some other cause. Studies have since been carried out with warfarin-poisoned rodents fed to dogs over several days. In general, these dogs tolerated the daily consumption of poisoned rodents without noticeable effects, and the possibility of secondary poisoning in the field was considered unlikely (e.g. Prier & Derse 1962).

The risk of secondary poisoning increased greatly following the introduction of the more potent second-generation rodenticides. Laboratory studies clearly showed the potential for predatory birds, especially owls (e.g. Mendenhall & Pank 1980), to be poisoned after eating rodents fed with second generation anticoagulants, but significant impacts on wild owl populations have not been demonstrated. While some studies (e.g. Duckett 1984, Hegdal & Colvin 1988, Young & De Lai 1997) implicate second generation rodenticides in the deaths of individual owls in the wild, others found no evidence that mortality was high enough to reduce population levels (Hegdal & Blaskiewicz 1984, Newton *et al.* 1990, Newton & Wyllie 2002, Eadsforth *et al.* 1996).

Racumin (*coumatetralyl*), a first generation rodenticide, has been identified by wildlife authorities in some countries as a possible 'low risk' rodenticide. For this reason, it has been used increasingly for conservation purposes in environmentally sensitive areas. In the sections below, I outline some of the salient findings that have led to its increased use.

PRIMARY POISONING HAZARD WITH COUMATETRALYL

Mammals seem more susceptible to coumatetralyl poisoning than are birds, but there are also marked differences between species. As expected, multiple feeding potentiates the toxicity of the

Table 1. Acute and subacute primary toxicity of coumatetralyl

	Animal species	LD_{50} (mg/kg b.w.)	Reference
Acute oral LD_{50} (single dose)	Rat	16.5–30.0	Enders 1970; Bomann 1992a
	Mouse	2000–4000	Hermann 1973
	Dog	[a] 35	Kimmerle 1958
	Guinea pig	[a] 250	Kimmerle 1958
	Cat	deaths from 50	Kimmerle 1958
	Rabbit	deaths from 10 >500	Kimmerle 1958; Bomann 1992b
	Chicken	>3000	Hermann 1963
	Japanese quail	>2000	Grau 1992a
Subacute oral LD_{50} (multiple doses over a number of days)	Rat	5 × 0.3	Hermann & Hombrecher 1962
	Mouse	18 × 0.19	Hermann 1973
	Dog	7 × 0.15	Ahmed *et al.* 1983
	Pig	<7 × 1.5	Dobson 1973
	Chicken	8 × 50	Hermann 1960
	Japanese quail	5 × 430	Grau 1992b
	Blackbird	[a] 23 × 6.7	Hermann 1963
	Cape sparrow	5 × 38.3	Hëyl 1986
	Pigeon	>24 × 57 >7 × 85.1	Unterstenhöfer & Hermann 1962 Lund 1983 Ten adult pigeons (*Columba livia*) were fed one of seven different commercial anticoagulant baits as their only food over seven days, followed by an observation period of at least four weeks. Deaths did not occur with any first generation baits, including coumatetralyl.

compound, especially in mammals. In rats, the cumultative lethal dose is more toxic by a factor of ten than the acute dose (Table 1). Birds seem able to tolerate longer periods of exposure to coumatetralyl than do mammals.

SECONDARY POISONING HAZARD WITH COUMATETRALYL

Several studies have tested for secondary poisoning of avian predators by coumatetralyl, but none was shown:

- A Steppe Buzzard (*Buteo buteo*) was fed in succession 59 coumatetralyl-killed Cape Sparrows (*Passer melanurus*), and a Spotted Eagle Owl (*Bubo africanus*) was fed 52 sparrows. Neither individual showed any signs of toxicity over 18 days, after which they were released (Hëyl 1986).
- Mice were fed under a range of regimes (see Table 2) in which Racumin 0.75% tracking powder was mixed with rolled oats and offered exclusively. After death, the mice were fed to

Table 2. Feeding of mice in preparation for feeding to caged Kestrels.

Group	% coumatetralyl	No. of mice	Time fed
I	0.0192	30	Till death (av. 5.1 days)
II	0.0375	33	Till death (av. 5.2 days)
III	0.075	19	Till death (av. 5.4 days)
IV	0.075	12	Fed 1 day & euthanased
IV	0.125	29	Till death (av. 4.9 days)

three caged Kestrels (*Falco tinnunculus*). Racumin administered at the recommended label rate and lower did not appear to affect the Kestrels following 22 days of feeding and 50 days of observation. When fed with mice killed with double or four times the label rates, the Kestrels did not die within the 12–23 day feeding period and showed no external symptoms. However, autopsy of the birds at the end of this period revealed some dose-related anticoagulant poisoning symptoms (Galanos 1991).

- Rats were fed coumatetralyl wax blocks for three nights, with each rat consuming an average of 30 g of block per night, before being euthanased on the fourth day. Ten captive Weka (*Gallirallus australis*) were then fed one rat per day for three days without alternative food. They preferred the internal organs and ate about 25% by weight of a rat per day. The Weka suffered no mortality and showed no indications of ill health (O'Connor & Eason 1999).
- Broad-winged hawks (*Buteo platypterus*) and Black-shouldered Kites (*Elanus caeruleus*) were monitored in an oil palm plantation in Honduras during a rat baiting campaign using Racumin and warfarin. No obvious effect was seen on either species, which maintained their numbers through the ten week trial period (Padilla *et al.*1995).

CONCLUDING REMARKS

Birds and other predators or scavengers are sometimes at risk from secondary rodenticide poisoning. The risk varies depending on the type of rodenticide used, on the care with which bait stations are set and maintained, as well as other factors. There is no 'perfectly safe' bait but, where necessary, the risk to non-target organisms can be reduced by the use of first generation anticoagulant rodenticides, such as coumatetralyl.

Racumin was registered in 1999 for use in sugar cane in Australia following the withdrawal of a second generation rodenticide. A number of measures were recommended to minimise exposure to non-target organisms, including the use of Racumin in bait stations as part of an integrated pest management programme. In addition, the advantages of Racumin have been recognised in its use in wildlife recovery programmes, including those on the Galapagos Islands and Norfolk Island. Compared to second generation rodenticides, its use could help to minimise the risks of secondary poisoning of owls and other rodent predators.

REFERENCES

Ahmed, A.A., Arif, H., Nounou, A.H. & Hamed, R.I. 1983. Haematological effect of the rodenticide 'Racumin' in dogs. *Vet. Med. J.* **31:** 115–120.

Bomann, W. 1992a. Racumin Techn. (C.n.: Coumatetralyl). Untersuchungen zur akuten oralen Toxizität an Ratten. Bayer AG, Fachbereich Toxikologie, Bericht Nr. 21726 vom 5 Oktober 1992.

Bomann, W. 1992b. Racumin Techn. (C.n.: Coumatetralyl). Untersuchungen zur akuten oralen Toxizität an Kaninchen. Bayer AG, Fachbereich Toxikologie, Bericht Nr. 21727 vom 5 Oktober 1992.

Dobson, K.J. 1973. Coumatetralyl poisoning in pigs and effectiveness of Vitamin K1. *Austr. Vet. J.* **49:** 98–100.

Duckett, J.E. 1984: Barn Owls (*Tyto Alba*) and the 'second generation' rat-baits utilised in oil palm plantations in peninsular Malaysia. *Plantar Kuala Lumpur* **60:** 3–11.

Eadsforth, C.V., Gray, A. & Harrison, E.G. 1996. Monitoring the exposure of barn owls to second-generation rodenticides in southern Eire. *Pestic. Sci.* **47:** 225–233.

Enders, E. 1970. Rodentizide. In Wegeler, R. (ed.) *Chemie der Pflanzenschutz- und Schädlingsbekämpfungsmittel*, Vol. 1: 624. Springer, Heidelberg.

Galanos, I. 1991. Beitrag zur Lebensweise des Turmfalken (*Falco tinnunculus*) in urbanen Ökosystemen und zur Kenntnis anthropogener Einflüsse auf die Population am Beispiel der Stadt Frankfurt am Main. [Study of the habits of the kestrel in an urban ecosystem with investigation of the man-made influences on the population using an example from the City of Frankfurt on Main]. *Doctoral thesis*, *Johann Wolfgang Goethe-University*, *Frankfurt am Main*, *Germany*.

Grau, R. 1992a. Coumatetralyl (Technical Grade) – acute oral toxicity to Japanese Quail. Bayer AG, Institute for Environmental Biology, Report No. Vw- 158, 30 June 1992.

Grau, R. 1992b. Coumatetralyl (Technical Grade) – 5–day dietary LC50 to Japanese Quail. Bayer AG, Institute for Environmental Biology, Report No. Vw- 159 of 30 June 1992.

Hegdal, P.L. & Blaskiewicz, R.W. 1984. Evaluation of potential hazard to Barn Owls of Talon (brodifacoum bait) used to control rats and house mice. *Environ. Toxicol.& Chem.* **3:** 167–179.

Hegdal, P.L. & Colvin, B.A. 1988. Potential hazard to Eastern Screech-Owls and other raptors of brodifacoum bait used for vole control in orchards. *Environ. Toxicol. & Chem.* **7:** 245–260.

Hermann, G. 1963. – Racumin 57- Vogeltoxizität. Bayer AG, Biologisches Institut, Brief vom 3 Oktober 1963.

Hermann, G. 1973. Orale Toxizität von Cumatetralyl (Racuminwirkstoff) für die weiße Labormaus. Bayer AG, Institut für Tierische Schädlinge, Bericht Nr: R 2/73 vom 28 Juni 1973.

Hermann, G. & Hombrecher, S. 1962. Ratten- und Mäusebekämpfung mit Racumin®57- Präparaten. *Pflanzenschutz-Nachrichten Bayer* **15:** 93–112.

Heÿl, C.W. 1986. Cumatetralyl as an avicide for use against the Cape Sparrow. *S. Afr. J. Enol. Vitic* **7(2):** 71–75.

Hunter, K. 1995. The poisoning of non-target animals. In Best, G.A. and Ruthven, A.D. (Eds.) *Pesticides-Developments*, *Impacts and Controls*: 74–86. Cambridge, RSC Publications.

Lund, M. 1983. The effect of various anticoagulants on non-target animals. *Danish Pest Inf. Lab. Ann. Rep. 1982* (**1983**): 93–95.

Kimmerle, G. 1958. Wirkstoff Dr Enders 11183b = E25634. Bayer AG, Toxicologisches und Gewerbehygieneisches Labor, Briefbericht vom 29 Oktober 1958.

Mendenhall, V.M. & Pank, L.F. 1980. Secondary poisoning of owls by anticoagulant rodenticides. *Wildl. Soc. Bull.* **8(4):** 311–315.

Newton, I., & Wyllie, I. 2002. Rodenticides in British Barn Owls. This volume.

Newton, I., Wyllie, I. & Freestone, P. 1990. Rodenticides in British Barn Owls. *Environ. Pollut.* **68:** 101–117.

O'Connor, C. & Eason, C. 1999. Secondary poisoning of Weka with coumatetralyl. Unpublished report of Manaaki Whenua Landcare Research No. LC9899/86: 1–8.

Padilla, M., Chinchilla, C., Arias, E. & Flores, I. 1995. Diurnal predatory birds and damage caused by rats in oil palm (*Elais guineensis* Jacq.) in Honduras. *ASD Oil Palm Papers* **10:** 1–12.

Prier, R.F. & Derse, P.H. 1962. Evaluation of the hazard of secondary poisoning by warfarin-poisoned rodents. *J.A.V.M.A.* **140(4):** 351–354.

Stone, W.B., Okoniewski, J.C. & Stedelin, J.R. 1999. Poisoning of wildlife with anticoagulant rodenticides in New York. *J. Wildl. Dis.* **35:** 187–193.

Unterstenhöfer, G. & Hermann, G. 1962. Le A 3763-Ho (holl. Patentanmeldung 220 331): Aralkyl-oxycoumarin-Anwendung. Bayer AG, Biologisches Institut, Brief vom 4 Juli 1962.

Young, J. & De Lai, L. 1997. Population declines of predatory birds coincident with the introduction of Klerat rodenticide in North Queensland. *Aust. Bird Watcher* **17:** 160–167.

Part 4

Voice, structure and taxonomy

This Page Intentionally Left Blank

28

VOCALISATIONS USED BY SOUTHERN BOOBOOKS (*NINOX NOVAE-SEELANDIAE*) IN THE AUSTRALIAN CAPITAL TERRITORY

JERRY OLSEN[1]*, S. TROST*[2] *& G. HAYES*[3]

[1]Applied Ecology Research Group, Division of Communication and Education, University of Canberra, ACT, Australia 2601.
[2]Erindale College, McBryde Cres., Wanniassa, ACT, Australia 2903.
[3]Environment Australia, GPO Box 787, Canberra, ACT 2600.
Currently, National Parks and Wildlife Service of New South Wales, GPO Box 2115, Queanbeyan, NSW, 2620.

Three adjacent nesting territories of Southern Boobooks *Ninox novaeseelandiae* were studied from October 1996 to October 1999; six adults were colour-marked, four of them radio-tagged. Observations were made several nights per week from just before the birds left their day roost each evening until one hour after. During 529 observation nights, we attempted to identify ten vocalisations for adults: (1) boobook call, (2) single hoot, (3) por (croak), (4) squeal, (5) bray, (6) trill, (7) yelp, (8) growl, (9) scream, and (10) squeak, and seven vocalisations recorded on a commercial audio tape. Where possible, we determined the sex of the calling owls and counted the frequency per month of boobook, single hoot, por, squeal, and bray calls. Both sexes used most calls, though there were individual differences, and different authors may label the same calls differently. We classified the boobook calls as contact or territorial, and suggest that por calls may be two types of call, that the single hoot call in some descriptions was more likely the por call, and that males did not give the bray call, though both sexes gave a quieter 'purr' call. We investigated the relationship between the frequency of some of these calls and (1) moon phase, (2) moon visibility, (3) temperature, (4) cloud cover, (5) wind speed, (6) wind direction, (7) rain, and (8) season, and found that most of the variation in frequency of calling in different months was related to (1) season, (2) social context, and (3) individual differences. These findings differed from those of earlier studies.

INTRODUCTION

Much of what is known about the behaviour and status of *Ninox* species in Australia is inferred from their vocalisations and not based on observation of the owls. However, no detailed studies have been done on vocalisations even in common species, such as the Southern Boobook *Ninox novaeseelandiae* (Higgins 1999). This paper is part of a long-term study of the behaviour and vocalisations of *N. novaeseelandiae*.

The Southern Boobook is the smallest of the nine owl species, five *Tyto* and four *Ninox*, that breed on mainland Australia (Schodde & Mason 1980; Hollands 1991; Higgins 1999). Fleay (1968), Schodde & Mason (1980), Hollands (1991), and Debus (1996, 1997) described vocalisations of this species in Australia, but none were from studies of colour-marked or radio-tagged owls. Imboden (1975) was the first to report on vocalisations from radio-tagged Southern Boobooks, in New Zealand. The significance of using marked birds is that the sex is known with certainty.

Here we report on 529 observation nights from 3 October 1996 to 22 October 1999 on three adjacent nesting territories of Southern Boobooks. We noted all vocalisations heard, categorised the vocalisations according to Higgins (1999), and attempted to identify the callers. Our aims were to: (1) document the frequency per month that males and females used the ten main vocalisations listed by Higgins (1999), and the seven call segments recorded by Buckingham & Jackson (1990); and (2) investigate the relationship between the frequency of Territorial and Contact Boobook calls (see below), Por calls, Bray calls, and 'duelling' (Olsen & Trost 1997), and seven weather and temporal variables in four seasons.

PREVIOUS STUDIES

Previous audio recordings of vocalisations of Southern Boobooks reveal a number of calls given by both sexes. For example, Buckingham & Jackson (1990) have seven audio-tape segments and list the calls, in order, as Duet, Higher-pitched call, Aggressive calling by two males, Call when disturbed, Churring calls and mating squeal, Falsetto call, and Food begging call from juvenile. These differ from descriptions of vocalisations in the literature, which often differ from one another. For example, Olsen & Trost (1997) described five vocalisations, Boobook, Croak, Bray, Single Hoot, and Trill, commonly heard during a study of colour-marked Southern Boobooks observed mainly during the nestling and post-fledging periods. Debus (1996, 1997), reported similar calls but heard females give Boobook and Croak calls, and males give Bray calls, while Olsen & Trost did not. Olsen & Trost also described 'duelling': neighbours calling with bouts of Boobook (and Por) calls overlapping. However, in contrast to Debus (1996, 1997), they heard no duetting. Higgins (1999) described the Single Hoot as a series of deep guttural calls used as a prelude to Boobook Calls, and as a response to the Boobook calls of rivals. In contrast, Olsen & Trost (1997) described the Single Hoot as predominantly an alarm call, given by males and females, especially in defence of fledged young. Fleay (1968), Debus (1996), and Olsen (1997) reported that females had deeper voices than males, but Stephenson (1998), in New Zealand, could not sex radio-tagged Southern Boobooks by call.

In the latest review, Higgins (1999) described ten main vocalisations given by adults of this species: (1) Boobook, (2) Single hoot, (3) Por call (Croak), (4) Squeal, (5) Bray, (6) Trill, (7) Yelp, (8) Growl, (9) Scream, and (10) Squeak.

Some observers have attempted to relate the frequency of certain calls to time of year, time of night, or weather conditions. Kavanagh & Peake (1993) used two survey techniques, a one-hour census followed by a 15 minute tape playback and spotlighting, to determine the distribution and detectability of seven nocturnal bird species. With Southern Boobooks, they found no seasonal differences in detectability, but heard them more often on nights with little or no wind, no visible moon and clear skies. Nights when the moon was not visible, regardless of moon phase, appeared to stimulate calling.

Debus (1997) noted that Southern Boobooks in New South Wales called spontaneously (not responding to playback) throughout the night, with a peak in the first half of the night. Moon visibility and cloud cover did not affect calling rates, but rain and wind depressed calling, though there were individual exceptions. Calls given were usually the disyllabic hoot, sometimes preceded by low croaks. The Bray and Yelp calls were occasionally heard in autumn and winter. Calling declined from February through autumn to a low in winter then rose in late winter or spring. Southern Boobooks responded to playback throughout the winter, but activity was still lowest then, even when playback was used. Certain owls tended to call even during rain and moderate wind during the days or weeks pre-laying.

STUDY AREA

The owls we studied near Canberra ranged over all of the 80 ha Aranda Bushland, and the north-western corner of the 600 ha Black Mountain Reserve, the suburbs of Cook and Aranda, open grazing land to the south of Aranda Bushland and Cook, and occasionally the wooded northern flank of Mount Painter (see map, Figure 1). Except for Mount Painter and the grazing land, the area is primarily open forest and tall woodland, with dominants of Scribbly Gum *Eucalyptus rossii*, Brittle Gum *E. mannifera*, Red Stringybark *E. macrorhyncha*, Blakely's Red Gum *E. blakelyi*

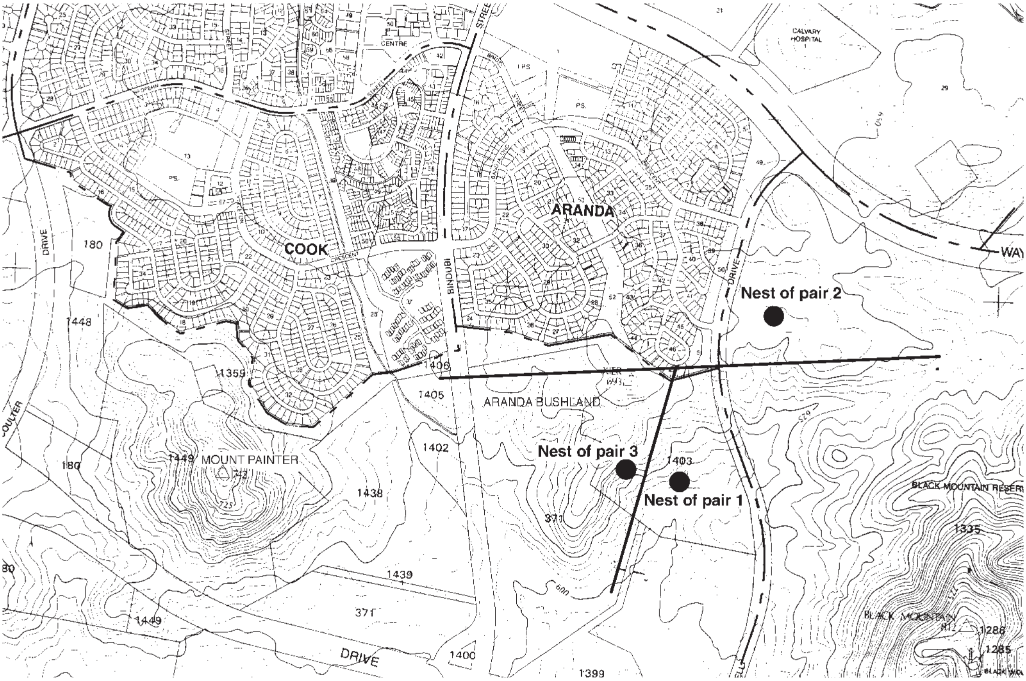


Fig. 1. Location of three Southern Boobook nests in Black Mountain Reserve and Aranda Bushland, Canberra, ACT in 1996 at the beginning of this study. Heavy line denotes territory borders between nests. Distance between Nest 1 and Nest 2 = 1080m; between Nest 2 and Nest 3 = 1140m; between Nest 1 and Nest 3 = 460m.

woodland with Red Box *E. polyanthemos* and Yellow Box *E. melliodora* in more open areas (NCDC 1988). The understorey has abundant tussock grasses (*Poa* spp.), with the shrub *Cassinia longifolia* dominating areas that are more open.

Aranda Bushland is bordered on the north by the suburb of Aranda, on the west by Bindubi Street, on the south by grazing land, and on the east by Caswell Drive, with woodland similar to Black Mountain Reserve. Wildfire has been largely absent and a regime of prescription burning has created a mosaic effect on the understorey. The suburbs of Cook and Aranda have retained a significant element of eucalypt overstorey of large Brittle Gums and Yellow Box with a mix of native and non-native understorey plants along roadsides, bushland corridors, and backyards. A common tree in all areas is the Native Cherry *Exocarpus cupressiformis*, which contains dense foliage that was favoured as daytime roosts by the owls.

METHODS

Trapping, banding, and radio-telemetry

We used wire bal-chatri traps (Olsen & Woollard 1975) baited with a House Mouse *Mus musculus*, a noose mounted on the end of a surf-casting rod, and fishing nets on extended poles, to trap adults and fledged young. All adults were sexed (Olsen & Trost 1997), fitted with a stainless steel, numbered Australian Bird and Bat Banding Scheme band, and a plastic colour-band sealed with super-glue ($n = 6$ adults). Some individuals removed the plastic colour-bands, so we banded them again with coloured aluminium bands attached with two rivets. Four of the adults had back-pack style Sirtrack single-stage transmitters fitted with a string harness and weak link designed to break if the bird became entangled by its transmitter and harness (Karl & Clout 1987). Radios weighed 5.4 g and harnesses 1.0 g, making 6.4 g on a 270 g male (2.4% of body wt.) and on a 340 g female (1.9% of body wt.). Batteries lasted 10–12 months.

Survey methods

We located the nests (see Figure 1) in three adjacent nesting territories straddling Aranda Bushland and Black Mountain Reserve; the larger of the pair, by weight, that had a brood patch, was determined to be the female (Olsen & Trost 1997).

