THE ECOLOGY OF THE KOOMAL (*TRICHOSURUS VULPECULA HYPOLEUCUS*) AND NGWAYIR (*PSEUDOCHEIRUS OCCIDENTALIS*) IN THE JARRAH FORESTS OF SOUTH-WESTERN AUSTRALIA

Adrian Francis Wayne

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The Australian National University, Canberra

To Julia Northin and all of my family,

for their love and support

DECLARATION

This thesis is my own work except where otherwise acknowledged (see Acknowledgements and Preface).

Adrian Francis Wayne

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PREFACE

With the exception of Chapter 1 (Introduction) and Chapter 8 (Synthesis), this thesis is presented as a series of logically connected manuscripts. All of these (except Chapter 6) have been submitted for publication and are at various stages of review. It is intended that Chapter 6 will be submitted for publication in scientific journals as two separate manuscripts. Because core chapters of this thesis are intended as stand-alone pieces of work for publication in scientific journals, some repetition between chapters was unavoidable. In addition, there are some stylistic differences according to the target journals. For example, in the chapters regarding the life history of possums, species are referred to using binomial nomenclature; in the remainder of the thesis common names are predominantly used. While the content remains the same, minor changes have been made to the formatting of each submitted manuscript for general presentation consistency within the thesis. Citation details of these submissions are provided at the beginning of the chapters. The work presented here is original, and the intellectual development and writing of this thesis was conducted by the author.

All of the manuscripts (core chapters) list co-authors to acknowledge the contributions of other workers and collaborators. David Lindenmayer was the Principal Supervisor of this research project and made useful contributions to all parts of this thesis, through helpful discussions and editorial comments on earlier drafts. Ann Cowling provided statistical advice and assistance with the statistical analysis in Chapters 2, 3 and 7. Under direction and consultation, Christine Donnelly assisted with many of the statistical analyses in these same chapters. With close collaboration, Simon Knapp assisted with the logistic regression and Poisson regression modelling in Chapter 6. Colin Ward, Chris Vellios, John Rooney and Ian Wheeler assisted me with the fieldwork in addition to a large number of volunteers. These same people also assisted with the initial stages of data processing (i.e. data entry into electronic databases and data validation). Co-supervisor, Mike Calver, made some particularly useful suggestions and editorial comments to improve the final draft of the manuscript presented in Chapter 7. The specific contributions of others to each of the studies presented in this thesis are described in the respective Acknowledgment sections of each core chapter and in the previous section of this thesis. The author took all photographic images presented in the thesis, except the first image in Chapter 2 by Chris Vellios, and the first image in Chapter 3 and the three images in Chapter 6 by Colin Ward.

THESIS SUMMARY

The jarrah (*Eucalyptus marginata*) forest in south-western Australia is recognised as one of the most important Australian bioregions for the conservation of many mammal species that have disappeared from much of their former ranges. Among these species are the only two large possums that occur in south-western Australia, the koomal (the south-western Australian subspecies of the common brushtail possum, *Trichosurus vulpecula hypoleucus,* Phalangeridae, Wagner 1855) and the ngwayir (pronounced ‘n-waar-ear’, or western ringtail possum, *Pseudocheirus occidentalis,* Pseudocheiridae, Thomas 1888). The aim of this study was to improve substantially the biological and ecological understanding of these species within the jarrah forest to acquire information essential both for their conservation and for ecologically sustainable forest management. With particular emphasis on the ngwayir, this study focused on the jarrah forest in the Upper Warren region, east of Manjimup, Western Australia (see Figure 1.1, p. 5), where the last substantial inland population of ngwayir remains.

The thesis is composed of four sections. Section A examines various survey methods. Section B investigates aspects of the life history of both possum species. Section C investigates habitat selection at multiple spatial scales, while Section D presents a brief synthesis of the research to date.

First, the survey methods used to study koomal and ngwayir were examined for the purpose of improving detection efficiencies, which have previously hindered the development of scientific understanding of the ngwayir in particular. Environmental and procedural factors such as the time of year, the amount of rain on the day prior to the spotlight survey, the minimum temperature and survey duration were related with the number of individuals of both species detected by vehicle-based spotlighting. Cloud cover also affected sightings of koomal. The importance of standardising travelling speed and accounting for potential observer differences was emphasised (Wayne *et al.* 2005a [Chapter 2]).

Arboreal trapping captured 2.3 and 9.3 times more koomal and ngwayir, respectively, than conventional ground trapping. Flour dough baits with rose oil or *Eucalyptus* oil as fragrant lures caught significantly more koomal (125%) than conventional ‘universal’ bait (peanut butter, rolled oats and sardines). Significantly more ngwayir were detected using 50- or 100-watt pedestrian-based spotlights than using 20-watt lights. There were no significant differences in the detection of either species when red or white lights were used and the number of detected koomal did not differ significantly with light intensity. There were, however, significant differences in the number of spotlight sightings between experienced

observers for both possum species. It was concluded that arboreal trapping with baits using rose or *Eucalyptus* oils were the most effective means of surveying koomal. Spotlighting with 50- or 100-watts lights detected more ngwayir than trapping, despite the vast improvements achieved in the latter. An abundance index based on scat surveys was significantly related with the abundance figures of ngwayir derived from spotlighting. Given the practicalities of the scat survey method and the lack of significant observer differences for this method, scats surveys also were considered a potentially useful means of surveying ngwayir (Wayne *et al.* 2005b [Chapter 3]).

An 18-month study of the life history of koomal revealed adult sexual dimorphism and a single autumn breeding season, in which the onset of births coincided with the end of the seasonal drought. All adult females produced a single young each year, of which at least 83% survived to pouch emergence. Growth was linear within the pouch but approached an asymptote after about five months of age. Both sexes matured from one year of age and male body condition varied significantly over time – condition was poorest in winter. Individuals are known to live for more than 10 years in the jarrah forest. Comparisons with the few other life history studies of non-jarrah forest populations of koomal revealed considerable variation in life history traits within the subspecies in south-western Australia and also within the species throughout Australia and New Zealand (Wayne *et al.* 2005c [Chapter 4]).

An 18-month study of the life history of ngwayir highlighted the reduced capacity of this population to withstand exogenous pressures in addition to those already being experienced. Compared with coastal populations, ngwayir at the jarrah study site were less fecund (about one young per adult female per year). Individuals have been observed in the jarrah forest surviving to four years of age and are rarely expected to exceed five years. Autumn (May – June) and secondary spring (October – November) breeding periods by ngwayir in the jarrah forest were more strongly seasonal than those of coastal populations. Male and female body condition varied significantly over time and was poorest in autumn and winter. Eighty-four percent of deaths, most of which were caused by predation, were between April and September. The timing of breeding, body condition and mortality were related with the seasonal quality and quantity of food, principally young jarrah leaves. Ngwayir population viability in the jarrah forest could be improved substantially through strategic predator control that minimises fox (*Vulpes vulpes*) and cat (*Felis catus*) densities when ngwayir are particularly vulnerable (April – September) (Wayne *et al.* 2005d [Chapter 5]).

Habitat use and the selection of diurnal refuges revealed the high dependence of koomal and ngwayir on hollow-bearing trees. Hollow logs, balga, (*Xanthorrhoea preissii*), forest debris, root cavities, dreys (ngwayir) and hollow stumps were rarely used (i.e. collectively 2% and 4% of the time for koomal and ngwayir respectively). Most diurnal refuges were visited rarely while a few were visited frequently, indicating that some refuges are more important than others. Co-use and sharing between conspecifics and species was rare. Logistic regression modelling demonstrated that tree diameter was the single most reliable predictor that a tree was used as a diurnal refuge by both possum species. Multivariate models revealed that crown senescence, canopy connectivity, possum signs and tree species also were important predictors of tree use for both possum species, though the preferred tree species was different for each. The habitat adjacent to trees also was important. The implications of these findings for sustainable forest management are discussed, including the protection of vegetation adjacent to 'habitat trees' to create 'habitat islands' in forests available for logging, thereby increasing the value of retained trees as potential refuges for these and potentially other fauna (Chapter 6).

Ngwayir abundance in the jarrah forest of the Upper Warren was significantly and positively related with areas that had limited anthropogenic disturbance at both the local and landscape scales and negatively associated with fire intensity, forest fragmentation and distance from non-native, non-remnant vegetation. Abundance was positively associated with fox control effort and was greatest in predominantly unlogged landscapes and regrowth forests averaging 40 years since the landscape was last logged (i.e. when logging was least intense) (Wayne *et al.* 2005e [Chapter 7]).

The new ecological information on the koomal and ngwayir presented in this thesis is synthesised and discussed in relation to (1) the timing, intensity, frequency and scale of disturbance; (2) ecological processes and patterns; and (3) interactions between ecological factors. The decline of the ngwayir throughout most of its former northern and inland distribution includes its loss from extensive areas of extant jarrah forest habitat. This study indicates that the pattern of decline is the result of this species' relatively poor capacity to withstand and recover from anthropogenic disturbances, due principally to nutrition-associated constraints on fecundity and a greater vulnerability to predation caused by climate-associated variation in habitat structure. It is probable that ngwayir have persisted in the Upper Warren but not elsewhere in the jarrah forest because of relatively low fox predation pressure and fewer extreme fire events since European settlement. The decline of the ngwayir has been more dramatic than that of the koomal because the koomal (1) has greater reproductive potential; (2) has a longer life expectancy; (3) is biologically and ecologically a generalist with greater adaptability; (4) is less susceptible to predation; and (5) is a more successful competitor than the ngwayir (Chapter 8).

The findings reported in this thesis are of particular importance for improving the conservation of both possum species and improving ecologically sustainable management of the jarrah forest. Preliminary management recommendations are briefly summarised from Chapter 8 and include the following:

(1) An approach based on ecological processes should be used to find solutions to mitigate the impacts of disturbance (i.e. consider species' responses and seek

solutions that take account of food, shelter, competition, predation and reproductive fitness).

(2) The intensity, scale (patchiness and extent), timing and frequency of disturbances, which affect wildlife responses, should be managed to reduce negative impacts.

(3) Management strategies and priorities should be specific to individual populations in view of their differences.

(4) Key habitats need to be identified and appropriately protected.

(5) Additional pressure on fauna populations resulting from climate change should be considered.

(6) Spatially and temporally strategic control of fox and possibly cat numbers is critical to the successful conservation of the koomal and ngwayir, and should be integrated with other management activities such as logging and fire.

(7) Logging intensity should be minimised in the jarrah forest to improve conservation outcomes. Effective predator control during and after disturbance, and the protection of important habitats at multiple spatial scales is necessary.

(8) Fire management for conservation purposes is necessary in the jarrah forest and adequate consideration of the complexity of different ecological factors in a spatially and temporally heterogeneous landscape is essential for ecological sustainability.

(9) Forest fragmentation has negative impacts on ngwayir abundance yet native vegetation in agricultural landscapes has an important conservation role. Further land clearance in high-value fauna habitats that may threaten the long-term viability of populations at risk of extinction should be prevented.

(10) Active adaptive management approaches should be adopted as an efficient and effective means of developing applied ecological understanding and improving integrated conservation and management practices.

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1.1 Context and reasons for this research

Globally, Mediterranean-type vegetation stands out as one of the world's most disturbed biomes (Hannah *et al.* 1995). In Mediterranean south-western Australia, only 30% of the native vegetation remains (Department of Environment and Heritage 2001). Of the 2.8 million ha of jarrah (*Eucalyptus marginata*) forest present at the time of European settlement (i.e. 1826) and within the area covered by the 'Regional Forest Agreement'), 65% remains (Conservation Commission 2004). Of the present extent (1.8 million ha), 87% (1.6 million ha) is vested in the Conservation Commission and managed by the Western Australian Department of Conservation and Land Management (CALM). Due to recent improvements in the forest reservation system, just over half (817 300 ha) of the jarrah forest managed by CALM is now formally or informally reserved (i.e. of what remains, irrespective of tenure, 34% is formally reserved and 11% is informally reserved, Conservation Commission 2004, see Figure 1.1). The remainder is available for timber harvesting. By comparison, 60% remains of the pre-1788 distribution of Australian forests (Dargavel 1995; Lamb and Smyth 2003); 14% of what remains is formally protected (National Land and Water Resources Audit 2001).

The CALM-managed areas of jarrah forest are subject to the principles of ecologically sustainable forest management described in section 19(2) of the Western Australian Government *Conservation and Land Management Act 1984*. The conservation of biodiversity also is required to be consistent with the 'National Strategy for the Conservation of Australia's Biological Diversity' (Commonwealth of Australia 1996). Other legislation relevant to the management of jarrah forests for biodiversity conservation include the Western Australian Government *Wildlife Conservation Act 1950,* the *Environmental Protection Act 1986* and the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999.* The current strategic management of all land vested in the Conservation Commission including the publicly-owned jarrah forest is provided in the 'Forest management plan (2004-2013)' (Conservation Commission 2004).

Most of the CALM-managed jarrah forest, irrespective of tenure, has experienced at least one cycle of timber harvesting (Herberle 1997; Bradshaw 1999; Stoneman *et al.* 2005) and has been subject to prescribed burning since the 1950s (McCaw and Burrows 1989). 'Jarrah dieback', caused by the introduced pathogen *Phytophthora cinnamomi*, also has caused substantial changes to the structure and floristics of much of the jarrah forest. By 1977 an estimated 280 000 ha of Crown land (mainly jarrah forest) was infected and continues to spread (Shearer and Tippet 1989; Dell *et al.* 2004). Dieback induced changes to native vegetation also affect the fauna within these areas (Garkaklis *et al.* 2004).

The introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) have been implicated in the recent decline in, or extinction of, much of Australia's native fauna, especially many small and medium-sized mammals (e.g. Burbidge and McKenzie 1989; Dickman 1996a, 1996b; Calver and Dell 1998a; Risbey *et al.* 2000). For the purpose of conserving wildlife, most of the CALM-managed jarrah forest has been subject to extensive fox control since 1996 (i.e. 'Western Shield' Programme, Bailey 1996; CALM 2000; Orell 2004), although some areas have been continuously fox-baited since the 1970s (e.g. Burrows and Christensen 2002). Dell *et al.* (1989) provide more general information on the ecology, history and management of the jarrah forest.

The jarrah forest, in particular, has been identified as one of the most important Australian bioregions, critical for the conservation of species that have disappeared from much of their former ranges (National Land and Water Resources Audit 2002). Among these species are the only two large possums in south-western Australia, the koomal (the south-western Australian subspecies of the common brushtail possum, *Trichosurus vulpecula hypoleucus,* Phalangeridae, Wagner 1855) and the ngwayir (pronounced 'n-waar-ear', or western ringtail possum, *Pseudocheirus occidentalis,* Pseudocheiridae, Thomas 1888). Introduced predators, habitat loss and modification, changed fire regimes, disease and hunting for pelts have all been implicated as causes in the decline in both possum species (e.g. Maxwell *et al.* 1996; Jones 2004; Abbott 2005).

The koomal has been lost from over 50% of its former range since the time of European settlement in south-western Australia (i.e. since 1826, How and Hillcox 2000) and is the only subspecies of the common brushtail possum with a conservation listing ('Lower Risk-near threatened'; Maxwell *et al.* 1996). The jarrah forest bioregion now supports the most extensive remaining koomal populations. The ngwayir has been lost from 80-90% of its pre-1826 distribution and now persists in reasonable numbers in only three areas, the most extensive of which is in the southern jarrah forest (Jones 2004). The ngwayir is consequently classified as Vulnerable according to the World Conservation Union (1994) criteria (de Tores 2000) and as 'fauna which is rare or likely to become extinct' under the Western Australian Government *Wildlife Conservation Act 1950*. Having been the subject of an interim recovery plan (Burbidge and de Tores 1998), the preparation of a formal 'Recovery Plan' for the ngwayir is currently underway within the framework of CALM Policy Statements, Numbers 44 and 50 (J. Richardson personal communication).

Limited empirical research has been conducted on wild populations of both species (see How and Hillcox 2000 and Jones 2004), particularly in the jarrah forest. Insufficient knowledge of these species currently constrains the ability to make a more reliable assessment of the conservation status of the ngwayir in particular (de Tores 2000). There are considerable differences of opinion concerning the effects on the koomal and the ngwayir of logging (e.g. Calver and Dell 1998a, 1998b; Abbott and Whitford 2002), fire (Christensen and Abbott 1989; Friend and Wayne 2003) and fox control (Jones 2004). To improve the conservation and management of south-western Australian forests, several scientific publications have identified, as a matter of priority, the need for a better understanding of the biology and ecology of the koomal and the ngwayir (e.g. McComb *et al.* 1994; Calver and Dell 1998a, 1998b; Abbott and Whitford 2002; Jones 2004; Wardell-Johnson *et al.* 2004).

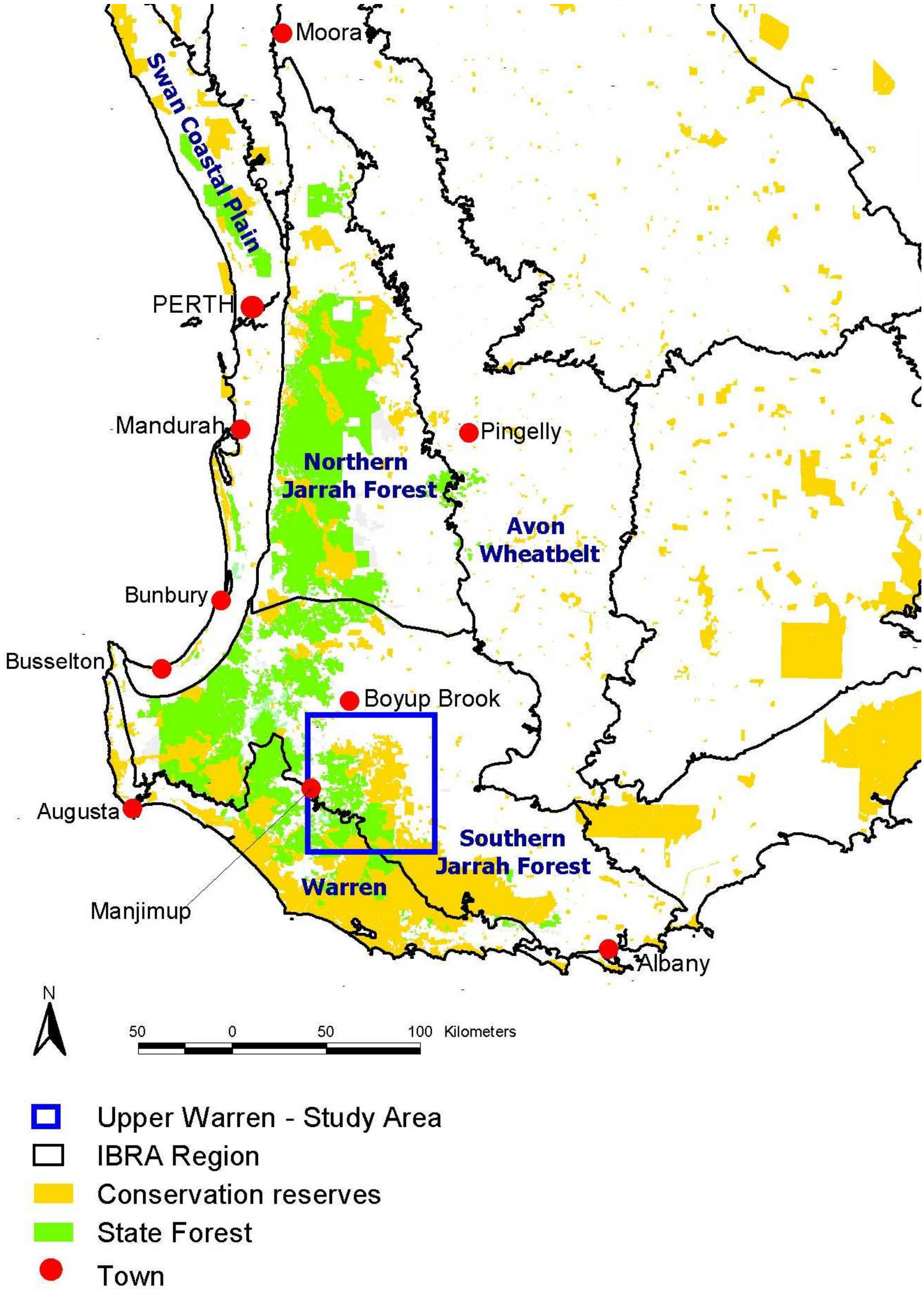

Figure 1.1. The jarrah forest and adjacent IBRA regions of south-western Australia, including conservation estate and State Forest, with reference to the Upper Warren study area.

1.2 Aim and scope

The aim of this study was to improve substantially the biological and ecological understanding of the koomal and the ngwayir within the jarrah forest to provide essential information for their conservation and ecologically sustainable forest management. This thesis places particular emphasis on the ngwayir because of concerns over its conservation status as a threatened species (de Tores 2000). The study was confined to the jarrah forest in the Upper Warren (i.e. upper catchment area of the Warren River), east of Manjimup, Western Australia (Figure 1.1), where the last remaining substantial inland population of ngwayir exists. This thesis presents only part of the ongoing research in which the author is engaged.

1.3 Overview of the thesis

The thesis is composed of four sections. Section A relates to the investigation and development of survey methods to improve possum detection. Section B investigates aspects of the life history of the koomal and the ngwayir. Section C investigates habitat selection at multiple spatial scales, while Section D presents a synthesis of the research to date.

1.3.1 Section A: Development of survey methods to improve possum detections

To complete this thesis successfully, it was necessary to explore and assess ways of improving the survey methods used for studying the ngwayir, in particular. Earlier difficulties in surveying the ngwayir are partly responsible for the current paucity of ecological knowledge of this species (e.g. Inions 1985; Jones *et al.* 1994; de Tores 2000). Improving the understanding of the biology and ecology of the ngwayir in particular was therefore dependent on improving the efficiency and reliability of survey efforts to detect and study this rare and elusive species. Trapping and spotlighting have traditionally been the most common methods for surveying koomal. Trapping has so far proved ineffective as a means of surveying ngwayir and spotlighting has therefore been the most commonly used method. Low and highly variable detection rates between repeat surveys were recognised as significant constraints on the usefulness of this survey method. Chapter 2 investigates how environmental factors and survey method procedures relate to the detection of koomal and ngwayir. It presents data collected prior to and during the author's PhD candidature. The data were derived from vehicle-based spotlight monitoring conducted over an eight-year period. Chapter 3 compares different spotlighting and trapping methods in order to identify practical and efficient survey methods for koomal and ngwayir. Different pedestrian-based spotlight methods were investigated, rather than vehicle-based methods. This was because the former are more suitable for site-based surveys of small areas inaccessible to vehicles, such as those conducted in subsequent parts of this research. Chapter 3 also investigates the potential usefulness of scat surveys for deriving an index of possum abundance.