Over 529 nights, we noted all vocalisations heard in three territories and, where possible, identified the callers by triangulating the location of radio-tagged birds with a hand-held Sirtrack yagi-antenna and Telonics TR–4 receiver, and sighted colour-bands with a torch and binoculars. We concentrated our observations during the following time frames: **Territory 1** (colour-banded, not radio-tagged), **103** nights between 3 October 1996 and 24 September 1997; **Territory 2** (colour-banded, radio-tagged), **110** nights between 1 January 1999 and 22 October 1999; **Territory 3** (colour-banded, radio-tagged), **316** nights between 1 October 1997 and 31 December 1998. Because of common borders, we had observations and counted Territorial Boobook calls from all three pairs during each time frame, until the male disappeared from Territory 1. We also had observations of a fourth colour-banded male (in **Territory 4**, banded in 1993), when he and his fledglings moved close to the nest of Pair 2 in January 1999, and during his interactions with the female in Territory 2 from August to October 1999.

Observations were made throughout the year (Table 1) from just before the birds left their day roost or nest, to one hour after. We visited the area several nights per week at sundown and stood 10–30 m from the nest or roost of one of the three pairs, then followed individuals after they left

Table 1. Total number of observation nights by month, 3 October 1996 to 22 October 1999.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
50	37	33	21	23	17	25	48	68	79	53	75

the roost or nest as closely as possible without disturbing them. Olsen and Trost observed most intensively between August and February, the pre-breeding to post-fledging phases of breeding, while Hayes observed the pair in Territory 2 about once per week from 17 January 1999 to 17 July 1999.

Dependent variables

We divided Boobook calls into Territorial (louder, usually given from a high perch across the territory and often in long bouts up to one hour) or Contact (usually given facing and close to a mate or young, most often in short bouts of one to three calls). We also observed and counted 'duels', defined by Olsen *et al.* (2002) as two unmated owls from different territories, facing each other, up to 50 m apart and calling with Boobook or Por calls during overlapping bouts, but not in a co-ordinated or synchronised fashion. We scored each vocalisation as heard or not heard each night.

Independent variables

For each observation night, we obtained moon phase and moon visibility from the Australian Surveying & Land Information Group, Department of Industry Science Resources, Bruce, ACT, and weather data from the Canberra Meteorological Office (Station 70014, Canberra Airport). We used the weather data for that day measured as close as possible to one hour after sundown, when we did our observations, and checked these data for accuracy against weather we noted in the field each night. Weather data and seasons were categorised as follows, partly after Kavanagh & Peake (1993):

- *moon visibility*: one of two categories (visible; not visible).
- *moon phase*: one of four categories (1/4, 2/4, 3/4, 4/4), whichever was closest to the night of observation.
- *cloud cover*: corresponding to eighths of the sky covered, but for analysis reduced to three categories (clear 0–1; partly clouded 2–5; overcast 6–8).
- *rain*: recorded in mm, but classed in two categories (dry 0; we*t* >0).
- *wind speed*: in km/hr reduced to three categories modified from the Beaufort Scale adapted for use on land (equivalent Beaufort Scale in brackets): gentle 0 to 10 (0–3); moderate 11 to 21 (4–5); strong >21 (6+).
- *wind direction*: reduced to four categories: (W; N; E; S).
- *temperature*: in degrees Celsius: one of four categories (cold <9; mild 9–14; warm 15–21; ho*t* >21).
- *season*: we divided the year into four categories based on the annual cycle of the owls: **non-breeding** – from when parents stop feeding young to pre-breeding (1 March – 14 August); **pre-breeding** – from when pairs begin roosting together near potential nests and copulating to egg-laying (15 August – 30 September); **breeding** – from egg-laying to fledging (1 October – 1 January); **post-fledging** – from fledging to when parents stop feeding young (1 January – 28 February).

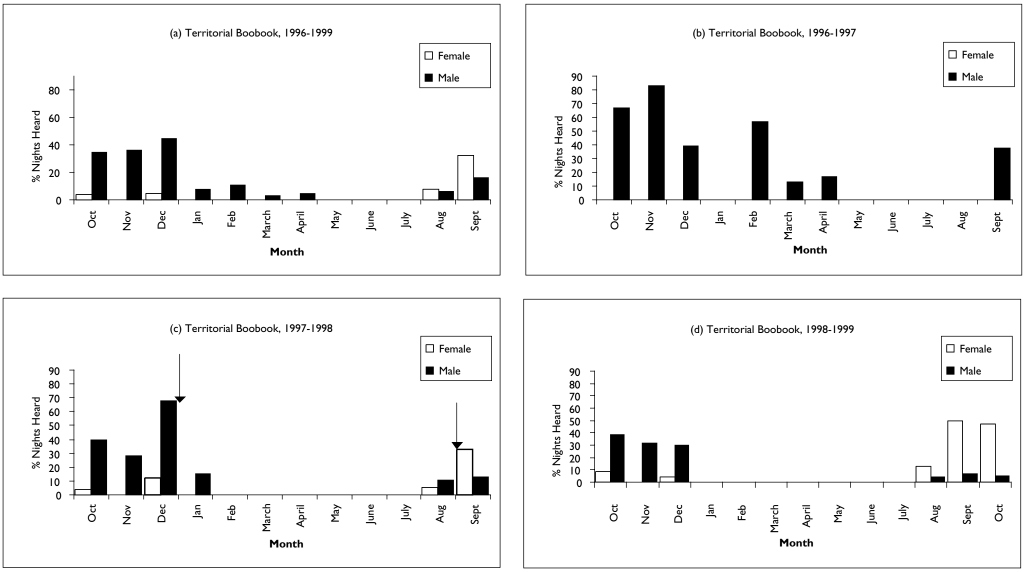


Fig. 2. (*a*) Percent of observation nights per month that we heard Territorial Boobook calls during 1996–99. Overall females 42/529 nights (7.9%) and males 103/529 nights (19.5%). (*b*) 1996–97. (c) 1997–98. (d) 1998–99. Arrows show when the Territory 1 male disappeared around 1 Jan, and the Territory 1 female was killed on 1 September.

Data analysis

We calculated nightly frequency per month of Territorial Boobook, Contact Boobook, Single Hoot, Por (Croak), Mating Squeal and Bray calls (Figs. 2 & 3). Using a separate analysis for duels, and the most common vocalisations observed (Territorial Boobook, Contact Boobook, Por (Croak) and Bray), we employed chi-square analyses (Zar 1984) to test if weather and temporal conditions or season had an effect on the calling of owls. Where there was one degree of freedom, a Fisher's Exact Test was used. In view of the large number of statistical tests involved, we used the Dunn-Sidak method (Sokal & Rohlf 1995) to correct for compounding Type I errors. Tests were carried out on data for the full year (Table 2) and, in order to eliminate seasonal effects, for the period in which calling was most common (September-December) (Table 4).

RESULTS

Territorial Boobook Calls. The two-note Territorial Boobook call has been likened to the call of the Common Cuckoo *Cuculus canorus* of Europe (Hollands 1991), which it superficially resembles. In this study Territorial Boobook calls were seasonal (Figs. 2a, b, c, d). Combining male, female and unidentified callers, we heard calling on 149 of 529 nights (28.2%). We saw females giving this call mainly when alone near the nest, and before egg-laying, and after nesting failure when females moved to a new nest location. They rarely called with males, but males commonly called on their own or in duels with other males (see Olsen *et al.* 2001). Around 3 July 1999, Female 2 left her breeding territory for a winter home range in a suburban street near Parliament House (7 km southeast of her nest). We did not hear her calling on this winter range, but she did commence calling on 25 August after she returned to her breeding territory.

We attempted, in three single blind trials of thirty minutes each, to sex individuals by ear in

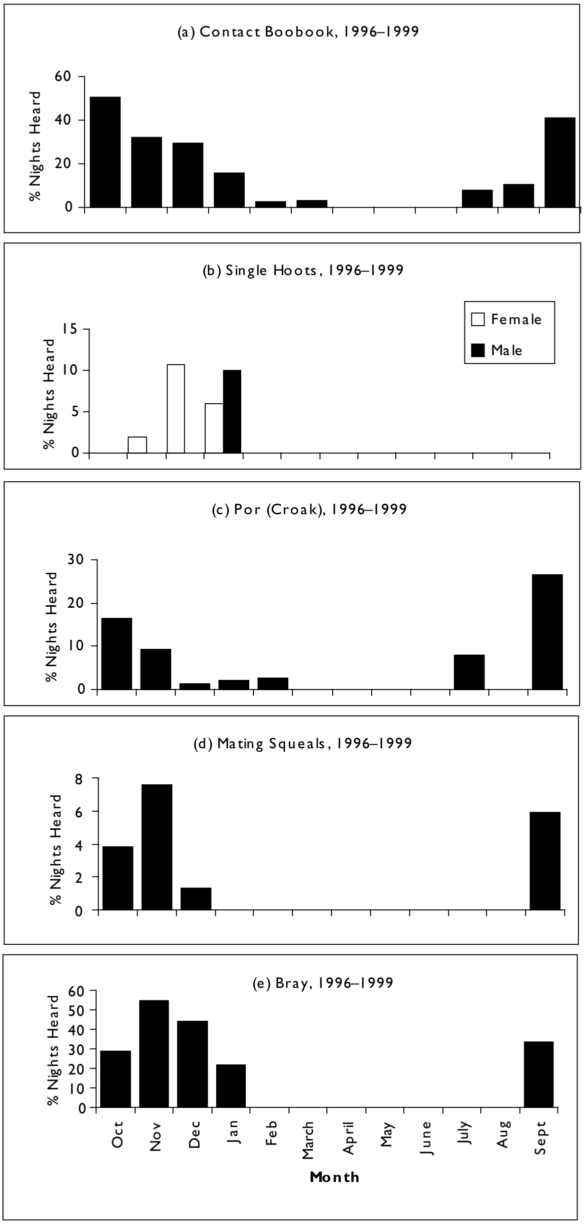


Fig. 3. (*a*) Percent of observation nights per month that we heard Contact Boobook calls during 1996–99. Total nights heard = 124/529 observation nights (23.4%); all male, except both male and female on two nights, and female alone on one night. (*b*) Percent of observation nights per month that we heard Single Hoot calls during 1996–1999. Total nights heard = 18 of 529 observation nights (3.4%); male 6 nights, female 12 nights. (*c*) Percent of observation nights per month that we heard Croaking Boobook and Por calls during 1996–1999. Total nights heard = 39 of 529 observation nights (7.4%); males alone 32 nights, females alone six nights, unknown one night. (*d*) Percent of observation nights per month that we heard Mating Squeals during 1996–1999. Total nights heard = 12 of 529 observation nights (2.3%); all, we believed, given by females. (*e*) Percent of observation nights per month that we heard Bray calls during 1996–1999. Total nights heard = 119 of 529 observation nights (22.5%); all, we believed, given by females.

Table 2. Calling behaviour of Southern Boobooks in relation to weather and season across 529 observation nights. Levels of significance of variation in calling behaviour are indicated by: ** $P < 0.001$. Data for each call type represents the number of nights in which owls were heard. n represents the total number of nights in which owls were surveyed. Contingency chi-square analyses and Fisher's Exact Tests used where appropriate. Dunn-Sidak method used to correct for compounding Type I errors.

	Moon		**Moon Phase**				**Cloud (oktas)**			**Rain**		**Wind speed (km/hr)**		
Call	Visible	Not visible	0	0.25	0.75	1	Clear (0–1)	Part (2–5)	Total (6–8)	Dry 0	Wet >0	Gentle (0–10)	Moderate (11–21)	Strong (>21)
n nights	249	265	120	120	135	153	303	100	126	495	33	197	244	88
Territorial	70	80	41	39	34	40	85	29	41	147	8	48	85	22
Duel	9	11	2	4	6	8	14	2	4	20	0	5	12	3
Por (Croak)	23	19	10	11	11	11	17	11	15	37	6	12	25	6
Bray	62	57	30	38	27	27	61	25	36	114	8	43	59	20
Contact	71	62	37	38	28	32	63	34	38	129	6	40	68	27

Call	Wind Direction				Temperature (C°)				Season			
	N	S	E	W	Cold <9	Mild 9–14	Warm 15–21	Hot >21	Non-breeding	Pre-breeding	Breeding	Post-fledging
n nights	178	26	131	155	67	185	218	59	111	122	208	88
Territorial	54	6	35	54	5	55	83	12 **	2	40	101	12 **
Duel	10	0	3	5	0	3	14	3	0	2	17	1 **
Por (Croak)	17	1	7	17	4	22	16	1	0	20	21	2 **
Bray	35	6	32	41	6	41	60	15	0	23	86	13 **
Contact	43	8	33	47	7	51	63	14	2	35	89	9 **

all three territories, and then confirmed the sex of the caller with radio-telemetry and colour-band. We could not reliably separate males from females, except in Territory 2 where the male had a particularly deep and loud voice compared with the female and with the males in Territories 3 and 4. However, the same male in Territory 2 occasionally gave a higher pitched series of Boobook calls that we could not distinguish from those of his mate, or from the males' calls in Territories 3 and 4.

Contact Boobook Calls. Contact Boobook calls followed a similar seasonal pattern to Territorial Boobook calls, but finished and started earlier in the year (Fig. 3a).

Single Hoot. This call sounded something like the first note, accentuated, of a Boobook call. Owls used the Single Hoot call most commonly after young fledged, so it was heard more often in December and January (Fig. 3b). Females used it when young first fledged, then males used it after parenting responsibilities transferred to them (Olsen & Trost 1997). In contrast, one female in late January 2000 (not included in Fig. 3b) after the male took over parenting, did not defend or feed the fledgling, as normal, though the fledgling sought her out each morning and roosted with her for the day. This female gave a series of Single Hoot calls if we approached her at her roost, or followed her after she left her roost, but ignored us if we approached her fledgling after it left the roost.

Por (Croak). Following previous authors, we have combined these two lower pitched calls (Fig. 3c), even though they are distinguishable. Por calls are single notes repeated; they are not uttered in two-note (disyllabic) segments. They contrast with low pitched 'Croaking Boobook calls' that, like other Boobook calls, are uttered in two-note segments. As with Boobook calls, Por (Croak) calls were seasonal.

Mating Squeal. Mating squeals (Fig. 3d) sounded like the squeal given by a European Rabbit *Oryctolagus cuniculus*, and lasted 2–3 seconds, as on the Buckingham & Jackson (1990) tape. They were given as copulation finished, probably by females, but we could not confirm this. Figure 3d may not represent normal frequencies for the species near Canberra, because Pair 3 failed twice in 1997 and copulated before each re-laying into December. Also, we began intensive observations of Pair 2 in 1999 and this female fledged young later each year, 1993–99, than the other females we observed.

Bray. Females gave a food-begging Bray call (Fig. 3e) that was like a deeper version of the Trill call given by nestlings, but both sexes also gave a softer Purr call (see Trill and Growl below).

Trill and Growl. On ten occasions in December – January, we heard calls given by adults of both sexes that we termed Purr. These were contact calls given mainly to their young, like quieter, subdued Bray calls, and could be confused with the Bray, Trill, or Growl calls described by Higgins (1999). Bray calls, given by females, were more 'whiney', as if given with an open beak, while Purr calls, given by both sexes, were even and more subdued, as if given with a closed beak.

Nestlings and fledglings used the cricket-like Trill call (food begging). Fledglings often called in this way for the entire one hour observation, and often while flying from perch to perch. On three occasions we saw neighbouring fledglings cross territorial borders, and territory owners did not drive them off or feed them, even though the fledglings begged for food. Adults seemed to recognise their own fledged young.

Yelp (yeo). Although we heard this call in an earlier study on these territories (Olsen & Trost 1997), the female that gave this call disappeared and we have not heard it subsequently.

Scream. Not heard.

Squeak. This was heard only once. The function was not clear.

Table 3. Comparison of calling behaviour of the Southern Boobook in relation to weather and season, according to findings of Kavanagh & Peake (1993), Debus (1997) and this study.

ns. = studied but not significant; – = not studied.

Variables	This study	Kavanagh & Peake (1993)	Debus (1997)
Moon phase	ns.	ns.	–
Moon visibility	ns.	$P < 0.01$	ns.
Wind	ns.	$P < 0.01$	$P < 0.01$
Temperature	$P < 0.001$	ns.	–
Rain	ns.	ns.	$P < 0.01$
Cloud	ns.	ns.	ns.
Season	$P < 0.001$	ns.	–

Chitter. We heard on three occasions a 'chitter' call (Olsen & Trost 1997) that occurred just before mating squeals, or when an owl fought with, or was displaced from a perch by, a fledgling or adult.

Weather and temporal variables

Although we found significant effects of temperature on Territorial Boobook calls and of season on all calling categories (Table 2), the effects of temperature disappeared when we limited the analysis to the four months, September–December, when Territorial Boobook calling was most common (Figure 2a; Table 4). This differed from the findings of Kavanagh & Peake (1993) and Debus (1997) (Table 3).

Social context and individual differences

Social context and individual differences appeared to account for some of the variation in Territorial Boobook calling. Although we had to stand within 30 m of the owls to hear most types of vocalisations, we could hear Territorial Boobook calls up to one km away; one of us could walk to and identify the caller with a torch, so we scored these calls from all territories during each of the study's three time frames (Table 5, Figs. 2b, 2c, 2d). The decrease in Territorial Boobook calling by males after 1 January 1998 reflected the end of a border dispute. From 1993, Pair 3 had nested further east each year, and ranged into Territory 2, and especially into Territory 1. The conflict continued until Male 1 disappeared around 1 January 1998 (Fig. 2c), though Female 1 remained.

In 1998 Male 3 moved into the nest tree vacated by Male 1, and reduced his Territorial Boobook calling. We observed him copulating with Female 1 at this tree, before Female 3 moved over the hill into this area. On 30 August and 1 September 1998, Females 1 and 3 called from high perches in the manner of singing males, and the two females duelled. On 1 September 1998, Female 3 apparently killed Female 1 and decapitated her; she carried the carcass from tree to tree for the 2.5 hours that we watched (Fig. 2c). From then, Pair 3 occupied the expanded territory and we saw no other adults there. From this new site, Female 3 continued to call during September–October 1998, as she had in October–December 1997 after each breeding failure and move to a new nest.

Table 4. Calling behaviour of Southern Boobooks in relation to weather and season in the four months when calling was heard close to 50% of nights – September to December. Data for each call type represents the number of nights in which owls were heard. n counts represents the total number of nights in which owls were surveyed. Contingency chi-square analyses and Fisher's Exact Tests used where appropriate, Dunn-Sidak method used to correct for compounding Type I errors. None reached levels of significance of $P < 0.001$.

	Moon		**Moon Phase**				**Cloud (oktas)**			**Rain**		**Wind speed (km/hr)**		
Call	Visible	Not visible	0	0.25	0.75	1	Clear (0–1)	Part (2–5)	Total (6–8)	Dry 0	Wet >0	Gentle (0–10)	Moderate (11–21)	Strong (>21)
n nights	130	136	72	68	65	68	136	62	76	254	19	75	143	56
Territorial	59	71	37	35	32	29	68	27	39	127	7	38	76	20
Duel	8	11	2	4	6	7	13	2	4	19	0	5	11	3
Por (Croak)	20	18	9	9	11	10	14	10	15	33	6	11	23	5
Bray	53	53	27	33	27	22	54	23	32	103	6	37	53	19
Contact	60	56	35	32	25	26	54	30	34	112	6	33	63	22

Call	Wind Direction				Temperature (C˚)			
	N	S	E	W	Cold <9	Mild 9–14	Warm 15–21	Hot >21
n nights	90	13	63	100	14	112	128	20
Territorial	49	5	27	50	5	48	71	10
Duel	10	0	2	5	0	3	13	3
Por (Croak)	17	1	5	16	5	44	59	10
Bray	32	6	26	41	6	41	53	9
Contact	37	6	27	45	3	21	14	1

Table 5. Number of nights we heard Territorial Boobook calls of identified male (M) and female (F) Southern Boobooks from the three territories each year between 1 October and 30 September 1996–1999.

Year of study	Sex and territory of identified calling owls							
	M1	M2	M3	Total males	F1	F2	F3	Total females
1996–1997	10	8	29	47	0	0	0	0
1997–1998	14	4	34	52	2	0	13	15
1998–1999	0	7	21	28	0	18	3	21
Totals	24	19	84	127	2	18	16	36

The increase in female calling during August-October 1999 (Figure 2d, Table 5) was mainly from Female 2, after a pair not included in this study (Pair 4) nested closer (500 m) to Pair 2's northern border. Since 1993, pair 4 had nested 850 m northwest of Pair 2. In 1998 we observed Male 4 with fledged young roosting 30 m from the Territory 2 nest; the previous Pair 4 nest was occupied by an unbanded pair. During August–October 1999, Female 2 called frequently from a high perch, facing Pair 4 on the border; Male 2 called little. Female 2 duelled twice with Male 4, on 25 August and 17 October. This was before Female 2, but after Female 4, had laid eggs.

DISCUSSION

Vocalisations heard

Territorial and Contact Boobook calls peaked during pre-breeding and breeding; the distribution of Contact Boobook calls was similar to Territorial Boobook calls though some earlier Contact Boobook calls, in July, we interpreted as pre-breeding behaviour. Like Stephenson (1998), we could not discriminate between male and female calls, although we would expect the males' calls to be generally lower in pitch, as with most other owls (Marks *et al.* 1999), but with considerable individual variation.

This study observed one of the same females that Olsen & Trost (1997) watched (2), but with a different mate (moved from Male 3 to Male 2), on a different territory, in a different year, and from an earlier stage (before egg-laying) in the breeding cycle. She was not heard giving Boobook calls in the earlier study, but did give Boobook calls in the later one, before egg-laying. Season, more than individual differences, could explain why Olsen & Trost (1997) did not hear females give Boobook calls. Much of the variation in Territorial Boobook calls from year to year in these three territories could be explained by (i) season, (ii) individual differences, and (iii) social context (owls called more during border conflicts, and duelled with some neighbours but not others). That females engaged in territorial disputes, perched alone on exposed branches, and engaged in territorial singing with Boobook and Por calls, was surprising, particularly as this happened before egg-laying when we expected males to guard females.

We heard Single Hoots used mainly in defence of young, but never as a prelude to a series of Boobook calls, or as a response to Boobook calls of a rival, as suggested by Higgins (1999). The calls referred to by Higgins were more likely Por or Croaking Boobook calls, a softer, lower pitched call than the Single Hoot, uttered by males or females in a different context – to their mates, or when alone, often when starting a series of Territorial Boobook calls. The three calls probably require separate classifications (see below). Similarly, two calls, the Por (Croak) call and the Croaking Boobook call, were combined here. Further study of the structure and context of the Por and Croaking Boobook calls is necessary to determine whether they are different calls or variations of the same call.

We did not observe males giving the Bray call, as reported by Higgins (1999). We wonder how commonly males use this call, and if observers confuse the Bray call with the Purr call which we saw both adults use, or the Trill or Growl Calls. The Purr call was used in a different context (often to young) from the Bray call (often the adult female to the adult male). This may be individual variation, and analysis of recorded calls from identified males and females should help determine if Purr and Bray are one call or two.

In this study we did not hear adults give Scream, Yelp (yeo), Trill or Growl calls. We heard Squeak calls rarely, and these seemed to be situation specific. We heard a call we termed 'Chitter' that may be the Scream call identified by Higgins (1999).

The seven recordings by Buckingham & Jackson (1990) could serve as an auditory guide to most of the calls we heard, but we would reclassify them as follows (Buckingham & Jackson description in quotes, followed by our classification in italics): (i) 'Duet' – more likely a *duel* between adults giving *Boobook calls*, sexes unknown; (ii) 'Higher-pitched call' – an adult of unknown sex giving *Boobook calls;* (iii) 'Aggressive calling by two males' – *Croaking* (*Por*) *calls* (not Croaking Boobook), sexes unknown; (iv) 'Call when disturbed' – adult giving *Bray calls* (food-begging), probably a female; (v) 'Churring' calls and 'mating squeal' – one adult giving *Boobook calls*, one giving *Croaking* (*Por*) *calls* (not Croaking Boobook), then *Mating Squeal* (vi) 'Falsetto call' – adult giving *Yeo calls*, sex unknown; and (vii) 'Food begging trill from juvenile' – Juvenile giving *Trilling calls*.

Weather and temporal variables

Although Territorial Boobook calling in this study varied with temperature, these variations disappeared when we controlled for season. We did not find variations in calling frequency with moon visibility or wind, as did Kavanagh & Peake (1993), or with rain or wind, as did Debus (1997).

In our study, because of the large number of statistical tests involved, we used the Dunn-Sidak method (Sokal and Rohlf 1995) to correct for compounding Type I errors. Also, we determined 'season' by dividing the year into four categories based on the annual breeding cycle of the owls in three territories, while Kavanagh & Peake (1993) observed seven species, including Southern Boobooks, and selected two periods in the year to census these species – winter/early spring, and late spring/summer. Finally, we observed the owls at close range, but Kavanagh & Peake (1993) and Debus (1997) mostly listened for the owls, sometimes at a distance. Although Debus (1997) found that rain and wind significantly depressed calling, certain owls in his study did call during rain and moderate wind in the pre-laying days or weeks. Owls in our study did not call significantly less often on rainy or windy nights, but moderate rain and wind might depress the *detectability* of calls to human listeners at a distance as much as depress the calling frequency itself. We would expect calling to stop during heavy rain or strong wind.

Evidence that the lunar cycle affects the calling behaviour of owls is inconsistent. For example, Ganey (1990) found that Spotted Owls *Strix occidentalis* called more than expected during the last quarter and new moon phases of the lunar cycle, but he summarised other studies that claimed that Tawny Owls *Strix aluco* reduced their calling in moonlight, that Western Screech Owls *Otus kennicotti* were most responsive under a bright waxing moon, that Boreal Owls *Aegolius funereus* and Northern Saw-whet Owls *Aegolius acadicus* were most responsive to playback when the moon was full, and that moon phase had no effect on the response rates of Eastern Screech Owls *Otus asio*, or on the calling behaviour of Spotted Owls in some other studies. Populations may differ, but we also wonder about differences in experimental conditions, and the likelihood of statistical artefacts and confounding variables in such studies. Recent reviews, such as that by Gutiérrez *et al.* (1995), have dropped the claim that Spotted Owl calling is affected by lunar conditions, and a number of researchers to whom we have spoken question the validity of such claims.

Conclusions

Three variables seemed to explain much of the variation in the frequency of calling we observed, namely, season, social context and individual differences. We limited our observations to the period just before the owls left their roost or nest to one hour after. We make no claim that the same patterns would hold later in the night.

There is much yet to understand about the delimitation and purpose of these calls. Given the current state of knowledge, we do not believe that observers can reliably sex Southern Boobooks by territorial calling alone. Care must be taken if behaviour, territory size, and status of these owls are inferred solely from surveys of vocalisations.

ACKNOWLEDGMENTS

Thanks to David Judge and Wayne Robinson for statistical advice, Dalice Trost for field assistance, Canberra Nature Park North, especially Odile Arman for access to nests and owls, and to the Applied Ecology Research Group, especially Arthur Georges, David Williams, Jim Hone, Tony Tucker, and Mike Palmer-Allen for advice and for supplying transmitters and receivers. Thanks also to Alan Nicol for help with figures, to Stephen Debus, John Penhallurick, Jim Hone, Rod Kavanagh, Ian Newton, two anonymous referees, and Tracy Fleming for helpful comments on the manuscript, to E. Forsman, J. Duncan, B. Marcot, D. Johnson, and T. Fleming for advice on lunar cycles and calling, and to Terry Dennis, Mark Holdsworth and Les Boyd for encouraging this research.

REFERENCES

Buckingham, R. & Jackson, L. (eds.) 1990. *A field guide to Australian bird song, Regent Parrot to Masked Owl*. Melbourne: Bird Observers Club of Australia.

Debus, S. 1996. Mating behaviour of the Southern Boobook *Ninox novaeseelandiae*. *Aust. Bird Watcher* **16:** 300–301.

Debus, S. 1997. Vocal behaviour of the Southern Boobook *Ninox novaeseelandiae* and other nocturnal birds. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Birds Australia Monograph **3:** 71–85. Melbourne: Birds Australia.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Milton, Qld.: Jacaranda.

Ganey, J. 1990. Calling behaviour of Spotted Owls in northern Arizona. *Condor* **92:** 485–490.

Gutierrez, R.J., Franklin, A.B. & LaHaye, W.S. 1995. Spotted Owl *Strix occidentalis*. *In* Poole, A. & Gill, F.

(eds.) *The Birds of North America*, No.179. The Academy of Natural Sciences, Philadelphia, and the A.O.U., Washington D.C.

Higgins, P.J. (ed.) 1999. *Handbook of Australian, New Zealand & Antarctic Birds. Vol. 4 Parrots to Dollarbird*. Melbourne: Oxford University Press.

Hollands, D. 1991. *Birds of the Night*. Balgowlah, N.S.W.: Reed.

Kavanagh, R.P. & Peake, P. 1993. Survey procedures for nocturnal forest birds: an evaluation of variability in census results due to temporal factors, weather and technique. In Olsen, P.D. (ed.) *Australian Raptor Studies*: 86–100. Melbourne. Royal Australian Ornithologists Union.

Imboden, C. 1975. A brief radio-telemetry study on moreporks. *Notornis* **22:** 221–230.

Karl, B.J. & Clout, N. 1987. An improved radio transmitter harness with a weak link to prevent snagging. *J. Field Orn.* **58:** 73–77.

Marks, J.S., Cannings, R.J. & Mikkola, H. 1999. Family Strigidae (Typical Owls). In del Hoyo, J., Elliott, A. & Sargatal, L. (eds.) *Handbook of Birds of the World. Vol.5. Barn owls to Hummingbirds*. 107–110. Barcelona: Lynx Edicions.

NCDC 1988. Sites of significance in the ACT Volume 2: Inner Canberra, Technical Paper 56.

Olsen, J. & Trost, S. 1997. Territorial and nesting behavior in Southern Boobook *Ninox novaeseelandiae*. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere. Second International Symposium*. General Technical Report NC – 190: 308–313. St. Paul MN: USDA Forest Service.

Olsen, J., Marcot, B. & Trost, S. 2002. Do Southern Boobooks *Ninox novaeseelandiae* duet? This volume.

Olsen, J. & Woollard, P. 1975. The use of the bal-cha-tri in banding. *Canberra Bird Notes*. **3:** 8–9.

Olsen, P. 1997. Egg weight loss during incubation, and growth and development of captive-bred Southern Boobooks *Ninox novaeseelandiae*. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Monograph **3:** 92–97. Melbourne: Birds Australia.

Schodde, R. & Mason, I. 1980. *Nocturnal Birds of Australia*. Melbourne: Lansdowne.

Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*: *The Principles and Practice of Statistics in Biological Research*. 3rd ed. NY: Freeman.

Stephenson, B.M. 1998. The ecology and breeding biology of Morepork, *Ninox novaeseelandiae*, and the risk from secondary poisoning, in New Zealand. Unpublished M.S. thesis. Palmerston North, N.Z.: Massey University.

Zar, J.H. 1984. *Biostatistical Analysis*. (2nd ed.) Englewood Cliffs, N.J.: Prentice-Hall.

29

DO SOUTHERN BOOBOOKS *NINOX NOVAESEELANDIAE* DUET?

JERRY OLSEN[1]*, B.G. MARCOT*[2] *& S. TROST*[3]

[1]Applied Ecology Research Group, Division of Communication and Education, University of Canberra, ACT, Australia 2616

[2]1221 S.W. Yamhill St., Suite 200, POB 3890, Portland OR USA 97208–3890

[3]Erindale College, McBryde Cres., Wanniassa, ACT, Australia 2903

There is disagreement about whether Southern Boobooks *Ninox novaeseelandiae* duet. A recent review of the species concluded that duetting does occur, based on (i) observations of captives and (ii) two reports from wild birds, including one from New Zealand. We examined definitions of duetting, and attempted to collect evidence for it in the calling behaviour of three mated pairs on adjacent territories observed from October 1996 to October 1999. To identify callers, six adults were colour-marked, and four of the six were radio-tagged. Observations were made on 529 nights from just before the birds left their day roost each evening until one hour after. Of 255 bouts of calling in which Territorial Boobook and Por calls were used, 30 (11.8%) overlapped (owls called at the same time); two (6.7%) of 30 overlapping bouts were between mated pairs, but without the temporal precision or sequential ordering of elements normally found in duetting. The other 28 overlapping bouts (93.3%) were mostly between neighbouring males. We found no convincing evidence in the field, or in the literature, that Southern Boobooks duet. We comment on behaviours that some may interpret as duetting, and suggest caution when estimating, solely from vocalisations, the densities of territorial pairs and sizes of home ranges of *Ninox*.

INTRODUCTION

There is some confusion as to whether Southern Boobooks *Ninox novaeseelandiae* duet, defined here as a mated pair calling with bouts overlapping in a synchronised and co-ordinated fashion (see below for detail). Here we contrast duetting with 'duelling' defined as two unmated owls from different territories, facing each other, up to 50 m apart and calling with Boobook or Por calls during overlapping bouts, but not in a co-ordinated or synchronised fashion.

Olsen (1997) claimed that captives duetted. Debus (1996, 1997) thought that wild pairs would duet in response to playback, sometimes emitting the mating squeal; he heard croaking duets and mating squeals through October. Where two birds were involved, hooting was call-and-answer in nature, with neighbours and/or mates giving call for call in long bouts. Olsen & Trost (1997) thought that some of the behaviours that observers interpreted as duetting between mated pairs might have been males 'duelling' with each other, probably over territorial boundaries. In a recent review of the literature on the Southern Boobook, Higgins (1999) concluded that duetting does occur, based on three pieces of evidence: (i) captive pairs duet, (ii) two birds, in the wild, apparently male and female, both giving Boobook calls, were collected together from the same tree by Whitlock (1923); and (iii) in New Zealand, birds close together sometimes seemed to duet rather than duel. None of these authors defined duetting, so none of these assertions has been checked.

Campbell & Lack (1985 p. 631) in their definition and description of duetting stated 'the complexity of song is increased by including contributions from two individuals, usually a mated pair. The songs produced are generally quite stereotyped and the two contributions so well coordinated that to the listener it seems to be produced by just one bird, …The precise timing of the different contributions to within hundredths of a second is a striking feature of duetting between mated pairs.' Marks *et al.* (1999 p. 109) said about duetting in the Spotted Eagle Owl *Bubo africanus* '… the two vocalisations sound like only one. Similarly, female Eurasian Scops-owls often duet so closely with their male partners that the monotonously repeated calls sound like a single, but two-part, call. The calls of two or more adjacent Scops-owls, while given at a very regular rate, are not synchronised with each other, and the pattern of calling thus differs from that of duetting mates.'

In an earlier definition, Farabaugh (1982, p. 87) first defined the term bout: 'Vocalisations, like other behaviours, are clumped rather than randomly distributed in time. These clumps are called bouts.' She described duetting as occurring when 'bouts of certain elements in the repertoire of one bird frequently overlap with bouts of certain elements in the repertoire of its mate. … Further, there is some organization of both participants' elements within the region of overlap. This view can be expressed in terms of three variables which can be measured for any species: one measure of bout overlap, ie., the percentage of bouts that overlap with bouts of the mate; and two measures of organization of male and female elements within overlapping bouts, ie., the precision of timing and the sequential ordering of elements. … The percentage of male bouts that overlap with female bouts, and vice versa, can be calculated for each type of bout (bouts of song, bout of each call type, etc.). If the percentage overlap is high, these overlapping bouts may be duets.'

According to Farabaugh there is 'temporal precision of timing' between male and female elements in an overlapping bout when the two calling birds sound like one synchronised two-part call, not like two birds calling in a non-synchronised way. If the calling sounds like two birds, the calling is less likely to be a duet. When elements in a bout are 'sequentially ordered', there is a clear, alternating, non-random pattern in the male and female contribution to the bout. Farabaugh gives the example of male and female elements ordered in the sequence fmfmfmfmfmfmfmfmfmf, as ordered sequentially and indicative of duetting, but male and female elements in the sequence mmmmmmmmmmfffffffff, as not sequential and not indicative of duetting.

Our aims in this study were to: (1) provide an assessment of duetting in three wild mated pairs of Southern Boobooks by documenting the percentage of male bouts that overlapped with female bouts, and in these overlapping bouts, estimating the precision of timing, and the sequential ordering of elements; and (2) evaluate existing claims in the literature for duetting in this species.

METHODS

Trapping, banding, and radio-telemetry of the three adjacent territorial pairs is described by Olsen *et al.* (2002). From 3 October 1996 to 22 October 1999, we visited the area several nights per week at sundown and stood near the nest or roost of one of the three pairs with a torch, binoculars and notebook. Observations were made throughout the year from just before the birds left their day roost or nest, to one hour after. During the hour, we stood 10–30 m from roosts or nests, or followed individuals after they left the roost or nest as closely as possible without disturbing them (see Olsen *et al.* 2002).

Over 529 nights we counted the number of overlapping bouts of calls, and, where possible, identified the callers by triangulating the location of radio-tagged birds with a hand-held yagi-antenna and Telonics TR–4 receiver, and sighting colour-bands with torch and binoculars. We concentrated our observations on the vocalisations of the three pairs as described in Olsen *et al.* (2002).

On three occasions, we played recordings of Southern Boobook calls, or Powerful Owl *Ninox strenua* calls, near to three pairs prior to egg laying. We describe the pairs' responses, but these nights are not counted in the 529 observation nights. From field observations, we calculated the percentage of bout overlap of Boobook and Por calls in unmated neighbours (duels), in mated pairs (indicating possible duetting), and noted other behaviours that might be interpreted as duetting. Throughout this paper the term 'Territorial Boobook' refers to a call and not an owl, and the word 'Por' denotes another type of call. Vocalisations that 'we heard' refers to vocalisations from owls we observed and identified individually.

RESULTS

Territorial Boobook and Por Calls

Bouts of Territorial Boobook and Por calls occurred on about half (275) of the 529 observation nights. We were able to identify callers in 255 of the 275 bouts, and 188 (74%) were uttered by males and 67 (26%) by females. We could not always discriminate between male and female calls by ear and had to rely on radio-tags and colour-bands. The calls were not stereotyped: either sex gave the Boobook call, sometimes the Por call, and both sexes progressed from Por to Boobook or Boobook to Por calls, or low-pitched to high-pitched calls, in one bout.

Bouts of Territorial Boobook and Por calls were seasonal (Fig. 1). Bouts for both males and females were highest in spring and summer, though female calling was less frequent, especially in November during the incubation and nestling phases, and in autumn; females tended to call more often than males before egg-laying, and less often than males after egg-laying.

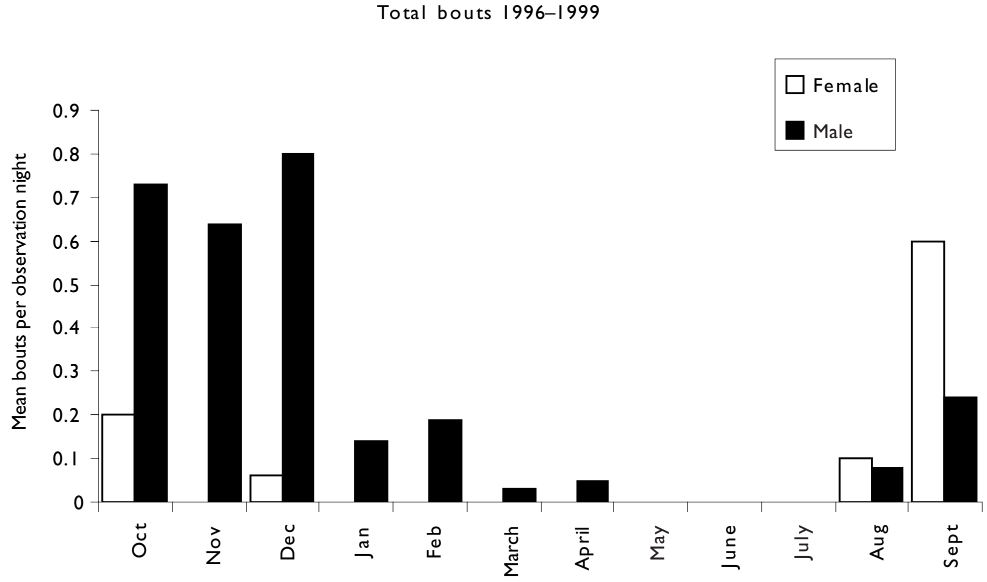


Fig. 1. Territorial Boobook calls identified as male or female (n = 255). Mean number of bouts per observation night by month.

Overlapping Bouts

Using Farabaugh's (1982) definition, we calculated percent of bout overlap between mated males and females. Only two of 255 bouts (0.8%) overlapped (Tables 1 & 2). The two overlapping bouts in mated pairs that we heard, one on 3 September 1998 (three disyllabic notes overlapped for nine seconds), and the second in a different pair on 31 August 1999 (three disyllabic notes overlapped for seven seconds), did not fit Farabaugh's definition of duetting. They were brief, and lacked discernible precision of timing or sequential ordering of elements; that is, both overlapping bouts sounded like two birds calling independently, not as one synchronised two-part call.

On several occasions we heard other overlapping (simultaneous) bouts:

Table 1. Percent of overlapping bouts (n = 30 of 255 bouts of Boobook or Por calls) that involved neighbours (duels), or mated pairs.

	Percent bouts overlapping between:	
	Neighbours (duels)	**Mated pairs**
Of 255 total bouts	11.0% (28/255)	0.8% (2/255)
Male/male	9.8% (25/255)	–
Female/female	0.4% (1/255)	–
Male/female	0.8% (2/255)	–
Of 30 overlapping bouts	93.3% (28/30)	6.7% (2/30)

Table 2. Percent of observation nights (*n* = 529 observation nights) when duels were heard between males, between females, or between males and females.

Duels heard:	Percent of observation nights
Between males	4.7% (25/529)
Between females	0.2% (1/529)
Between males & females	0.4% (2/529)
Total	5.3% (28/529)

Duelling

On 28 of 529 nights, we heard duelling bouts, mainly between neighbouring males (Table 2), but no more than one bout per night.

As duels and duetting are both forms of overlapped Boobook calls, we compared the percent bouts of duels (neighbours) with the percent bouts of overlapping calls between members of mated pairs (Table 1). Most overlapping bouts were between neighbouring males which lasted up to one hour on borders. In contrast, the two overlapping bouts between members of mated pairs lasted only a few seconds. At least 14 of 28 duels (50%) had three birds present, one to 50 m apart, but only two of the birds called using Boobook or Por calls.

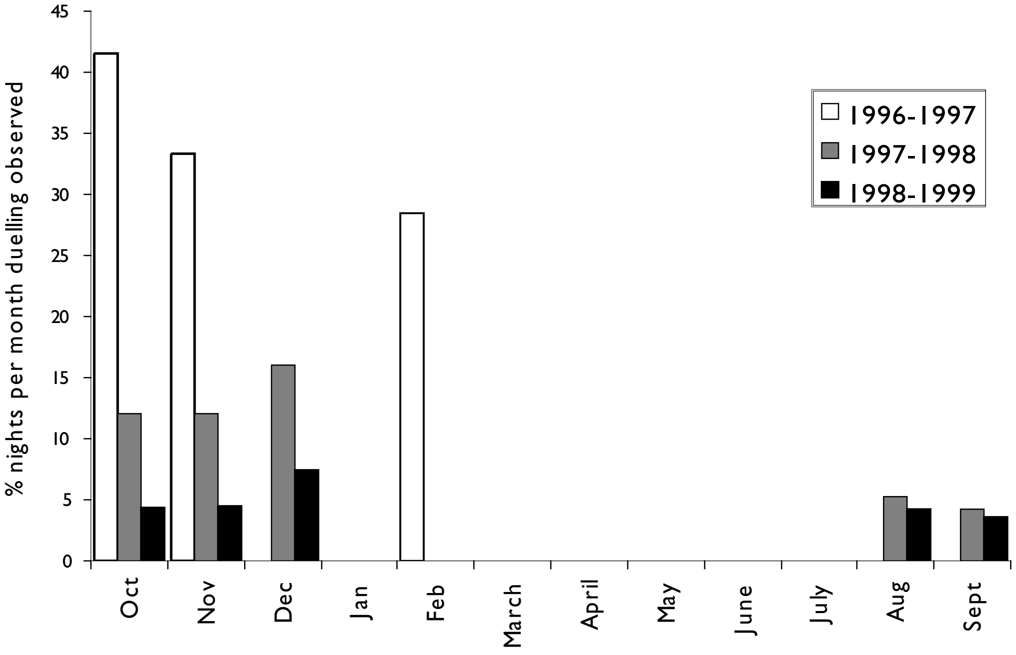


Fig. 2. Percent nights per month when duelling was observed in each of three years. Note: does not include one observation in October 1999.

Duelling was seasonal, beginning in late winter, and peaking when pairs had eggs and nestlings in October–December (Fig. 2). This differed slightly from the frequency of bouts of Territorial Boobook calls (Fig. 1). The frequency of duelling bouts changed between the three years of study, and increased duelling in the spring-summer of 1996–1997 reflected a territorial dispute between an incoming pair that had nested against the borders of two resident pairs (making three pairs in the area), until one of these original males disappeared at the end of December 1997 (see Olsen *et al.* 2002). We saw no duelling between the two original resident males. In August–October 1999 we moved to a nest that we had not studied during the pre-breeding stage and observed the female duelling with the neighbouring male twice, and her mate duelling with him once.

Alternating pitches in a bout

On one occasion (22 Sept 1997) a male in a tree alternated the pitch of his Boobook calls in a bout, low pitched, then high pitched, so he sounded like two birds calling from the same tree.

Playback

On the three occasions when we used playback near a pair before egg laying, the pairs gave simultaneous (overlapping) Boobook calls. Two males caught moths and tried to feed their mates. On one occasion, a male attempted to copulate with the female, and on another occasion the pair copulated and the female gave a Mating Squeal (Higgins 1999).

Simultaneous female Bray and male Boobook call

Males in this study gave Contact Boobook calls (see Olsen *et al.* 2002) when they delivered food to the female, and she sometimes gave simultaneous Bray calls; that is, the calls overlapped.

Mating

During copulation, males made a low croaking (Por call) and females simultaneously made a soft purr, similar to a quiet Bray call (see Olsen *et al.* 2002, Imboden 1975), then one of the pair gave the Mating Squeal.

DISCUSSION

During 529 observation nights over 37 months we twice observed some brief (seven and nine seconds) overlapping of Boobook and/or Por calls between mated pairs. In neither case did the overlapping calls sound coordinated with any precision, nor were they sequentially ordered. Nothing we heard, except perhaps mating, fitted the definitions of duetting given by Farabaugh (1982), Campbell & Lack (1985) or Marks *et al.* (1999).