1.3.2 Section B: Life history

Chapters 4 and 5 investigated aspects of the life history of koomal and ngwayir respectively. The purpose of these studies was to provide a general biological understanding of these species in the jarrah forest. This information provides an essential background for the development of a more holistic ecological understanding of these species in a specific forest habitat that is subject to intensive management and provides biological data that is relevant to the conservation and management of the species.

1.3.3 Section C: Ecology

Factors at multiple spatial scales influence the distribution and abundance of most species (e.g. Johnson 1980; Wiens 1989; Urban et al. 1987; Mackey and Lindenmayer 2001). In Section C of this thesis, habitat selection by koomal and ngwayir is examined at multiple scales. Chapter 6 examines diurnal refuge use by radio-collared individuals. Habitat selection was examined by comparing the attributes of diurnal refuges used by possums (‘micro-scale’) and their surrounding habitat (‘meso-scale’), with comparable habitat attributes generally available. This information is particularly relevant to identifying specific habitat elements that need to be protected and managed in order to ensure that adequate shelter resources remain available, particularly where forests are subject to timber harvesting. Chapter 7 examines how anthropogenic factors, such as logging, fire, fox control and forest fragmentation, relate to the distribution and abundance of ngwayir within the jarrah forest of the Upper Warren. An index of population abundance (derived from methods developed in Chapter 2) is used as the response measure for habitat preferences operating at the local scale (3 ha) and landscape scale (> 300 ha).

1.3.4 Section D: Synthesis

Chapter 8 is a synthesis of the information presented in earlier chapters and demonstrates how the aim of the thesis is fulfilled. The improvements to survey methods are discussed in relation to the facilitation of the research involved in the thesis and other wildlife monitoring programmes. New insights into the biology and ecology of the koomal and ngwayir generated in the thesis are broadly synthesised and integrated with other relevant published studies. A hypothesis for the pattern of decline by ngwayir is presented, as well as explanations as to why ngwayir have persisted in the Upper Warren, and not elsewhere in the jarrah forest, and why ngwayir have declined more dramatically than koomal in south-western Australia. Recommendations for conservation and forest management are presented. There also is a brief discussion of ongoing research regarding possum ecology in the jarrah forest in which the author is engaged and that this thesis constitutes a part as well as other priorities and opportunities for future research.

1.4 References

Abbott, I. (2005). Historical perspectives of the ecology of some conspicuous vertebrate species in south-west Western Australia. Manuscript (in preparation to be submitted for publication to *Conservation Science Western Australia*).

Abbott, I. and Whitford, K. (2002). Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: strategic risk assessment in relation to ecology, policy, planning and operations management. *Pacific Conservation Biology* **7**, 240-255.

Bailey, C. (1996). Western Shield: bringing wildlife back from the brink of extinction. *Landscope* **11**, 41-48.

Bradshaw, F. J. (1999). Trends in silvicultural practices in the native forests of Western Australia. *Australian Forestry* **62**, 255-264.

Burbidge, A. A. and de Tores, P. (1998). 'Western Ringtail Possum (*Pseudocheirus occidentalis*) Interim Recovery Plan.' Department of Conservation and Land Management – WA Threatened Species and Communities Unit, No.17, Perth.

Burbidge, A. A. and McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143-198.

Burrows, N. D. and Christensen, P. E. S. (2002). Long-term trends in native mammal capture rates in a jarrah forest in south-western Australia. *Australian Forestry* **65**, 211-219.

CALM (2000). 'Western Shield Fauna Recovery Program Strategic Plan (July 1999 – June 2004).' Western Australian Government Department of Conservation and Land Management, Perth.

Calver, M. C. and Dell, J. (1998a). Conservation status of mammals and birds in southwestern Australian forests. I. Is there evidence of direct links between forestry practices and species decline and extinction? *Pacific Conservation Biology* **4**, 296-314.

Calver, M. C. and Dell, J. (1998b). Conservation status of mammals and birds in southwestern Australian forests. II. Are there unstudied, indirect or long-term links between forestry practices and species decline and extinction. *Pacific Conservation Biology* **4**, 315-325.

Christensen, P. E. S. and Abbott, I. (1989). Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. *Australian Forestry* **52**, 103-121.

Conservation Commission (2004). 'Forest Management Plan 2004-2013.' Conservation Commission of Western Australia, Perth.

Dargavel, J. (1995). 'Fashioning Australia's Forests.' (Oxford University Press: Melbourne)

Dell, B., Havel, J. J. and Malajczuk, N. (1989). 'The Jarrah Forest: A Complex Mediterranean System.' (Kluwer Academic Publishers: Dordrecht)

Dell, B., Hardy, G. E. S. and Vear, K. (2005). History of *Phytophthora cinnamomi* in Western Australia. In 'Proceedings of the 6th National Conference of the Australian Forest History Society'. (Eds M. C. Calver, H. Bigler-Cole, G. Bolton, J. Dargavel, A. Gaynor, P. Horwitz, J. Mills and G. Wardell-Johnson) pp. 391-406. (Millpress Science Publishers, Rotterdam)

Department of Environment and Heritage (2001). National Vegetation Information System (NVIS) - Pre-European and Present Native Vegetation (Australian Natural Resources Atlas Data - Stage 1, Version 2). Department of Environment and Heritage, Canberra.

de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

Dickman, C. R. (1996a). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**, 185-195.

Dickman, C. R. (1996b). 'Overview of the impacts of feral cats on Australian native fauna.' Australian Nature Conservation Agency, Canberra.

Friend, G. R. and Wayne, A. F. (2003). Relationships between mammals and fire in south-west Western Australian ecosystems: what we know and what we need to know. In 'Fire in Ecosystems of South-West Western Australia: Impacts and Management'. (Eds I. Abbott and N. D. Burrows) pp. 363-380. (Backhuys: Leiden)

Garkaklis, M. J., Calver, M. C., Wilson, B. A. and Hardey, G. E. S. (2004). Habitat alteration caused by an introduced plant disease, *Phytophthora cinnamomi*: a potential threat to the conservation of Australian forest fauna. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 899-913. (Royal Zoological Society of New South Wales: Sydney)

Hannah, L., Carr, J. L. and Landerani, A. (1995). Human disturbance and natural habitat – a biome level analysis of a global data set. *Biodiversity and Conservation* **4**, 128-155.

Herberle, G. (1997). Timber harvesting of Crown land in the south-west of Western Australia: An historical review with maps. *CALMScience* **2**, 203-224.

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

Inions, G. (1985). The interactions between possums, habitat trees and fire. Honours thesis, Australian National University.

World Conservation Union (1994). 'IUCN Red List Categories.' Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **6**, 65-71.

Jones, B. (2004). The possum fauna of Western Australia: decline, persistence and status. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 149-160. (Surrey Beatty and Sons: Sydney)

Jones, B. A., How, R. A. and Kitchener, D. J. (1994). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Lamb, D. and Smyth, A. (2003). Forests. In 'Ecology: An Australian Perspective'. (Eds I. Attiwill and B. Wilson) pp. 331-351. (Oxford University Press: Melbourne, Victoria)

Mackey, B. G. and Lindenmayer, D. B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography* **28**, 1-21.

Maxwell, S., Burbidge, A. A. and Morris, K. (1996). 'The 1996 Action Plan for Australian Marsupials and Monotremes.' Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Project No. 500, Perth.

McCaw, W. L. and Burrows, N. D. (1989). Fire management. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem.' (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 317-334. (Kluwer Academic Publishers: Dordrecht)

McComb, W. C., Jones, B., Biggs, P., Collins, P. and Bradshaw, F. J. (1994). 'A comparison of jarrah harvest plans on brush-tailed possum (*Trichosurus vulpecula*) populations in central jarrah forests.' Western Australian Government Department of Conservation and Land Management, Perth.

National Land and Water Resources Audit (2001). Australian Native Vegetation Assessment 2001. National Land and Water Resources Audit, c/o Land & Water Australia on behalf of the Commonwealth of Australia, Canberra. http://audit.ea.gov.au/ANRA/vegetation/docs/Native_vegetation/nat_veg_contents.cfm.

National Land and Water Resources Audit (2002). Australian Terrestrial Biodiversity Assessment 2002. National Land and Water Resources Audit, Canberra. http://audit.deh.gov.au/ANRA/vegetation/docs/biodiversity/bio_assess_contents.cfm.

Orell, P. (2004). Fauna monitoring and staff training: Western Shield review – February 2003. *Conservation Science Western Australia* **5**, 51-95.

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S. and Wright, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* **27**, 223-235.

Shearer, B. L. and Tippet, J. T. (1989). 'Jarrah Dieback: The dynamics and management of *Phytophthora cinnamomi* in the jarrah (*Eucalyptus marginata*) forest of southwestern Australia.' Western Australian Government Department of Conservation and Land Management, Perth.

Stoneman, G. L., Hagan, R. and Rayner, M. E. (2005). Evolution of silvicultural practices in the jarrah forest of Western Australia. In 'Proceedings of the 6th National Conference of the Australian Forest History Society'. (Eds M. C. Calver, H. Bigler-Cole, G. Bolton, J. Dargavel, A. Gaynor, P. Horwitz, J. Mills and G. Wardell-Johnson) pp. 693-706. (Millpress Science Publishers, Rotterdam)

Urban, D. A., O'Neill, R. V. and Shugart, H. H. (1987). Landscape ecology. *Bioscience* **37**, 119-127.

Wardell-Johnson, G., Calver, M. C., Saunders, D. A., Conroy, S. and Jones, B. (2004). Why integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 394-417. (Royal Zoological Society of New South Wales: Sydney)

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385-397.

SECTION A

DEVELOPMENT OF SURVEY METHODS TO IMPROVE POSSUM DETECTION

This section comprises Chapters 2 and 3 and investigates aspects of the survey methods used to detect possums in the jarrah forest. The aim of this section was to identify practical and efficient means of surveying koomal and ngwayir in order to facilitate research into the biology and ecology of these species. Chapter 2 investigates how environmental factors and survey method procedures relate to the spotlight detection of koomal and ngwayir. Chapter 3 compares different trapping and spotlighting methods to identify which methods detect the most koomal and ngwayir. Chapter 3 also relates an abundance index derived from scat surveys with the number of animals detected by trapping and spotlighting, to assess its potential usefulness as an alternative survey method.

Chapter 2

FACTORS AFFECTING THE DETECTION OF POSSUMS BY SPOTLIGHTING

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Vehicle-based spotlighting

Ngwayir,

Pseudocheirus occidentalis

2.1 Abstract

This paper describes how environmental factors, survey method procedures and differences in forest structure resulting from logging relate to the detection of koomal (common brushtail possum, *Trichosurus vulpecula hypoleucus*) and ngwayir (western ringtail possum, *Pseudocheirus occidentalis*). A total of 169 vehicle-based spotlight surveys of possums within native jarrah (*Eucalyptus marginata*) forest was conducted on three transects over eight years (1996-2003). Up to 5.7 koomal and up to 3.3 ngwayir were detected per km per transect side. Only one ngwayir was detected during the eight surveys conducted between 2001 and 2003. More koomal were seen in spring and autumn (i.e. September – November and March – May respectively) and more ngwayir were seen between October and April. Although surveys were not conducted on very rainy or excessively windy nights, fewer possums were nonetheless seen on nights following rainy days and on cold nights. Cloud cover also affected sightings of koomal. The time taken to complete the surveys increased in conjunction with the number of possums detected, on account of the time required to record data. The importance of standardising travelling speed also is emphasised. Possum spotlight counts differed between recently logged and unlogged areas. However, these findings were not supported by complementary koomal abundance estimates derived from trapping, suggesting that vegetation structure may affect detectability. Factors such as the lunar cycle, wind speed and survey start time after sunset did not significantly affect detection rates of either species. On the basis of these findings, specific survey conditions can be selected to improve spotlight detection efficiency.

2.2 Introduction

Spotlighting is the most widely used field technique for studying arboreal marsupials (Lindenmayer *et al.* 2001). It also is often the most effective conventional method available for many species (e.g. Davey 1990; Catling *et al.* 1997). There are, however, some limitations associated with this method. Among these is the risk of poor detection efficiency (i.e. the small proportion of available individuals actually seen) (e.g. Fletcher *et al.* 1999; Lindenmayer *et al.* 2001; Goldingay and Sharpe 2004a, 2004b), which affects the data return for effort. Insufficient data resulting from poor rates of detection also compromises the statistical rigour of results. For rare species, in particular, increasing the survey effort may not be either sufficient or practical as a means to overcome these issues, which in turn has implications for the conservation and management of these species.

Various methods have been used to survey koomal (*Trichosurus vulpecula hypoleucus,* Phalangeridae, Wagner 1855), ngwayir (*Pseudocheirus occidentalis*, Pseudocheiridae, Thomas 1888) and other arboreal marsupials. These include trapping (e.g. Morris *et al.*

2001), scat counts (B. Jones personal communication) and spotlighting methods using a range of light intensities (e.g. Jones *et al.* 1994a). A comparative study of a number of these methods showed that pedestrian-based spotlight surveys detected, on average, only 4.9% of the koomal known to be alive, and that spotlighting and scat counts were more effective than trapping at detecting ngwayir (Wayne *et al*. 2005b [Chapter 3]).

The reason for this study was to find ways to improve the detection of koomal and ngwayir using vehicle-based spotlight surveys. Specifically, the aim was to examine how seasonal and lunar cycles, weather and spotlight procedures may influence the detection rates of possums in the jarrah forest (*Eucalyptus marginata*) of south-western Australia. Given the potential sensitivity of possums to logging (Wayne *et al.* 2000; Morris *et al.* 2001; Abbott and Whitford 2002), this paper also briefly examined how structural differences in the forest, due to logging, may affect the detection of possums.

2.3 Methods

2.3.1 Target species

The koomal is the south-western subspecies of the common brushtail possum (Kerle *et al.* 1991). It is an arboreal generalist capable of living in a range of habitats (Dyne and Walton 1987; How and Kerle 1995; Nowak 1999; Kerle 2001). Although the conservation status of this subspecies is considered ‘Lower Risk (near threatened)’ (Maxwell *et al.* 1996), it has disappeared from much of its former arid habitat and now occupies less than 50% of the area it did prior to the European settlement of Western Australia (How and Hillcox 2000). It is now abundant only in the more mesic forests and woodlands of the region (How and Hillcox 2000; Jones 2004).

The ngwayir (pronounced n-waar-ear, Abbott 2001) is a specialised arboreal folivore, endemic to south-western Australia (Dyne and Walton 1987; Jones 1995; Nowak 1999; Kerle 2001). It has undergone a substantial decline in distribution and abundance since the European settlement of Western Australia and is currently classified as ‘Vulnerable’ (Maxwell *et al.* 1996) and as ‘fauna which is rare or likely to become extinct’ under the Western Australian *Wildlife Conservation Act 1950*. Remaining populations are largely confined to the south-west coastal and near-coastal woodlands between Bunbury and the Albany region, especially around Busselton (Jones 2004). A few scattered remnant inland forest populations also remain, the largest of which includes animals within the Greater Kingston study area (Maxwell *et al.* 1996; de Tores 2000; Jones 2004).

2.3.2 Study area

Within the Greater Kingston area (Kingston and Warrup State Forest Blocks; 116° 37’ E, 34° 12’ S), jarrah and marri (*Corymbia calophylla*) dominate the dry open forest and woodland (Dell and Havel 1989; Mattiske and Havel 1997). The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters, with an annual average rainfall of approximately 900 mm. The topography is gently undulating with plateaux tops, low lateritic ridges and broad valleys, and ranges between 200 m and 340 m above sea level. Further details on the region are provided elsewhere (McArthur and Clifton 1975; Wilde and Walker 1984; Strelein 1988).

2.3.3 Survey transects

Two transects were established within the Greater Kingston forest in 1996. The ‘Northern’ transect was 10.9 km long and ran along the northern boundary and through the centre of Kingston forest block (Figure 2.1). The ‘Southern’ transect bisected parts of Warrup and Kingston forest blocks and was 10.6 km long, finishing at the same end point as the Northern transect, having approached it from the opposite direction. In March 1997, a third spotlight transect was established within Kingston 4 logging coupe as part of a species-specific study on the impact of logging on the ngwayir (Wayne *et al.* 2000). The Kingston 4 (‘K4’) transect followed various logging roads and had a total length of 10.3 km (Figure 2.1). Vegetation along the three survey transects was broadly similar. Only a few of the largest drainage lines that intermittently carried surface water supported a narrow belt of vegetation that differed markedly in its floristics and structure from the forest elsewhere in the profile. Recently logged areas also differed considerably in structure from the more mature forest stands. The proportions of the transect lengths immediately adjacent to recently logged forest (see ‘Forest Management History’ section below) were 34%, 10% and 58% for the ‘Northern’, ‘Southern’ and ‘K4’ transects respectively.

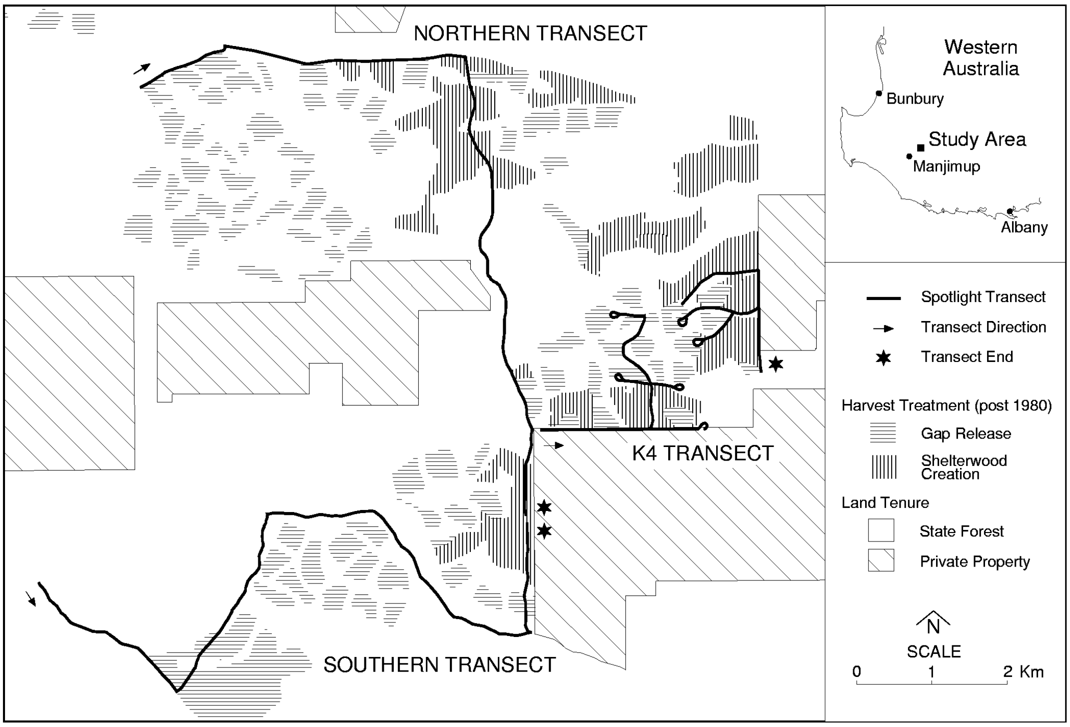

Figure 2.1. Location of three possum spotlight transects within the Greater Kingston jarrah forest.

2.3.4 The survey protocol

During 65 nights between February 1996 and December 2003, 169 spotlight surveys were completed. Before March 1997, the 'Northern' and 'Southern' transect spotlight surveys were conducted irregularly and generally on different nights. With the commencement of the 'K4' transect, all three transects were surveyed concurrently and fortnightly when possible and weather permitting. The frequency of surveys was reduced to monthly from April 1998 to January 2001 and to annually between 2001 and 2003 (Table 2.1).

Spotlight surveys began 36 to 174 minutes after sunset (mean = 97 minutes) and were conducted from vehicles travelling at an average speed of about five km hr^{-1}. Two spotlights were used per vehicle; one spotlight for each side of the road and both systematically conducted sweeping searches between the ground and tree crowns. The spotlighters were positioned either on the back of utility vehicles or on a specially adapted double seat fitted to the roof-rack of a four-wheel-drive station wagon.

To maintain consistency of technique, where possible each of the three spotlighting teams was led by one of four workers who are experienced spotlight operators (AW, JR, CW, IW), each of which used the same vehicle during most surveys. Occasionally, but particularly in

1996, other experienced workers replaced the principal spotlight leaders when they were not available. The spotlight leaders alternated between the three transects on successive spotlight nights in order to minimise observer bias. The second spotlighter and driver for each spotlight team were volunteers. Surveys were not conducted on rainy or very windy evenings.

For each survey, the weather conditions (temperature, wind and cloud cover), the start and finish times and the spotlight team were recorded. Data collected on possum sightings included their location in logged or unlogged forest. Weather data for the days preceding and including the survey nights were extracted from records maintained at the Department of Conservation and Land Management (CALM) Science Division office in Manjimup, 26 km south-west of the survey area. Most solar and lunar data for the study area were supplied by the Perth Observatory, while the proportion of luminous moon and the wax/wane moon phase data were extracted from the U. S. Naval Observatory website (http://aa.usno.navy.mil/cgi-bin/aa_pap.pl).

Table 2.1. Summary of the number of spotlight surveys along three transects in Greater Kingston between 1996 and 2003.