Evidence for duetting in the literature

None of the studies that reported duetting in Southern Boobooks defined terms, referred to criteria, or provided evidence. The claim for duetting in Higgins (1999) was based on (i) observations of captives, (ii) a report by Whitlock in 1923, and (iii) an unsourced claim that Southern Boobooks in New Zealand appear to duet. Take these claims in turn:

(i) Captive males and females occasionally give Boobook and Por calls simultaneously (J. Olsen pers. obs.). Wild pairs in our study often separated during the night and called from different parts of their territory, even during the pre-egg laying phase. Members of captive pairs cannot separate, and they are often housed in cages next to other calling pairs, and within the territories of calling wild pairs, producing a confusing and artificial situation. Other repeated claims from observations on captive birds, for example that extra females help at the nest (Fleay 1968; Schodde & Mason 1980; Olsen 1994), have yet to be confirmed in the wild.

(ii) Whitlock (1923) did not report duetting. He reported two owls of undetermined species or sex using a call he did not identify; he did not mention synchronisation or co-ordination of these calls.

(iii) None of the five studies of radio-tagged or colour-marked Southern Boobooks (Imboden 1975; Olsen & Bartos 1997; Olsen & Trost 1997; Stephenson 1999; this study), including two in New Zealand, have confirmed duetting with Boobook calls.

Even if the three pieces of evidence presented by Higgins (1999) are valid, two Southern Boobooks giving Boobook or Por calls in overlapping bouts are not necessarily duetting as defined by Farabaugh (1982), Campbell & Lack (1985), or Marks *et al.* (1999). Mated pairs of many other birds vocalise simultaneously but they are not necessarily duetting. For example, both sexes in mated pairs of Spotted Owls *Strix occidentalis* sing giving hooting calls, sometimes simultaneously (Gutiérrez *et al.* 1995), but this is not considered as duetting because their calling does not fit accepted definitions.

Other calling with overlapping (simultaneous) bouts

Duelling

Duelling may be the behaviour most often misidentified as duetting. On a number of nights we observed males duelling with neighbouring males (Table 2), while their mates sat nearby and did not respond. Stephenson (1998) described similar behaviour in Southern Boobooks in New Zealand. The assumption that two owls heard calling in a survey are duetting from inside a territory instead of duelling on their common border may affect an estimate of the breeding pairs in an area. In a survey of Powerful Owls in the ACT, Olsen & Rehwinkel (1995) identified clusters of vocalisations on a map which could be interpreted as pairs on territories. They cautioned that these clusters of vocalisations could be owls from different territories calling on territorial borders, as Southern Boobooks did in this study. Counting such clusters as owls calling from territory centres could over-estimate the density of pairs, and under-estimate their home range sizes, particularly since owls may call from one border then move and call from another.

Response to playback

Three mated pairs responded to recorded playback by calling simultaneously, but the calling was not synchronised, and the pairs were duelling with the recorded voice of an owl they could not identify. This may be particularly threatening to males just before egg laying. We believe these pairs were reacting to an unusual event: an owl, unknown to them, calling near their proposed nest. Individuals of the pair, whether they were together or not, would respond with alarm and confusion to such a threat, often by calling. We saw no similar behaviour during the 37 months of this study, or during a previous study (Olsen & Trost 1997). The circumstances were contrived, and the behaviour of birds towards playback may not reflect frequent behaviour in normal circumstances.

Simultaneous female Bray and male Boobook call

Olsen & Trost (1997) suggested that this simultaneous calling may be what some authors termed duetting. Most female birds food-beg when males feed them, and Southern Boobook males gave a Contact Boobook call when they arrived at the nest with prey (Olsen *et al.* 2002). This does not fit the definitions of duetting quoted earlier.

Mating

The mating calls made by males and females were simultaneous and we heard these particular calls in no other context. Moreover, many bird species vocalise during copulation and this generally is not considered duetting.

Farabaugh (1982) described three characteristics more common among duetting than non-duetting species: (i) occurrence in the tropics; (ii) year-round territoriality; and (iii) prolonged monogamous bonds. These characteristics did not fit pairs in our study, where: (i) nests were in temperate woodland; (ii) after her young fledged in 1999 and 2000, one female left the breeding territory for a non-breeding home range in a suburban street 7 km from her nest, then returned for the next breeding season; and (iii) during 1993–1999 one female switched mates, and four males obtained new mates (three females disappeared).

Conclusion

We failed to find conclusive evidence that Southern Boobooks duet, as defined by Farabaugh (1982), Campbell & Lack (1985) or Marks *et al.* (1999). We do not believe that duetting with Boobook or Por calls is a normal part of the annual breeding sequence of Southern Boobooks. Verification of duetting is best done in the wild, without artificial means, such as recorded playback, that may modify natural behaviours.

Given our current knowledge of the species, we do not believe that observers can reliably sex callers without sighting colour-bands, nor can they assume that pairs of calling owls in surveys are mated pairs calling from territory centres. They may be neighbours or mated pairs calling at borders.

ACKNOWLEDGMENTS

Thanks to David Judge for statistical advice, Greg Hayes and Dalice Trost for field assistance, Canberra Nature Park North, especially Odile Arman for access to nests and owls, and to the Applied Ecology Research Group, especially Arthur Georges, David Williams, Jim Hone, Tony Tucker, and Mike Palmer-Allen for advice and for supplying transmitters and receivers. We are also grateful to Alan Nicol for help with figures, to D. Kroodsma, I. Rowley, S. Petty, J. Marks, and J. Duncan for help with definitions, to Stephen Debus, John Penhallurick, Jim Hone, Rod Kavanagh, Ian Newton, two anonymous referees, and Tracy Fleming for helpful comments on the manuscript, and to Terry Dennis, Mark Holdsworth and Les Boyd for encouraging this research.

REFERENCES

Campbell, B. & Lack, E. (eds.) 1985. *A Dictionary of Birds*. Calton, England: T. & A.D. Poyser.

Debus, S. 1996. Mating behaviour of the Southern Boobook *Ninox novaeseelandiae*. *Aust. Bird Watcher* **16**: 300–301.

Debus, S. 1997. Vocal behaviour of the Southern Boobook *Ninox novaeseelandiae* and other nocturnal birds. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Birds Australia Monograph **3**: 71–85. Melbourne: Birds Australia.

Farabaugh, S.M. 1982. The ecological and social significance of duetting. In Kroodsma, D.E., Miller, E.H. & Ouellet, H. (eds.) *Acoustic Communication in Birds*: 85 – 123. NY: Academic Press.

Fleay, D. 1968. *Nightwatchmen of Bush and Plain*. Milton, Qld.: Jacaranda.

Gutierrez, R.J., Franklin, A. B. & LaHaye, W. S. 1995. In Poole, A. & Gill, F. (eds.) *The Birds of North America*, No.179. The Academy of Natural Sciences, Philadelphia, and the A.O.U., Washington D.C.

Higgins, P.J. (ed.) 1999. *Handbook of Australian*, *New Zealand & Antarctic Birds. Vol. 4*, *Parrots to Dollarbird*. Melbourne: Oxford University Press.

Imboden, C. 1975. A brief radio-telemetry study on moreporks. *Notornis* **22**: 221–230.

Karl, B.J. & Clout, N. 1987. An improved radio transmitter harness with a weak link to prevent snagging. *J. Field Orn*. **58:** 73–77.

Marks, J.S., Cannings, R.J. & Mikkola, H. 1999 Family Strigidae (Typical Owls) – Voice. *In* del Hoyo, J., Elliott, A. & Sargatal, L. (eds.). *Handbook of Birds of the World. Vol.5*, *Barn owls to Hummingbirds*: 107–110. Barcelona: Lynx Edicions.

Olsen, J. & Woollard, P. 1975. The use of the bal-cha-tri in banding. *Canberra Bird Notes*. **3:** 8–9.

Olsen, J. & Rehwinkel, R. 1995. Peregrines and Powerful Owls in Namadgi and Tidbinbilla: A report for the National Estates Grants Programme. Unpublished report, Environment ACT.

Olsen, J. & Trost, S. 1997. Territorial and nesting behavior in Southern Boobook *Ninox novaeseelandiae*. In Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.) *Biology and Conservation of Owls of the Northern Hemisphere. Second International Symposium*: 308–313 General Technical Report NC – 190: 308–313. St. Paul MN: USDA Forest Service.

Olsen, J., Trost, S., & Hayes, G. 2002. Vocalisations used by Southern Boobooks (*Ninox novaeseelandiae*) in the Australian Capital Territory. This volume.

Olsen, P. 1994. Southern Boobook. *In* Strahan, R. (ed.) *Cuckoos*, *Nightbirds & Kingfishers of Australia*: 79. Pymble, N.S.W.: Angus & Robertson.

Olsen, P. 1997. Egg weight loss during incubation, and growth and development of captive-bred Southern Boobooks *Ninox novaeseelandiae*. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Monograph **3**: 92–97. Melbourne: Birds Australia.

Olsen, P. & Bartos, R. 1997. Home range of the Southern Boobook *Ninox novaeseelandiae* near Canberra ACT. In Czechura, G. & Debus, S. (eds.) *Australian Raptor Studies II*. Monograph **3**: 86–91. Melbourne: Birds Australia.

Schodde, R. and Mason, I. 1980. *Nocturnal Birds of Australia*. Melbourne, Aust.: Lansdowne.

Stephenson, B.M. 1998. The ecology and breeding biology of morepork, *Ninox novaeseelandiae*, and the risk from secondary poisoning, in New Zealand. Unpublished M.S. thesis. Palmerston North, N.Z.: Massey University.

Whitlock, F.L. 1923. A trip to the Fortescue River and Hamersley Ranges, North-West Australia. *Emu* **22**: 259 – 273.

30

INDEPENDENT EVOLUTION OF OUTER EAR ASYMMETRY AMONG FIVE OWL LINEAGES; MORPHOLOGY, FUNCTION AND SELECTION

R. ÅKE NORBERG

Department of Zoology, Zoomorphology, University of Göteborg, Box 463, 405 30
Göteborg, Sweden. email: ake.norberg@zool.gu.se

Asymmetry of the outer ear occurs among owls belonging to five phyletic lines, represented by the following genera: (1) *Tyto*; (2) *Phodilus*; (3) *Strix*; (4) *Rhinoptynx*, *Asio*, *Pseudoscops*; and (5) *Aegolius*. Various *Strix* species differ considerably in their degree of ear asymmetry, and in the structures involved. Within each of the other groups, however, ear morphology is rather uniform among species, but strikingly different between groups. In fact, differences in the form and structure of the asymmetry are so great between groups that ear asymmetry almost certainly originated independently in each one of the five owl lineages. Ear asymmetry makes the auditory directional sensitivity pattern for high frequencies different in elevation between the two ears. This enables the owl to localize sound in the vertical plane, by comparing the intensity and spectral composition of sound between the two ears. When an owl localizes ground-living prey by hearing, it usually sits or flies low in order to be close to the sound source, thereby improving detection. The direction of the sound source then forms a shallow angle with the ground. Therefore, a vertical angle of error, with respect to the true direction to the target, converts into a longer error in distance along the ground than does an equally large, horizontal, angular error. This trigonometrical relationship causes selection for high accuracy in the vertical localization of sound, which presumably underlies the evolution of ear asymmetry in owls.

INTRODUCTION

My aims in this paper are to: (1) describe briefly the anatomy of the five major types of ear asymmetry among owls, and show why each one of them must have evolved independently in a separate phyletic line; (2) explain the functional significance of ear asymmetry; and (3) expose the selection pressures that are likely to lead to the evolution of ear asymmetry. Much of the presentation is based on Norberg (1968; 1977; 1978 and on references therein), with new material and interpretations added.

MORPHOLOGY AND TERMINOLOGY OF THE OUTER EAR OF OWLS

External or outer ear

By *external* or *outer ear* is meant those ear structures that are outside of the eardrum. Parts of the external ear are thus the *external auditory meatus* or *acoustic meatus*, the *aural skin folds* or *flaps* bordering the ear aperture, the cavities between these skin folds and the skull, and also feathers around the ear.

Outer ear opening

I distinguish between two outer ear openings in owls.

1. The *ear opening in the skin* is the most external opening and is bounded by a skin fold that in some species is developed into conspicuous *preaural* and *postaural folds* or *flaps*. In some species the ear opening is merely a small oval hole in the skin, with its long axis shorter than the eye diameter. In others, the ear opening in the skin is narrow but very high, forming a *slit*, that reaches from below the lower jaw up to the top of the head.
2. The *ear opening in the skull* is the orifice of the external auditory meatus, and is formed by skeletal bone, covered by very thin skin. The lateral border of the opening is usually formed partly by a curved bone flange, the *squamoso-occipital wing*, vaulting over the ear canal, and often forming the most lateral part of the skull. The inner, medial, border of the ear opening is formed by the *postorbital process*, on which the eye rests, and by the *sclerotic eye ring*. This is a bone ring, or short tube, formed by a series of bone lamellae, encircling the eye ball and making the eye almost immobile.

Ear flaps

Most owl species have merely a narrow skin fold around the rim of the ear opening. But some species have a strongly developed *preaural skin fold* or *flap* that more or less overlaps the ear opening in the skin. And others have a well developed *postaural skin fold*, whose anterior part is deflected laterally, forming a broad, anteriorly facing rim, the edge of which bears the most anterior feathers of the *facial ruff*.

Ear feathers

Facial ruff. Behind and to the sides of the ear openings there are specialised, dense feathers that are extremely densely packed and form a *facial ruff*. Indeed, nowhere else on the owl's body are any feathers even nearly as densely packed as in the facial ruff. The ruff forms a concave surface to the sides of the ears. It is sound-reflecting and increases the sound intensity in the ear like a parabolic reflector. Some of the facial ruff feathers attach to the deflected edge of the postaural skin fold, or skin ridge, behind the ear opening, while the remaining ruff feathers are densely packed behind this rim.

The facial ruff is ill-defined or almost lacking in some species, whereas it is very prominent and almost encircling the face in those species that rely most heavily on hearing for prey localization.

Facial disc. In front of the ear opening lie modified, very sparse, 'sound-transparent' feathers, which attach to the rim and anterior surface of the preaural skin fold. They are arranged radially around the eye and form a rounded *facial disc*. The facial disc feathers easily let sound through, their main function obviously being to protect the ear canal from objects coming into it, and probably also preventing air turbulence and aerodynamic noise from arising at the ear opening. Usually the facial disc feathers only partly overlap the ruff as seen from in front, leaving an often dark-coloured rim of the ruff visible outside the disc. The facial ruff and disc together often give the owl face a distinctive, species-specific character.

External auditory meatus or ear canal

The *external auditory meatus* or *ear canal* is the canal between the ear opening and the eardrum. Inside the ear opening in the skull the ear canal expands behind the eye and runs backwards-downwards, then contracts as it passes outside the quadrate, after which it curves sharply downwards-inwards, and finally flattens and spreads out over the eardrum, which is located to either side at the bottom of the skull.

Between-ear, or binaural or bilateral ear asymmetry

Species of most owl genera have each ear shaped as a perfect mirror image of the other, the contralateral ear. However, pronounced *bilateral asymmetry* of the outer ear, meaning that the two ears are *not* mirror images of each other, is known in seven owl genera, and is referred to below simply as *asymmetry* of the ears. This must not to be confused with *monaural asymmetry*, meaning that in no way can one or more planes be oriented so as to divide one ear into two or more equal parts. The human pinna shows a familiar example of monaural asymmetry. This kind of ear asymmetry will not be further mentioned here.

The bilateral ear asymmetry among owls always concerns the outer ear only. From the eardrum and inwards, perfect bilateral symmetry prevails. This is also to be expected for theoretical reasons. Once the outer ear asymmetry has caused different, direction-dependent, transformation – coding – of the incoming sound in the two ears, that information should be transmitted unaltered through the middle ear, inner ear and onto the auditory nervous system, with no further differentiation between the ears. This is because bilateral asymmetry in the eardrum or structures inside of it could not perform any direction-dependent transformation of the incoming sound, situated far from the outside sound field as they are.

FIVE INDEPENDENT EVOLUTIONARY LINES OF EAR ASYMMETRY AMONG OWLS

The five major morphological types of outer ear asymmetry among owls will be briefly described here, presented by genera.

1. Tyto

The *Tyto* species have very complete facial ruffs and discs. They form a conspicuously heart-shaped face, with the ruff and disc completing nearly the full 360°. The facial ruff forms a concave surface, made up of compact and densely packed feathers. It collects sound over the entire face of the owl and guides the sound to the ear openings in the skin. The ear openings are about the size of the eye, and nearly square. They are of about the same size on both sides and each is covered by a big, almost square preaural skin flap, which reaches far lateral to the ear opening.

Ear asymmetry.

- Ear openings in the skin at different vertical levels. *Left* opening highest.
- Skin flaps in front of the ear of slightly different form on the left and right side and set at different vertical levels. *Left* flap highest. Because the flap is located further down in the concave face in the right ear than in the left ear, the right flap faces about 15° more upwards than the left flap.
- Ear asymmetry is caused by soft anatomy structures only, confined here to left-right differences in shape and position of the preaural flaps and to the position of the ear openings in the skin (Fig. 1).

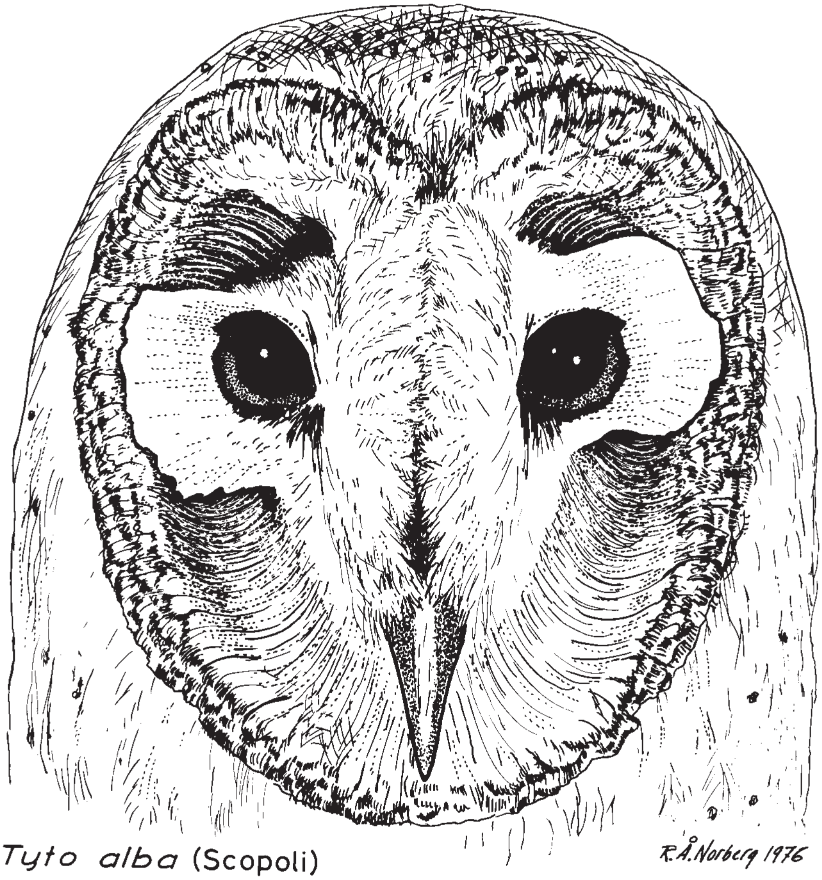


Fig. 1. Frontal view of *Tyto alba*, whose facial disk feathers have been removed from the drawing. The ear openings in the skin are small and nearly square and entirely overlapped by the preaural flaps, which are somewhat different in form in the left and right ear. The ear opening and the preaural flap are located higher on the left side. The facial ruff is extremely well developed, nearly completing the full 360°, and makes the entire face into two concave surfaces. In effect, because of the shape and structure of the facial ruff, each half-face forms a sound-collecting outer ear, which in its function, and even in its form, is like the human pinna. The facial disc feathers are normally attached radially around the eyes and onto the preaural flaps, and they overlap the facial ruff, except for a narrow peripheral border of the ruff, which comes to enframe the facial disc. All illustrations, except Fig. 2, bottom, are made by R. Å. Norberg.

2. Phodilus

Phodilus has a well developed facial ruff and disc, but unlike *Tyto*, *Phodilus* has a wide tract of forehead feathers, which separate the left and right parts of the facial ruff and disk above the beak. The facial ruff and disc extend upwards, above the top of the head, and are unlike those of any other owl. They give a unique and strange appearence to the owl.

The ear openings in the skin are small, oval, and of about the same relative size as in *Tyto alba*. There is no preaural skin flap.

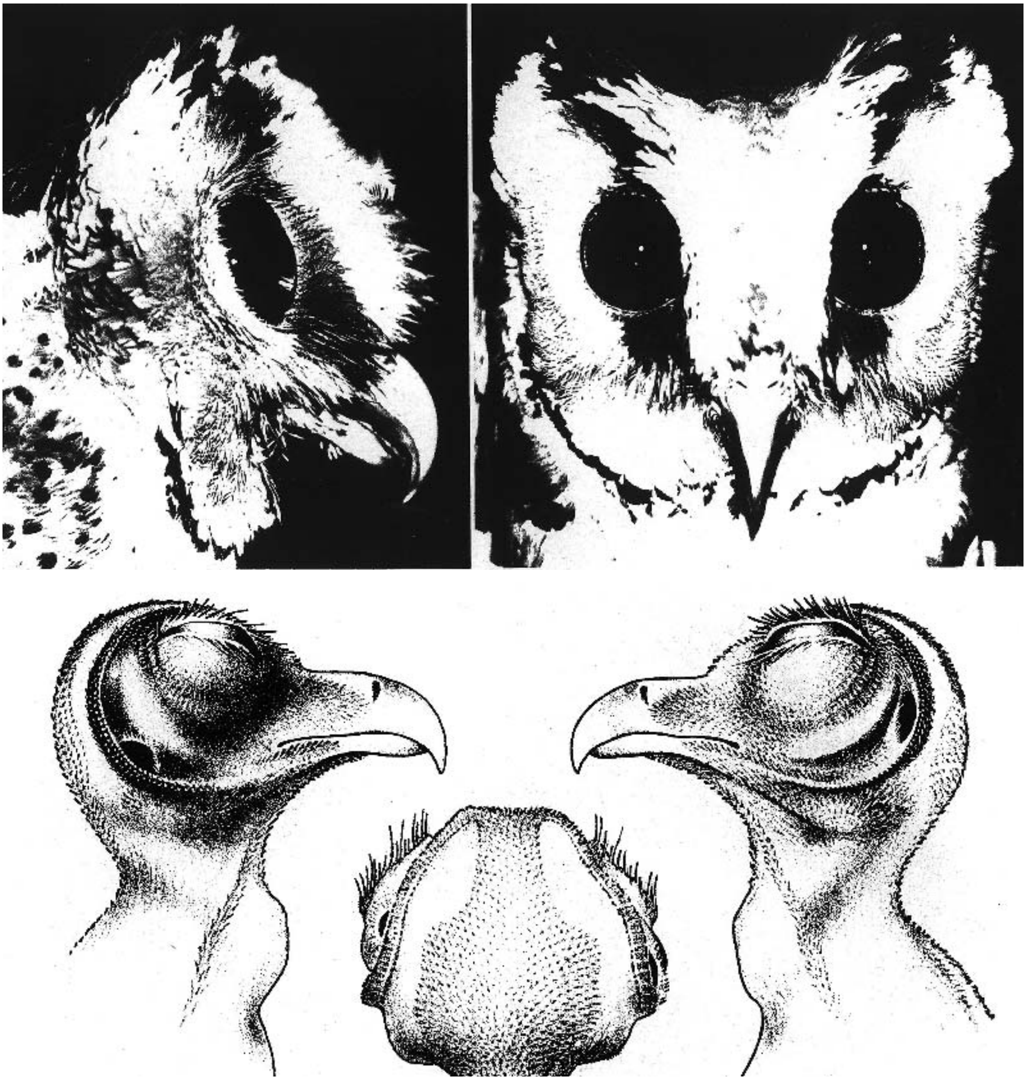


Fig. 2. *Top. Phodilus badius*. The form of the facial disc and ruff is unique among owls, and the eyes are enormously large. Photo: R. Å. Norberg. *Bottom.* Lateral and posterior views of the head of *Phodilus badius*. All feathers have been removed to show the different vertical locations of the ear openings in the skin, behind which lies a curved, dermal ridge on which the facial ruff feathers attach. From Pycraft (1903, Plate 2).