TRANSECT/YEAR	1996	1997	1998	1999	2000	2001	2002	2003	TOTAL
North	7	15	15	12	8	1	1	1	**60**
South	8	13	14	12	8	1	1	1	**58**
K4	0	14	15	12	8	1	0	1	**51**
Annual total	**15**	**42**	**44**	**36**	**24**	**3**	**2**	**3**	**169**

2.3.5 Forest management history

According to local CALM fire history records, the study area has generally been subject to prescribed burning on a 7-10 year rotation basis since the 1960s. The area was selectively logged for premium jarrah sawlogs in the 1920s and again between 1940 and 1980 (Herberle 1997; Bradshaw 1999). The most recent logging in Kingston forest occurred predominantly between 1995 and 1998. Two silvicultural systems were applied in this cycle: (1) ‘shelterwood creation’ aimed at reducing the tree basal area to 10-12 m^2 ha^{-1} with the objective of establishing regeneration from seedlings; and (2) ‘gap release’ in which most of the overstorey was removed with the objective of establishing regeneration by the release of lignotubers from suppression (CALM 1995) (Figure 2.1). The recent cycle of logging in Kingston forest resulted in ‘shelterwood creation’ over 16% of the area, ’gap release’ over 17% and 67% remaining unlogged. Possums spotlighted in forest logged using either of these methods between 1995 and 1998 were recorded as being within ‘logged’ forest.

Possums sighted in the remaining forest were recorded as located within contemporarily ‘unlogged’ forest, although the forest stand may have been previously logged in earlier cutting cycles (Table 2.2).

‘Logging disturbance’ occurred between February 1995 and November 1996 along the ‘Northern’ transect, between May 1995 and December 1997 along the ‘Southern’ transect and between March 1997 and November 1998 along the ‘K4’ transect. The term ‘post-logging disturbance’ was used to define surveys conducted after the completion of the silvicultural burn used to stimulate regeneration following logging. Because of the possible indirect effects of logging on possum abundance in nearby unlogged forest – as well as direct effects in logged areas – it was logical to analyse the interaction between logging activity and logging treatment (Table 2.2).

2.3.6 Data analysis

Of interest to this study was the identification of environmental and survey procedure covariates that influenced possum detection. Twenty-three covariates were classified into three groups: temporal, weather and survey procedures. Logging was included as an experimental treatment (Table 2.2). To avoid ‘over-fitting’ covariates within a single model, three separate initial models (one for each group of related covariates) were used to analyse the spotlight detection data for both possum species. The logging covariates were included in each of the three models for each species. Because there were correlations between covariates, these three initial models should be regarded as different explanations of the variation in detection rates of possums. These initial models were used to determine those covariates that were potentially important in predicting transect counts. Statistically significant variables from each of these initial models were then included in a fourth and final model for each of the two species. This procedure allowed us to identify variables that influenced the detection of each species.

Only one ngwayir was detected during the eight surveys conducted between 2001 and 2003. This was the only source of information on ngwayir for those years. Therefore, all models for ngwayir used data only from 1996 to 2000 inclusive.

The response variable used was the number of possums detected per transect side (i.e. $km^{-1}ts^{-1}$), which was a count variable and was best modelled using a model appropriate for a discrete distribution. Poisson generalised linear mixed models (Schall, 1991) were fitted to each covariate group using GenStat (2003). The survey night, the transect and their two-way interaction were included as random effects. All other covariates were included as fixed effects. The log transformation of transect length was included as an offset in each model to adjust for the different lengths of ‘logged’ and ‘unlogged’ forest sections. Transformations were otherwise not necessary for any of the explanatory variables. Wald tests were used to assess the significance of the fixed effects, and stepwise backward elimination was used to remove unimportant covariates from the models (i.e. model reduction). Since the main interest was in screening terms to determine which covariates were potentially influential, a 10% significance level was used as the criterion for removing covariates from the model.

Table 2.2. The covariates used in statistical modelling of which factors affect the spotlight detection of koomal and ngwayir.

COVARIATES BY MODEL	DEFINITION
TEMPORAL	
Year	1996-2003 inclusive
Season	Spring (Sept-Nov); Summer (Dec-Feb); Autumn (Mar-May); Winter (June-Aug)
Month	Month in which the survey was conducted
Darkness	Period of darkness on night of survey (minutes)
% Moon luminous	Proportion of moon illuminated
Moon wax/wane	Wane or Wax Moon phase
% Time moon up during survey	Proportion of time during the survey that the moon was above the horizon
WEATHER	
Rain day of survey	Rain on the day of the survey (i.e. 24 hours prior to 0900 on the day after the survey)
Cumulative rain 2 days prior	Total Rain on the day of and the day prior to the survey
Cumulative rain 3 days prior	Total Rain on the day of and the two days prior to the survey
Max temp. day of survey	Maximum temperature taken on the day of the survey.
Min temp. day of survey	Minimum temperature recorded on the day of the survey.
Max temp. day before survey	Maximum temperature on the day prior to the survey.
Min temp. day before survey	Minimum temperature on the day prior to the survey.
Survey temp. class	Cold = 0 to 9 ^{o}C, Cool = 10 to 14 ^{o}C, Warm = 15 to 21 ^{o}C, estimated at the start of survey
Survey wind class	Wind Nil = 0 km/hr, Light = 1-9, Moderate = 10-19, Strong = 20+km/hr, estimated at the survey start
Survey cloud cover	Cloud cover estimated at the beginning of the spotlight survey, expressed in eighths
SURVEY	
Observer team	Spotlight team leaders; AW; CW; JR; IW; Others
Survey start after sunset	Time lag between sunset and start of survey (minutes)
Survey duration	Survey finish time minus start time (minutes)
LOGGING	(included in all three models based on temporal, weather and survey covariates)
Logging activity	‘During’ or ‘After’ logging activity (start of logging to completion of silvicultural burn)
Logging treatment	Contemporarily (1995-1998) ‘Logged’ or ‘Unlogged’ areas adjacent to transect
Logging treatment*activity	Interaction between logging activity and logging treatment covariates

2.4 Results

There were 2674 and 1499 spotlight detections of koomal and ngwayir, respectively. The numbers of koomal detected per km per transect side ($km^{-1}ts^{-1}$) varied between 0 and 5.7 (raw mean = 0.9 $km^{-1}ts^{-1}$), and the number of ngwayir detected varied between 0 and 3.3 $km^{-1}ts^{-1}$ (raw mean = 0.5 $km^{-1}ts^{-1}$).

2.4.1 Koomal

2.4.1.1 Koomal models 1-3: Temporal, weather and survey procedures

In the reduced temporal model, using a 10% significance level, there were mild effects of ‘year’ ($\chi^2_7 = 12.50$, $p = 0.085$) and ‘season’ ($\chi^2_3 = 6.60$, $p = 0.086$), and a strong effect of ‘logging treatment’ ($\chi^2_1 = 34.81$, $p < 0.001$).

In the reduced weather model, using a 10% significance level, there were significant effects of ‘rain day of’ ($\chi^2_1 = 3.77$, $p = 0.052$), ‘min temp day before’ ($\chi^2_1 = 3.06$, $p = 0.080$), and ‘survey cloud cover’ ($\chi^2_8 = 14.26$, $p = 0.075$). There also was a strong effect of ‘logging treatment’ ($\chi^2_1 = 35.55$, $p < 0.001$).

In the reduced survey procedure model, using a 10% significance level, there was an effect of ‘observer team’ ($\chi^2_4 = 9.47$, $p = 0.050$), and strong effects of ‘survey duration’ ($\chi^2_1 = 12.97$, $p < 0.001$) and ‘logging treatment’ ($\chi^2_1 = 33.73$, $p < 0.001$).

2.4.1.2 Model 4: All significant variables combined

In the final reduced and combined model, again using a 10% significance level, there were significant effects of ‘survey duration’, ‘rain day of’, ‘season’ and ‘logging treatment’ (Table 2.3).

The back-transformed number of koomal (i.e. the expected count of animals if all other variables in the model were held at their mean values) was highest in spring and lowest in winter: Spring = 0.93 $km^{-1}ts^{-1}$, summer = 0.76 $km^{-1}ts^{-1}$, autumn = 0.86 $km^{-1}ts^{-1}$, winter = 0.72 $km^{-1}ts^{-1}$ (Figure 2.2). The number of koomal also was higher in logged than in unlogged areas: 1.03 $km^{-1}ts^{-1}$ and 0.64 $km^{-1}ts^{-1}$ respectively. The effect of both ‘survey duration’ and ‘rain day of’ was linear on the log scale but was not linear when back-transformed. The number of koomal detected increased as the survey duration increased, and decreased with increasing rain on the day of the survey (Table 2.3).

Table 2.3. Summary of the final combined Poisson generalised linear mixed model with a log link function for the significant variables that affected the spotlight detection of koomal in Greater Kingston.

Variable	df	Coefficient	Std. Error	Wald Chi-square	p-value
Logging treatment	1	Unlogged 0.000 Logged 0.477	0.080	35.89	<0.001
Survey duration	1	0.006	0.001	29.6	<0.001
Rain on day of survey	1	-0.040	0.016	6.06	0.014
Season	3	Autumn 0.000 Winter -0.189 Spring 0.077 Summer -0.132	0.105	7.84	0.049

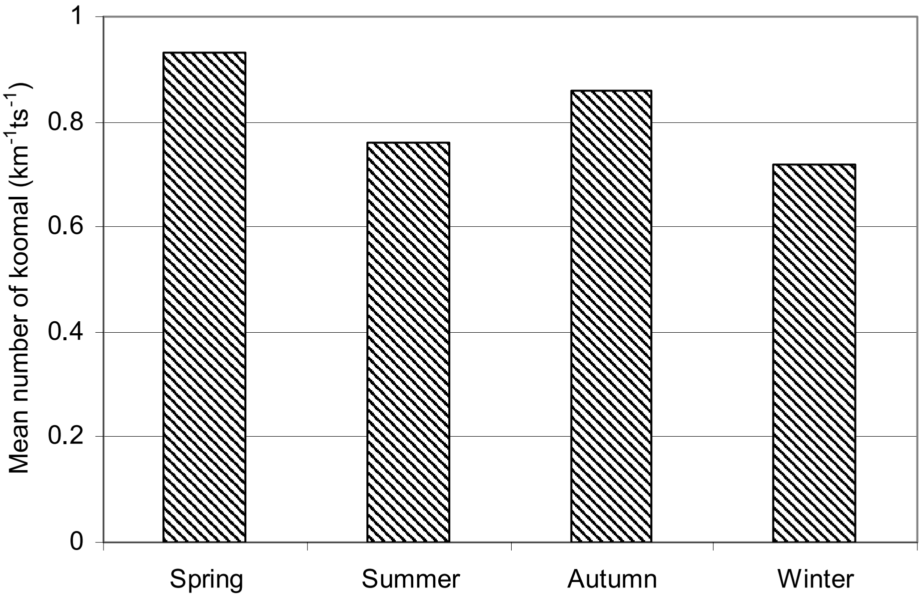

Figure 2.2. The annual back-transformed numbers of koomal per kilometre per transect side for spotlight transects in Greater Kingston, between 1996 and 2000.

2.4.2 Ngwayir

2.4.2.1 Ngwayir models 1-3: Temporal, weather and survey procedures

In the reduced temporal model, using the 10% significance level, there were strong effects of 'year' (χ^2_4 = 58.25, $p < 0.001$), 'season' (χ^2_3 = 9.70, $p = 0.021$) and 'month' (χ^2_8 = 16.54, $p = 0.035$). There also was a mild interaction between 'logging activity' and 'logging treatment' (χ^2_1 = 3.60, $p = 0.058$).

In the reduced weather model, using the 10% significance level, there was a strong effect of 'min temp day before' (χ^2_1 = 14.72, $p < 0.001$), a significant effect of 'rain day of' (χ^2_1 = 4.68, $p = 0.031$) and strong effects of 'logging activity' (χ^2_1 = 15.20, $p < 0.001$) and 'logging treatment' (χ^2_1 = 26.51, $p < 0.001$).

In the reduced survey procedure model, using the 10% significance level, there was a strong effect of 'survey duration' (χ^2_1 = 33.24, $p < 0.001$), a significant effect of 'survey start after sunset' (χ^2_1 = 3.81, $p = 0.051$) and a significant interactive effect between 'logging activity' and 'logging treatment' (χ^2_1 = 4.07, $p = 0.044$).

2.4.2.2 Model 4: All significant variables combined

In the final reduced and combined model, again using a 10% significance level, there were strong effects of 'year' and 'survey duration'. There were significant effects of 'month' and the interaction between 'logging activity' and 'logging treatment'. There also were mild effects of 'rain day of' (Table 2.4).

The back-transformed number of ngwayir was greatest in 1998 and least in 2000 (Figure 2.3). Within years, more ngwayir were detected between October and April (Figure 2.4). The back-transformed number of ngwayir detected was greatest in logged areas during logging activity and the least numbers of ngwayir detected were in the unlogged areas after logging activity in the vicinity had been completed: the number of ngwayir detected in logged forest was 0.51 $km^{-1}ts^{-1}$ during logging and 0.43 $km^{-1}ts^{-1}$ after logging; the number of ngwayir detected in contemporarily unlogged forest was 0.43 $km^{-1}ts^{-1}$ during logging activity in the vicinity and 0.25 $km^{-1}ts^{-1}$ after logging activity. The effect of both 'survey duration' and 'rain day of' was linear on the log scale but was not linear when transformed back to the original scale. The number of ngwayir detected increased with 'survey duration' and was inversely related to the amount of rain recorded on the day of the survey (Table 2.4).

Table 2.4. Summary of the final combined Poisson generalised linear mixed model with a log link function for the significant variables that affected the spotlight detection of ngwayir in Greater Kingston.

Variable	df	Coefficient	Std. Error	Wald Chi-square	p-value
Year	4	1996; 0.000 1997; 0.473 1998; 0.615 1999; 0.280 2000; -0.780	0.240	37.69	<0.001
Survey duration	1	0.007	0.001	26.15	<0.001
Month	11	Jan; 0.000 Feb; -0.001 Mar; 0.085 Apr; -0.037 May; -0.605 Jun; -0.180 Jul; -0.625 Aug; -0.458 Sep; -0.332 Oct; 0.186 Nov; -0.101 Dec; 0.037	0.261	24.39	0.011
Logging treatment*activity	1	Logged.During; -0.370 Logged.After; 0.000 Unlogged.During; 0.000 Unlogged.After; 0.000	0.173	4.58	0.032
Rain on day of survey	1	-0.045	0.23	3.77	0.052

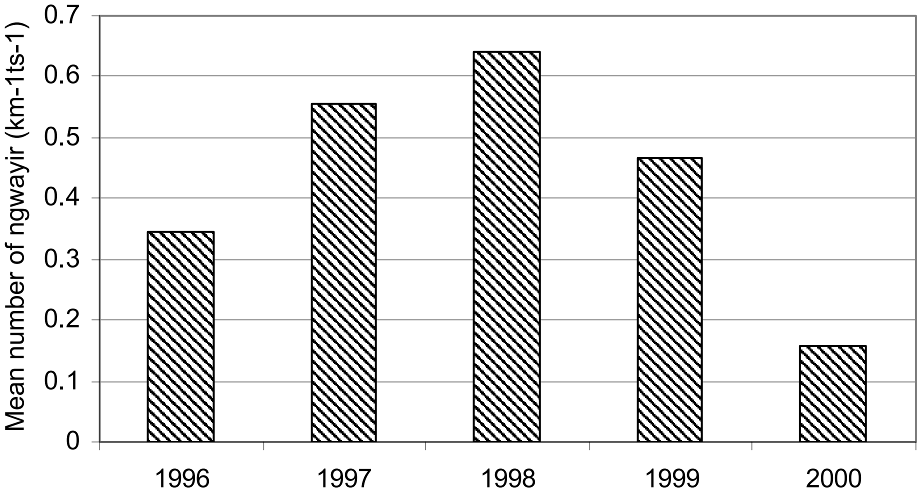

Figure 2.3. The annual back-transformed numbers of ngwayir per kilometre per transect side for spotlight transects in Greater Kingston, between 1996 and 2000.

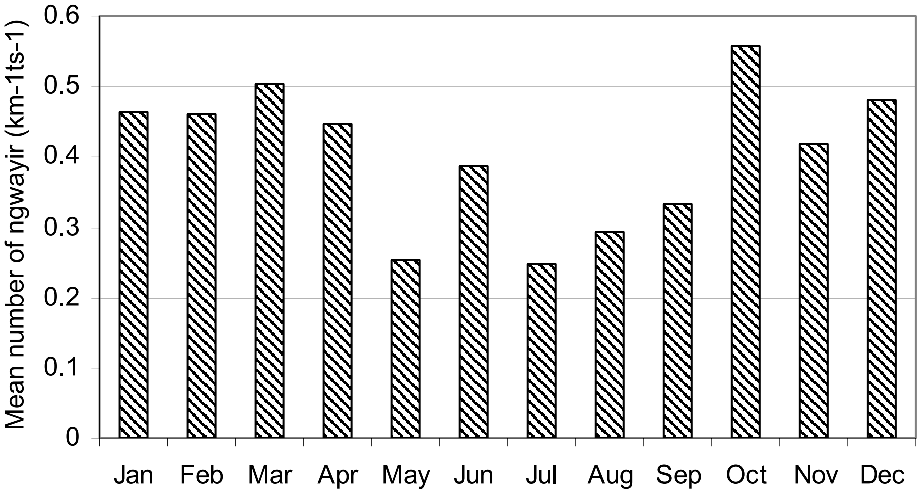

Figure 2.4. The monthly back-transformed numbers of ngwayir per kilometre per transect side in Greater Kingston.

2.5 Discussion

Many studies have commented on how factors such as weather and moonlight may affect the detection of animals by spotlighting (e.g. Bell 1981; Fletcher *et al.* 1999). Other studies also provide insight on how Australian arboreal marsupial activity may be influenced by these variables or change during a given night (e.g. Goldingay 1984; Kavanagh and Rohan-Jones 1982; Proctor-Gray 1984; Maher 2001). There are, however, few studies of Australian arboreal mammals that have explicitly and rigorously tested how these variables relate to spotlight detection. For the purpose of increasing the detection of koomal and ngwayir, the principal focus of this study was to determine which factors should be accounted for when conducting vehicle-based spotlight surveys on these species.

The advantages of vehicle-based spotlight surveys compared with pedestrian-based spotlighting include the ability to survey more extensive areas and, when riding on top of a vehicle, a higher perspective above the ground reduces visual obstructions by ground vegetation. Other differences between the two types of survey include: speed; a potentially greater element of surprise to animals in vehicle-based surveys, given the speed of approach; and, again in vehicle-based surveys, a lower probability of detecting animals by sound (not of major concern for koomal and ngwayir, which rarely vocalise and are stationary much of the time (e.g. MacLennan 1984; A. Wayne personal observation). Other researchers who have used vehicle-based spotlight surveys for arboreal marsupials include Davey (1990), Bennett *et al.* (1991) and Jones *et al.* (1994a). Comparisons are made between the findings of our study and those of other relevant studies of Australian arboreal marsupials, including studies using pedestrian-based surveys. In making these comparisons it is assumed that seasonal, lunar, weather and procedural effects on the detectability of possums do not differ fundamentally between vehicle-based and pedestrian-based survey methods.

2.5.1 Temporal effects

There were significant differences between years in the number of koomal detected at the 10% level of significance within the temporal model but not in the final combined model. The lack of significance of this factor in the final combined model means that some other significant effect is also partially explaining the same phenomenon in this model.

Significant annual differences in the numbers of ngwayir detected suggest that annual population levels were variable (Figure 2.3). After increasing in 1997 and 1998, the numbers declined from their 1998 peak. Despite only one ngwayir being detected during the eight surveys conducted between 2001 and 2003, there were insufficient data to use statistical inference to determine whether there had been a significant decline over time. The longitudinal data also were insufficient to determine whether population changes were cyclical or otherwise. Nonetheless, these initial data should give cause for concern, given that the ngwayir is a threatened species about which relatively little is known. Clearly, there is considerable value in continuing spotlight monitoring over a longer term to examine population changes.

Seasonal effects on the spotlight detection of koomal indicate that more animals were seen in spring and autumn than in summer and winter (Figure 2.2). The highest detection rates in spring coincide with the emergence of six-month-old pouch-young, beginning in August – September (Wayne *et al.* 2005c [Chapter 4]). Mortality can be very high between 6 and 18 months of age (< 83%), after the possums emerge from the pouch (e.g. How 1978, 1981). Higher detection rates in spring thus support the expectation that the population of koomal peaks at this time of year.

A secondary autumn peak in koomal spotlight detection rates coincides with the breeding season (Wayne *et al.* 2005c [Chapter 4]). Activity at this time of year is expected to be particularly high as individuals seek mates. Increased rates of activity probably make it easier to detect possums during this period.

Most ngwayir breeding activity (77%) occurs in March – April with a minor second peak in September – October (Wayne *et al.* 2005d [Chapter 5]). After approximately 2-4 weeks of gestation, ngwayir remain in the pouch for three to four months (Pahl 1987; Ellis and Jones 1992; Jones *et al.* 1994b). They are then weaned at age 6-8 months and disperse at 8-12 months (How 1978). Mortality of ngwayir is predominantly between April and September (Wayne *et al.* 2005d [Chapter 5]). The greater detection rates of ngwayir between October and April (Figure 2.4) therefore correspond with the breeding activity, weaning and maturation of young, and when the population is seasonally at its greatest.

Seasonal changes in the number of possums detected due to juvenile recruitment have been considered elsewhere for other arboreal marsupials (e.g. Goldingay and Kavanagh 1988; Goldingay and Sharpe 2004a), but also may result from seasonal differences in habitat use and food availability (e.g. Kavanagh 1984; Davey 1990; Eyre 2004). Other studies have found no seasonal effects on detection. One study of the habitat preference of the yellow-bellied glider (*Petaurus australis*) also found no significant relationships for any of the other covariates examined – moon phase, moonlight, cloud cover, temperature, wind, precipitation, time after dusk, or *Eucalyptus* flowering (Eyre and Smith 1997).

The moon did not significantly relate to the number of koomal or ngwayir detected in this study. The lunar cycle also was not a significant main effect for four glider species (yellow-bellied glider, feathertail glider *Acrobates pygmaeus*, sugar glider *Petaurus breviceps*, and greater glider *Petauroides volans*) in southern New South Wales (Davey 1990), or for coppery brushtail possums (*T. v. johnstoni*) and Lumholtz's tree-kangaroos (*Dendrolagus lumholtzi*) in northern Queensland (Laurance 1990). On the other hand, fewer Herbert River ringtail possums (*Pseudocheirus herbertensis*), green ringtail possums (*Pseudochirops archeri*) and lemuroid ringtail possums (*Hemibelideus lemuroides*) were detected on clear moonlit nights (Laurance 1990). Fewer common ringtail possums were detected during surveys with a full moon in south-eastern Australia (How *et al.* 2004). Moonlight also influenced the terrestrial activity of common brushtail possums near Brisbane (MacLennan 1984) and the detection of the common brushtail possum, mountain brushtail possum (*Trichosurus caninus*), greater glider, sugar glider and feathertail glider in southern Queensland (Eyre 2004) and the feathertail glider in New South Wales (Goldingay and Kavanagh 1988). The effect of moonlight on the activity and/or detectability of many eutherian species also have been reported (e.g. Gannon and Willig 1997; Gursky 2003 and references therein).

Changes in behaviour in response to moonlight have been associated with predator avoidance for a number of arboreal marsupials (MacLennan 1984; Goldingay and Kavanagh 1988; Laurance 1990). The Powerful Owl (*Ninox strenua*) and other larger native nocturnal carnivores that are major predators of many arboreal marsupials in eastern Australia are absent from Western Australia. The largest native nocturnal predator in south-western Australia is the threatened chuditch (*Dasyurus geoffroii*). While it is capable of preying on ngwayir and possibly on koomal, the extent to which it does so is unknown. It is possible that prior to the introduction of the red fox (*Vulpes vulpes*) and the cat (*Felis catus*), possums in the south-west may have had less cause than eastern Australian arboreal marsupials to modify their behaviour on moonlit nights to avoid predation.

2.5.2 Weather

Because rainy or very windy evenings were avoided, we did not examine the effects of spotlight detection in the full range of weather conditions that can occur in the study area. Nonetheless, fewer possums of both species were detected with increasing rain experienced in the 24 hours before 0900 hrs on the day of the survey. The reduction in detection abundance is probably due to two factors; 1) increased light reflectance (i.e. visual ‘noise’) off moist foliage, making it more difficult to detect eye shine and 2) change in possum behaviour in wet conditions. According to Thomson and Owen (1964), the activity of common ringtail possums (*P. peregrinus*) was reduced more by wind than by light rain, while it was completely suppressed by heavier rain or fog. Other observations of common ringtail possums (Owen and Thomson 1965; How 1972; Davey 1990), koomal and ngwayir (A.Wayne personal observation) also suggest that they may be less active in wet conditions, presumably to avoid heat loss and discomfort associated with getting wet.

Colder nights prior to the spotlight evening reduced the number of possums of both species that were detected. While this difference was significant in the weather models for both species, it was not significant in the final combined models. Given that cold nights are associated with winter, the covariates ‘season’ and ‘month’ most likely function as proxies for minimum temperature in explaining this phenomenon in the latter models. Similarly, cloud cover on the survey evening may have an effect on the detection of koomal but is otherwise explained by season and rain on the day of the survey. Cloud cover did not significantly influence the detection of ngwayir in this study or common ringtail possums and common brushtail possums in eastern Australia (e.g. How *et al.* 2004; Eyre 2004).

Laurance (1990) found that of the five variables he tested, temperature had the greatest effect on the spotlight detection of coppery brushtail possums, Herbert River ringtail possums and lemuroid ringtail possums. In agreement with the findings of our study, Laurance (1990) detected fewer animals on relatively cooler nights. In southern Queensland, however, temperature apparently had a negative influence on the detection of common ringtail possums (Eyre 2004).

Strong-to-gale-force wind was found to reduce the nocturnal foraging ranges of common brushtail possums in New Zealand (Paterson *et al.* 1995). Wind also was shown to reduce the activity of common ringtail possums in Victoria (Thomson and Owen 1964), but did not relate to detection rates in another study in south-eastern Australia (How *et al.* 2004). Changed behaviour in response to wind also was found to facilitate the detectability of feathertail gliders during the full moon (Davey 1990). Nonetheless, wind did not significantly affect the detection rates of koomal or ngwayir within the range of conditions experienced in our study.

The responses of arboreal marsupials to general conditions found by other researchers include the reduced detectability of yellow-bellied gliders by calling in adverse weather (Kavanagh and Rohan-Jones 1982). Goldingay and Kavanagh (1988) found for the detection of feathertail gliders that the moon was the only variable with a significant correlation with detection rates, while other variables, including temperature, cloud cover, rain, wind and survey duration, had no effect. Perceived ‘dreariness’, wind velocity, incidence of flowering, cloud cover and rain intensity were related to the detectability of gliders in a study that concluded that the most efficient survey nights were humid, warm, still and dark (Davey 1990). In fact, many researchers limit the weather and/or lunar cycle conditions in which they spotlight, whether or not these factors have been demonstrated to affect their specific circumstances (e.g. Kavanagh 1984; Lindenmayer *et al.* 2001; Goldingay and Sharpe 2004a).

Differences in the findings of various studies in relation to arboreal marsupial responses to the same factor result from one or a combination of the following: different species or population responses; different temporal and spatial ranges of survey conditions (e.g. habitat, weather); different measurement approaches to the same variable; over-fitting of statistical models providing spurious results; different analytical approaches. The gathering of accurate, quantitative measurements of variables rather than subjective estimations will improve the rigour of the study and reliability of the results. For similar reasons, measuring variables such as moonlight directly, rather than indirectly (e.g. astronomical tables that do not account for horizons, cloud cover, forest density, etc) as in this study, is also strongly recommended.

2.5.3 Survey procedures

The time taken to complete standardised spotlight transect lengths (i.e. survey duration) was significantly related to the numbers of koomal and ngwayir detected in this study. This was probably due, in part, to the time taken to identify and record data on sightings – i.e. the more possums seen, the longer it takes to complete the survey – especially since the number of possums detected on any one survey ranged from 3 to 71 (mean = 25). Additionally, even a small difference in the travel speed will have a substantial effect on the survey time, given the transect lengths. The ability to spotlight possums within a structurally complex forest system also is particularly sensitive to survey speed – something which was only approximated in this study – highlighting the importance of tightly controlling survey speed. Goldingay and Sharpe (2004b) also emphasised the importance of a slow pace for improving the pedestrian-based spotlight detection of feathertail gliders. The optimal detection efficiency is, in part, a compromise between allowing sufficient time to scan and search the vegetation adequately while minimising the time available for possums to hide.

An observer team effect ($p = 0.050$) on the detection of koomal in the survey procedures model, but not in the final models for either species, roughly reflected the relative experience of the observer team-leaders. The influence of observer expertise on the detection of arboreal marsupials has been recognised by others (e.g. Goldingay and Sharpe 2004a). It is therefore advisable that the same observer be used where possible, and this factor needs to be considered in both the design of the study and subsequent data analyses (e.g. Cunningham *et al*. 1999; Field *et al.* 2002).

In the final models, the start time of the spotlight survey in relation to sunset did not significantly affect the number of koomal or ngwayir detected. Interestingly, other researchers have observed differences in the diel activity patterns of these and other arboreal marsupials. These activity patterns may in turn influence their detectability throughout the night (e.g. Goldingay 1984; Newell 1999; Eyre 2004). Ngwayir emerge shortly after dark (Jones *et al.* 1994b), and their activity has been found to vary during the course of the night (Maher 2001). The closely-related common ringtail possum is the last of a number of species to emerge after darkness (Lindenmayer *et al.* 1991) and is normally most active before midnight (Thomson and Owen 1964); its activity and detectability also may vary throughout the evening (Roberts *et al.* 1990; How *et al.* 2004). Common brushtail possum activity also varies throughout the night (e.g. Ward 1978; MacLennan 1984; Cowan and Clout 2000) and may affect their detectability. For example, Paterson *et al.* (1995) found that relatively more possums were observed between 2300 and 0230 hours in New Zealand, while in north Queensland, coppery brushtail possums were most active in the first half of the night and green ringtails were most active during the two hours before dawn (Proctor-Gray 1984).

Given the evidence for differing diel activity patterns and the research findings for other species, it remains advisable to include the timing of surveys into the design of a study. This can be approached in a number of ways. For example, Kavanagh (1984) designed a spotlight method to overcome potential temporal differences in detection by surveying each transect twice in each of two periods, once in each direction in each period (Goldingay and Kavanagh 1988). Alternatively, the start times for spotlight surveys can be fixed in relation to sunset or astronomical definitions of darkness.

While the frequency of surveys was not examined in this study, if surveys are conducted too frequently it may affect the behaviour or welfare of the study animals (e.g. Lindenmayer 2002). This in turn may cause a change in detectability and possibly compromise the value of research results. For instance, experiments on three species of ringtail possum in Queensland found that their response to repeated spotlighting within the same night was to move away from the road transects and higher up into the trees with each subsequent visit (Wilson 1999). Active avoidance by greater gliders also was found after eight nights of spotlighting (Davey and Robinson 1986). The frequency of spotlight surveys therefore needs to be considered in the research methodology.

2.5.4 Differences in habitat structure due to logging

Fewer ngwayir were detected in the years after logging and more koomal and ngwayir were detected in recently logged than in unlogged areas. The differences in detection levels between logged and unlogged areas could result from several factors: (1) differential detectability due to (a) structural differences in vegetation and/or (b) behavioural differences; and (2) real differences in possum densities. The latter factor is unlikely for koomal at least, given that a simultaneous trapping study to examine the effects of logging in the same area found fewer koomal in the logged areas commensurate with the intensity of the logging treatment (Morris *et al.* 2001; A. Wayne unpublished). Given that the ngwayir was not easily trapped there are no complementary trapping data available for this species for comparison.

Differences in detectability in response to vegetation structure are the most logical and parsimonious explanation as to why more koomal and ngwayir were detected in logged areas. It has been suggested by other researchers that habitat structure may affect the ability to observe arboreal mammals (e.g. Bell 1981; Davey 1990), although this has not yet been comprehensively demonstrated for any Australian arboreal marsupials. Nonetheless, some studies have attempted to account for detectability differences due to habitat in order to compare abundance estimates between habitat types (e.g. Kavanagh 1984). Other studies have restricted the distances over which animals were counted in order to control for differences in detectability associated with habitat structure (e.g. Kavanagh 1988).

Alternatively, others have limited their research scope to one forest type in order to avoid potential detectability differences (e.g. Lindenmayer *et al.* 2001).

Possum behaviour is expected to respond differently to logged and unlogged forest on account of variations in the type and distribution of food and shelter resources, travel routes and relative vulnerability to predation. For instance, we would expect possums (ngwayir in particular) to travel on the ground more in logged areas than in mature forest, where greater tree crown connectivity may provide more preferable travel routes. This is supported by the spotlight data, with proportionally twice as many ngwayir being detected on the ground in logged areas as in unlogged areas (i.e. 3.5 % and 8.3% of ngwayir were initially located on the ground in logged and unlogged forest respectively; Wayne *et al.* 2001). These differences in behaviour also may affect the chances of animals being detected by spotlighting in ways that may not be so easily measured.

As regrowth forest structure changes over time, it is likely that possum detection efficiencies may vary with changes in habitat structure and possum behavioural responses to the vegetation. Therefore, careful consideration of habitat effects over space and time is required for a reliable comparison of detection rates. Priority should be accorded to improving the reliability of abundance estimates by determining the effect of habitat structure on the spotlight detectability of arboreal marsupials.

2.6 Conclusion

Spotlight detection counts may be influenced by spatial and temporal differences in the detection efficiency or possum behaviour. Technical aspects of the survey method, even apparently subtle ones, also can influence the number of possums detected. Key recommendations when considering how to maximise the detection of possums using vehicle-based spotlight methods include the following: (1) Survey koomal in spring and autumn and ngwayir between October and April. If the objective is to survey both species simultaneously then March – April and October – November are the best times; (2) Avoid surveying on rainy days or in particularly cold weather (i.e. weather most commonly associated with winter in the jarrah forests); (3) Control the travel speed of surveys. This is because detection efficiencies are likely to be sensitive to even small variations in survey speed; (4) Restrict the number of observers. When multiple observers are used, account for this in the study design and data analysis; (5) When surveying different habitats over space and/or time, account for the potential effect of vegetation structure, which can affect detection efficiency; and (6) Depending on the populations and their habitat, other temporal, weather and procedural factors (including survey frequency) may affect the spotlight detection efficiency and precision. Understanding an animal's life history, behaviour and ecology can inform and improve survey methodology. It will also increase awareness of specific factors that may need to be taken into account when conducting further research and interpreting the results.

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2.8 References

Abbott, I. (2001). Aboriginal names of mammal species in south-west Western Australia. *CALMScience* **3**, 433-486.

Abbott, I. and Whitford, K. (2002). Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: strategic risk assessment in relation to ecology, policy, planning, and operations management. *Pacific Conservation Biology* **7**, 240-255.

Bell, D. J. (1981). Estimating the density of possums *Trichosurus vulpecula*. In 'Proceedings of the first symposium on marsupials in New Zealand'. (Ed. B. D. Bell) No. 74 pp. 177-182. (Zoology Publications from Victoria University: Wellington)

Bennett, A. F., Lumsden, L. F., Alexander, J. S. A., Duncan, P. E., Johnson, P. G., Robertson, P. and Silveira, C. E. (1991). Habitat use by arboreal mammals along an environmental gradient in north-eastern Victoria. *Wildlife Research* **18**, 125-146.

Bradshaw, F. J. (1999). Trends in silvicultural practices in the native forests of Western Australia. *Australian Forestry* **62**, 255-264.

CALM (1995). 'Silvicultural Guidelines 1/95: Silvicultural Practice in Jarrah Forest. 'Western Australian Government Department of Conservation and Land Management, Perth.

Catling, P. C., Burt, R. J. and Kooyman, R. (1997). A comparison of techniques used in a survey of the ground-dwelling and arboreal mammals in forests in north-eastern New South Wales. *Wildlife Research* **24**, 417-432.

Cowan, P. and Clout, M. (2000). Possums on the move: Activity patterns, home ranges and dispersal. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 24-34. (Manaaki Whenua Press: Lincoln, New Zealand)

Cunningham, R. B., Lindenmayer, D. B. and Nix, H. A. (1999). Quantifying observer heterogeneity in bird counts. *Australian Journal of Ecology* **24**, 270-277.

Davey, S. M. (1990). Methods for surveying the abundance and distribution of arboreal marsupials in a south coast forest of New South Wales. *Australian Wildlife Research* **17**, 426-445.

Davey, S. M. and Robinson, N. (1986). Methods appraisal of techniques for behavioural observations of greater gliders. *Bulletin of the Australian Mammal Society* **9**, 42.

Dell, B. and Havel, J. J. (1989). The jarrah forest, an introduction. In 'The Jarrah Forest: A Complex Mediterranean System'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 1-10. (Kluwer Academic Publishers: Dordrecht)

de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

Dyne, G. R. and Walton, D. W. (1987). (Ed.) 'Fauna of Australia: Volume 1B, Mammalia.' (Australian Government Publishing Service: Canberra)

Ellis, M. and Jones, B. (1992). Observations of captive and wild western ringtail possums *Pseudocheirus occidentalis*. *Western Australian Naturalist* **19**, 1-10.

Eyre, T.J. (2004). Distribution and conservation status of the possums and gliders of southern Queensland. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 1-25. (Surrey Beatty and Sons: Sydney)

Eyre, T. J. and Smith, A. P. (1997). Floristic and structural habitat preferences of yellow-bellied gliders (*Petaurus australis*) and selective logging impacts in southeast Queensland, Australia. *Forest Ecology and Management* **98**, 281-295.

Field, S. A., Tyre, A. J. and Possingham, H. P. (2002). Estimating bird species richness: How should repeat surveys be organized in time? *Austral Ecology* **27**, 624-629.

Fletcher, D. J., Moller, H. and Clepperton, K. B. (1999). Spotlight counts for assessing abundance of rabbits (*Oryctolagus cuniculus* L.). *Wildlife Research* **26**, 609-620.

Gannon, M. R. and Willig, M. R. (1997). The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). *Biotropica* **29**, 525-529.

GenStat (2003). GenStat for Windows. Seventh Edition. VSN International Ltd., Hemel Hempstead, U.K.

Goldingay, R. L. (1984). Photoperiodic control of diel activity in the sugar glider (*Petaurus breviceps*). In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 385-391. (Australian Mammal Society: Sydney)

Goldingay, R. L. and Kavanagh, R. P. (1988). Detectability of the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Burramyidae), in relation to measured weather variables. *Australian Mammalogy* **11**, 67-70.

Goldingay, R. L. and Sharpe, D. J. (2004a). How effective is spotlighting for detecting the squirrel glider? *Wildlife Research* **31**, 443-449.

Goldingay, R. L. and Sharpe, D. J. (2004b). Spotlight versus nestboxes for detecting feathertail gliders in northeast New South Wales. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 298-305. (Surrey Beatty and Sons: Sydney)

Gursky, S. (2003). Lunar philia in a nocturnal primate. *International Journal of Primatology* **24**, 351-367.

Herberle, G. (1997). Timber harvesting of Crown land in the south-west of Western Australia: An historical review with maps. *CALMScience* **2**, 203-224.

How, R. A. (1972). The ecology and management of *Trichosurus* species (Marsupialia) in New South Wales. PhD thesis, University of New England.

How, R. A. (1978). Population strategies of four species of Australian "possums". In 'Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery) pp. 305-313. (Smithsonian Institution Press: Washington)

How, R. A. (1981). Population parameters of two congeneric possums, *Trichosurus* spp., in north-eastern New South Wales. *Australian Journal of Zoology* **29**, 205-215.

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

How, R. A. and Kerle, J. A. (1995). Common Brushtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan). (Reed Books: Chatswood)

How, T., Carthew, S. M. and Tap, P. (2004). A comparison of survey techniques for detecting possums and gliders in forest patches in southern Australia. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 564-578. (Surrey Beatty and Sons: Sydney)

Jones, B. (1995). Western Ringtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan) pp. 252-254. (Reed Books: Chatswood)

Jones, B. (2004). The possum fauna of Western Australia: decline, persistence and status. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 149-160. (Surrey Beatty and Sons: Sydney)

Jones, B. A., How, R. A. and Kitchener, D. J. (1994a). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175-187.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994b). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Kavanagh, R. P. (1984). Seasonal changes in habitat use by gliders and possums in south eastern New South Wales. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 527-543. (Australian Mammal Society: Sydney)

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. and Rohan-Jones, W. G. (1982). Calling behaviour of the yellow-bellied glider *Petaurus australis* Shaw (Marsupialia: Petauridae). *Australian Mammalogy* **5**, 95-111.

Kerle, J. A. (2001). 'Possums: the brushtails, ringtails and greater glider (First edn).' (University of New South Wales Press: Sydney)

Kerle, J. A., McKay, G. M. and Sharman, G. B. (1991). A systematic analysis of the brushtail possum, *Trichosurus vulpecula* (Kerr, 1792) (Marsupialia, Phalangeridae). *Australian Journal of Zoology* **39**, 313-331.

Laurance, W. F. (1990). Effects of weather on marsupial folivore activity in north Queensland upland tropical rainforest. *Australian Mammalogy* **13**, 41-47.

Lindenmayer, D. B. (2002). 'Gliders of Australia: A Natural History.' (University of New South Wales Press Ltd.: Sydney)

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T. and Nix, H. A. (1991). Aspects of the use of den trees by arboreal and scansorial marsupials inhabiting montane ash forests in Victoria. *Australian Journal of Zoology* **39**, 57-65.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F., Incoll, R. D., Pope, M. L., Tribolet, C. R., Viggers, K. L. and Welsh, A. H. (2001). How effective is spotlighting for detecting the greater glider (*Petauroides volans*)? *Wildlife Research* **28**, 105-109.

MacLennan, D. G. (1984). The feeding behaviour and activity patterns of the brushtail possums, *Trichosurus vulpecula*, in an open eucalypt woodland in southeast Queensland. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 155-161. (Australian Mammal Society: Sydney)

Maher, M. (2001). Nocturnal and diurnal activity patterns of the western ringtail possum, *Pseudocheirus occidentalis*, and its relevance to the Western Shield Program. Unpublished Directed Environmental Research Project. University of Notre Dame.

Mattiske, E. M. and Havel, J. J. (1997). 'Review and integration of floristic classifications in the south-west forest region of Western Australia: A report to the Commonwealth and Western Australian Governments for the Western Australian Regional Forest Agreement.' Mattiske Consulting Pty. Ltd., Perth.

Maxwell, S., Burbidge, A. A. and Morris, K. (1996). 'The 1996 Action Plan for Australian Marsupials and Monotremes.' Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Project No. 500, Perth.

McArthur, W. M. and Clifton, A. L. (1975). 'Forestry and agriculture in relation to soils in the Pemberton area of Western Australia. Soils and Land Use Series No. 54 ' C.S.I.R.O., Melbourne.

Morris, K., Johnson, B., Rooney, J. and Ward, C. (2001). The short-term impacts of timber harvesting and associated activities on the abundance of medium-sized mammals in the jarrah forest of Western Australia. In 'Nature Conservation 5: Conservation in the Production Environments: Managing the Matrix'. (Eds J. L. Craig, N. Mitchell and D. A. Saunders) pp. 60-70. (Surrey Beatty and Sons: Sydney)

Newell, G. R. (1999). Home range and habitat use by Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) within a rainforest fragment in north Queensland. *Wildlife Research* **26**, 129-145.

Nowak, R. M. (1999). 'Walker's Mammals of the World, Volume 1 (Sixth edn).' (The John Hopkins University Press: Baltimore)

Owen, W. H. and Thomson, J. A. (1965). Notes on the comparative ecology of the common brushtail possum and mountain possums in eastern Australia. *Victorian Naturalist* **82**, 216-217.

Pahl, L. I. (1987). Survival, age determination and population age structure of the common ringtail possum, *Pseudocheirus peregrinus*, in a *Eucalyptus* woodland and a

Leptospermum thicket in southern Victoria. *Australian Journal of Zoology* **35**, 625-639.