Ear asymmetry

- Ear openings in the skin at different vertical levels. *Left* opening highest.
- Ear asymmetry caused by soft anatomy structures only, confined here to left-right differences in vertical position of the ear openings in the skin (Fig. 2).

3. Strix

Among *Strix* species there is extreme diversity in ear morphology. This genus now contains all those species formerly placed in the genus *Ciccaba*. In fact, *Ciccaba* was formerly placed in subfamily Buboninae and *Strix* in subfamily Striginae. These two subfamilies were separated on the basis of the relative size of the ear openings in the skin. However, I have argued that *size* of the ear opening in the skin is a character of such small complexity, that it is much too easily modifiable by evolution to be adequate for taxonomic separation at subfamily level; so I rejected this division into subfamilies and also questioned the validity of the genus *Ciccaba* (Norberg 1977). These two former subfamilies and the genus *Ciccaba* are now suppressed. But this taxonomic history highlights the diversity of ear structure among species in the present genus *Strix* – an ear diversity once thought important enough to justify splitting at subfamily level.

The facial ruff and disc are moderately developed in some *Strix* species, like *Strix virgata*, whereas *Strix nebulosa* exhibits a facial ruff and disc that are huge in size and as well developed and complete as in *Tyto*, forming nearly a full 360°.

Ear asymmetry

Most species formerly assigned to the genus *Ciccaba* are now those *Strix* species which have the least developed ear asymmetry. Their asymmetry is the simplest and least complex in the genus *Strix*, and is exemplified here by *Strix virgata*:

- Ear openings in the skin of different size. *Right* opening largest, its height being about 55% larger than that of the left ear.
- Ear asymmetry caused by soft anatomy structures only, confined here to left-right differences only in the size of the ear openings in the skin (Fig. 3).

Between this simple kind of asymmetry, and the most complex one, there is a range of different asymmetries of varying complexity in the genus *Strix*. Below I describe the most complicated, extreme ear asymmetry, which occurs in *Strix nebulosa*:

- Ear openings in the skin of different size. *Right* opening largest.
- Skin flaps in front of the ear large, overlapping the ear opening in the skin, and of different shape in left and right ears.
- A nearly horizontal skin fold, or septum, located inside the ear opening in the skin, and above the ear opening in the skull, present in both ears, but with a slightly different position in the two ears.
- Asymmetry of the skull. The squamoso-occipital wing reaches farther antero-dorsally on the left side than on the right side, and the dorsal part of the postorbital process extends farther laterally on the right side. Because of this skull asymmetry, the ear openings in the skull are of different shape, and the left ear canal is directed more upwards than the right canal.
- Ear asymmetry caused by soft anatomy structures, but also by the skeleton of the skull; left-right differences in the size of the ear openings in the skin, in the shape of the preaural skin

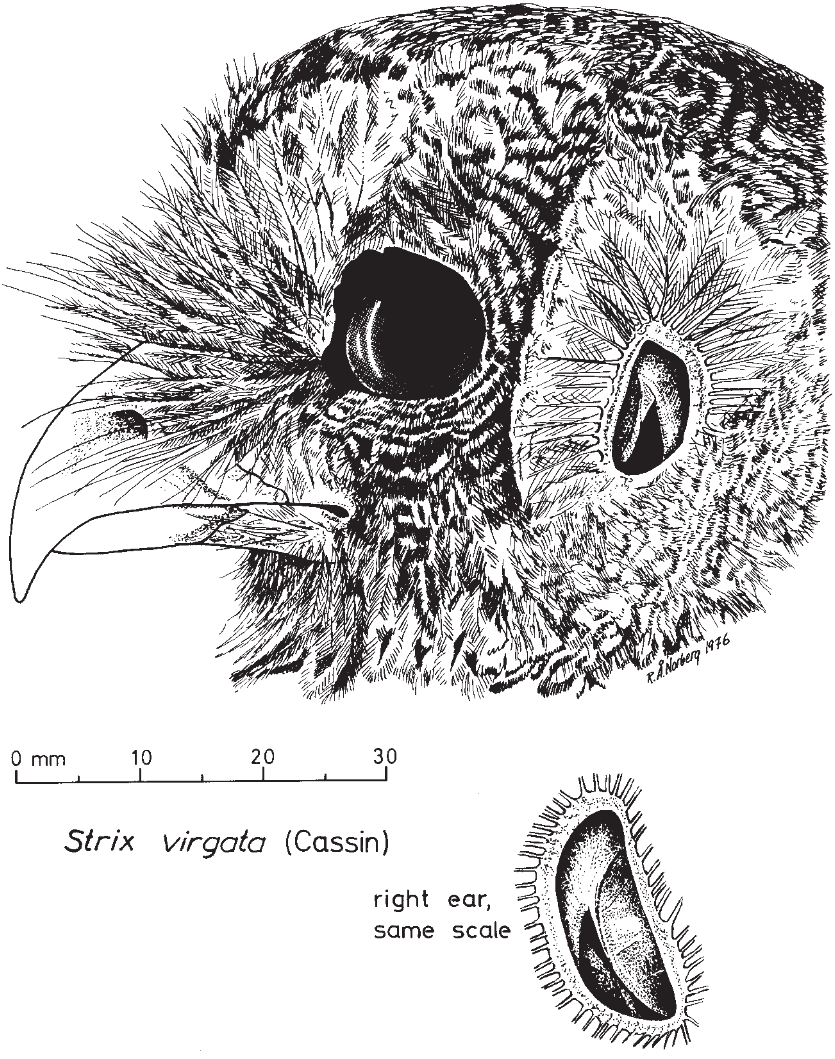


Fig. 3. Lateral view of the head of *Strix virgata*. The facial disc feathers over the ear opening are folded forwards and the facial ruff feathers behind the ear are folded backwards, to expose the unequally large ear openings in the skin.

flaps, in the position of a nearly horizontal skin septum above the ear opening in the skull, and also in the shape of the skull bones bordering the ear aperture in the skull.

4. Bubo

In *Bubo bubo* the right ear opening is larger than the left, just as among *Strix* species. But the right opening was only about 15% higher than the left one in the eight specimens examined. And no ear asymmetry has been reported in any other *Bubo* species. The edges of the ear opening in the skin in owls are rather lax, and the ear opening can easily be stretched and deformed, so it is rather difficult to take reliable and reproducible measurements. Therefore, I feel that the possible

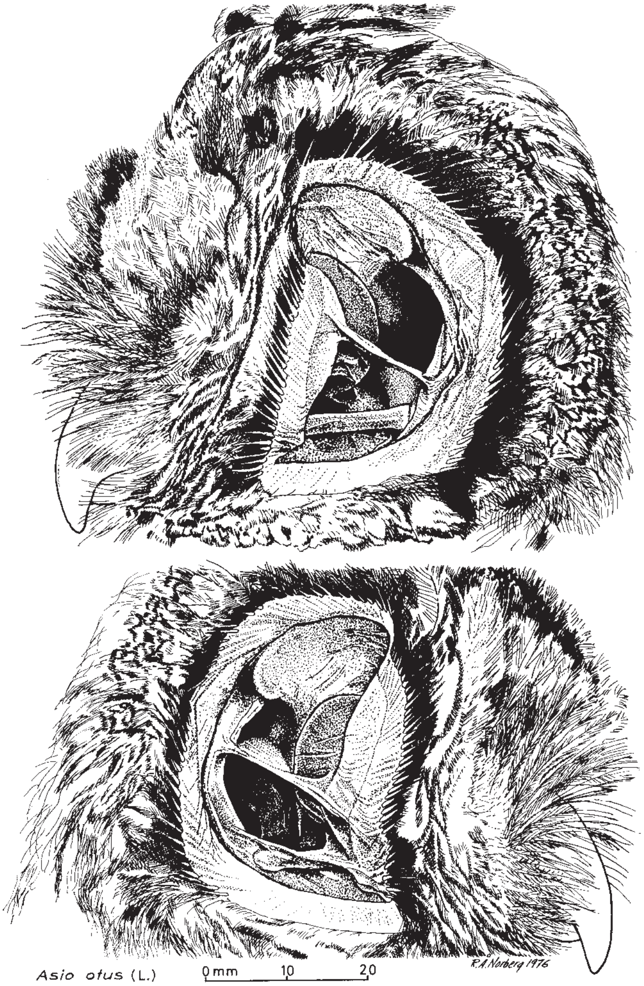


Fig. 4. Lateral view of the head and ear of *Asio otus*, with the jugal bar lying in the plane of the figure, so that the head is seen slightly from in front. The head and ears are intact, but the preaural flap is folded forwards and the postaural flap is displaced backwards to expose underlying structures of the outer ear. The bilateral ear asymetry is caused entirely by the different orientation of the nearly horizontal intra-aural skin septum in the left and right ear.

ear asymmetry in *Bubo* needs to be examined further – for its definition, consistency and occurrence among species.

5. Asio, Rhinoptynx, Pseudoscops

The ear openings in the skin are slit-like and very large, extending from below the lower jaw up to the top of the head, thus occupying the entire height of the head. The preaural flaps overlap the ear openings, which therefore open towards the side of the head. The ear openings in the skin, the postaural skin folds and the preaural flaps are perfectly symmetrical between the left and right side.

Rhinoptynx clamator of the new world was formerly placed in a monotypic genus but is now

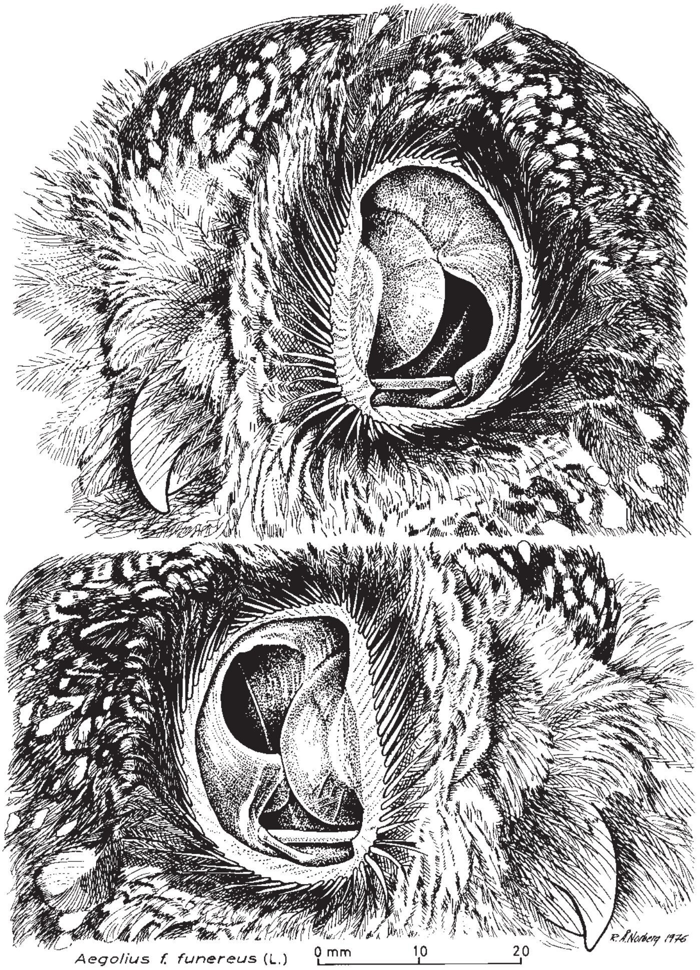


Fig. 5. Lateral view of the head and ear of *Aegolius funereus*, with the jugal bar lying in the plane of the figure, so that the head is seen slightly from in front. The head and ears are intact, but the preaural flap is folded forwards and the postaural flap is displaced backwards to expose underlying structures of the outer ear. The bilateral ear asymetry is caused entirely by the asymmetry of the head skeleton, namely the different position and orientation of the squamoso-occipital wing.

usually referred to as *Asio clamator*. *Pseudoscops grammicus* is endemic to the island of Jamaica and has a monotypic genus named for it.

Ear asymmetry

- Ear openings in the skull are perfectly symmetrical between the left and right sides, but a nearly horizontal intra-aural skin septum is oriented in different ways in the two ears. By very simple means, namely by different attachments of the septum to the inner and outer walls of the ear opening in the skull, the septa produce dramatic bilateral ear asymmetry.
- The functional ear openings in the skull are of different form and are located at different vertical levels, due entirely to the delimitation by the skin septum; *left* opening highest,

resulting in the left ear canal being directed markedly upwards, whereas the right canal is directed horizontally.

- Ear asymmetry caused by soft anatomy structures only, confined here entirely to the different orientation of a nearly horizontal skin septum in the left and right ear (Fig. 4).

6. Aegolius

The ear openings in the skin are slit-like and very large, extending from the level of the lower jaw up to near the top of the head, thus occupying almost the entire height of the head, but not quite as large as in *Asio*. The preaural flaps overlap the ear openings, which therefore open towards the side of the head. The ear openings in the skin, the postaural skin folds and the preaural flaps are perfectly symmetrical between the left and right side.

Ear asymmetry

- Ear openings in the skull are located at strikingly different vertical levels, due entirely to the different positions and orientations of the squamoso-occipital wing on each side of the skull, which produces a dramatic bilateral skull and ear asymmetry.

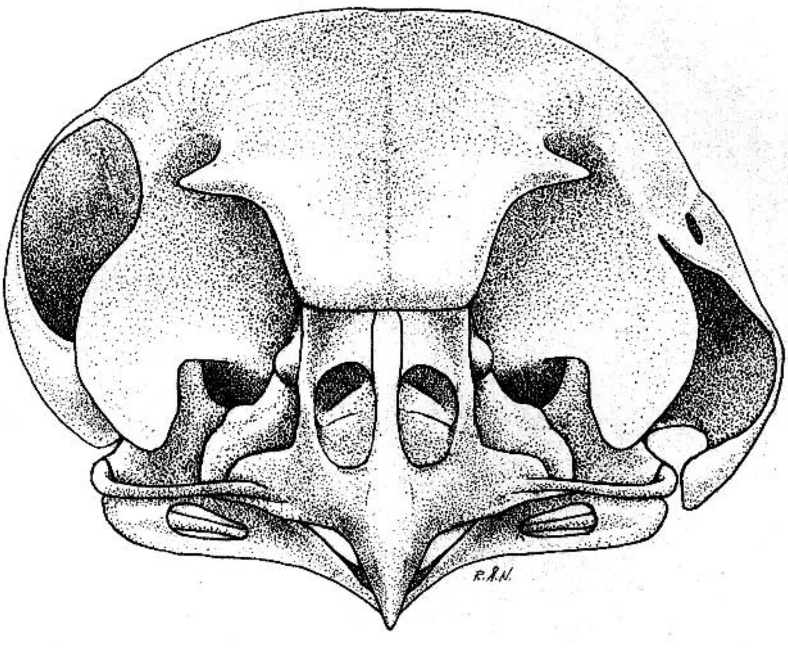


Fig. 6. Frontal view of the skull of *Aegolius funereus*, with the sclerotic eye rings and the rhamphotheca (horny beak sheath) removed. The asymmetry of the skull and of the ear openings in the skull is caused by the asymmetric position and orientation of the squamoso-occipital wings, which vault over, and form the outer wall of the ear canal. Apart from the squamoso-occipital wing, the asymmetry extends also to the neighbouring skull elements – orbitosphenoid, squamosal, parietal, and frontal. When the skull is viewed from in front, a line connecting the centres of the ear openings deviates 12° from the horizontal. And lines through the centre of the eardrum and the centre of the ear opening in each ear diverge vertically by 40° when the head is seen from the side, i.e. in a projection onto the vertical median plane of the head. This is the projected, vertical divergence angle between the left and right ear canal.

- The ear openings in the skull are of different form and are located at different vertical levels; *right* opening highest, resulting in the right ear canal being directed markedly upwards, whereas the left canal is directed horizontally – opposite to the situation in *Asio*.
- Ear asymmetry caused by head skeleton structures only, confined here entirely to the different positions and orientations of the squamoso-occipital wing and adjacent bones on the left and right sides.

Conclusion

Various *Strix* species differ considerably in their degree of ear asymmetry, and in the structures involved. Within each of the other groups, however, ear morphology is rather uniform among species, but strikingly different in structure and geometry between groups. Consideration of the probabilities that various anatomical similarities and dissimilarities in the outer ear have shared or independent evolutionary origins, leads to the conclusion that ear asymmetry has evolved independently at least five times among owls (Norberg 1977). The phylogenetic distribution of ear asymmetry supports this conclusion.

FUNCTION OF EAR ASYMMETRY

Symmetrical ears

Whenever the direction to a sound source is determined binaurally – by comparison of sounds received in the two ears – the all-important reference directions are those in which the sound is perceived equally in both ears. For animals with symmetrical head and ears these reference directions lie in the vertical, median plane of the head. When a sound source lies in this median plane, sound reaches the two ears simultaneously, and with the same intensity and spectral composition, i.e. with the same intensity in both ears for any frequency component of the sound (Fig. 7).

The *azimuth*, or *horizontal direction*, may therefore be determined, with reference to the vertical median plane, by using differences between the two ears in *arrival time* of sound, and in *intensity* and *spectral composition* of sound. The *vertical direction* can be determined *binaurally* only by tilting the head so that the reference median plane becomes oriented more or less horizontally, and then repeating the process.

Owls with symmetrical ears must determine the horizontal and vertical directions of a sound separately, one after the other, by tilting the head in between (Fig. 7). Therefore, a moving prey undividual will be in a different position when the vertical localization is made.

Asymmetrical ears

The description above applies also to owls with asymmetrical ears when sound contains low frequencies only, because the morphological ear asymmetry has no effect on the ears' directional sensitivity for low frequencies. But for *high frequencies* ear asymmetry makes the auditory directional sensitivity pattern different in elevation – in the vertical plane – between the two ears, which enables the owl to localize in the vertical plane by comparing intensity and spectral composition of *high-frequency sound* in the two ears without tilting the head (Fig. 8). Rustling sounds made by prey in vegetation or snow contain low as well as high frequency components and also transients. Moving prey, can therefore be localized both in the horizontal and vertical planes

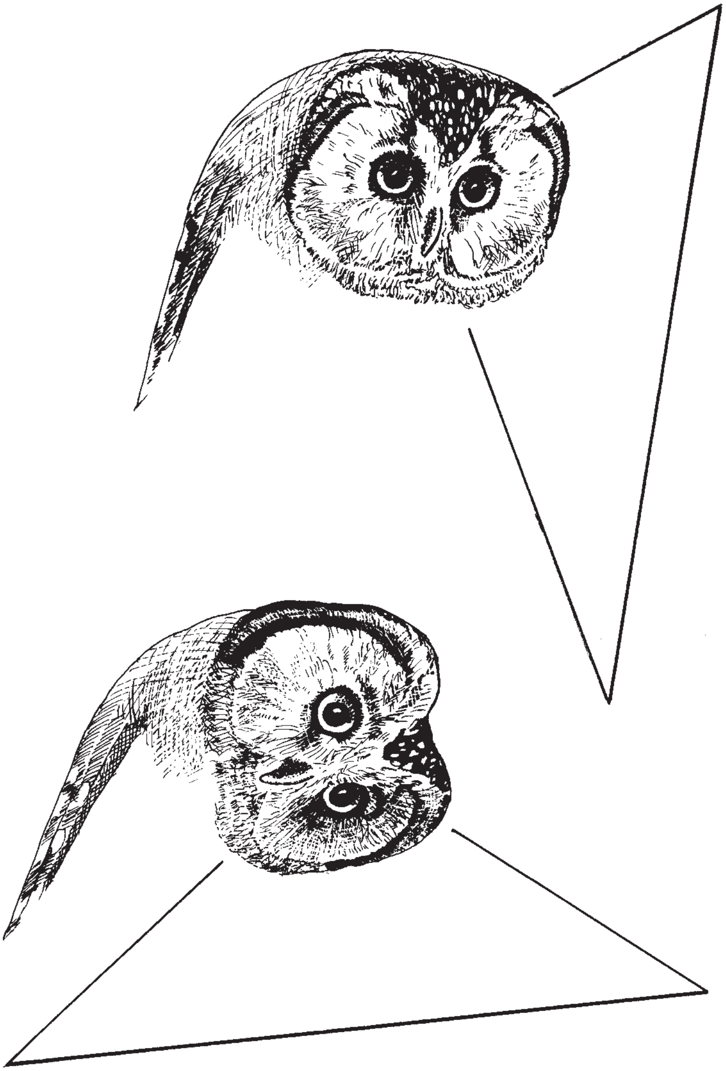


Fig. 7. With symmetrical ears, sound reaches the two ears simultaneously, and with the same intensity and spectral composition, whenever the source lies in the vertical median plane of the head – which is an all-important reference plane. Using binaural cues – differences in arrival time and intensity of sound between the two ears – and keeping the head upright, it is possible to localize only horizontally, in azimuth, i.e. with reference to the vertical, median plane of the head. Therefore, vertical direction can be determined *binaurally* only after tilting the head – again with reference to the vertical median plane of the owl's head, now tilted. And the azimuth must be remembered and combined with the succeeding vertical localization. Because of this time interval, a moving prey individual will be in different positions at the two localization events. These conditions and the associated localization difficulties apply also to owls with asymmetrical ears when sound contains low frequencies only, because then the structural ear asymmetry does not impose any vertical disparity between the directional sensitivity patterns of the two ears.

simultaneously, using binaural comparison. This is the great acoustical advantage with ear asymmetry. It saves time and avoids directional ambiguity with moving prey (Norberg 1968; 1978).

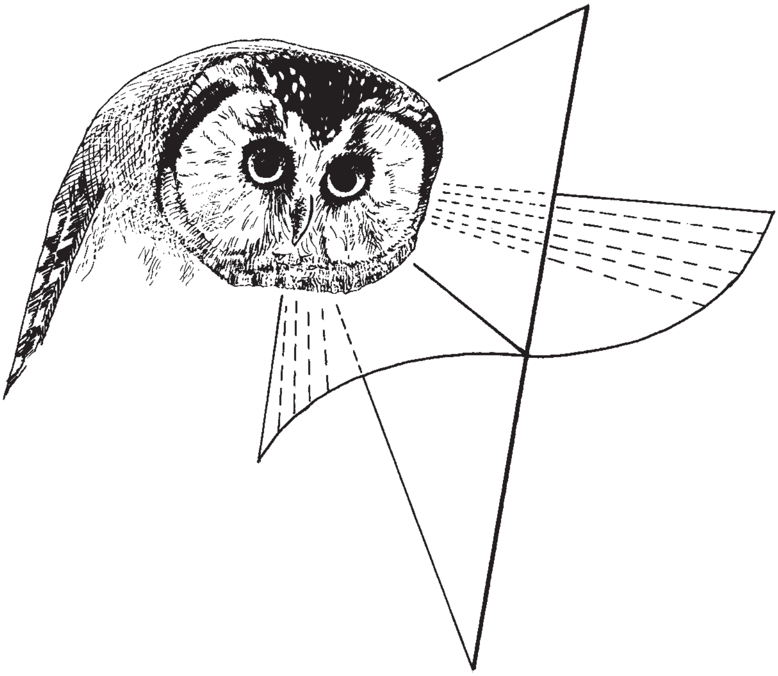


Fig. 8. With asymmetrical ears, time of arrival of sound to the two ears, and intensity of *low-frequency sound*, can still be used to localize in azimuth – horizontally, with reference to the vertical, median plane of the head. But owing to ear asymmetry, high frequency sounds are heard with equal intensity in directions lying on a curved surface that is almost horizontal near the owl's line of sight. Vertical localization can be made with reference to this surface by comparing intensity and spectral composition of *high-frequency sound* in the two ears. Therefore, broadband sound with transients can be localized *simultaneously* – without head tilting – both in azimuth and elevation, by binaural comparison of arrival time and intensity of low and high frequency sound components.

STEPS IN THE EVOLUTIONARY ORIGIN OF EAR ASYMMETRY IN OWLS

The following chain of causes and conditions must have been important for the evolutionary origin of ear asymmetry among owls.

- Selection by the owl of ground-living prey for food.
- Selection by the owl of habitats with dense forest or dense ground vegetation or with temporary snow cover.
- This makes visual hunting less useful but favours aural detection and localization.
- The use of hearing for detection requires that the owl is close enough to the sound source. In order to maximize its detection area, the owl must therefore select low perches or fly low if it hunts in flight.
- The direction to prey must be localized in two planes, both horizontally and vertically, whenever predator or prey are off ground level.
- From a low listening position, the direction to prey forms a shallow angle with the ground. Therefore, a given angle of error, with respect to the true direction to the target, converts into

a longer off-target in distance along the ground for a vertical angular error than for an equally large, horizontal angular error (Norberg 1977).

- This trigonometrical relationship causes selection for high localization accuracy in the vertical plane (in elevation).
- Directional localization must be quick, before prey reaches cover. With symmetrical ears horizontal and vertical localization can only be made successively, with head tilting in between, and with memorization of the horizontal direction, to be combined later with the vertical localization. This takes time, and allows prey to run into a new position between the two localization events.
- Ear asymmetry is an adaptive answer to the selection pressures described above. It enables the owl to localize *quickly* and *simultaneously* both in the horizontal and vertical planes.

ACKNOWLEDGMENTS

I gratefully acknowledge a travel grant from The Royal Society of Arts and Sciences in Göteborg.

REFERENCES

Norberg, R. Å. 1968. Physical factors in directional hearing in *Aegolius funereus* (Linné)(Strigiformes), with special reference to the significance of the asymmetry of the external ears. *Arkiv för Zoologi* **20:** 181–204.

Norberg, R. Å. 1977. Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. *Phil. Trans. Roy. Soc. Lond. Ser. B.* **280:** 375–408. Plates 1–4.

Norberg, R. Å. 1978. Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's Owl, *Aegolius funereus* (Linné). *Phil. Trans. Roy. Soc. Lond. Ser. B.* **282:** 325–410. Plates 1–10.

Pycraft, W. P. 1903. On the pterylography of *Photodilus*. *Ibis* **1903:** 36–48.

31

THE TAXONOMY AND CONSERVATION STATUS OF THE OWLS OF THE WORLD: A REVIEW

JOHN M. PENHALLURICK

Applied Ecology Group, Division of Communication and Education, University of Canberra, A.C.T., Australia 2601

This paper reviews the current taxonomy and status of the owls of the world. It compares the number of genera and species in the accounts of Peters (1940) and König *et al.* (1999). Based on the analysis of mtDNA sequencing and other methodologies, several genera in Peters, including *Pseudoptynx* and more recently *Ketupa*, are lumped into *Bubo*, and it is suggested that *Nyctea* should also be so placed; *Ciccaba* is merged into *Strix*; *Speotyto* into *Athene*; and *Rhynoptynx* into *Asio*. Recent mtDNA evidence also suggests that *Otus* is polyphyletic and should be split into at least four distinct genera: African *Ptilopsis* for *leucotis* and its sister species *granti*; *Otus* for Eurasian and other African species; and *Megascops* for all American species except for the aberrant *flammeolus*, which should be transferred to a monotypic genus *Psiloscops*. It is similarly argued, on the basis of mtDNA data, that the Old World species under *Glaucidium* should be split between *Glaucidium* and *Taenioglaux*, and that all the New World species should be transferred to *Phalaenopsis*. The addition of species through the discovery of new taxa and the splitting up of particularly *Otus scops* and *O. bakkamoena* is discussed. I examine, and provide brief comment, on the four owl species classed as Critical, the five classed as Endangered, and the 17 classed as Vulnerable. A plea is made for more attention to be paid to subspecies or 'ultrataxa', and the extremely threatened status of several subspecies is mentioned.

INTRODUCTION

The number of owl taxa that have been recognised as species has increased greatly over the past 60 years or so, mainly because of advances in taxonomic research, but also because of discoveries of previously unknown species. At the same time, attempts have been made to classify the conservation status of different species, according to different categories of risk. In this paper, I attempt to review both the taxonomic and conservation status of different species. I make the point that several taxa, currently classed as subspecies, might after investigation be proved to be more appropriately classed as species, or in any case, are worthy of special conservation efforts. Throughout the text, the use of single letters is intended to refer the reader to the endnotes.

RESULTS

Taxonomic status of owls

The numbers of recognised species have increased greatly in the last 60 years. Peters (1940: 77–174) lists 141 species of owls in the families *Tytonidae* and *Strigidae*. del Hoyo *et al.* (1999) list 195 species in the same two families, and drawing on even more recent research, König *et al.* (1999:35) recognise 'at least 212 species'. The numbers in Table 1 represent the number of species

Table 1. Genera and numbers of owl species listed in Peters (1940) and König *et al.* (1999).

From Peters, 1940		**From König *et al.* 1999**	
TYTONIDAE		TYTONIDAE	
Tyto	8	Tyto	17
Phodilus	1	Phodilus	1
STRIGIDAE		STRIGIDAE	
Otus	36	Otus	62
Pyrroglaux	1	Pyrroglaux	1
Gymnoglaux	1	Gymnoglaux	1
		Ptilopsis[xxx]	2
Mimizuku	1	Mimizuku	1
Jubula	1	Jubula	1
Lophostrix	1	Lophostrix	1
Pseudoscops	1	Pseudoscops	1
Bubo	11	Bubo[xxxi]	20
Pseudoptynx	1		
Ketupa	4		
Scotopelia	3	Scotopelia	3
Nyctea	1	Nyctea	1
Pulsatrix	3	Pulsatrix	4
Strix	12	Strix[xxxii]	21
Ciccaba	5		
Glaucidium	13	Glaucidium	30
Xenoglaux			1 (new)
Micrathene	1	Micrathene	1
Athene	3	Athene[xxxiii]	4
Speotyto	1		
Aegolius	3	Aegolius	4
Ninox	18	Ninox	21
Uroglaux	1	Uroglaux	1
Sceloglaux	1	Sceloglaux	1
Surnia	1	Surnia	1
Neasio	1	Nesasio	1
Asio	6	Asio[xxxiv]	7
Rhynoptynx	1		

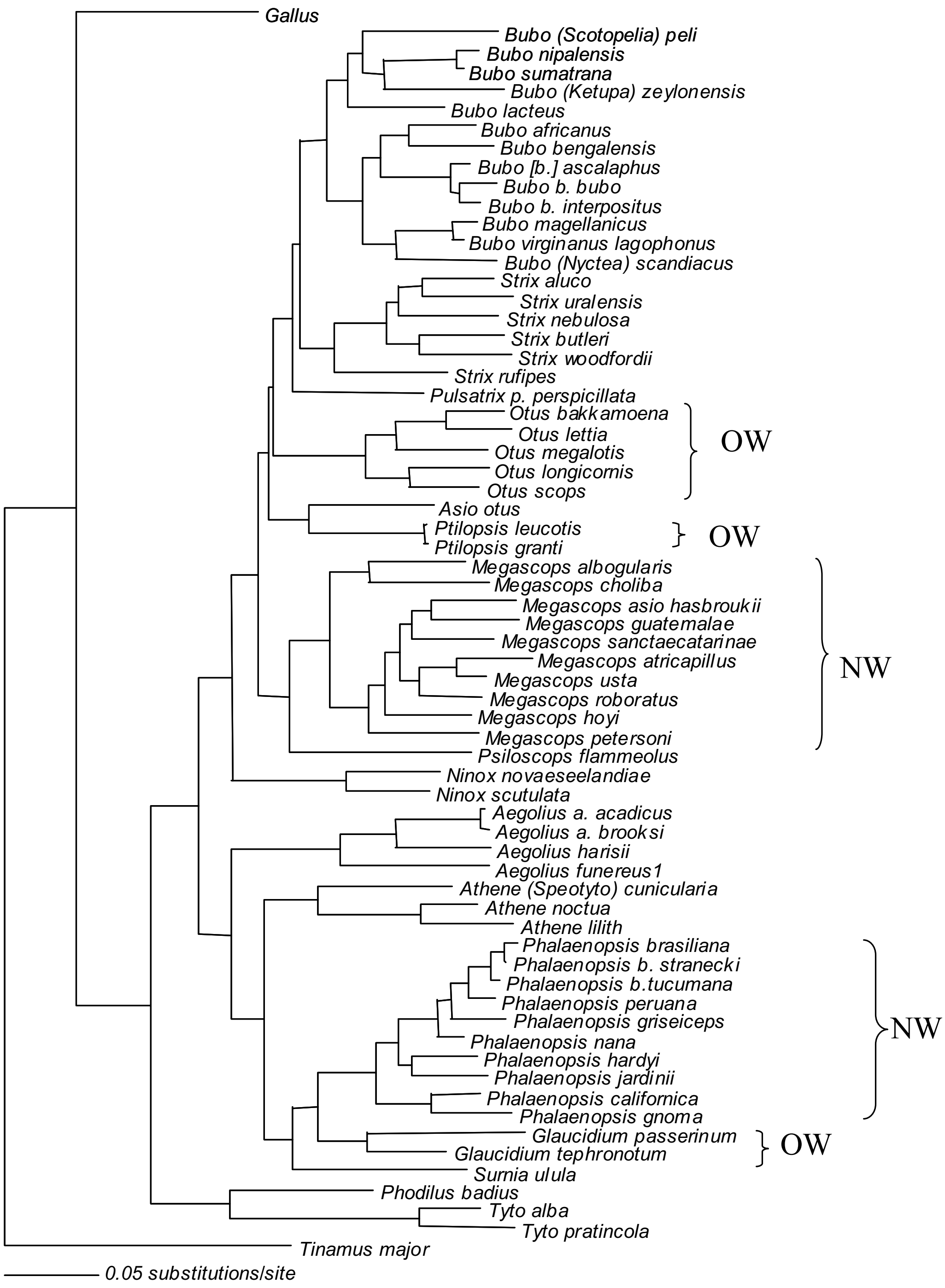


Fig. 1. Maximum Likelihood Tree showing relationships of owls as determined by sequencing of mtDNA cytochrome b (1040 base pairs).[xxxv] NW = New World, OW = Old World

in each genus, as given by Peters (1940) and König *et al.* (1999), with genera listed in the sequence of König *et al.*(1999).

At the generic level, relatively little change is apparent. *Xenoglaux* O'Neill & Graves 1977 is a new genus for the newly discovered Long-whiskered Owlet *Xenoglaux loweryi* from the Peruvian Andes. The reasons for most of the other changes at the generic level can be seen by considering Fig. 1[i]. This represents genetic relationships within the *Tytonidae* and *Strigidae* based on analyses of the cytochrome b gene from mitochondrial DNA.[ii] The tree is based on the Maximum Likelihood method, which '...has been considered as the best tree reconstruction method available at present.' (Wink & Heidrich in König *et al.* 1999:40).

Ketupa Lesson 1830 (as represented in Fig. 1 by Brown Fish Owl formerly *Ketupa zeylonensis*) has as its closest relatives three *Bubo* owls: Verreaux's Eagle Owl *B. lacteus*, Forest Eagle Owl *B. nipalensis*, and Barred Eagle Owl *B.sumatrana*. Given the relatively shallow depth of the link, corresponding to a genetic (mt DNA, cytochrome *b* gene) distance of 10.2% between *zeylonensis* and *nipalensis*, and 9.2% between *zeylonensis* and *sumatrana* (cf.König *et al.*1999: 51–54), the maintenance of *Ketupa* at the generic level is untenable. König *et al.* (1999:43) therefore merge *Ketupa* into *Bubo* Duméril 1806.[iii] A similar logic dictates that *Nyctea* Stephens 1826, the monotypic genus containing the Snowy Owl *Nyctea scandiaca*, should become a subgenus of *Bubo* (although Köning *et al.* do not take this step), reflecting genetic distances of 8.1% between *scandiaca* and *B.virginianus*, and 9.0% between *scandiaca* and *B. magellanicus* (cf.König *et al.*1999: 51–54). Similar analyses (Fig. 1) suggest that *Scotopelia* should also be reduced to a subgenus of *Bubo*. The Burrowing Owl, formerly *Speotyto cunicularia*, clusters unambiguously with *Athene*, which means that the former monotypic genus *Speotyto* Gloger 1841 should be submerged in *Athene*, surviving only at subgeneric level.

Ciccaba Wagler 1832, as represented by the African Wood Owl *Ciccaba woodfordi* (Peters 1940:155), clearly groups with *Strix*. [iv] The monotypic genus *Rhinoptynx* Kaup 1851 with *R. clamator*, has been submerged in *Asio*, which accounts for the extra species in *Asio*. Similarly, the monotypic *Pseudoptynx* Kaup 1851, with *P. philippensis*, has been merged with *Bubo*. The former *Otus leucotis* has been transferred to *Ptilopsis* Kaup 1848.[v]

Some of the most interesting data in Fig.1 relate to two of the biggest genera, *Otus* and *Glaucidium*, although this is not adequately reflected in the generic names used by König *et al.* (1999). Not only is the genus *Otus* Pennant 1769, polyphyletic in relation to the taxa now assigned to *Ptilopsis*; but also in relation to the New World and Old World representatives of *Otus*. The Old World *Otus* species have as a sister-clade the entire remainder of the family *Strigidae*, whereas the New World *Otus* species have as a sister-clade a group incorporating *Bubo*, *Pulsatrix* and *Strix* (Fig. 1). It is clearly incorrect to place the New World taxa in the genus *Otus*, which has as its type *Otus bakkamoena* Pennant 1769. The oldest available generic name applicable to the New World taxa is *Megascops* Kaup 1848, whose type species is *Otus asio* Linnaeus 1758, so at least some of the New World taxa formerly in *Otus* should be transferred to *Megascops* and perhaps other genera.[vi]

However, König *et al.* (1999: 227) retain the New World *Otus flammeolus* in *Otus* on both morphological and vocal grounds.[vii] That *flammeolus* is distinct from other New World '*Otus*' species is clear. Ridgway (1914: 686 and 728) emphasized the many points of morphology in which *flammeolus* differs from other New World '*Otus*' species; but he also (1914:628) points out how, despite 'superficial' morphological similarities with *Otus scops* Linnaeus,1758, *flammeolus* differs from the Old World species.

The mtDNA data of Wink & Heidrich (in König *et al.*1999) clinches the case that *flammeolus* is odd among both New and Old World Scops Owls. *Otus flammeolus* is indeed distant, in genetic terms, from other New World '*Otus*' owls: 14.8% from *O. asio*; 14.5% from *O. atricapillus*; 14.0% from *O. guatemalae*; 15.9% from *O. choliba*; 14.3% from *O. hoyi*; 14.6% from *O. petersoni*; 15.1% from *O. roboratus*; 14.5% from *O. sactaecaterinae*; and 14.3% from *O. usta*. But it shows even greater percentage distances from all the Old World *Otus* species included in the sample: 15.8% from *O. 'bakkamoena'*; 15.9% from *O. lempiji*; and 17.6% from *O. scops*. The tree in Fig. 1 (like Fig. 55a, König *et al.* 1999: 45) places *O. flammeolus* as a sister-clade to a clade representing the entire remainder of the New World '*Otus*' species, but with an equally distant relationship to the Old World *Otus* species[viii]. The position of *O. flammeolus* also requires that it be assigned to a new genus distinct from both *Megascops* and *Otus*. The oldest (in fact apparently the only) available name appears to be *Psiloscops* Coues 1899[ix].

Another interesting genus in Fig.1 is *Glaucidium*. Wink & Heidrich (in König *et al.* 1999:41) state that '…the Old and New World species cluster in separate monophyletic clades which possess a common ancestry but diverged more than 7–8 million years ago.' We read further(1999: 348): 'Most African and some Asian species lack the 'occipital face' but have barred head and nape, and do not cock and flick tail. These should probably be removed from this genus, as they seem to be more closely related to the genus *Athene*; we consider them to be members of a subgenus *Taenioglaux*. According to DNA evidence, the American pygmy owls are not closely related to those of the Old World.' Resorting to subgenera seems inadequate to capture accurately the phylogeny of the taxa hitherto grouped under *Glaucidium*. The revised *Glaucidium* should include its type species, *G. passerinum*, together with *G. perlatum* and *G. tephronotum*. Other Old World species should be referred to *Taenioglaux* Kaup 1848 (Type species *Strix radiata* Tickell, 1833): namely, *T. radiata*, *T. castanonota*, *T. sjostedti*, *T. capensis*, *T. castanea*, *T. albertina*, *T. cuculoides*, *and T. castanoptera*. The New World taxa hitherto assigned to *Glaucidium* also need to be reassigned. The earliest available name is *Phalaenopsis* Bonaparte 1854.[x]

In relation to changes in the number of species, the situation with *Ninox* is a little complicated. The extra three species in König *et al.* (1999) are partly the result of splitting Christmas Hawk-Owl *Ninox natalis* from Moluccan Hawk-Owl *N. squamipila*, a split which is universally accepted; and also of separating Southern Boobok *Ninox boobook* from Morepork *Ninox novaeseelandiae*. However, L. Christidis has publicly stated that the similar split in P.Olsen (in del Hoyo *et al.* 1999:232) is based on a misinterpretation of his DNA results, and that the Australian and New Zealand boobooks (together with those of New Guinea and Wallacea[xi]) should be seen as one species.[xii] The recent description of Cinnabar Hawk-Owl *Ninox ios* Rasmussen, 1999, from Sulawesi, still takes us back to an extra two species in the genus *Ninox*.

Some of the other increases in species numbers result from newly described species. This includes the little-known Congo Bay Owl *Phodilus* (or *Tyto*) *prigogenei* Schouteden, 1952.[xiii] It also includes twelve species of *Otus*, namely Sokoke Scops Owl *O. ireneae* Ripley 1966; Mindanao Scops Owl *O. mirus* Ripley & Rabor 1968; Moheli Scops Owl *O. moheliensis* Lafontaine & Moulaert 1999; Comoro Scops Owl *O. pauliani* Benson 1960; Sangihe Scops Owl *O. collari* Lambert & Rasmussen 1998; Nicobar Scops Owl *O. alius* Rasmussen 1998; and, in the New World (and hence better placed in *Megascops*; see above) Balsas Screech Owl *O. seductus*[xiv] Moore 1941; Koepcke's Screech Owl *O. koepckeae* Hekstra 1982; Hoy's Screech Owl *O. hoyi* König & Stranek 1989; Colombian Screech Owl *O. colombianus* Traylor 1952; Cloud-forest Screech Owl *O. marshalli* Weske & Terborgh 1981; and Cinnamon Screech Owl *O. petersoni* Fitzpatrick & O'Neill 1986.

Seven new species have been described in the genus *Glaucidium* (or better, since they are all from the New World, *Phalaenopsis*; see above), namely Cloud-forest Pygmy Owl *G. nubicola*[xv] Robbins & Stiles 1999; Tamaulipas Pygmy Owl *G. sanchezi* Lowery & Newman 1949; Subtropical Pygmy Owl *G. parkeri* Robbins & Howell 1995; Yungas Pygmy Owl *G. bolivianum* König 1991; Hardy's Pygmy Owl *G. hardyi* Vieillard 1990; Peruvian Pygmy Owl *G. peruanum* König 1991; and Albertine Owlet *G.* (better *Taenioglaux*) *albertinum* Prigogine 1983.

The increase of seven species in *Bubo*, except in the case of the lumping of *Pseudoptynx* mentioned above, is a result of splits, rather than newly described species. The Magellanic Owl *B. magellanicus* (J.F.Gmelin 1788), p.287 has been split from Great Horned Owl *B. virginianus*[xvi] (J.F.Gmelin) 1788, p.286; the Rock Eagle Owl *B. bengalensis* (Franklin 1831) and Pharaoh Eagle Owl *B. ascalaphus* Savigny 1809 have both been split from the Eurasian Eagle Owl *B. bubo* (Linnaeus 1758). In all three species, both DNA data and voice support the split (König *et al.* 1999:295 and 296).

The twelve new *Otus* species mentioned above account for less than fifty percent of the twenty-six additions to '*Otus*' overall in Table 1, so splits have also played an important part with this genus.[xvii] In the Old World, the major splits in what Peters (1940) considered species have been with *Otus scops*, from which *O.mirus*, *O.sunia*, *O.elegans*, *O.longicornis*, *O.mindorensis* and *O.mantanensis* have been separated; and with *Otus bakkamoena*, from which *O. semitorques*, *O.lettia*, *O.lempiji*, *O. mentawi* and *O.fulginosus* have been separated.

The judgments of Peters (and of ornithologists up to and including at least Burton (1973)) were largely based on appearance. This was true of many of the judgments on which species limits in the traditional taxonomy were based. Ornithologists in museums examined skins. With what was available to them, they did a magnificent job. But they often lacked information on calls and song, habitat, behaviour and precise location, all of which played a role in recent separations.[xviii]

Calls are critical in relation to species boundaries among owls. The discussion of systematics by Marks, Cannings and Mikkola in del Hoyo *et al.* (1999:76–151) indicates that similarities in appearance have made classification of some species of *Otus* difficult, and stresses the need to focus on the most important isolating mechanisms, which for nocturnal owls are vocalisations.[xix] If the vocalisations of the males of two taxa differ, they are likely to represent distinct species.

In relation to the forms formerly included in *Otus scops*, the combination of different vocalizations and DNA evidence supports separation of the sub-Saharan *O. senegalensis* and East Asian *O. sunia*. Of the East Asian forms largely subsumed formerly in *O. bakkamoena*, the forms *O.lettia*, *O.lempiji*, *O. semitorques* and *O.bakkamoena* should be separated, as they are in del Hoyo *et al.* (1999: 157–159).

Since *ussuriensis*, which del Hoyo *et al.* (1999: 158) put in *O.lettia*, is closer to *O. semitorques* in voice and plumage, and intermediate in eye colour, it seems logical to include that subspecies in *semitorques*, as König *et al.* (1999:248) do. Also *Otus* (*?lempiji*) *cnephaeus*, the form resident in southern peninsular Malaysia, has distinct vocalisations, so is probably a species separate from *O.lempiji*.

The other major problematic group is the New World '*Glaucidium*' complex, which would more appropriately be referred to a new genus (or genera). König *et al.* (1999:354) affirm decisively that the Northern Pygmy Owl *G. californicum* and Cape Pygmy Owl *G. hoskinsii* are specifically distinct from *G. gnoma* by vocalisations, ecology and DNA evidence. *G. minutissimum* is confined to eastern Brazil. As König *et al.* (1999:365) state of another supposedly widespread species, *G. jardinii* is endemic to the NW Andes of west Venezuela, north-central Colombia, central and east Ecuador and Peru south to the Marañon depression, and specifically distinct from all other taxa which traditionally have been merged with it. As mentioned above, all of these species are better placed in *Phalaenopsis*.