Paterson, B., Morris, R. S., Weston, J. and Cowan, P. E. (1995). Foraging and denning patterns of brushtail possums, and their possible relationship to contact with cattle and the transmission of bovine tuberculosis. *New Zealand Veterinary Journal* **43**, 281-288.

Proctor-Gray, E. (1984). Dietary ecology of the coppery brushtail possum, green ringtail possum and Lumholtz's tree-kangaroo in north Queensland. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 129-135. (Australian Mammal Society: Sydney)

Roberts, M., Phillips, L. and Kohn, F. (1990). Common ringtail possum (*Pseudocheirus peregrinus*) as a management model for the Pseudocheiridae – Reproductive scope, behavior, and biomedical values on a browse-free diet. *Zoo Biology* **9**, 25-41.

Schall, R. (1991). Estimation in generalised linear models with random effects. *Biometrika* **78**, 719-727.

Strelein, G. J. (1988). 'Site classification in the southern jarrah forest of Western Australia. 'Western Australian Government Department of Conservation and Land Management, Perth.

Thomson, J. A. and Owen, W. H. (1964). A field study of the Australian ringtail possum *Pseudocheirus peregrinus* (Marsupialia : Phalangeridae). *Ecological Monographs* **34**, 27-52.

Ward, G. D. (1978). Habitat use and home range of radio-tagged opossums *Trichosurus vulpecula* (Kerr) in New Zealand lowland forest. In 'Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery) pp. 267-287. (Smithsonian Institution Press: Washington)

Wayne, A. F., Ward, C., Rooney, J. and Wheeler, I. (2000). 'The immediate impacts of timber harvesting and associated activities on the ngwayir (*Pseudocheirus occidentalis*) in the jarrah forest of Kingston State Forest Block.' Progress Report. Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Rooney, J., Ward, C., Wheeler, I. and Mellican, A. (2001). 'Spotlight surveys to investigate the impacts of timber harvesting and associated activities within the jarrah forest of Kingston State Forest, with particular reference to the koomal (*Trichosurus vulpecula*) and ngwayir (*Pseudocheirus occidentalis*).' Progress Report. Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Cowling, A., Ward, C. G., Rooney, J. F., Vellios, C. V., Lindenmayer, D. B. and Donnelly, C. F. (2005b [Chapter 3]). A comparison of survey methods for arboreal possums in jarrah forest, Western Australia. *Wildlife Research* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005c [Chapter 4]). The life history of *Trichosurus vulpecula hypoleucus* (Phalangeridae), in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005d [Chapter 5]). The life history of *Pseudocheirus occidentalis* (Pseudocheiridae) in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wilde, S. A. and Walker, I. W. (1984). Pemberton-Irwin Inlet, Western Australia. Geological Survey Series Explanation Notes. Geological Survey of Western Australia, Perth.

Wilson, R. (1999). Possums in the spotlight. *Nature Australia*, 34-41.

Chapter 3

A COMPARISON OF SURVEY METHODS FOR KOOMAL AND NGWAYIR

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Arboreal trap

Pedestrian-based spotlighting with red filter

3.1 Abstract

Comparative trials of survey methods were conducted in the southern jarrah (*Eucalyptus marginata*) forest to determine the most efficient means of detecting koomal (common brushtail possum, *Trichosurus vulpecula hypoleucus*) and ngwayir (western ringtail possum, *Pseudocheirus occidentalis*). In particular, we examined different trapping and spotlighting methods and compared these with scat surveys.

Six different trapping methods (derived by combining three bait types and two trap positions) were compared at six sites. Significantly fewer koomal were caught on 'universal' bait (i.e. peanut butter, rolled oats and sardines) than on flour-based baits using rose oil or *Eucalyptus* oil as lures. Significantly more individuals of both possum species were caught in arboreal traps than in ground traps ($p < 0.001$ in both cases). Recapture rates of koomal were high, while ngwayir were rarely retrapped.

Six different spotlighting methods (derived by combining three spotlight intensities with two filter colours) were compared at the same six sites. There were no detection differences between the six methods for koomal. Significantly more ngwayir were detected using 50 watt or 100 watt lights than 20 watt lights ($p = 0.01$). There were no significant differences in the detection rates for ngwayir using red or white light. There were, however, significant observer differences in the number of possums of both species detected (koomal, $p = 0.025$; ngwayir, $p = 0.004$).

Spotlighting detected on average only 4.9% of the koomal 'known to be alive' (KTBA) by trapping. However, spotlighting with a 50 watt or 100 watt spotlight detected more ngwayir than did trapping. Koomal abundance measures derived from scat surveys were not significantly related to trapping or spotlight abundance estimates. For ngwayir, however, scat counts were strongly related to spotlight counts and there were no significant observer differences for the former. We conclude that koomal are more effectively surveyed using arboreal trapping with rose or *Eucalyptus* lures. Ngwayir are best surveyed using scat surveys or 50 W spotlights.

3.2 Introduction

Improving the understanding of the ecology or biology of any animal species or population depends on being able to detect reasonable numbers of individuals. The survey methods used will influence the amount, quality and type of data that can be collected. The methods commonly used to survey (i.e. count, catch and/or observe) Australasian arboreal marsupials include direct techniques such as trapping, spotlighting and stag watching, and indirect methods such as hair tubes, bait interference and scat surveys (Table 3.1). General descriptions of these methods are provided elsewhere (e.g. Sutherland 2003; Warburton

2000; Wilson and Delahay 2001). The detection efficiency of a survey method relates to the 'return' (i.e. the number of individuals recorded) for effort. This is especially pertinent when studying difficult-to-detect species where the results can have implications for conservation. In these cases in particular, the efficiency of the survey methods in detecting animals also may be critical to the success of the study. Consequently, the scientific knowledge of species may be reflected as much by the ease with which they can be studied, as by research interests or conservation priorities.

The ngwayir (western ringtail possum, *Pseudocheirus occidentalis*, Thomas 1888; Pseudocheiridae) is endemic to south-western Australia (Jones 1995; Kerle 2001), and according to sub fossil and historic records, its distribution has declined substantially since European settlement (de Tores 2000). An understanding of its ecology and conservation status has been constrained by the relative difficulty in surveying this species in the wild (Inions 1985; Jones *et al.* 1994b; de Tores 2000).

Conventional trapping methods, while useful for studying the sympatric koomal, (south-western subspecies of the common brushtail possum, *Trichosurus vulpecula hypoleucus,* Wagner 1855), have proved ineffective for ngwayir (Morris *et al.* 2001*;* A. Wayne unpublished data). Studies requiring the capture of ngwayir individuals have been limited to hand-catching or use of a tranquilliser dart gun (Jones *et al.* 1994b; P. de Tores unpublished data; A. Wayne unpublished data). In addition to being inefficient and labour intensive, such methods raise questions about the welfare of target animals. Spotlighting has been the most commonly used method for deriving abundance estimates of ngwayir and also is frequently used for koomal. Its usefulness, however, can be diminished by poor detection efficiency and high variability between repeat surveys (e.g. A. Wayne unpublished data).

This study examined variants of both live trapping (bait type and trap position) and spotlighting methods (light intensity and light colour) to identify which detected the most koomal and ngwayir individuals. Faecal pellet (scat) surveys were considered the most promising of the indirect survey methods and were also examined to assess their suitability as an alternative abundance measure for koomal and ngwayir.

Table 3.1. Summary of the most common direct (*) and indirect (#) survey methods used to study common Australasian arboreal marsupials.

TECHNIQUE	DESCRIPTION	EXAMPLE REFERENCES
Spotlighting*	Vehicle or pedestrian based surveys along transects or within plots using a torch or spotlight to visibly detect animals by eye-shine, movement or shape	Pahl 1987a; Jones and Hillcox 1995; Lindenmayer *et al.* 1999a; Kavanagh 2000; Soderquist and MacNally 2000; Warburton 2000; Kanowski *et al.* 2001; van der Ree and Loyn 2002; Wormington *et al.* 2002
Trapping*	Typically using wire cage or box traps with bait to entrap animals unharmed	How 1981; Pahl 1987b; Brockie *et al.* 1997; Kerle 1998; Runcie 1999; Efford *et al.* 2000; How and Hillcox 2000; Viggers and Lindenmayer 2000
Stag watching*	Sit and observe animals emerge from potential or known den trees during early evening	Lindenmayer *et al.* 1991; Lindenmayer and Cunningham 1997; van der Ree and Loyn 2002
Thermography*	Infrared thermal imaging using cameras	Dymond *et al.* 2000
Nest boxes*	Monitoring artificial day rest sites, generally species specific	Soderquist *et al.* 1996; Rhind and Bradley 2002; Lindenmayer *et al.* 2003
Hand Capture*	Search (usually by spotlight at night or dreys during the day) and capture either by hand or with the aid of equipment, e.g. tranquilliser dart gun	Pahl 1987b; Jones *et al.* 1994a, 1994b; Munks 1995; Salas and Stephens 2004
Vocalisation and Playbacks*	Listen for vocalisations or elicit responses using recordings of calls	Kavanagh and Bamkin 1995
Opportunistic observations*	e.g. detections made by logging crews, also road-kills and public sightings	Braithwaite *et al.* 1984; Bennett *et al.* 1991
Hair tubes#	Capture of hair that can be identified by their species specific characteristics	Lindenmayer *et al.* 1999b, 1999c
Bait interference#	Identify species by bite marks on wax block lures	Thomas 1999; Warburton 2000; Warburton *et al.* 2004
Scats#	Presence/absence, frequency of detection or relative abundance	Jones *et al.* 1994a; Munks *et al.* 1996
Predator Scat Analysis#	Species presence using remains found in the scats of predators	Friend 1978; Lunney 1987; Goldingay and Daly 1997
Other sign#	Possum tracks and other marks up trees, sand pads, smoked/ink papers	Inions *et al.* 1989; Jones *et al.* 1994a

3.3 Methods

3.3.1 Study area

The study area was within the southern portion of Perup Nature Reserve (Boyicup and Chariup forest blocks), 270 km south-south-east of Perth, and 40 km east of Manjimup, Western Australia. Perup is 52,000 hectares of dry sclerophyll forest dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*), which has been managed as a Nature Reserve since the 1971. The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters. The local average annual rainfall is around 700 mm. The region is on the Darling Plateaux underlain by the Archaean Yilgarn Craton composed of granites and gneiss (Wilde and Walker 1984; CALM 1998). The topography is gently undulating plateaux tops, low lateritic ridges and broad valleys, ranging from 220 m to 280 m above sea level.

3.3.2 Study sites

Six study sites were used to conduct comparative trials for the trapping, spotlighting and scat surveys (Figure 1; Boyicup Dense, 116.59^{o}E, 34.28^{o}S; Chariup Open, 116.63^{o}E, 34.28^{o}S; DeLandrafft Dense 116.59^{o}E, 34.26^{o}S; Glendale Dense, 116.60^{o}E, 34.29^{o}S; Glendale Open, 116.59^{o}E, 34.29^{o}S; Orient Open, 116.61^{o}E, 34.27^{o}S). To maximise detection rates, the study sites were selected in areas of jarrah forest known to have had relatively high possum densities. To provide representativeness across a range of jarrah forest conditions, three sites were selected with a dense mid-storey (valley sites) and three with an open mid-storey (upland sites).

Each study site consisted of five parallel 600 m transects, spaced 100 m apart. Ground trap points were spaced every 50 m along these transects, and arboreal trap platforms were positioned at every second ground trap point (i.e. 35 arboreal trap platforms per site, 65 ground trap positions). Spotlight surveys were conducted on the central and two outer transects (i.e. spaced 200 m apart, 1800 metres total spotlight survey length per site). This was to minimise repeat counting of the same individuals, given that most possums were detected < 50 m from the transect lines and possum movements are generally limited (e.g. MacLennan 1984; A. Wayne personal observation). Scat surveys were conducted adjacent to the same three transects but offset by about 10 metres to avoid areas disturbed by trapping and spotlight activity. Each scat transect comprised of 60 scat survey quadrats (1 m x 1 m).

Spotlighting and trapping surveys were conducted on different days to avoid confounding between survey methods. Altogether 18 spotlight surveys were conducted on each of the six study sites between November 2001 and March 2002. Six trapping sessions (each involving three consecutive nights of trapping) were conducted between November 2001 and February 2002 at each of the same six sites. The scat surveys were completed in four weeks during April and May 2002.

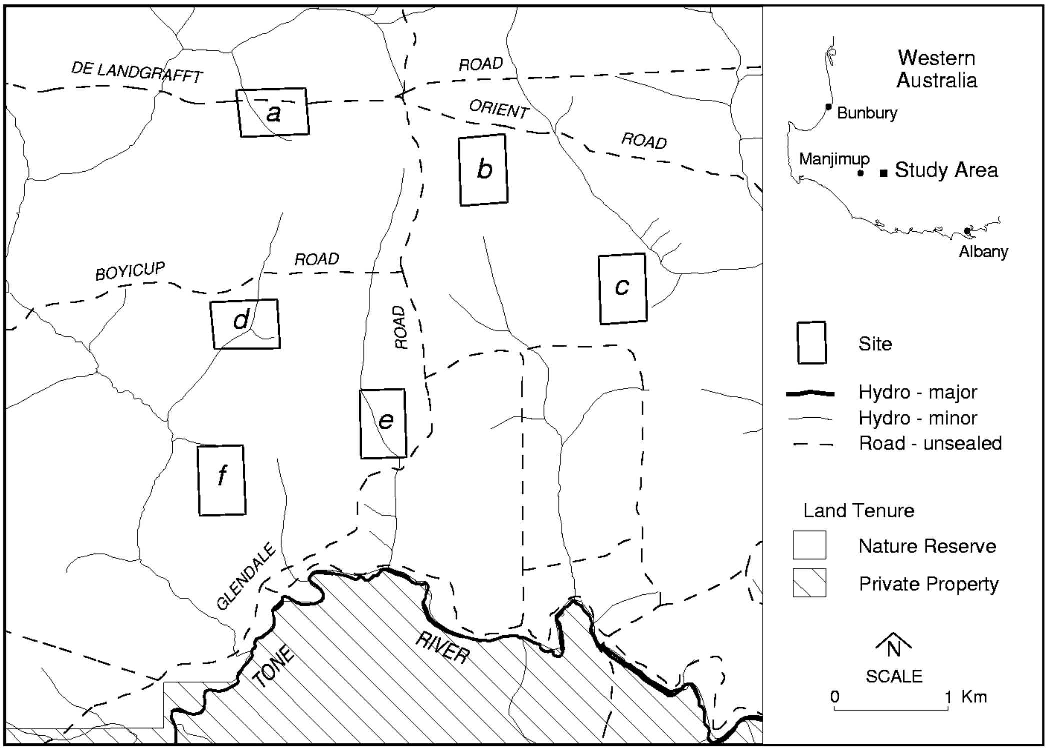

Figure 3.1. The location of the six study sites used in the comparative survey method trials for koomal and ngwayir in Perup Nature Reserve.

The six sites are (a) DeLandgrafft Dense, (b) Orient Open, (c) Chariup Open, (d) Boyicup Dense, (e) Glendale Dense and (f) Glendale Open.

3.3.3 Trapping method trials

Six trapping methods comprised of all combinations of three bait types ('universal', rose oil and *Eucalyptus* oil) with two trap positions (ground and arboreal) were applied to the six sites over six fortnights (Table 3.2). The 'Latin Square' design was balanced with respect to carry-over effects (Cochran and Cox 1957). Three sites were trapped in a given week and the other three sites in the alternate weeks. A break of at least 11 days between trapping sessions on the same site also reduced the influence of any carry-over effects. Each trapping session was conducted for three consecutive nights (i.e. a total of 195 ground trap nights or 105 arboreal trap nights per session). All traps were checked and reset daily, in the early morning. Animals were immediately processed then released at the site of capture having recorded species, sex, age and individual identity (based on uniquely numbered small titanium tags applied one to each ear of all adults captured for the first-time).

Table 3.2. 'Latin Square' design balanced for carry-over effects for the assignment of six trapping methods to the six sites over a 12-week trapping programme.

The six trapping methods are a combination of two trap positions (Ground and Arboreal) and three baits (Universal, Rose oil and *Eucalyptus* oil).

WEEK	Glendale Open	Glendale Dense	Orient Open	DeLand-grafft Dense	Chariup Open	Boyicup Dense
1	Ground Universal	Ground Rose Oil	Arboreal Eucalyptus Oil	-	-	-
2	-	-	-	Arboreal Rose Oil	Ground Eucalyptus Oil	Arboreal Universal
3	Arboreal Eucalyptus Oil	Arboreal Rose Oil	Ground Eucalyptus Oil	-	-	-
4	-	-	-	Arboreal Universal	Ground Universal	Ground Rose Oil
5	Ground Rose Oil	Arboreal Eucalyptus Oil	Arboreal Rose Oil	-	-	-
6	-	-	-	Ground Eucalyptus Oil	Arboreal Universal	Ground Universal
7	Ground Eucalyptus Oil	Arboreal Universal	Ground Universal	-	-	-
8	-	-	-	Ground Rose Oil	Arboreal Eucalyptus Oil	Arboreal Rose Oil
9	Arboreal Universal	Ground Universal	Ground Rose Oil	-	-	-
10	-	-	-	Arboreal Eucalyptus Oil	Arboreal Rose Oil	Ground Eucalyptus Oil
11	Arboreal Rose Oil	Ground Eucalyptus Oil	Arboreal Universal	-	-	-
12	-	-	-	Ground Universal	Ground Rose Oil	Arboreal Eucalyptus Oil

For arboreal trapping, platforms were constructed from a metal frame with reinforced plywood decking (1200 mm x 200 mm x 10 mm). The platform was attached to a tree approximately 1.8 m above ground with two tech screws. The same type of Sheffield wire mesh cage that was used for ground trapping (220 mm x 220 mm x 590 mm) was secured to the platform using elastic hooks. A small straight bush stick was placed under the entrance of all traps to avoid injury to captured possums and facilitate complete trap door closure and locking. A thick hessian bag covered the traps to provide protection from the weather and exposure. Data were collected on the characteristics of the trees to which arboreal trapping platforms were attached to examine whether particular attributes influenced trap success (Table 3.3).

Two baits using novel lures, (1) rose oil, (PE1993, Range Products, Unit 6/138 Radium St, Welshpool, WA 6106); and (2) *Eucalyptus* oil ('Goanna' brand, Herron Pharmaceuticals, 17 Curzon St, Tennyson, QLD 4105) and a third, 'universal' bait (2 kg peanut butter, 500 g rolled oats and 636 g sardines) were used in the comparative trapping trials. These novel fragrances were chosen from a total of six (including aniseed oil, vanilla essence, tea tree oil and cod liver oil) that were involved in a preliminary bait selection trial (A. Wayne unpublished data). The *Eucalyptus* and rose baits consisted of 12 ml of oil per kilogram of plain flour and sufficient blended vegetable oil (50% canola, 50% soya bean) to produce moist firm dough. The proportions of ingredients used in the different bait types were maintained throughout the study. The bait in each trap was approximately squash ball size and was replaced only when an animal was caught. Given that the trap sessions were only three days long and in fine weather, the baits appeared to maintain their appearance and smell throughout each trap session. The results from these trials only apply to these trapping and bait conditions.

Table 3.3. Characteristics of the trees on which arboreal trapping platforms were attached, used to investigate whether particular attributes further improved trap success.

PARAMETER	DEFINITION
SPECIES	Tree Species; *Corymbia calophylla, Eucalyptus marginata, Eucalyptus wandoo*
DBHOB	Diameter at breast height over bark, (centimetres)
HEIGHT	Tree height to top of crown (metres)
SENESCENCE SCALE	Crown Senescence Scale (Whitford 2002)
TREE LEAN	Visual assessment of the degree of bole lean; V = vertical or near vertical; SL = Slightly leaning; L = Leaning
DEAD OR ALIVE	D = Dead; A = Alive tree or shrub
ANIMAL SIGN (0-5)	Extent of possum activity (score 0-5) on the bole and major branches of the tree
TRAP DIRECTION	Compass direction that the mouth of the trap faces on the platform
CONTACTS	The number of tall shrubs or trees within 2 m of the trap tree providing potential access for a possum

3.3.4 Spotlight method trials

Six spotlight methods were examined, which comprised of all combinations of three light intensities (20 W, 50 W, 100 W) with two light colours (white and red – approximately 85% of the red light transmission was 620-1100 nm from a Lightforce ‘Filter Red Striker’). Each of the six methods was used at the six sites by each of three observers (AW, CW, JR). Within an evening, each observer conducted two surveys (Period: early = start time one hour after 'civil darkness', i.e. one hour after the sun had reached three degrees below the horizon; and late = start time four hours after ‘civil darkness’). The start time of the early survey accounted for the different emergence times of arboreal marsupials (e.g. Thomson and Owen 1964; Lindenmayer *et al.* 1991). The spotlight methods were assigned to sites and nights using three 6 x 6 ‘Latin Squares’ balanced for carry-over effects. The 18 spotlight nights were generally conducted once per week. To limit environmental effects on the detection efficiency (Davey 1990; Laurance 1990; Wayne *et al.* 2005a [Chapter 2]), spotlighting was not conducted on evenings of extreme or inclement weather.

Surveys were conducted using handheld spotlights. Given the sensitivity of spotlight detection efficiencies to travel speed (Goldingay and Sharpe 2004a; Wayne *et al.* 2005a [Chapter 2]), this factor was tightly controlled in this study. A stopwatch and reflective markers every 50 m along transects ensured a consistent search speed of 1000 m per hour. Because of illness, a substitute observer (CV for JR) was used during five spotlight surveys. Cloud cover, wind, temperature, moon phase and presence were recorded during each survey. All possums that could be confidently identified to species level, either by the naked-eye or with the aid of binoculars, were recorded. Data recorded for each detected animal included time, number observed together (within approximately 10m), species, perpendicular distance from transect (m), height above ground (m), animal location (tree species, log, ground, etc), and where applicable, tree maturity (Sapling < 15 cm DBHob; Pole 15-40 cm DBHob; Mature > 40 cm DBHob, Overmature > 40 cm DBHob and advanced state of decay), and general comments on their activity, possible responses to spotlight disturbance, etc.