Conservation status of owls

Many species of owls are at risk to some degree. The standard categories of risk are defined by the IUCN (Collar *et al.* 1994:14–15, based on Mace & Stuart, 1994, which, in turn, built on Mace & Lande, 1991).

Critical Species. Under Critical[xx] are found: Anjouan Scops Owl *Otus capnodes*; Comoro Scops Owl *O. pauliani*; Seychelles Scops Owl *O. insularis*; and Forest Owlet *Athene blewitti*. The first three are restricted to small islands. *O. capnodes* is confined to Anjouan in the Comoros, specifically to a very small area of less than 20 square kilometres, where habitat continues to be destroyed. The owl is also hunted for food and current numbers are unlikely to exceed 200 breeding pairs. *O. pauliani* is confined to Grand Comoro, in an area of about 1,000 square kilometres, also subject to habitat destruction. Current numbers are about 1,000 pairs. The Seychelles Scops Owl *O. insularis* is apparently restricted to one island, Mahé, in the Seychelles, where it was rediscovered in 1959. Current numbers are estimated at about 200 breeding pairs, but the species is vulnerable from habitat destruction, and probably from introduced predators. It is better off than the two Comoros species in that some conservation measures are in place.

Of the other species whose status is considered Critical, few ornithologists can be unaware of the rediscovery of the Forest Owlet *Athene blewitti* in India in 1997. The species is restricted to plains and low foothills of the Akrani Range in northwest Maharashtra, and possibly also in eastern Madhya Pradesh and western Orissa, though there are no twentieth century records from these latter areas. The main threat is habitat destruction from increasing human population pressure (Ishtiaq *et al.* 2002).

Endangered species. Five species are categorized as Endangered:[xxi] Madagascar Red Owl *Tyto soumagnei*; Lesser Eagle Owl *Mimizuku gurneyi* of the Philippines; Philippine Eagle Owl *Bubo philippensis*; Blakiston's Fish Owl *Bubo* (*Ketupa*) *blakistoni* of northeast Asia; and Rufous Fishing Owl *Bubo* (*Scotopelia*) *ussheri* of West Africa.[xxii]

With no records of *Tyto soumagnei* between 1934 and 1973, a few birds were caught and radio-tagged on the Masoala Peninsula in the 1990s. The species appears restricted to the rainforest of eastern Madagascar and is apparently rare, the main threat being continuing habitat destruction.

The Lesser (or Gurney's) Eagle Owl *Mimizuku gurneyi* of the islands of Mindanao, Dinagat and Siargao is apparently found mainly in lowland forest, although it also occurs on Mt. Kitanglad and Mt. Apo. Anyone who has visited the Philippines cannot help but be aware of the extent of habitat destruction and fragmentation, particularly in the lowlands, and this constitutes the main threat to this species.

The same pressures threaten the Philippine Eagle-Owl *Bubo* (*Pseudoptynx*) *philippensis*, also a bird mainly of lowland rainforest. Although recorded historically from Catanduanes, Mindanao, Samar and Leyte, all the few recent records have come from Luzon. It is clearly very rare, and may also be subject to hunting pressure.

Blakiston's Fish Owl or Eagle Owl *Bubo* (*Ketupa*) *blakistoni* has been transferred by König *et al.* (1999:43) from *Ketupa* to *Bubo*, along with the other former members of *Ketupa*, as discussed above. Probably fewer than 500 pairs remain in Ussuriland, Sakhalin, the south Kuriles, northeast China (including western Manchuria) and Hokkaido. The main threats to this owl are destruction of its riverside habitat through logging and human settlement, and also overfishing.

The Rufous Fishing Owl *Bubo* (*Scotopelia*) *ussheri* is confined to the upper Guinea Forest of Sierra Leone, Liberia, Ivory Coast and Ghana. Although it occurs in several protected areas,[xxiii] given the recent civil wars in the first three of those countries, little if any protection is presumably afforded. In addition to habitat destruction, this rare owl is threatened in places by pollution from mining, and also by capture for pets.

Vulnerable Species. Seventeen species are listed as Vulnerable[xxiv] in Collar *et al.* (1994:113–116): Taliabu Masked Owl *Tyto nigrobrunnea*; Manus Masked Owl *T. manusi*; Bismarck Masked Owl *T. aurantia*; Congo Bay Owl *Phodilus* or *Tyto*[xxv] *prigoginei*; White-fronted Scops Owl *Otus sagittatus*; Sokoke Scops Owl *O. ireneae*; Javan Scops Owl *O. angelinae*; Mindanao Scops Owl *O. mirus*; Luzon Scops Owl *O. longicornis*; Mindoro Scops Owl *O. mindorensis*; Palawan Scops Owl *O. fuliginosus*; Usambara Eagle Owl *Bubo vosseleri*; Albertine Owlet *Glaucidium albertinum*; Sumba Boobook *Ninox rudolfi*; Sichuan Wood Owl *Strix davidi*; and Fearful Owl *Nesasio solomonensis*. The assignment by Collar *et al.* (1994:116) and del Hoyo *et al.* (1999:231) of the Powerful Owl *Ninox strenua* of eastern Australia to this category is clearly not warranted.[xxvi]

The list includes four *Tyto* owls from the New Guinea-Wallacean region, all at risk from habitat destruction and low numbers. The same applies to other owls from the Wallacean and Southeast Asian regions, including *Ninox rudolfi* of Sumba, where only about 10 per cent of the original closed canopy forest remains; *Otus angelinae* of Java, known from only two localities; *O. sagittatus* of peninsular Myanmar, Thailand and Malaysia is thought to be a lowland forest specialist, and thus at particular risk. *Strix davidi* from central and western Sichuan and southeast Qinghai also suffers from extensive deforestation of its open coniferous and mixed forest habitat.

Five *Otus* species endemic to the Philippines are all at risk from the massive and widespread destruction of forest in these islands. Of the four African species, *Otus ireneae* is mainly known from the Sokoke-Arabuko forest of coastal Kenya[xxvii] which, despite its protected status, still suffers from logging. *Phodilus progoginei* and *Glaucidium albertinum*,[xxviii] both of the Albertine rift mountains of eastern Zaire, Rwanda and Burundi, also have limited habitat remaining. *Bubo vosseleri* of northeast Tanzania was not seen between its discovery in 1908 and 1962 and is thought to be an altitudinal migrant. Lowland forest in the Usambaras is limited and subject to clearing. However, the discovery of a population in the Uluguru Mountains of Tanzania, and the fact that the species can tolerate some kinds of agriculture, such as cardamom plantations which require a closed canopy, suggest that *Bubo vosseleri* may be less at risk than previously thought. Finally, the monotypic *Nesasio solomonensis* is confined to Bougainville, Choiseul and Ysabel of the north Solomons. It is little known and rare, and presumably threatened by forest destruction.

In conclusion, if one goes through the list of owls in either del Hoyo *et al.* (1999) or König *et al.*(1999), one can quickly see that there are many threatened species not formally listed as such in the IUCN's Red Data Book. That list is clearly in need of revision in relation to owls. The main reason why some of these species are not listed is that, at the time the list was compiled, they were classed as subspecies.

Ornithologists (and bird-watchers) should pay more attention to the listing of subspecies, or more accurately, ultrataxa. This latter term was coined by Schodde & Mason (1999), in their account of Australian Passerine birds. They commented that subspecies are viewed pejoratively by many ornithologists and most birdwatchers, but suggest strongly that this neglect is unwarranted: first because subspecies, as genetically distinct regional populations, are the real building blocks of evolution; and second, because many more subspecies than biological species are rare and endangered. So in the hope of remedying the neglect of subspecies, they introduced the term 'ultrataxon', which applies to both monotypic species and subspecies (1999: 2–3).

In the past, what were often thought of as subspecies have later been recognised as species. Take *Otus manadensis siaoensis* (Schlegel 1873). This is restricted to the small island of Siao in the Sulawesi subregion. According to the unknown author of the account for *Otus manadensis* (del Hoyo *et al.* 1999:167), it is known only from its type specimen; two recent searches for it have failed to find it, and the forest on Siao is almost gone. If it could be examined by modern methods, this owl might well be elevated to the level of species, but in any case, the status of this taxon must be adjudged Critical (if not extinct)[xxix].

Other ultrataxa merit recognition as Threatened:

(1) Biak Scops Owl *Otus beccarii*, restricted to Biak Island off NW West Papua, formerly treated as a race of *O.magicus*. 'The species is only known from three specimens and a few sight records. Much of the forest on Biak has been destroyed or degraded, posing a serious threat to the long-term survival of this little-known species.' (König *et al.* 1999:238).

(2) *Otus brookii brookii* of the mountains of NW Borneo is known from two specimens from Sarawak collected in the nineteenth century. It was not recorded as seen by ornithologists in the twentieth century and must be considered at least Endangered if it is not already extinct.

(3) The Tytonid form *insularis* of the Lesser Antilles (St.Lucia, St.Vincent, Bequia, Carriacou, Union and Grenada) has been variously assigned. M.D. Bruce, in del Hoyo *et al.* (1999: 72), groups *insularis* with *T.glaucops*: 'Several recent works consider nominate *glaucops* as part of a natural group including *insularis* and *nigrescens* (last two forms possibly comprising a separate species, *T.insularis*...). On present evidence, best option may be to treat the three extant races as one species...' Although König *et al.* (1999:195–197) treat *T.glaucops* as a species distinct from *T.alba*, they treat *insularis* (and *nigrescens*) as a subspecies of *T.alba*, and suggest further that *insularis* may, together with *T.punctatissima* of the Galapagos, form a separate species. But while debate on the systematics of the owl goes on, the fact remains that it is rare and presumably endangered within its restricted range.

ACKNOWLEDGMENTS

The author gratefully acknowledges the kind assistance of Prof. Michael Wink of the University of Heidelberg, not only as the source of the phylogenetic tree shown in Fig. 1, but as the main researcher on the mtDNA sequencing data published in König *et al.* (1999) on which this discussion has drawn heavily. He made helpful comments on many of the taxonomic and nomenclatural issues discussed in this paper. I would also like to thank three anonymous reviewers for constructive comments.

REFERENCES

Burton, J. (ed) 1973. *Owls of the World: their evolution, structure and ecology*. Peter Lowe, No locality given.

Collar, N. J., Crosby, M. J. & Stattersfield, A. J. 1994. *Birds to Watch 2: The World List of Threatened Birds*. Cambridge, BirdLife International.

del Hoyo, J.,Elliott, A. & Sargatal, J. (eds.) 1999. *The Handbook of the Birds of the World*, Vol.5. Barcelona, Lynx Edicions.

Garnett, S. G. 1992. RAOU Report 82.

Higgins, P. (ed.) 1999. *Handbook of Australian, New Zealand & Antarctic Birds*, Vol. 4. Melbourne: Oxford University Press.

Ishtiaq, F., Rahmani, A.R. & Rasmussen, P.C. 2002. Ecology and behaviour of the Forest Owlet *Athene blewitti*. This volume.

König, C.,Weick, F. & Becking, J.-H. 1999. *Owls: A guide to the Owls of the World*. The Banks, Mountfield: Pica Press.

Mace, G. M. & Lande, R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.* **5**: 148–157.

Mace, G. M. & Stuart, S. 1994. Draft IUCN Red List categories. Species 21–22, 13–24.

Penhallurick, J. M. & Gregory, M. S. 2001. A note on the correct type of *Macabra* Bonaparte, 1854 (*Strigidae*). *Bull. Brit. Orn. Club.* **121:** 213–215.

Peters, J. L. 1940. *Checklist of Birds of the World*, Vol. 4, Cambridge, Mass.: Harvard University Press.

Ridgway, R. 1914. The Birds of North and Middle America: A Descriptive Catalogue Bulletin of the U.S. National Museum, No.**50**, pt. 6.

Schodde, R. & Mason, I. J. 1999. *The Directory of Australian Birds. Passerines*. Collingwood, Vic., CSIRO Publishing.

Wolters, H. E. 1975–82, *Die Vogelarten der Erde*. Hamburg and Berlin: Paul Parey.

ENDNOTES

[i] This is an update from Table 55a in Wink & Heidrich's chapter in König *et al.*(1999) in that it includes *Bubo [Streptopelia] peli*, and also includes the new names that Professor Wink and I propose in a forthcoming joint paper on the taxonomy and nomenclature of New World Owls.

[ii] Wink & Heidrich state: 'Distances (p-distance) are calculated as the proportion of nucleotide substitutions (in %) between pairs of taxa....Distances correlate with divergence through time: a 2% nucleotide substitution is estimated to be crudely equivalent to a million years of separation ...Distances can be used to decide whether a taxon can be regarded as a distinct species: in owls a divergence of more than 1.5% is usually indicative of species level, and we advocate species recognition at this level where there is clear support from morphological or acoustic characters.' (in König *et al.*,1999: 40). We urge interested readers to consult the matrix of percentage separations in König *et al.* (1999: 51-54). While the structure of the tree is suggestive, when making decisions about taxa at the generic and species levels, the absolute percentage values in the input matrix are crucial.

[iii] An anonymous reviewer questioned whether the two *Bubo* clades should perhaps not be assigned to distinct genera, given the logic of our treatment of *Glaucidium* below. Yet the percentage difference of 9.4% between *B. africanus* and *B. lacteus* (representing the two clades) is much less than the distances found between Old World and New World *Otus* and *Glaucidium* clades.

[iv] The genetic data here are completely consistent with the morphological data. Marks, Cannings & Mikkola in del Hoyo *et al.* (1999:82) summarise: 'An additional genus, *Ciccaba*, was separated from *Strix* by Peters on the basis of the size of the external ears and their dermal flaps, but subsequent work by K.H.Voous showed that these genera could not be reliably separated by ear characters. N.L.Ford found no osteological characters that distinguished the two genera and recommended that they be merged, a conclusion also supported by DNA-DNA hybridization data.'

[v] Wink & Heidrich state: 'The African *Otus leucotis* and *O.granti* differ both morphologically and genetically from the other Old World *Otus* species and have been placed in the genus *Ptilopsis*. In all reconstructions…they figure as a sister group to *Asio*, to which they have a superficial resemblance' (in König *et al.*, 1999:42). On the southern form *granti*, the same authors state: 'It is likely that '*P.leucotis*' represents two species: *P.leucotis* and *P.granti*, which are similar in size and plumage, but differ strikingly in voice and range; moreover, our DNA data…indicate a clear difference between them.' (ibid.)

[vi] König *et al.* (1999:35) state:'We treat the American screech owls *Otus* as members of subgenera *Megascops* and *Macabra*, as they differ from the Old World scops owls in having two songs.' Several points might be made in relation to this statement. First, the relationship revealed between the Old World and New World *Otus* owls in both Fig. 1 and in Fig. 55a (1999:45) is not adequately reflected by recourse to subgenera. Elsewhere, Wink & Heidrich state: 'According to our genetic analysis (Figs.55-57),members of the genus *Otus* appear in at least three different monophyletic clades, indicating that the genus is polyphyletic; it therefore needs a systematic revision. The screech owls of the New World represent a distinct group which is separated from Old World *Otus* by genetic distances of between 12 and 16%, equivalent to 6-8 million years.' (1999:42). Yet König *et al.* themselves leave the New World representatives in *Otus*. Second, one might propose that *Megascops* and *Macabra* be raised to generic level. While there is no problem with *Megascops*, *Macabra* does not appear to be available for New World '*Otus*' owls. *Macabra* was originally proposed by Bonaparte, 1854, with two species listed: *Strix hylophila* Temminck, 1825; and *Syrnium albo-gularis* Cassin, 1848. Since these relate to two distinct generic taxa Sharpe's 1875, subsequent designation of *Strix hylophila* Temminck 1825, as the type of the genus must prevail. Therefore *Macabra* Bonaparte, 1854, would appear to be either a junior subjective synonym of *Strix* Linnaeus, 1758, or if one accepts Wolter's (1975-82: 71) treatment of subgenera, would replace *Tacitathena* Kelso & Kelso 1937 as the subgenus containing *Strix hylophila*. See Penhallurick and Gregory (forthcoming).

[vii] König *et al.* (1999: 227) state: 'We consider this owl to be more closely related to the Old World *Otus* than to the American screech owls, both morphologically and vocally. The latter have more or less trilling songs or rather rapid sequences of generally higher pitched notes, whereas that of *O.flammeolus* is similar to the songs of scops owls of the Old World.'

[viii] By way of comparison, the distance between *Asio otus* and *Bubo bubo bubo*, two taxa in different genera, is 13 %.

[ix] *Psiloscops* Coues, 1899, *The Osprey*, 3, p.144. Type, by original designation, *Scops flammeola* Kaup,1852.

[x] *Revue et Magasin de Zoologie pure et appliquée*, 6, pt.2, p.544.Type by original designation, *Strix nana* King, 1828.

[xi] *Plesseni* in east Lesser Sundas: Alor:Tanglapoi; *rotiensis* in Roti; *fusca* in Timor, Roma and Leti; *cinnamomina* in Babar.Is: Tepa;and *ocellata* in Kai.Is.and Sawu.I.

[xii] The following direct quote from L.Christidis was posted to Birding-aus on 26.10.99 by M.Mules in response to an earlier question about the grouping of the Tasmanian Boobook with the New Zealand Boobook in P.D.Olsen, '*Ninox novaeseelandiae*' in del Hoyo *et al.* (1999:232). 'The section in HBW has misrepresented our papers on DNA studies of the Boobook owls. In these papers the Tasmanian Boobook Owl samples were included to represent the Australian Boobook. There was never any suggestion that the mainland and Tasmanian Boobook were different species. We are in the process of writing up our data on variation in the Australian forms of boobook, mainland and Tasmanian, and there is no suggestion that they are different species. So far as the molecular data is concerned, Australia (including Tasmania), Norfolk Island and New Zealand share the one species of Boobook Owl, *Ninox novaeseelandiae*.'

[xiii] Or *Tyto prigogenei*, according to König *et al.* (1999:208).

[xiv] In keeping with the comments above, all of the New World '*Otus*' species which follow would be better reassigned to *Megascops.*

[xv] As pointed out above, the New World *Glaucidium* species are better assigned to *Phalaenopsis.*

[xvi] The taxonomic history of these taxa is complex, with *virginianus* earlier often being put in *magellanicus*.

[xvii] In fact, three of the twelve additional species were themselves described as subspecies: *Otus mirus* as *Otus scops mirus*; *Otus pauliani* as *Otus rutilus pauliani*; and *Otus koepckeae* as *Otus choliba koepckeae*.

[xviii] A recent example of the problems of uncertain provenance comes from *Otus obsti* Eck, 1973, whose type locality was given as 'Java'. P. Rasmussen (pers.comm.) stated : 'I have studied [Eck's] specimen in Dresden and concluded that it was inseparable from *manadensis* of Sulawesi, being a rather (but not exceptionally) dark example, and that it was almost certainly simply mislabeled by a dealer.'

[xix] König *et al.* (1999:35), talking of the idea of Biological Species as having evolved different patterns from members of other reproductive communities, continue: 'These patterns are often most easily perceptible vocally. Owls have not evolved distinct regional dialects and all vocalisations are inherited; therefore bioacoustics are the most

important taxonomic criterion used to separate difficult species groups.' They continue: 'Morphology varies relatively little in many owl species...If phylogenetic relationships are reconstructed on the basis of morphological characters alone, errors may result from the confusion caused by convergent traits that have nothing to do with underlying phylogeny.' (1999:40).

[xx] Defined as a 50% chance of going extinct in 5 years (Collar *et al.*, 1994:14).

[xxi] Defined as a 20% chance of going extinct in 20 years (Collar *et al.*, 1994:14).

[xxii] The bracketed name in *Bubo (Ketupa) blakistoni* and *Bubo (Scotopelia) ussheri* indicate that, as discussed below, *Ketupa* and *Streptopelia* should be maintained only as subgenera of *Bubo*.

[xxiii] Gola Forest Reserve, Sierra Leone; Sapo National Park, Liberia; and Tai Forest National Park, Ivory Coast.

[xxiv] Defined as a 10% chance of going extinct in 100 years (Collar *et al.*1994:14).

[xxv] König *et al.* (1999:208) transfer *prigogenei* to *Tyto*, with the comment: 'A photograph of the recently netted bird shows what is to us a typical *Tyto* owl with its heart-shaped facial disc, very different from the disc of Bay Owl.' They continue: 'Nothing is known about the vocalisations and DNA of Itombwe Owl, and research in these fields is urgently requested. The results may show that this owl should indeed be placed in the genus *Tyto*, as we suggest here, or in a separate genus within *Tytonidae*.'

[xxvi] Collar *et al.* (1994:p.116) and del Hoyo *et al.* (1999:231) also list *Ninox strenua*, Powerful Owl, of eastern Australia, as Vulnerable, though the later source does state: '...probably more common and less habitat-specific than previously supposed.' Although the most recent authoritative source, *Handbook of Australian, New Zealand and Antarctic Birds*, 4 (Higgins 1999:820), lists its Status as 'Rare (Garnett,1992).Vulnerable in Qld and NSW(*Nature Conservation Regulation* 1994 [Qld];*Threatened Species Conservation Act* 1995 [NSW];Rare in Vic. (CNR 1995).', the estimated population of over 2,000 breeding pairs (cf. Higgins 1999:820), and the wide variety of habitats in which the bird occurs, and its apparent tolerance of lightly and selectively logged forests (cf Higgins 1999:820), combine to suggest that its classification by the IUCN as Vulnerable is unwarranted.

[xxvii] It has also been confirmed that numbers of this species occur in the Kamgai and Kwamgumi Forest Reserves on northern Tanzania. Cf del Hoyo *et al.* (1999:154).

[xxviii] Reasons for preferring to assign this taxon to the genus *Taenioglaux* are discussed below.

[xxix] Unknown author,'*Otus manadensis*' in del Hoyo *et al.*(1999: 167) states:'... *siaoensis*, with shorter wings and much shorter and narrowly barred tail may well be specifically distinct.'

[xxx] Split from *Otus*

[xxxi] Includes *Pseudoptynx* & *Ketupa*

[xxxii] Includes *Ciccaba*

[xxxiii] Includes *Speotyto*

[xxxiv] Includes *Rhynoptynx*

32

DISTRIBUTION, TAXONOMY, STATUS AND MAJOR THREATENING PROCESSES OF OWLS OF THE AUSTRALASIAN REGION

STEPHEN DEBUS

Division of Zoology, University of New England, Armidale, NSW 2351, Australia

The Australasian Faunal Region is the centre of diversity for the genera *Tyto* and *Ninox*. Coupled with the distribution of other tytonid owls (*Phodilus* in Southeast Asia, *Phodilus* or *Tyto prigoginei* in Africa and *T. soumagnei* in Madagascar), this pattern suggests a Gondwanan origin for the Tytonidae. Evidence suggests an endemic Australasian clade of strigid genera, also with a possible Gondwanan origin: *Ninox* (with outliers in Southeast Asia and possibly Madagascar), *Uroglaux*, and *Sceloglaux*. *Otus*, with several regionally endemic species, penetrates Wallacea from Asia and occurs marginally in northwestern Melanesia. Other than the probably extinct New Zealand Laughing Owl (*Sceloglaux*), the regionally most threatened owls are endemic species of tropical forest on islands in Wallacea and Melanesia. *Ninox natalis* (Christmas I.) is Critically Endangered. Several species are Vulnerable: *Tyto nigrobrunnea* (Taliabu I.), *T. aurantia* (New Britain), *T. manusi* (Manus I.), *Otus collari* (Sangihe I.), *O. beccarii* (Biak I.), *Ninox rudolfi* (Sumba), *Nesasio solomonensis* (Solomon Is.). Several are Data Deficient: *Tyto sororcula* (Moluccas, Tanimbar Is.), *T. inexspectata* (Sulawesi), *Uroglaux dimorpha* (New Guinea), and probably *Ninox ios* (Sulawesi). One is Near Threatened: *Otus silvicola* (Lesser Sundas). The remainder, including all Australian species, are Least Concern (= not globally threatened). However, some Australian subspecies of *Tyto novaehollandiae*, *Ninox rufa* and *N. connivens* are Endangered or Near Threatened, and two of *N. novaeseelandiae* are Extinct. For most of the threatened and near-threatened taxa in the region, the major threatening impacts are from deforestation and logging. Unresolved taxonomic problems include: species limits in the masked-owl complex (*Tyto sororcula*, *nigrobrunnea*, *manusi*), the sooty-owl complex and the grass-owl complex; species limits in the Wallacean *Otus* complex, including the identity of an *Otus* on Sumba; species limits in the *Ninox novaeseelandiae* and *N. squamipila* complexes; generic allocation of *Ninox superciliaris* (Madagascar); and the affinities of *Nesasio*.

INTRODUCTION

This paper reviews current opinion on the distribution, taxonomic status, conservation status and major threatening processes of owls in the Australasian Region. This region includes Australia and islands east of Wallace's Line: the eastern Indonesian islands (Sulawesi, Lesser Sundas, Moluccas, collectively Wallacea), New Guinea, Bismarck Archipelago and the Solomon Islands, to Fiji and New Zealand. Within this region occur 36 species of owl, of which 33 are endemic: 15 in Wallacea, ten in Melanesia (New Guinea to the Solomons) and eight in Australia and New Zealand. Only three of these species or species-complexes also occur beyond Australasia: the cosmopolitan Barn Owl *Tyto alba* complex, the (Eastern) Grass Owl *T. capensis/longimembris* complex which extends to Southeast Asia and Africa, and the Brown Hawk-Owl *Ninox scutulata* which is a winter migrant from Southeast Asia to Indonesia.

For endemic Australian species, systematic treatment follows Higgins (1999), and for other species del Hoyo *et al.* (1999) and König *et al.* (1999). The review of unresolved taxonomic issues is also drawn largely from Higgins (1999), del Hoyo *et al.* (1999) and König *et al.* (1999), and the illustrations therein. For Australian species, conservation status follows Garnett & Crowley (2000), and for other species del Hoyo *et al.* (1999). Included in this review is a new species, the Cinnabar Hawk-Owl *Ninox ios* of Sulawesi (Rasmussen 1999), described after the publication of del Hoyo *et al.* (1999) and König *et al.* (1999).

IUCN definitions of conservation status (level of threat), and the criteria used to define each category, are given by del Hoyo *et al.* (1999), Garnett & Crowley (2000) and key references therein.

DISTRIBUTION

The Australasian Region is the centre of diversity for the genera *Tyto* and *Ninox*. *Tyto* is represented in Australasia by eleven of the world's 16 species, including nine regional endemics showing wide morphological and ecological differentiation. By contrast, the rest of the world is occupied by the Barn Owl and its island allospecies, the grass owls (*T. capensis/longimembris*) in the Old World tropics and subtropics, and the Madagascar Red Owl *T. soumagnei*. The other tytonid genus, *Phodilus*, is a divergent genus sometimes ascribed subfamilial status. It occurs in Southeast Asia; the relict form in Africa previously known as *Phodilus prigoginei* is doubtfully congeneric and is now regarded as a *Tyto* or possibly warranting its own monotypic genus (del Hoyo *et al.* 1999, König *et al.* 1999). These patterns suggest a Gondwanan origin for the genus *Tyto* (Schodde 1993) and indeed for the family Tytonidae.

Ninox is represented in Australasia by 16 of the world's 20 species: 15 are regional endemics showing wide morphological and ecological differentiation, and the other is a small hawk-owl that extends to mainland Southeast Asia. The remaining four species, all small hawk-owl types, occur extralimitally in insular Southeast Asia and, if generic allocation is correct, on Madagascar (*N. superciliaris*). This pattern suggests an old Eurasian (Schodde 1993) or perhaps Gondwanan origin for *Ninox*. Genetically, *Ninox* clusters with the *Glaucidium/Athene* complex, both genera of which have divergent Old World (African/Eurasian) and New World (predominantly South American) groups (Wink & Heidrich 1999). This pattern lends support to the notion of a Gondwanan origin for the *Ninox* clade, which includes *Uroglaux* and *Sceloglaux*.

Genus Tyto

The endemic *Tyto* species include two sooty owls of Australo-Papuan rainforests; a large masked owl of forest and woodland in Australia and New Guinea, with five smaller members of the masked-owl group in the forests of Wallacean and Melanesian islands; and a member of the barn-owl group (Sulawesi Barn Owl *T. rosenbergii*) in Wallacea (Table 1).

Table 1. Owl species of the Australasian Region, their distribution, status and threats.

Location: M = Moluccas, T = Tanimbar Is., LS = Lesser Sundas, W = Wallacea, NG = New Guinea. Level of threat (IUCN classification): ? = Extinct, CE = Critically Endangered, V = Vulnerable, DD = Data Deficient, NT = Lower Risk (Near Threatened), LC = Lower Risk (Least Concern). Sources of information: Higgins (1999), del Hoyo *et al.* (1999), Garnett & Crowley (2000). Christmas Island included with Wallacea.

Species	Distribution	Status	Likely threats
Wallacea:			
Tyto sororcula	M, T	DD	Deforestation? Logging?
T. nigrobrunnea	Taliabu	V	Deforestation, logging
T. inexspectata	N. Sulawesi	DD	Deforestation, logging
T. rosenbergii	Sulawesi	LC ?	
Otus alfredi	Flores	LC	Deforestation?
O. silvicola	Flores, Sumbawa	NT	Deforestation
O. magicus	LS, M	LC	Deforestation
O. manadensis	*Sulawesi*	LC	Deforestation
O. collari	Sangihe	V	?
Ninox rudolfi	Sumba	V	Deforestation, fire
N. scutulata	W	LC	?
N. ochracea	Sulawesi	LC	Deforestation
N. squamipila	M, T	LC	Deforestation
N. natalis	Christmas I.	CE	Ant invasion
N. punctulata	Sulawesi	LC	?
N. ios	Sulawesi	DD?	Deforestation? Logging?
Melanesia:			
Tyto aurantia	N. Britain	V	Deforestation, logging
T. manusi	Manus	V	Deforestation?
Otus beccarii	Biak	V	*Deforestation*
Ninox theomacha	NG	LC	?
N. meeki	Manus	LC	?
N. variegata	Bismarcks	LC	Deforestation?
N. odiosa	N. Britain	LC	?
N. jacquinoti	Solomons	LC	Deforestation?
Uroglaux dimorpha	NG	DD	Deforestation
Nesasio solomonensis	Solomons	V	Deforestation, logging
New Zealand:			
Sceloglaux albifacies		X?	Deforestation, fire, introduced carnivores (mustelids)

(Table 1 continued)

Table 1. Owl species of the Australasian Region, their distribution, status and threats (continued).

Species	Distribution	Status	Likely threats
Australia:			
Tyto tenebricosa	+NG	LC	Deforestation, logging
T. multipunctata		LC	Deforestation, logging
T. novaehollandiae	+s. NG	LC	Deforestation, logging, rodenticides (brodifacoum)
T. alba	+W, NG, Solomons	LC	Loss of old hollow trees, rodenticides (brodifacoum)
T. longimembris	+NG, Fiji	LC	Intensive agriculture, urbanisation, rodenticides (brodifacoum), foxes
Ninox rufa	+NG, Aru Is.	LC	Deforestation, logging, fire, rodenticides (brodifacoum)
N. strenua		LC	Deforestation, logging
N. connivens	+M, NG	LC	Deforestation, loss of old hollow trees, rodenticides (brodifacoum)
N. novaeseelandiae	+W, NG, NZ	LC	Loss of old hollow trees, rodenticides (brodifacoum); competition from introduced Little Owl (NZ)

Ninox *and other endemic genera*

The endemic *Ninox* species include three medium to large forest or woodland hawk-owls in Australia, New Guinea and Wallacea, and a variety of small, generalised boobook or hawk-owl types found in forest and woodland throughout the region (Table 1). The other genera occur (or occurred) in New Guinea (*Uroglaux*), Solomon Islands (*Nesasio*) and New Zealand (*Sceloglaux*).

An asionine owl (*Nesasio*) in the Solomon Islands is well isolated from related species, as the distribution of *Asio* species is fairly remote from Australasia. Their nearest occurrence is mainland Southeast Asia and some islands in the North Pacific Ocean (Hawaii, those off Japan, and Micronesia; del Hoyo *et al.* 1999, König *et al.* 1999). Nomadic or migratory *Asio* species are good dispersers, but *Nesasio* is a resident forest bird. The centre of diversity for the asionine owls is Central and South America, with a lesser centre in Africa/Madagascar. Coupled with the occurrence of a relict, primitive asionine owl in Australasia, this pattern might also suggest a Gondwanan origin for some sections of the Strigidae.

Genus Otus

Otus (in the narrow sense, following Wink & Heidrich 1999) is evidently a colonist from Southeast Asia, occurring on islands in Wallacea and extreme northwestern Melanesia where six regionally endemic forms have attained species status (Table 1).

TAXONOMIC ASPECTS

Species limits in the masked-owl complex

Species limits in the island masked-owl complex (*Tyto sororcula*, *nigrobrunnea*, *manusi*) require resolution. These forms are regarded as having differentiated sufficiently from the Masked Owl

T. novaehollandiae to be ascribed specific status. However, the Taliabu Owl *T. nigrobrunnea* is known from only one specimen in 1939, a dark female, and this specimen may represent a dark morph of the Lesser Masked Owl *T. sororcula*. This suggestion is tenable on geographical grounds, as *nigrobrunnea* occurs in the Sula Islands (Taliabu) and *sororcula* occurs in the adjacent southern Moluccas and nearby Tanimbar Islands. The contrary view (reviewed in del Hoyo *et al.* 1999), that *nigrobrunnea* is related to or even conspecific with the Minahassa Masked Owl *T. inexspectata* of Sulawesi, seems unlikely, as the latter is morphologically distinct and resembles more closely the Golden Owl *T. aurantia* of the Bismarck Archipelago. There are also taxonomic questions regarding *T. sororcula*: it is thought either that subspecies *cayelii* on Buru is specifically distinct from nominate *sororcula* on the Tanimbar Islands, and that the population on Seram is subspecifically distinct from *cayelii*, or, conversely, that all these island forms of *sororcula* constitute a monotypic species (del Hoyo *et al.* 1999, König *et al.* 1999).

Species and subspecies limits within *T. novaehollandiae* also require resolution. Tasmanian *T.n. castanops* may or may not have attained species status, with some current opinion favouring the latter view. Similarly, the New Guinea Masked Owl *T.n. calabyi* may be approaching species status, and south-western mainland *T.n. novaehollandiae* might be subspecifically distinct. The recognition of *T.n. galei* of Cape York Peninsula, as distinct from *T.n. kimberli*, is debatable on current, limited evidence (Higgins 1999).

Species limits in the sooty-owl complex

The Lesser Sooty Owl *Tyto multipunctata* of northern Queensland is recognised as specifically distinct from the Sooty Owl *T. tenebricosa* of southeastern Australia, on grounds of morphology, ecology and slight differences in vocalisations. However, there has been no biochemical or genetic comparison of the two species that includes the New Guinea form *T.t. arfaki*, which resembles *tenebricosa*, even though *multipunctata* occupies an intervening geographical position (del Hoyo *et al.* 1999, Higgins 1999, König *et al.* 1999).

Species limits in the grass-owl complex

It is debatable whether the African Grass Owl *Tyto capensis* and the Eastern Grass Owl *T. longimembris* of Asia and Australasia should be considered conspecific. One view is that they might resemble each other convergently (König *et al.* 1999). They are now widely separated geographically, although they may have been connected across the Middle East in the past, and they are morphologically fairly distinct. The number of subspecies in the *longimembris* group, and their distributions, requires resolution (del Hoyo *et al.* 1999).

Species limits in the Wallacean Otus *complex*

The Sangihe Scops Owl *O. collari* has recently been elevated to species status, and the Biak Scops Owl *O. beccarii* is now recognised as specifically distinct from the Moluccan Scops Owl *O. magicus*. Some island subspecies of *O. magicus* and of the Sulawesi Scops Owl *O. manadensis* might be assigned to the wrong species, or might be specifically distinct (del Hoyo *et al.* 1999). The *Otus* inhabiting Sumba requires identification, and taxonomic description if it is a new taxon.

Racial affinity of south-western Ninox connivens

Barking Owls in south-western Australia resemble nominate *N.c. connivens* and are treated as belonging to that subspecies, but they are geographically closer to *N.c. peninsularis* and may be genetically closer to the latter (Higgins 1999). Perhaps they are a relict population of southern *connivens* that has hybridised with *peninsularis*. Pending further taxonomic (including genetic) analysis, they might require recognition as a separate subspecies.

Species limits in the Ninox novaeseelandiae *complex*

One school of thought would separate the New Zealand form *novaeseelandiae*, Norfolk Island form *undulata*, Lord Howe Island form *albaria* and Tasmanian form *leucopsis* as species separate from the mainland Australian *boobook* (del Hoyo *et al.* 1999). However, the current genetic evidence is equivocal and its interpretation limited. The rainforest form *lurida* of northeastern Queensland may also be specifically distinct (König *et al.* 1999).

Species limits in the Ninox squamipila *complex*

There are two morphological forms within the species currently classified as *Ninox squamipila* (Moluccan Hawk Owl), and apparently some differences in vocalisations. The dark forms *hypogramma* and *squamipila* on the North Moluccas and Seram resemble each other, as do the rufous forms *hantu* and *forbesi* on Buru and the Tanimbar Islands, although Seram and Buru are nearest neighbours. This pattern suggests that more than one species might be involved (del Hoyo *et al.* 1999, König *et al.* 1999).

Generic allocation of Ninox superciliaris

The White-browed Hawk Owl of Madagascar is classified as *Ninox superciliaris*, but its distribution is remote from other *Ninox*, and it might warrant classification in a separate genus whose affinities would then require clarification (del Hoyo *et al.* 1999).

Uroglaux

The Papuan Hawk Owl *Uroglaux dimorpha* is regarded as separable from *Ninox* on account of its relatively shorter, more rounded wings and longer tail (del Hoyo *et al.* 1999, König *et al.* 1999). However, it is a rainforest species that combines the barred upperparts of the Rufous Owl *N. rufa* with the streaked underparts of the Barking Owl *N. connivens* and it is sometimes included in *Ninox* (del Hoyo *et al.* 1999), as its morphology suggests. Its wing and tail proportions probably reflect its closed-forest habitat.

Affinities of Sceloglaux

The affinities of *Sceloglaux* of New Zealand are unclear. It is regarded as part of the *Ninox* clade and close to if not congeneric with *Ninox*, and also close to *Uroglaux* (which is doubtfully separable from *Ninox*) (del Hoyo *et al.* 1999).

Affinities of Nesasio

The affinities of the Fearful Owl *Nesasio solomonensis* are uncertain. It is regarded as a primitive asionine owl on skull characters (Olson 1995), but it lacks ear tufts and it differs from *Asio* in some aspects of external morphology such as the facial disc and plumage. The juvenile does not resemble the juveniles of well-known Old World *Asio* species (Loyn & Debus 2000). *Nesasio* is said to share some features, such as general appearance of plumage, strong bill and feet, and perhaps voice, with *Sceloglaux* (König *et al.* 1999). The distribution of other asionine owls is fairly remote from the Solomon Islands; for instance, they do not penetrate peninsular or insular Southeast Asia (e.g. the Philippines) nor cross the equator in the western Pacific (del Hoyo *et al.* 1999).

STATUS AND MAJOR THREATENING PROCESSES

Thirteen (i.e. one-third) of the Region's owl species are classified in one of the 'threatened' categories according to IUCN criteria and 'red list' data (Table 1). One, the Laughing Owl *Sceloglaux albifacies* of New Zealand, is probably extinct, although rumours of its existence persist. Another, the Christmas Island Hawk Owl *Ninox natalis*, is now Critically Endangered, owing to invasion by the predatory Yellow Crazy Ant *Anoplolepis gracilipes* which might prey on eggs or nestlings as well as reduce the owl's prey base. Seven species are classed as Vulnerable: Taliabu Owl *Tyto nigrobrunnea* (Taliabu I.), Golden Owl *T. aurantia* (New Britain), Manus Masked Owl *T. manusi* (Manus I.), Sangihe Scops Owl *Otus collari* (Sangihe I.), Biak Scops Owl *O. beccarii* (Biak I.), Sumba Boobook *Ninox rudolfi* (Sumba) and Fearful Owl *Nesasio solomonensis* (Solomon Is.). Three are Data Deficient: Lesser Masked Owl *Tyto sororcula* (Moluccas, Tanimbar Is.), Minahassa Masked Owl *T. inexspectata* (Sulawesi) and Papuan Hawk Owl *Uroglaux dimorpha* (New Guinea). One is Near Threatened: Wallace's Scops-Owl *Otus silvicola* (Lesser Sundas). The newly described Cinnabar Hawk Owl *Ninox ios* (Sulawesi) might be threatened, and probably should be classified as Data Deficient. The remainder, including all Australian species, are in the category of Least Concern (= not globally threatened). Regionally the most threatened owl species are island endemics of tropical forest in Wallacea and Melanesia, and the New Zealand Laughing Owl (if it survives).

Some Australian subspecies of the Masked Owl *Tyto novaehollandiae*, Rufous Owl *Ninox rufa* and Barking Owl *N. connivens* are Endangered or Near Threatened, and two subspecies of the Southern Boobook *N. novaeseelandiae* are extinct. These subspecies are classified by Garnett & Crowley (2000) as follows. *Tyto n. novaehollandiae*: Near Threatened; *T.n. kimberli*: Near Threatened; *T.n. melvillensis*: Endangered; *T.n. castanops*: Endangered; *Ninox rufa queenslandica*: Near Threatened; *N.r. meesi*: Near Threatened; *Ninox c. connivens*: Near Threatened (south-western birds, if racially distinct, Vulnerable or Endangered?); *Ninox novaeseelandiae albaria*: Extinct; *N.n. undulata*: technically Extinct, although genes survive in a hybrid population.

For most of the threatened and near-threatened taxa in the region, the major destructive processes are deforestation and logging (Table 1; also Higgins 1999, Garnett & Crowley 2000). Deforestation is a major concern in the lowlands of Wallacea (Brooks *et al.* 1999). Other important threats in Australia and New Zealand include loss of old hollow trees from agricultural landscapes, rodenticides (especially brodifacoum), fire, and introduced carnivores (foxes, mustelids) (Higgins 1999). Although forestry activities are a potential threat to regional populations of some near-threatened owl taxa in Australia, the populations of these taxa and the scale of threat do not warrant placing these owls in any of the 'threatened' categories at a national level (Garnett & Crowley 2000).

Deforestation and logging are likely to result in increased owl mortality (through broadscale loss of habitat, roost sites and food supply, and inhibited dispersal across cleared country); and reduced fecundity (through loss of nesting hollows, reduced food supply, and loss of prey den sites) (Higgins 1999, Garnett & Crowley 2000 and key relevant references therein).

DISCUSSION

The Australasian Region is a major centre of diversity and endemism for the two families of owls represented here. Some of the unresolved taxonomic issues are of wide scientific interest. For instance, the affinities of *Ninox superciliaris* and of *Nesasio*, and the existence of an endemic Australasian clade, bear on the notion of a Gondwanan origin for some sections of the Strigiformes and on ideas on their evolution and radiation.

The most outstanding taxonomic issues relate to species and subspecies limits in the endemic island owls of Wallacea and Melanesia. All the taxonomic questions herein require resolution by modern taxonomic methods, including molecular analysis, particularly in view of the small populations on some islands and the implications for their conservation. Recording and comparative analysis of the vocalisations of the problematic taxa might also help to resolve species limits. Issues regarding the problematic Australian taxa will be addressed by Schodde & Mason (forthcoming).

Regionally, the most important conservation issues are associated with deforestation and logging in Wallacea and Melanesia, particularly in the lowlands. The impending loss of biodiversity in these developing nations, in the face of growing human population and economic pressure, will require addressing with the assistance of developed nations such as Australia. Ongoing deforestation is also an important issue in Australia itself. Land clearance is not one of the 'key threatening processes' listed by the Australian *Endangered Species Protection Act 1992*, but is a major threat to many avian taxa of mainland terrestrial habitats (Garnett & Crowley 2000). The federally listed factors are therefore inadequate, and need to be modified to incorporate factors threatening owls in Australia.

Finally, the probable extinction of the New Zealand Laughing Owl, a regionally endemic genus, is especially tragic. Although its decline began in the pre-conservation era, unconfirmed reports of its presence persisted until the 1970s and 1980s. In a country renowned for conservation efforts on other endangered birds, it seems a case of 'out of sight, out of mind'. A cryptic, nocturnal species slid to extinction at a time when expensive, intensive and pioneering work was done to save popular diurnal birds from near extinction. If the rumours are sufficient indication that the Laughing Owl might still exist, then perhaps it is not too late for remedial action to be taken.

ACKNOWLEDGMENTS

I thank Hugh Ford, John Penhallurick and three referees for comments on a draft, and Price Webb for comments on the systematics of *Nesasio*.

REFERENCES

Brooks, T.M., Pimm, S.L., Kapos, V. & Ravilious, C. 1999. Threats from deforestation to montane and lowland birds and mammals in insular South-east Asia. *J. Anim. Ecol.* **68:** 1061–1078.

del Hoyo, J., Elliott, A. & Sargatal, J. (eds) 1999. *Handbook of the Birds of the World, Vol. 5*. Barcelona: Lynx Edicions.

Garnett, S.T. & Crowley, G.M. 2000. *The Action Plan for Australian Birds 2000*. Canberra: Environment Australia.

Higgins, P.J. (ed.) 1999. *Handbook of Australian, New Zealand and Antarctic Birds, Vol. 4*. Melbourne: Oxford University Press.

König, C., Weick, F. & Becking, J.-H. 1999. *Owls, A Guide to the Owls of the World*. Mountfield (UK): Pica Press.

Loyn, R.H. & Debus, S.J.S. 2000. Description of juvenile Fearful Owl *Nesasio solomonensis*. *Aust. Bird Watcher* **18:** 288–289.

Olson, S.L. 1995. The genera of owls in the Asioninae. *Bull. Brit. Orn. Club* **115:** 35–39.

Rasmussen, P.C. 1999. A new species of hawk-owl *Ninox* from North Sulawesi, Indonesia. *Wilson Bull.* **111:** 457–464.

Schodde, R. 1993. Origins and evolutionary radiations of Australia's birds of prey. In Olsen, P.D. (ed.) *Australian Raptor Studies*: 12 [abstract only]. Melbourne: Australasian Raptor Association, Royal Australian Ornithologists Union.

Schodde, R. & Mason, I.J. Forthcoming. *The Directory of Australian Birds: Non-passerines*. Melbourne: CSIRO Publishing.

Wink, M. & Heidrich, P. 1999. Molecular systematics and evolution of the owls. In König, C., Weick, F. & Becking, J.-H. *Owls, A Guide to the Owls of the World*: 39–57. Mountfield (UK): Pica Press.