3.3.5 Scat surveys

The 1 x 1 m scat quadrats (i.e. 180 quadrats per site) were located under tree canopies to maximise the chances of detection of ngwayir scats in particular. Each quadrat was searched for the presence of koomal and ngwayir scats for two minutes by the same observer (CV) at all sites. With training and the use of reference collections, the species of most intact possum scats can be distinguished on the basis of shape, size, the content material and particle size. Those scats that could not be confidently attributed to either species were not recorded (<10% of samples). A relative index of abundance was then derived as the number of quadrats in which scats from each possum species were detected out of 60 quadrats (i.e. a scat detection rate). Scat surveys were conducted toward the end of the seasonal summer drought to allow for comparable data and maximum scat accumulation due to minimum moisture-driven scat decay rates (e.g. Chapman 2002).

3.3.5.1 Testing for scat survey observer differences

To examine observer differences in the use of the scat survey method, three observers (AW, CW, CV), each with a volunteer assistant, independently surveyed 11 transects at another nearby study area (Orient study site, Chariup Block). The 500 m long transects were spaced 50 m apart. The presence/absence of koomal and ngwayir scats was assessed at 33 one-metre diameter plots spaced at 15 m intervals along each transect. Each observer avoided sampling from those areas disturbed by a previous observer or by recent animal activity. Each plot was searched for two minutes. The surveys were conducted in five weeks, February – March 2003.

3.3.6 Data analysis

3.3.6.1 Trapping

Data were analysed using Poisson generalised linear mixed models (GLMMs, Schall, 1991). The number of individuals of each species trapped per survey at each site was the response variable. The fixed effects were the six methods (bait*position) and the corresponding carry-over effects. Site and week were included as random effects. An offset was used to correct for the different trap effort used for arboreal and ground traps. Consequently, results are expressed in units of possums per trap per survey. Models were reduced using Wald tests at the 5% significance level.

3.3.6.2 Arboreal trap success and tree characteristics

The capture data from the arboreal traps were analysed to examine whether trap success was related to tree characteristics. GLMMs were used for both possum species with the nine tree characteristic variables (Table 3.3) and all their two-way interactions as fixed effects and site as a random effect.

For koomal, a Poisson model was used with the response variable as the number of individuals caught in each arboreal trap during 18 survey nights. Because so few ngwayir were trapped, the success or failure of individual traps was used as the response in binomial models. Backward elimination was used to remove non-significant terms, based on Wald tests at the 5% significance level.

3.3.6.3 Spotlighting

Data were analysed using Poisson GLMMs. The number of individuals of each possum species detected on any night at each site was the response variable. The fixed effects were the six methods (intensity*colour), the corresponding carry-over effects, observer, period and mid-storey density. Site and week were included as random effects. Models were reduced using Wald tests at the 5% significance level.

3.3.6.4 Scat surveys

To investigate whether detection rates differed between observers, binomial GLMMs were fitted. The response variable was the number of plots per transect (out of 33) on which scats were recorded, observer was a fixed effect and transect was a random effect.

3.3.6.5 Comparison of methods

For trapping, the number of individuals known-to-be-alive (KTBA, or minimum number alive, MNA, Krebs 1999) was calculated by totalling the number of individuals that were trapped over the entire trapping trials along each transect of each site. The use of mark-recapture methods to estimate population abundance was not necessary because the aim of this study was to compare the actual number of individuals detected by trapping and spotlight methods, and how these compared with an index of abundance derived from scat surveys. Therefore, for each species, linear regression was used to determine whether there was a relationship between trapping (KTBA), spotlighting (total count of sightings along each transect over the entire study period), and scat surveys (prevalence of scats out of 60 quadrats), examining two methods at a time. Splines were fitted in an initial analysis to see whether each relationship was best modelled as linear or curvilinear. Subsequent analyses used polynomial models if appropriate. Linear models were fitted in all but one case; a quadratic term was fitted to the ngwayir scat data when modelled with the ngwayir spotlight data.

3.4 Results

3.4.1 Trapping

There were 1886 captures of koomal (350 individuals) and 80 captures of ngwayir (73 individuals) during 5400 trap nights (Table 3.4a and 3.4b respectively). On average, each koomal individual was caught five times during the trials, although two individuals were caught on all of the 18 trapping days conducted at their sites. Recapture rates of ngwayir were very low, with only seven instances where an individual was caught a second time.

Table 3.4. Summary of the number of a) koomal and b) ngwayir individuals captured at each of the six study sites using a combination of three baits and two trap positions, the total number of individuals captured by each method, and the number of individuals known-to-be-alive (KTBA) per site.

a) Koomal

Bait	Trap Position	Boyicup Dense	Chariup Open	DeLandgrafft Dense	Glendale Dense	Glendale Open	Orient Open	**Total Individuals**
Eucalypt	Arboreal	42	36	55	68	18	6	**225**
Eucalypt	Ground	35	25	52	40	22	15	**189**
Rose	Arboreal	48	35	46	61	22	17	**229**
Rose	Ground	24	28	37	36	17	16	**158**
Universal	Arboreal	18	28	22	64	21	20	**173**
Universal	Ground	23	20	48	41	10	15	**157**
KTBA per site		**59**	**46**	**74**	**118**	**30**	**23**	

b) Ngwayir

Bait	Trap Position	Boyicup Dense	Chariup Open	DeLandgrafft Dense	Glendale Dense	Glendale Open	Orient Open	**Total Individuals**
Eucalypt	Arboreal	0	3	0	1	4	7	**15**
Eucalypt	Ground	0	9	1	0	1	1	**12**
Rose	Arboreal	0	4	9	3	3	5	**24**
Rose	Ground	0	0	0	0	0	0	**0**
Universal	Arboreal	7	8	0	1	2	3	**21**
Universal	Ground	1	2	0	0	1	0	**4**
KTBA per site		**8**	**25**	**10**	**5**	**10**	**15**	

3.4.1.1 Trapping methods: bait types and trap positions

In the final model for the number of individual koomal trapped per survey, there was a highly significant difference between trap positions (X^2_1 = 134.54, p < 0.001). There also was a significant trap position carry-over effect (i.e. a retrappability effect; X^2_2 = 7.05, p = 0.029), and a significant difference between the three bait types (X^2_2 = 6.47, p = 0.039).

The back-transformed number of koomal is the expected count of animals if all other variables in the model were held at their mean value. This considered, the back-transformed number of koomal individuals caught per trap per survey using arboreal traps was 0.85 compared with 0.37 for ground traps. The number of koomal individuals caught for the first time was 0.44 per trap per survey, but for recaptures it was 0.64 and 0.61 per trap per survey for arboreal and ground traps, respectively. This indicated that once trapped, koomal were frequently retrapped. The trap rate of koomal individuals for universal, *Eucalyptus* and rose bait was 0.48, 0.60 and 0.60 per trap per survey, respectively.

In the final model for the number of individual ngwayir trapped, there was a highly significant difference between trap positions ($X^2_1 = 67.20$, $p < 0.001$), a significant trap position carry-over effect (i.e. retrappability) ($X^2_2 = 12.95$, $p = 0.002$), but no difference between the three bait types.

The trap rate of ngwayir individuals caught using arboreal traps was 0.08 per trap per survey and 0.01 for ground traps. The number of ngwayir individuals caught for the first time was 0.08 per trap per survey. Recapture rates of the same individuals were 0.01 and 0.02 per trap per survey for arboreal and ground traps, respectively. This indicated that ngwayir were rarely retrapped.

The success of arboreal traps at capturing koomal or ngwayir was not related to the characteristics of the tree to which the trap was attached (Table 3.3), or the orientation of the trap.

3.4.2 Spotlighting

The mean number of koomal individuals detected per spotlight survey was 2.5 (count range = 1-15; Table 3.5a). The mean number of ngwayir individuals detected per spotlight survey was 9.1 (count range = 1-26; Table 3.5b).

In the final models for both koomal and ngwayir, there were significant observer differences ($X^2_3 = 9.37$, $p = 0.025$; and $X^2_3 = 13.43$, $p = 0.004$ respectively). This was due to one observer detecting relatively more koomal, and the substitute observer detecting significantly fewer ngwayir.

In the final koomal model, there were significantly more sightings ($X^2_1 = 10.37$, $p = 0.001$) on the sites that had dense mid-storey vegetation (3.91 koomal per survey at dense sites, 1.43 koomal per survey at open sites). Spotlight detection rates for koomal did not differ in response to light intensity, colour, the interaction between light intensity and colour, or survey period.

In the final ngwayir model, there were significantly fewer sightings ($X^2_2 = 9.18$, $p = 0.010$) using a 20 W spotlight compared with 50 W and 100 W (back-transformed mean of 7.54, 9.48 and 9.06 ngwayir per survey respectively). Spotlight detection rates for ngwayir did not differ significantly in response to mid-storey vegetation, light colour, the interaction between light intensity and colour, or survey period.

Table 3.5. The mean number of a) koomal and b) ngwayir detected at each of the six sites by three different observers during spotlight trials of six methods derived from the combinations of three spotlight intensities and two colours.

a) Koomal

Intensity (watts)	Colour	Boyicup Dense	Chariup Open	DeLandgrafft Dense	Glendale Dense	Glendale Open	Orient Open	**Method Average**
20	RED	3.0	1.0	2.0	6.3	0.0	1.0	**2.2**
20	WHITE	4.3	3.7	2.0	4.3	0.3	0.3	**2.5**
50	RED	4.7	2.7	2.0	7.0	1.7	2.7	**3.4**
50	WHITE	4.0	1.3	3.3	8.0	0.7	1.0	**3.1**
100	RED	4.3	1.0	3.3	1.0	2.0	2.0	**2.3**
100	WHITE	3.0	1.7	3.3	9.3	1.3	2.0	**3.4**
Site Average		**3.9**	**1.9**	**2.7**	**6.0**	**1.0**	**1.5**	

b) Ngwayir

Intensity (watts)	Colour	Boyicup Dense	Chariup Open	DeLandgrafft Dense	Glendale Dense	Glendale Open	Orient Open	**Method Average**
20	RED	7.3	13.7	5.3	6.3	6.3	16.0	**9.2**
20	WHITE	3.7	18.7	8.7	6.7	6.7	17.3	**10.3**
50	RED	7.7	20.3	10.7	9.7	9.3	21.7	**13.2**
50	WHITE	5.0	16.3	15.3	6.0	5.3	22.3	**11.7**
100	RED	8.3	21.7	13.3	4.0	5.7	23.7	**12.8**
100	WHITE	4.7	13.3	10.0	11.0	6.7	18.0	**10.6**
Site Average		**6.1**	**17.3**	**10.6**	**7.3**	**6.7**	**19.8**	

3.4.2.1 Relative rates of detection between trapping and spotlighting

A three-day trapping survey using the optimal trapping methods for koomal (i.e. rose or *Eucalyptus* oil for bait and arboreal traps) caught on average 65.5% of the KTBA individuals (range = 26.1-81.3%). By comparison, a spotlight survey detected only an average of 4.9% of the koomal individuals KTBA (range = 0.8-21.7%). Compared to a three-day trapping survey using optimal methods, a spotlight survey detected on average 7.7% (range = 5.0-13.0%) of the koomal individuals caught per site.

A three-day trapping survey using the optimal trapping methods for ngwayir (i.e. arboreal traps) caught on average 29.3% of the total number of ngwayir individuals trapped at each site throughout the entire study (i.e. KTBA). By comparison, a single spotlight survey using 50 W or 100 W light detected more individuals per site (mean = 359.6%, range = 225-411%) than a three-day trapping session using optimal trapping methods, and detected a similar number of individuals (mean = 106.5%, range = 20-220%) as was trapped over the entire study (i.e. KTBA).

Both the trapping and spotlight trials showed similar trends to each other in the relative abundance of koomal and ngwayir between sites. There were more koomal individuals at the three sites with dense mid-storeys (p < 0.001 for both trapping and spotlight measures, Table 3.4a and 3.5a). Conversely, there tended to be more ngwayir at the open sites (p < 0.001 for spotlight abundance, p = 0.072 for trapping, Table 3.4b and 3.5b), despite Glendale Open having moderate to low numbers of both species relative to the other sites.

3.4.3 Scat surveys

Koomal scats were detected on average in 84% of plots per transect (range = 65-95%). Ngwayir scats were detected on average in 26% of the plots per transect (range = 3-50%). While the relative prevalence of scats varied moderately among sites for koomal (range = 67.3-93.3%), the detection rates differed more among sites for ngwayir (range = 6.1-46.7%; Table 3.6).

The regression models for koomal revealed no significant relationship between the prevalence of scats along each transect with either the KTBA from trapping or counts from spotlighting. The regression model relating ngwayir abundance from trapping and scat surveys indicated a very weak association (p = 0.067), principally because of the very low trap-capture rates of ngwayir. The regression model relating the total number of ngwayir detected by spotlighting along each transect and the prevalence of scats indicated a strong association (p < 0.001, 78.5% of the variance explained). The separate scat trials at the Orient study site specifically testing for observer differences revealed no significant differences.

Table 3.6. The mean scat detection prevalence for koomal and ngwayir at the six survey method trial sites in the jarrah forest of Perup Nature Reserve.

The prevalence of scats at each site was derived from the aggregation of three 600 m transects, each with 60 scat quadrats (1 m x 1 m).

	Boyicup Dense	Chariup Open	DeLandgrafft Dense	Glendale Dense	Glendale Open	Orient Open
Koomal	88.3%	93.3%	90.6%	85.0%	67.2%	78.9%
Ngwayir	21.7%	41.1%	27.2%	16.1%	6.1%	46.7%

3.5 Discussion

3.5.1 Trapping

3.5.1.1 Bait type

The comparisons made here of survey methods for koomal and ngwayir contribute to other comparative studies of various survey methods for other arboreal species (Table 3.7). Here, universal bait caught significantly fewer individual koomal than rose oil or *Eucalyptus* oil baits. Bait type did not, however, significantly affect capture rates of ngwayir. The findings for koomal in particular, are interesting given that universal bait has been the broadly accepted general trapping bait for many small-to-medium-sized mammals (including brushtail possums) throughout Australia. The results of this study (conducted over summer) should be considered in the context that it is possible that the success of baits may vary as a result of seasonal differences in nutritional demands and dietary differences in food types, quality and quantity. These seasonal aspects of bait effectiveness were not investigated here. The success of rose oil or *Eucalyptus* oil as a general, non-specific bait for other species is also unknown.

Different bait types have substantially improved the trap success rates of other species (e.g. chuditch, *Dasyurus geoffroii*, A. Wayne unpublished data; Laurance 1992; Ji *et al.* 1999). Alternative sound, visual and food lures have, however, generally resulted in little or no improvement in the capture rates of common brushtail possums (*Trichosurus vulpecula*) (e.g. Cowan 1987; Morgan *et al.* 1995; Carey *et al.* 1997; Todd *et al.* 1998). Other lures not tested here might further improve the trap success rates for koomal or ngwayir. Their effectiveness, however, will be limited by the range over which possums can detect them (Morgan *et al.* 1995).

Table 3.7. Some comparisons of different survey methods used to study Australasian arboreal marsupials.

Including; *Acrobates pygmaeus, Cercartetus nanus, Gymnobelideus leadbeateri, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Phalanger carmelitae, Phalanger sericeus, Pseudocheirus occidentalis, Pseudocheirus peregrinus, Pseudchirops cupreus, Trichosurus caninus, Trichosurus vulpecula.*

		COMPARED METHODS		
SPECIES	**REGION**	**BEST**	**OTHER**	**SOURCE**
P. breviceps, *P. peregrinus,* *T. vulpecula*	NSW	Foot spotlighting	Vehicle spotlighting, ground and arboreal trapping (Elliott traps, wire cages), hair tubes, smoked papers	Davey 1990
P. volans, *P. australis*	NSW	Vehicle spotlighting	Foot spotlighting, ground and arboreal trapping, hair tubes, smoked papers	Davey 1990
P. volans, *P. breviceps,* *P. peregrinus*	NSW	Foot spotlighting	Ground trapping (Elliotts, wire cages), soil plots, hair tubes, opportunistic sightings	Catling *et al.* 1997
T. caninus, *T. vulpecula*	NSW	Soil plots / foot spotlighting	Ground trapping, hairtubes, opportunistic sightings	Catling *et al.* 1997
P. norfolcensis	NSW	Spotlighting	Arboreal trapping (Elliotts)	Goldingay and Sharpe 2004b
A. pygmaeus	NSW	Foot spotlighting	Nestboxes, although may be appropriate when rare or monitored over several years	Goldingay and Sharpe 2004a
C. nanus	Vic.	Predator scat analysis	Ground trapping (wire cages) and foot spotlighting	Friend 1978
G. leadbeateri, *P. australis,* *P. breviceps,* *T. caninus*	Vic.	Stag watching	Foot spotlighting, arboreal trapping	Smith *et al.* 1989
P. volans, *P. peregrinus*	Vic.	Foot spotlighting and stagwatching were complementary		Smith *et al.* 1989
P. volans, *P. australis,* *P. peregrinus,* *T. caninus,* *T. vulpecula*	Vic.	Vehicle spotlighting	Foot spotlighting, arboreal trapping, incidental observations	Bennett *et al.* 1991
A. pygmaeus	Vic.	Foot spotlighting	Vehicle spotlighting, arboreal trapping, incidental observations	Bennett *et al.* 1991
A. pygmaeus	Vic.	Nestboxes	Foot spotlighting	Ward 2000
P. occidentalis, *T. vulpecula*	SA/Vic	Spotlighting	Hair tubes, response to call playback	How *et al.* 2004
P. breviceps	SA/Vic	Listening for calls	Spotlighting, hair tubes	How *et al.* 2004
P. occidentalis	WA	Foot spotlighting / Scat surveys	Ground and arboreal trapping	this paper
T. vulpecula	WA	Arboreal trapping	Ground trapping, foot spotlighting, scat surveys	this paper
T. vulpecula	NZ	Leg-hold trap	Kill trap	Miller 1993
T. vulpecula	NZ	Leg-hold trap	Wax blocks	Warburton *et al.* 2004
P. carmelitae, *P. sericeus,* *P. cupreus*	PNG	Locate by night-search, catch by day	Night search, day search, trapping	Salas and Stephens 2004

3.5.1.2 Trap placement

Arboreal traps caught 2.3 times as many koomal and 9.3 times as many ngwayir as ground traps. An advantage of arboreal traps is that non-target terrestrial species are not caught unnecessarily and more traps are left available to catch possums. Arboreal traps have been used elsewhere to study a number of species (e.g. Kays 1999 and references within), including common ringtail possums (*Pseudocheirus peregrinus*; Pahl 1987b) and other arboreal marsupials (e.g. Mawbey 1989; Davey 1990; Bennett *et al.* 1991; Meggs *et al.* 1991; Traill and Coates 1993).

There was no additional capture efficiency demonstrated in our study by selecting specific attributes of the tree upon which the traps were placed, although such an effect has been shown for other arboreal marsupials. For example, the trap rate of the sugar glider (*Petaurus breviceps*) is significantly related to the tree species on which the arboreal trap is attached (Smith and Phillips 1984). The height of the trap above ground also has been found to affect the trap rate of other arboreal animals, such as southern flying squirrels (*Glaucomys volans*) in North America (Risch and Brady 1996). Optimising trap height may lead to further improvements in the trap success rates for koomal and ngwayir, but any increase may be outweighed by the difficulties of setting up and checking less accessible traps. Potential sampling bias may occur from differences in animal behaviour according to sex and age (e.g. Coleman and Green 1984). These potential biases between different trapping methods were not examined in this study.

3.5.2 Spotlighting

While the detection of koomal did not differ between spotlight methods, 50 W and 100 W lights detected more ngwayir than 20 W lights. Similarly, no differences were found between 50 W and 100 W spotlights in detecting squirrel gliders (*Petaurus norfolcensis*; based on 28 sightings; Goldingay and Sharpe 2004b) and feathertail gliders (*Acrobates pygmaeus*; based on 12 sightings in 24.7 hours using 50 W spotlight and eight sightings in 22.6 hours with 100 W spotlight; Goldingay and Sharpe 2004a).

A practical advantage of 50 W light compared with 100 W is that a smaller, lighter battery can be carried to complete the same period of surveying. Furthermore, concerns about the impact of high intensity light on the eyes and welfare of nocturnal animals (e.g. Wilson 1999) can be addressed to some extent by the use of 50 W spotlights without compromising detection efficiency of ngwayir. If spotlight surveys in jarrah forest are specifically targeting only koomal, then 20 W lights can be used without a significant reduction in detection efficiency.

The colour of the light used (white or red filter) did not significantly affect detection rates for either possum species. To our knowledge, suggestions that red light potentially causes less disruption to Australian arboreal marsupials have not yet been substantiated in the published literature. Nevertheless, the results from this study suggest that red light can be used without compromising the detectability of koomal and ngwayir.

Possum spotlight detection rates did not differ between those surveys that commenced one hour versus four hours after ‘civil darkness’. These results are similar to those of another study in jarrah forest (Wayne *et al.* 2005a [Chapter 2]) that found vehicle-based spotlight detection rates of koomal and ngwayir did not relate to the survey start times (36 to 174 minutes after sunset, i.e. approximately 0-2.5 hours after ‘civil darkness’). The detection of common brushtail possums in southern Australia also did not vary between three different start times after sunset (How *et al.* 2004). The same study, however, detected significantly more common ringtail possums in surveys which started 30 minutes after sunset compared with 120 minutes and 240 minutes after sunset (How *et al.* 2004). Other researchers also have observed variation over time in the activity and detection of other arboreal species (e.g. Proctor-Gray 1984; Paterson *et al.* 1995). Therefore, while koomal and ngwayir detection rates are comparable over a range of survey times within the southern jarrah forest, the same may not necessarily apply to other populations or species elsewhere.

There were observer differences in spotlight detection of both koomal and ngwayir. These results suggest that despite extensive experience, there may be skill differences between observers. Goldingay and Sharpe (2004b) acknowledged that the influence of observer differences should not be underestimated and that it required testing when spotlighting squirrel gliders. Therefore, if multiple observers are used to spotlight arboreal mammals, potential variation between observers needs to be appropriately addressed in the design and analysis of the research (e.g. Lindenmayer *et al.* 1999a).

Spotlight detection rates are also likely to be sensitive to the survey speed (e.g. Goldingay and Sharpe 2004a; Wayne *et al.* 2005a [Chapter 2]). For this reason we highly recommend that speed be tightly controlled, as was the case in this study. Similar speeds to that used in this study (1000 m/h) have been used elsewhere for various arboreal marsupials (e.g. Ward 2000; Kanowski *et al.* 2001; How *et al.* 2004), however, further spotlight detection efficiencies may be gained by determining the optimal speed for particular species in particular habitats. For example, slower speeds (e.g. 500 m/h) were thought to be generally better for feathertail gliders (Goldingay and Sharpe 2004a). Optimal speeds are likely to be a compromise between sufficient time to carefully search for animals throughout the vegetation and allowing too much time for animals to detect observer presence and avoid detection (Wayne *et al.* 2005a [Chapter 2]). Spotlighting can be further improved by selecting optimal procedural and environmental conditions that influence detection rates, such as season and weather (Wayne *et al.* 2005a [Chapter 2]).

3.5.3 Comparisons between trapping and spotlighting methods

Overall, a spotlight survey for koomal detected an average of 4.9% (range = 0.8-21.7%) of the individuals KTBA from the trapping trials. By comparison, a three-day arboreal trapping survey with either rose oil or *Eucalyptus* oil bait, caught on average 65.5% (range = 26.1-81.3%) of the koomal individuals KTBA. Therefore, arboreal trapping was a more effective means of obtaining a population measure of koomal relative to spotlighting and other conventional trapping methods (i.e. ground traps and universal bait).

The detection rates of ngwayir individuals with 50 W or 100 W spotlights were similar (106.5%) to the total number of individuals (KTBA) detected throughout the entire trapping trial. On any one night, however, up to 220% more ngwayir were detected by spotlighting than were KTBA by trapping. Therefore, repeated spotlighting provides similar or better detection rates than extensive trapping, but requires substantially less effort. It would require further testing to determine how these methods might comparably perform in other habitats.

The comparison of survey methods with KTBA is considered a valid approach for koomal but is problematic for ngwayir. Having conducted 900 trap nights at each of six sites within a 14-week period, no or few new koomal individuals were caught at these sites towards the end of the trapping trials. Therefore, the number of koomal individuals KTBA at these sites is considered a reasonable but conservative estimate of the trappable population. The number of trapped ngwayir individuals KTBA were, however, poor estimates of the actual population given that few ngwayir were trapped relative to the number of possums detected within any one evening of spotlighting.

3.5.3.1 Detection comparisons by other studies

The spotlight detection efficiency for greater gliders (*Petauroides volans*) was found to be on average 26% (range = 0-50% per survey night per site; Lindenmayer *et al.* 2001). The relative spotlight detection efficiency for squirrel gliders was similar, at an average of 25% (range = 0-57%; Goldingay and Sharpe 2004b). In both the squirrel glider study (Goldingay and Sharpe 2004b) and this study a similar approach was used to compare methods, by which the rates of detection efficiency between survey methods were relative (not absolute) given that the areas of effective spotlight detection and individuals KTBA from trapping were not identical. Because they were relative measures of efficiency, the survey effort per unit area needs to be comparable for the results of different studies to be directly compared. This was not the case between this study and that of Goldingay and Sharpe (2004b) (e.g. distance between transects and the travel speed of surveys were different). Within this study, it was expected that less than 50% of the possums would be potentially detected, given that the mean distance of spotlighted possums from the transects was 26 m for both koomal and ngwayir and the transects were 200 m apart. ‘Distance sampling’ models (Buckland *et al.* 2004) may be used to overcome some of these differences but were not used here.

3.5.4 Scats

Scat detection rates for koomal did not significantly relate to trapping (KTBA) or spotlighting counts. This is most likely due to the high proportion of quadrats (mean = 84%) containing koomal scats (i.e. close to saturation) and the relatively low levels of variation in the prevalence of scats along different transects, resulting in limited distinction between sites. Therefore, while this method may be useful for detecting the presence of koomal, in its current form it is not considered a useful index of population size. Measures of scat abundance within quadrats rather than just presence/absence, or scat accumulation rates (e.g. Putman 1984; Warburton 2000; Wilson and Delahay 2001) may be alternative approaches to scat surveys that may provide better indices of population size.

Scat detection rates of ngwayir were strongly related to those derived from spotlighting (the regression model explained 78.5% of the variance). Scat surveys may therefore be a useful alternative relative measure of abundance. The poor relationship between ngwayir scat detection rates and ngwayir KTBA derived from trapping was not surprising given the relative ineffectiveness of the latter.

There are several advantages to the scat survey method for studying ngwayir distribution and abundance. There were no observer differences in the scat detection rates, whereas there were observer differences for spotlighting. In addition, scat surveys are quick, cost effective, simple and do not directly impact on the behaviour or welfare of the possums.

Of the indirect survey techniques commonly available, scat surveys are potentially the most useful, especially for herbivores (Triggs 1996) and inconspicuous or nocturnal animals (e.g. Taylor and Williams 1956; Southwell 1989; Bulinski and McArthur 2000). Other general advantages of indirect versus direct counts include; their accuracy is less dependent on the skill of the observer, and they are less affected by viewing conditions (Caughley 1977). It is important to note, however, that indirect survey methods have limitations (e.g. Neff 1968; Bulinksi and McArthur 2000). For example, variable defecation rates and scat decay rates (e.g. Bell 1981; Putman 1984; Southwell 1989; Lehmkuhl *et al.* 1994; Chapman 2002) may affect the comparable nature of the data and the calculation of population estimates.

3.5.5 Survey method comparisons by other studies

Bearing in mind that the relative suitability of various methods may differ with habitat and populations, our findings suggest that trapping was more effective than spotlighting for detecting koomal in the jarrah forest. By contrast, Catling *et al.* (1997) found that soil plots and spotlighting on foot provided higher detection rates of common brushtail possums. Spotlighting on foot was similarly the best method according to Davey (1990) and How *et al.* (2004), while Bennett *et al.* (1991), found that spotlighting from a vehicle detected more brushtail possums. Davey (1990) and Bennett *et al.* (1991) fixed arboreal traps directly to the trees. By comparison, the design and use of platforms used in this study appeared to considerably improve the effectiveness of the arboreal traps in the jarrah forest. The results from other comparative method studies are summarised in Table 3.7.

The results for the common ringtail possum in other studies were similar to those found for the ngwayir in this study (Table 3.7). Spotlighting on foot was generally the most effective detection method for common ringtail possums and many other arboreal marsupials (Smith *et al.* 1989; Davey 1990; Catling *et al.* 1997; How *et al.* 2004). Bennett *et al.* (1991), however, found that vehicle spotlighting was better. Stagwatching also has been recommended as a complementary method for common ringtail possums, given that this method detected individuals in areas where spotlighting failed to do so and vice versa (Smith *et al.* 1989). Scat surveys were not compared with other survey methods in these other studies.

The strong relationship between spotlighting and scat surveys for ngwayir does not indicate how well either of these methods relates to true abundance (i.e. precision and accuracy). To do so would depend on testing these methods on populations in which all individuals were confidently known (e.g. Perry and Braysher 1986). The effort required to do this is substantial. Alternatively, a measure of population density using scat surveys may be achieved less directly. For instance, with accurate knowledge of both the defecation rate and scat decay rate, a potentially reliable measure of population can be derived (e.g. Taylor and Williams 1956; Neff 1968; Putman 1984). These rates, however, would need to be specifically accounted for in each population given that they can vary over space and time.

3.5.6 Site differences

Both trapping and spotlighting showed that koomal were most abundant on the valley sites with relatively dense mid-storey vegetation. Ngwayir, on the other hand, were most abundant on two of the open mid-storey sites on the upper-slopes. In other habitats, ngwayir (Jones *et al.* 1994a) and the common ringtail possum (Soderquist and MacNally 2000) have been considered more abundant in valleys and more mesic areas. Therefore, the question remains as to whether the trends observed in our study reflect potential differences in habitat preference, predation differences, and/or competition between the two possum species. Nonetheless, variation in animal densities across the landscape will also affect rates of detection.

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3.7 References

Bell, D. J. (1981). Estimating the density of possums *Trichosurus vulpecula*. In 'Proceedings of the first symposium on marsupials in New Zealand'. (Ed. B. D. Bell) No. 74 pp. 177-182. (Zoology Publications from Victoria University: Wellington)

Bennett, A. F., Lumsden, L. F., Alexander, J. S. A., Duncan, P. E., Johnson, P. G., Robertson, P. and 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. and Kelly, J. (1984). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales: III. Relationships between faunal densities, eucalypt occurrence and foliage nutrients and soil parent materials. *Australian Wildlife Research* **11**, 41-48.

Brockie, R. E., Ward, G. D. and Cowan, P. E. (1997). Possums (*Trichosurus vulpecula)* on Hawke's Bay farmland: spatial distribution and population structure before and after a control operation. *Journal of The Royal Society of New Zealand* **27**, 181-191.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2004). 'Advanced distance sampling: Estimating abundance of biological populations.' (Oxford University Press: Oxford)

Bulinski, J. and McArthur, C. (2000). Observer error in counts of macropod scats. *Wildlife Research* **27**, 277-282.

CALM (1998). 'Draft Management Plan: Perup Forest and Lake Muir/Unicup Nature Reserves.' Western Australian Government Department of Conservation and Land Management, Perth.

Carey, P. W., O'Connor, C. E., McDonald, R. M. and Matthews, L. R. (1997). Comparison of the attractiveness of acoustic and visual stimuli for brushtail possums. *New Zealand Journal of Zoology* **24**, 273-276.

Catling, P. C., Burt, R. J. and Kooyman, R. (1997). A comparison of techniques used in a survey of the ground-dwelling and arboreal mammals in forests in north-eastern New South Wales. *Wildlife Research* **24**, 417-432.

Caughley, G. (1977). 'Analysis of Vertebrate Populations.' (John Wiley and Sons: London)

Chapman, K. (2002). Differential decay rates of brushtail possum (*Trichosurus vulpecula*) and western ringtail possum (*Pseudocheirus occidentalis*) scats. Honours thesis, University of Western Australia.

Cochran, W. G. and Cox, G. M. (1957). 'Experimental Design (Second edn).' (John Wiley and Sons: New York)

Coleman, J. D. and Green, W. Q. (1984). Variations in the sex and age distributions of brush-tailed possum populations. *New Zealand Journal of Zoology* **11**, 313-318.

Cowan, P. E. (1987). The influence of lures and relative opportunity for capture on catches of brushtail possums, *Trichosurus vulpecula*. *New Zealand Journal of Zoology* **14**, 149-161.

Davey, S. M. (1990). Methods for surveying the abundance and distribution of arboreal marsupials in a south coast forest of New South Wales. *Australian Wildlife Research* **17**, 426-445.

de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

Dymond, J. R., Trotter, C. M., Shepherd, J. D. and Wilde, H. (2000). Optimizing the airborne thermal detection of possums. *International Journal of Remote Sensing* **21**, 3315-3326.

Efford, M., Warburton, B. and Spencer, N. (2000). Home-range changes by brushtail possums in response to control. *Wildlife Research* **27**, 117-127.

Friend, G. R. (1978). A comparison of predator scat analysis with conventional techniques in a mammal survey contrasting habitats in Gippsland, Victoria. *Australian Wildlife Research* **5**, 75-83.

Goldingay, R. L. and Daly, G. (1997). Surveys of arboreal and terrestrial mammals in the montane forests of Queanbeyan, New South Wales. *Australian Mammalogy* **20**, 9-19.

Goldingay, R. L. and Sharpe, D. J. (2004a). Spotlight versus nestboxes for detecting feathertail gliders in northeast New South Wales. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson). pp. 298-305. (Surrey Beatty and Sons: Sydney)

Goldingay, R. L. and Sharpe, D. J. (2004b). How effective is spotlighting for detecting the squirrel glider? *Wildlife Research* **31**, 443-449.

How, R. A. (1981). Population parameters of two congeneric possums, *Trichosurus* spp., in north-eastern New South Wales. *Australian Journal of Zoology* **29(2)**, 205-215.

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

How, T., Carthew, S. M. and Tap, P. (2004). A comparison of survey techniques for detecting possums and gliders in forest patches in southern Australia. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 564-578. (Surrey Beatty and Sons: Sydney)

Inions, G. (1985). The interactions between possums, habitat trees and fire. Honours thesis, Australian National University.

Inions, G. B., Tanton, M. T. and Davey, S. M. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**, 449-458.

Ji, W., Veitch, C. R. and Craig, J. L. (1999). An evaluation of the efficiency of rodent trapping methods: The effect of trap arrangement, cover type, and bait. *New Zealand Journal of Ecology* **23**, 41-51.

Jones, B. (1995). Western Ringtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan). pp. 252-254. (Reed Books: Chatswood)

Jones, B. and Hillcox, S. (1995). A survey of the possums *Trichosurus vulpecula* and *Pseudocheirus occidentalis* and their habitats in forest at Ludlow, Western Australia. *Western Australian Naturalist* **20**, 139-150.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994a). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175-187.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994b). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Kanowski, J., Hopkins, M. S., Marsh, H. and Winter, J. W. (2001). Ecological correlates of folivore abundance in north Queensland rainforests. *Wildlife Research* **28**, 1-8.

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. *Pacific Conservation Biology* **6**, 18-30.

Kavanagh, R. P. and Bamkin, K. L. (1995). Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biological Conservation* **71**, 41-53.

Kays, R. W. (1999). A hoistable arboreal mammal trap. *Wildlife Society Bulletin* **27**, 298-300.

Kerle, J. A. (1998). The population dynamics of a tropical possum, *Trichosurus vulpecula arnhemensis* Collett. *Wildlife Research* **25**, 171-181.

Kerle, J. A. (2001). 'Possums: the brushtails, ringtails and greater glider (First edn).' (University of New South Wales Press: Sydney)

Krebs, C. J. (1999). 'Ecological Methodology.' (Addison-Wesley Educational Publishers: California)

Laurance, W. F. (1990). Effects of weather on marsupial folivore activity in north Queensland upland tropical rainforest. *Australian Mammalogy* **13**, 41-47.

Laurance, W. F. (1992). Abundance estimates of small mammals in Australian tropical rain-forest – a comparison of four trapping methods. *Wildlife Research* **19**, 651-655.

Lehmkuhl, J. F., Hansen, C. A. and Sloan, K. (1994). Elk pellet-group decomposition and detectability in coastal forests of Washington. *Journal of Wildlife Management* **58**, 664-669.

Lindenmayer, D. B. and Cunningham, R. B. (1997). Patterns of co-occurrence among arboreal marsupials in the forests of central Victoria, southeastern Australia. *Australian Journal of Ecology* **22**, 340-346.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T. and Nix, H. A. (1991). Aspects of the use of den trees by arboreal and scansorial marsupials inhabiting montane ash forests in Victoria. *Australian Journal of Zoology* **39**, 57-65.

Lindenmayer, D. B., Cunningham, R. B., Pope, M. L. and Donnelly, C. F. (1999a). The response of arboreal marsupials to landscape context: A large-scale fragmentation study. *Ecological Applications* **9**, 594-611.

Lindenmayer, D. B., Cunningham, R. B. and Pope, M. L. (1999b). A large-scale "experiment" to examine the effects of landscape context and habitat fragmentation on mammals. *Biological Conservation* **88**, 387-403.

Lindenmayer, D. B., Incoll, R. D., Cunningham, R. B., Pope, M. L., Donnelly, C. F., MacGregor, C. I., Tribolet, C. and Triggs, B. E. (1999c). Comparison of hairtube types for the detection of mammals. *Wildlife Research* **26**, 745-753.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F., Incoll, R. D., Pope, M. L., Tribolet, C. R., Viggers, K. L. and Welsh, A. H. (2001). How effective is spotlighting for detecting the greater glider (*Petauroides volans*)? *Wildlife Research* **28**, 105-109.

Lindenmayer, D. B., MacGregor, C. I., Cunningham, R. B., Incoll, R. D., Crane, M., Rawlins, D. and Michael, D. R. (2003). The use of nest boxes by arboreal marsupials in the forests of the Central Highlands of Victoria. *Wildlife Research* **30**, 259-264.

Lunney, D. (1987). Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, N.S.W. *Australian Wildlife Research* **14**, 263-274.

MacLennan, D. G. (1984). The feeding behaviour and activity patterns of the brushtail possums, *Trichosurus vulpecula*, in an open eucalypt woodland in southeast Queensland. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 155-161. (Australian Mammal Society: Sydney)

Mawbey, R. B. (1989). A new trap design for the capture of sugar gliders, *Petaurus breviceps*. *Australian Wildlife Research* **16**, 425-428.

Meggs, R. A., Lindenmayer, D. B., Linga, T. and Morris, B. J. (1991). An improved design for trap brackets used for trapping small mammals in trees. *Wildlife Research* **18**, 589-591.

Miller, C. J. (1993). An evaluation of two possum trap types for catch-efficiency and humaneness. *Journal of The Royal Society of New Zealand* **23**, 5-11.

Morgan, D. R., Innes, J., Frampton, C. M. and Woolhouse, A. D. (1995). Responses of captive and wild possums to lures used in poison baiting. *New Zealand Journal of Zoology* **22**, 123-129.

Morris, K., Johnson, B., Rooney, J. and Ward, C. (2001). The short-term impacts of timber harvesting and associated activities on the abundance of medium-sized mammals in the jarrah forest of Western Australia. In 'Nature Conservation 5: Conservation in the Production Environments: Managing the Matrix'. (Eds J. L. Craig, N. Mitchell and D. A. Saunders) pp. 60-70. (Surrey Beatty and Sons: Sydney)

Munks, S. (1995). The breeding biology of *Pseudocheirus peregrinus viverrinus* on Flinders Island, Bass Strait. *Wildlife Research* **22**, 521-534.

Munks, S. A., Corkrey, R. and Foley, W. J. (1996). Characteristics of arboreal marsupial habitat in the semi-arid woodlands of northern Queensland. *Wildlife Research* **23**, 185-195.

Neff, D. J. (1968). Pellet-group count technique for big game trend census and distribution – a review. *Journal of Wildlife Management* **32**, 597-614.

Pahl, L. I. (1987a). Feeding-behaviour and diet of the common ringtail possum, *Pseudocheirus peregrinus*, in *Eucalyptus* woodlands and *Leptospermum* thickets in southern Victoria. *Australian Journal of Zoology* **35**, 487-506.

Pahl, L. I. (1987b). Survival, age determination and population age structure of the common ringtail possum, *Pseudocheirus peregrinus*, in a *Eucalyptus* woodland and a *Leptospermum* thicket in southern Victoria. *Australian Journal of Zoology* **35**, 625-639.

Paterson, B., Morris, R. S., Weston, J. and Cowan, P. E. (1995). Foraging and denning patterns of brushtail possums, and their possible relationship to contact with cattle and the transmission of bovine tuberculosis. *New Zealand Veterinary Journal* **43**, 281-288.

Perry, R. J. and Braysher, M. L. (1986). A technique for estimating the numbers of eastern grey kangaroos, *Macropus giganteus*, grazing a given area of pasture. *Australian Wildlife Research* **13**, 335-338.

Proctor-Gray, E. (1984). Dietary ecology of the coppery brushtail possum, green ringtail possum and Lumholtz's tree-kangaroo in north Queensland. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 129-135. (Australian Mammal Society: Sydney)

Putman, R. J. (1984). Facts from faeces. *Mammal Review* **14**, 79-97.

Rhind, S. G. and Bradley, J. S. (2002). The effect of drought on body size, growth and abundance of wild brush-tailed phascogales (*Phascogale tapoatafa*) in south-western Australia. *Wildlife Research* **29**, 235-245.

Risch, T. S. and Brady, M. J. (1996). Trap height and capture success of arboreal small mammals: Evidence from southern flying squirrels (*Glaucomys volans*). *The American Midland Naturalist* **136**, 346-351.

Runcie, M. J. (1999). Movements, dens and feeding behaviour of the tropical scaly-tailed possum (*Wyulda squamicaudata*). *Wildlife Research* **26**, 367-373.

Salas, L. A. and Stephens, S. A. (2004). Capture and immobilisation of cuscuses and ringtail possums in Papua New Guinea. *Wildlife Research* **31**, 101-107.

Schall, R. (1991). Estimation in generalized linear models with random effects. *Biometrika* **78**, 719-727.

Smith, A. P. and Phillips, K. (1984). A systematic technique for census of sugar gliders and other small arboreal mammals. *Australian Wildlife Research* **11**, 83-87.

Smith, A. P., Lindenmayer, D. B., Begg, R. J., Macfarlane, M. A., Seebeck, J. H. and Suckling, G. C. (1989). Evaluation of the stag-watching technique for census of possums and gliders in tall open forest. *Australian Wildlife Research* **16**, 575-580.

Soderquist, T. R. and Mac Nally, R. (2000). The conservation value of mesic gullies in dry forest landscapes: mammal populations in the box-ironbark ecosystem of southern Australia. *Biological Conservation* **93**, 281-291.

Soderquist, T. R., Traill, B. J., Faris, F. and Beasley, K. (1996). Using nest boxes to survey for the brush-tailed phascogale *Phascogale tapoatafa*. *The Victorian Naturalist* **113**, 256-261.

Southwell, C. (1989). Techniques for monitoring the abundance of kangaroo and wallaby populations. In 'Kangaroos, Wallabies and Rat Kangaroos'. (Eds G. Grigg, P. Jarman and I. D. Hume) pp. 659-693. (Surrey Beatty and Sons: Sydney)

Sutherland, W. J. (2003). 'Ecological Census Techniques: A Handbook (Eighth edn).' (Cambridge University Press: Cambridge)

Taylor, R. and Williams, R. M. (1956). The use of pellet counts for estimating the density of populations of rabbits, *Oryctolagus cuniculus* (L.). *New Zealand Journal of Science and Technology* **38B**, 236-256.

Thomas, M. D. (1999). Feasibility of using wax-blocks to measure rodent and possum abundance and changes in population size. *Science for Conservation* **127C**, 39-48.

Thomson, J. A. and Owen, W. H. (1964). A field study of the Australian ringtail possum *Pseudocheirus peregrinus* (Marsupialia : Phalangeridae). *Ecological Monographs* **34**, 27-52.

Todd, J. H., O'Connor, C. E. and Waas, J. R. (1998). Laboratory evaluation of odour preferences of the brushtail possum. *Journal of Chemical Ecology* **24**, 439-449.

Traill, B. J. and Coates, T. D. (1993). Field observations on the brush-tailed phascogale *Phascogale tapoatafa* (Marsupialia: Dasyuridae). *Australian Mammalogy* **16**, 61-65.

Triggs, B. (1996). 'Tracks, Scats and Other Traces: A Field Guide to Australian Mammals.' (Oxford University Press: Melbourne)

van der Ree, R. and Loyn, R. H. (2002). The influence of time since fire and distance from fire boundary on the distribution and abundance or arboreal marsupials in

Eucalyptus regnans - dominated forest in the Central Highlands of Victoria. *Wildlife Research* **29**, 151-158.

Viggers, K. L. and Lindenmayer, D. B. (2000). A population study of the mountain brushtail possum (*Trichosurus caninus*) in the Central Highlands of Victoria. *Australian Journal of Zoology* **48**, 201-216.

Warburton, B. (2000). Monitoring possum populations. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 132-142. (Manaaki Whenua Press: Lincoln, New Zealand)

Warburton, B., Barker, R. and Coleman, M. (2004). Evaluation of two relative-abundance indices to monitor brushtail possums in New Zealand. *Wildlife Research* **31**, 397-401.

Ward, S. J. (2000). The efficacy of nestboxes versus spotlighting for detecting feathertail gliders. *Wildlife Research* **27**, 75-79.

Wayne, A. F., Cowling, A., Rooney, J. F., Ward, C. G., Wheeler, I. B., Lindenmayer, D. B. and Donnelly, C. F. (2005a [Chapter 2]). Factors affecting the detection of possums by spotlighting in Western Australia. *Wildlife Research* – revised manuscript in review.

Whitford, K. R. (2002). Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees: I. Hollow sizes, tree attributes and ages. *Forest Ecology and Management* **160**, 201-214.

Wilde, S. A. and Walker, I. W. (1984). Pemberton-Irwin Inlet, Western Australia. Geological Survey Series Explanation Notes. Geological Survey of Western Australia, Perth.

Wilson, R. (1999). Possums in the spotlight. *Nature Australia*, 34-41.

Wilson, G. J. and Delahay, R. J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* **28**, 151-164.

Wormington, K. R., Lamb, D., McCallum, H. I. and Moloney, D. J. (2002). Habitat requirements for the conservation of arboreal marsupials in dry sclerophyll forests of southeast Queensland, Australia. *Forest Science* **48**, 217-227.

SECTION B

POSSUM BIOLOGY IN JARRAH FOREST

This section comprises Chapters 4 and 5 and focuses on aspects of the life histories of koomal and ngwayir in the jarrah forest. These studies used the improved survey methods developed and identified in Section A, namely arboreal trapping, to collect relevant data on individuals within an area of jarrah forest in Chariup (part of Perup Nature Reserve), east of Manjimup, over an 18 month period. The purpose of this section is to provide a general biological understanding of these possum species in the jarrah forest. This provides particularly valuable background information necessary for the development of a more holistic ecological understanding, which will be addressed in Section C and synthesised in Section D.

Chapter 4

LIFE HISTORY OF KOOMAL

Citation: A. F. Wayne, C. G. Ward, J. F. Rooney, C. V. Vellios, and D. B. Lindenmayer (2005c) The life history of Trichosurus vulpecula hypoleucus *(Phalangeridae) in the jarrah forest of south-western Australia. Australian Journal of Zoology – revised manuscript in review*

Koomal,
Trichosurus vulpecula hypoleucus

4.1 Abstract

The common brushtail possum, *Trichosurus vulpecula* is noted for its morphological, biological and ecological variability across its range. Despite having suffered substantial population declines since European settlement, relatively little has been published on the south-western Australian subspecies, the koomal, *T. v. hypoleucus*. This study reports morphological, reproductive and general life history data from an 18-month study of a population in the southern jarrah (*Eucalyptus marginata*) forest at Chariup (part of Perup Nature Reserve), near Manjimup, in south-western Australia.

As one of the smallest subspecies, *T. v. hypoleucus* adult males averaged 1616 g and females averaged 1470 g. Sexual dimorphism also occurred with head length and pes length, but not tail length. A single autumn breeding season occurred in both 2002 and 2003, in which all adult females bred and produced a single young between February and May. The onset of autumn births was associated with the end of the summer drought. Unlike many other *Trichosurus* populations, no spring breeding pulse or 'double-breeding' events were observed. At least 83% of pouch-young survived to pouch emergence. The growth rate of offspring was initially linear, but became curvilinear and approached an asymptote after about 5 months. Most females bred for the first time when they were one year old. Based on testis size, males also matured at one year old. The body condition of adult males, but not adult females, changed significantly over time and followed an apparently seasonal pattern in which their condition was poorest in winter and best in summer. While many of the life history traits of the Chariup population were similar to other south-western Australian populations of *T. v. hypoleucus*, the most striking variations included age at maturity, extent of spring breeding pulse and female fecundity. Further comparisons with conspecifics elsewhere in Australia and New Zealand, also highlight the variability exhibited by *T. vulpecula* across its range. Some aspects of the biology of *T. v. hypoleucus* were particularly similar to those observed for *T. v. arnhemensis* in northern Australia.

4.2 Introduction

The koomal, *Trichosurus vulpecula hypoleucus* (Wagner 1855; Phalangeridae), is the south-western subspecies of the common brushtail possum (Kerle *et al.* 1991; Taylor and Foulkes 2004). *T. v. hypoleucus* is geographically isolated and morphologically distinct from other brushtail possum populations. In particular, it is smaller in size and has longer, dense fur (Kerle *et al.* 1991). *T. v. hypoleucus*, like some other subspecies of *T. vulpecula*, has undergone a widespread decline in distribution and a substantial reduction in abundance since European settlement (How and Hillcox 2000; Kerle 2001). *T. v. hypoleucus* is the only subspecies of *T. vulpecula* that has a conservation listing, being classed as 'Lower Risk (near threatened)' (Maxwell *et al.* 1996). The decline of *T. v. hypoleucus* has been attributed to predation by the introduced red fox (*Vulpes vulpes*), habitat alteration and habitat loss, disease and past hunting for pelts (Shortridge 1909; Maxwell *et al.* 1996; I. Abbott unpublished data). In areas where extensive and systematic fox-baiting using 1080 poison has been undertaken, populations of *T. v. hypoleucus* have recovered to some extent (e.g. Burrows and Christensen 2002; Kinnear *et al.* 2002; Orell 2004).

Variability in the morphology, reproduction and behaviour of *T. vulpecula* across its distribution has long been recognised and has been attributed to its ability to live in a broad range of habitats (Kerle 1984; How and Hillcox 2000). Although the general biology and ecology of *T. vulpecula* has been well studied in many parts of Australia (see Tyndale-Biscoe 1973; Kerle 1984; Kerle 2001; Goldingay and Jackson 2004) and New Zealand where it was introduced (see Green 1984; Cowan 1990; Montague 2000), there is relatively little published on *T. v. hypoleucus* (i.e. Sampson 1971; Inions 1985; Inions *et al.* 1989; Patt 1995; Tan 1999; How and Hillcox 2000).

Only three field studies have investigated the life history of *T. v. hypoleucus* populations: (1) in mixed open woodlands (including *Eucalyptus wandoo*) at Tutanning Nature Reserve, within the wheatbelt near Pingelly (Sampson 1971); (2) in coastal *Banksia* woodlands at Harry Waring Marsupial Reserve (HWMR) in Perth (Tan 1999); and (3) in coastal tuart (*Eucalyptus gomphocephala*) and peppermint (*Agonis flexuosa*) woodlands at Abba River near Busselton (How and Hillcox 2000; see Figure 4.1 for locations). Free-living *T. v. hypoleucus* also has been studied at the Perth Zoo (Patt 1995; Tan 1999). No studies have yet reported on the life history of *T. v. hypoleucus* in the jarrah (*Eucalyptus marginata*) forest – the most extensive forest type in south-western Australia. Of the pre-European distribution of jarrah forest (2.8 million ha within the Regional Forest Agreement area), 35% has been cleared (Conservation Commission 2004). Of the present extent, 87% (1.6 million ha) is vested in the Conservation Commission and managed by the Department of Conservation and Land Management (CALM). Most of this forest has been subject to prescribed burning every 7-12 years since the 1950s (CALM 1998; McCaw and Burrows 1989) and has experienced at least one cycle of logging (Herberle 1997; Bradshaw 1999). Just over half (817,300 ha) of the jarrah forest managed by CALM is formally or informally reserved (Conservation Commission 2004). For the purpose of conserving wildlife, most of the CALM-managed jarrah forest is also subject to extensive fox control ('Western Shield' Programme; Bailey 1996; CALM 2000; Orell 2004). This study investigated the general biology and ecology of *T. v. hypoleucus* in the southern jarrah forest and describes aspects of their reproduction, morphology, temporal changes in condition and mortality.

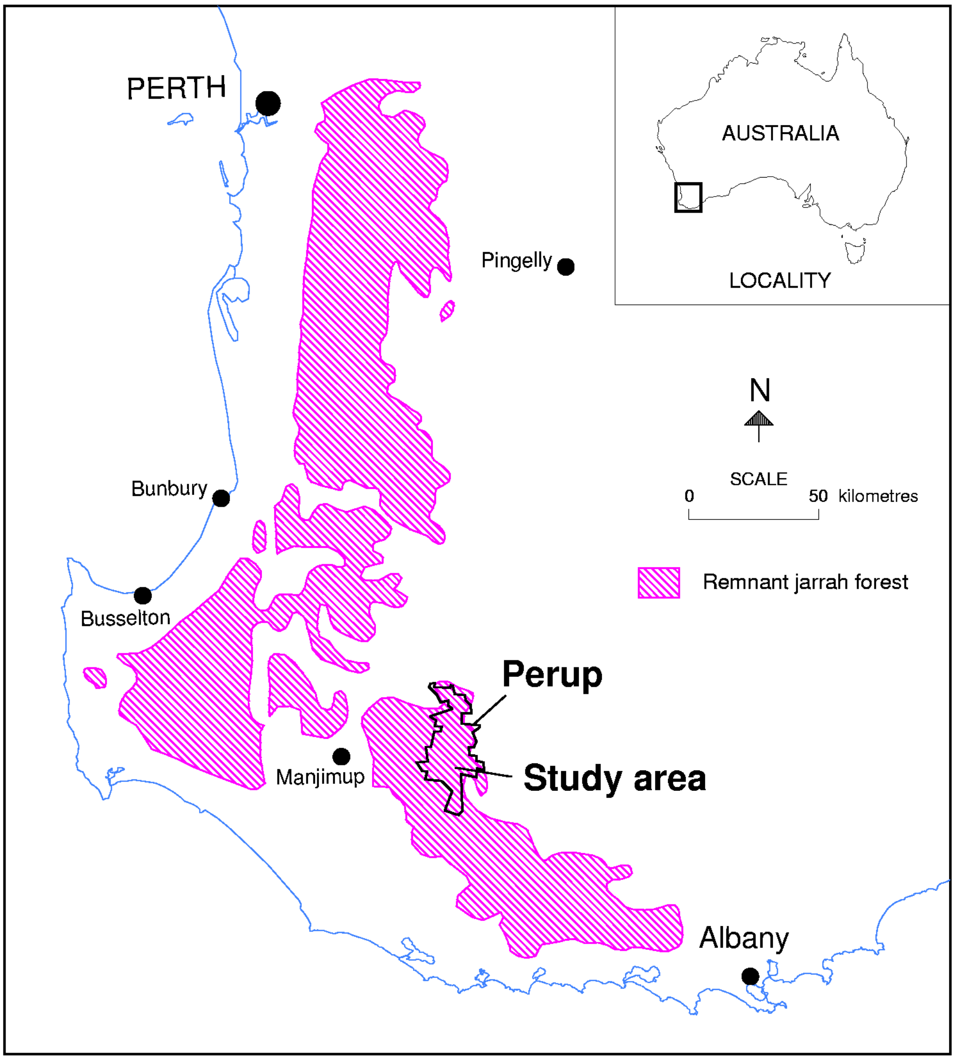

Figure 4.1. Study area used to examine the life history of *Trichosurus vulpecula hypoleucus* in the jarrah forest (hatched area) at Chariup, Perup Nature Reserve.

Note: Other studies on the life history of *T. v. hypoleucus* have been conducted at Tutanning near Pingelly (Sampson 1971), Perth (Patt 1995; Tan 1999) and Abba River near Busselton (How and Hillcox 2000).

4.3 Methods

4.3.1 Study area

The study area was in Chariup forest block, in the southern portion of Perup Nature Reserve, 270 km south-south-east of Perth, and 40 km east of Manjimup, in south-western Australia (116° 37'E, 34° 16'S; Figure 4.1). Perup is 52,000 hectares of dry sclerophyll forest dominated by jarrah and marri (*Corymbia calophylla*) and has been managed as a nature reserve since 1972 (CALM 1998). Prior to this, the area was vested as State forest and commercially logged for timber. In recognition of the value of the remnant native fauna and the predation threat from the introduced red fox, irregular baiting in some areas using 1080 toxin began in 1977. Regular broad scale aerial fox-baiting commenced in 1990 (Burrows and Christensen 2002). The Chariup study site had not been burnt for 18 years prior to this study. The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters. The local long-term average annual rainfall is around 700 mm, and the monthly mean minimum and maximum temperature range is approximately 5°C to 28°C (ANUCLIM 2001 data, Hutchison *et al.* 1999). More detailed management history and habitat attributes of the study area are described by McArthur and Clifton (1975), Wilde and Walker (1984), Strelein (1988), CALM (1998) and Burrows and Christensen (2002).

4.3.2 Trapping

Arboreal traps were shown in a previous study to capture more than twice as many *T. v. hypoleucus* as the same traps placed on the ground (Wayne *et al.* 2005b [Chapter 3]). Hence, a 500 m by 500 m grid consisting of 121 arboreal trapping points spaced 50 m apart (i.e. 11 parallel transects with 11 points each) was used in this study. The arboreal platforms were constructed from a metal frame with a reinforced plywood decking (1200 mm x 200 mm x 10 mm) and were attached to trees approximately 1.8 m above ground. Sheffield wire mesh cages (220 mm x 220 mm x 590 mm) were secured to the platform using elastic hooks. A small straight bush stick was placed under the mouth of all traps to avoid tail injury to captured possums (i.e. to stop the tail potentially being 'wedged' between the trap door and the platform decking). A thick hessian bag covered the traps to provide protection from the weather and exposure. In addition to the use of arboreal traps, capture rates were maximised by baiting traps with flour and vegetable oil dough scented with rose essence (12ml rose fragrance per kg of flour) – shown to catch 125% more *T. v. hypoleucus* than the peanut-butter based 'universal' bait (Wayne *et al.* 2005b [Chapter 3]). During 18 months between June 2002 and November 2003, 10 trapping sessions were conducted, each for a duration of three or four consecutive days, and generally eight weeks apart (Table 4.1).

Table 4.1. Trapping dates and the number of *T. v. hypoleucus* individuals captured at Chariup.

Note: J = Juvenile, S = Sub-adult, A = Adult (trapping effort varied between months)

TRAP SESSION	TRAPPING DATES	TOTAL NO. INDIVIDUALS	MALES J	MALES S	MALES A	FEMALES J	FEMALES S	FEMALES A
1	5 -7 June 2002	18		1	8			9
2	11-14 June 2002	25		1	10			14
3	16-18 July 2002	26		1	12			13
4	6-8 August 2002	33		1	15			17
5	23-25 October 2002	57	6	1	24	9		17
6	3-6 December 2002	54	4	3	22	7	1	17
7	11-13 February 2003	48		5	21		5	17
8	8-10 April 2003	55			30		1	24
9	4-6 June 2003	50			23			27
10	18-20 November 2003	60	1	3	29	1	1	25

4.3.3 Animal handling and data collection

During the initial stages of the study (June and July 2002), possums captured for the first time were sedated using an intramuscular (quadricep) injection of Ketamine (20mg / kg) and Xylazine (7 mg / kg), or Zoletil (10mg / kg) to minimise stress and to facilitate the examination of tooth wear and pouch-young and the fitting of radio-collars. Unlike *T. vulpecula* in south-eastern Australia and New Zealand, *T. v. hypoleucus* is generally not aggressive or overtly stressed when trapped and can be easily handled with minimum restraint when the eyes remain covered and if the eyes are only briefly exposed. Therefore, individuals were not sedated after this initial phase of the study. The main morphological measurements collected from captured individuals are summarised in the Appendix at the end of this chapter. Tooth-wear and the extent of exposed dentine (Winter 1980) were used to derive a relative and approximate measure of age. Coat condition was subjectively assessed on the extent of hair loss and matting, density, uniformity and general appearance. Ectoparasites (Arachnida; Acarina) visible to the naked eye were counted on the head. Sternal gland activity was subjectively assessed by the amount of fresh (moist) staining present on the chest. Subjective assessments of coat condition and sternal gland activity were standardised between observers (AW, CW, JR, CV) by initial training and consensus in the allocation of score values.

Individuals were considered to be pouch-young when suckling within the pouch and juveniles when they had emerged from the pouch but were dependent on their mother (i.e. back young). Sub-adults were at least semi-independent but sexually immature. Adults were considered mature after their testes grew rapidly in size (> 10 mm wide, > 15 mm long) or the presence of a well-developed pouch.

4.3.4 Mortality events

Mortality-sensitive radio-transmitting collars (Biotrack, U.K.) were fitted to a subset of the adult population (14 males, 15 females) as part of a complementary study on habitat selection (Wayne *et al*. in preparation-a [Chapter 6]). Radio-collared individuals were scanned weekly to check that they were still alive. When mortality radio-signals were detected, the collars were located and possum remains examined. Where possible, necropsies and biopsies were conducted to assist with identifying factors contributing to the cause of death.

4.3.5 Condition index

Indices of 'body condition' attempt to quantify a 'gestalt' of attributes that describe the general health and fitness of individuals (Humphreys *et al.* 1984; Viggers *et al.* 1998). The interpretation and usefulness of condition indices that relate body mass with body size rely on assumptions that these measures reflect actual body condition and the relative fitness of individuals within a population. These assumptions and the usefulness of condition indices have been addressed elsewhere (e.g. Bamford 1970; Humphreys *et al.* 1984; Parker and Krokenberger 2002; Viggers *et al.* 1998). Using head-length, a measure of adult body condition was derived as a measure of the deviation of its actual body mass from the average given its size (e.g. Viggers *et al.* 1998; Johnson *et al.* 2001).

There are, however, inherent differences in the body mass and size of individuals within the same population (e.g. Viggers *et al.* 1998). Furthermore, for most possums involved in this study, there were multiple measures of the same individual over time. Both of these issues are often not explicitly incorporated in the development of condition indices presented in the literature. Here, we accounted for within- and between-possum variation, by using a linear mixed model in which possum identity (ID) was included as a random effect. In this model, the response of body mass to the fixed effects of head length, sex and their two-way interaction was investigated. This model demonstrated a significant relationship between body mass and head length ($F_{1, 256} = 8.362$, $p = 0.0042$) and a significant difference between the sexes ($F_{1, 72} = 18.934$, $p < 0.0001$), but no significant interaction between these effects. The residuals from this mixed model provided a condition index (CI) that was specific for each individual and relative to its own 'usual' condition. Having accounted for individual differences, this provided an independent measure of body condition for each measurement whether on the same individual or on different individuals.

To assess the assumption that CI was a true measure of body condition, CI was tested in a linear model with a subjective score of body condition (score range 1-5). This relationship was highly significant (see Results). These results, therefore, suggested that CI was a true measure of body condition. We therefore chose to use CI because it was an objective measure and was expected to be more accurate than the alternative subjective scoring system used.

4.3.6 Data analysis

Morphometric measurements were tested for differences between the sexes using linear mixed models that accounted for multiple measurements of the same individual over time (i.e. ID was included as a random effect). Analysis of variance (ANOVA) was used to examine whether there was a temporal difference with respect to CI. Month, sex and their two-way interaction were included in the model as factors. Temporal variation in sternal gland activity was modelled using ANOVA with season as a factor (i.e. insufficient data to test temporal variation by month). The variation in the number of ectoparasites in relation to season was examined using Pearson's Chi-square test. ANOVA also was used to examine relationships of CI with body condition, coat condition and ectoparasites. Because testis size in *T. vulpecula* does not vary significantly with season (e.g. Dunnet 1956; Fletcher and Selwood 2000) it was not examined in this study.

Head length is considered the most reliable measure to characterise the growth of developing young *T. vulpecula* (e.g. Lyne and Verhagen 1957; Pilton and Sharman 1962; Kerle and Howe 1992). A preliminary exploration of multiple measures of pouch-young was consistent with the findings of other researchers who observed linear head length growth of *Trichosurus* pouch-young (e.g. How 1976; Kerle and Howe 1992; How and Hillcox 2000). The development of a growth curve was a two-stage process: (1) characterisation of the linear growth of head length for early pouch life; and (2) modelling the non-linear growth thereafter. Firstly, the growth of small pouch-young was determined for 10 individuals with repeated measures over time. These were then used to derive an overall average linear rate of growth. This average growth rate was then applied to the first head length measurement for each pouch-young to estimate their birth date (assuming a 7 mm head length at birth; How and Hillcox 2000). These ages and corresponding head measurements were then used to examine *T. v. hypoleucus* growth from birth to maturity. The second stage of analysis involved measurements from individuals arbitrarily older than 149 days (i.e. 61 observations, approximating when growth rate appears to change). To make the relationship between head length and age linear, age was transformed to the negative reciprocal of age squared. This transformation was biologically more meaningful than, for example, quadratic functions, given that growth was likely to be asymptotic. A linear mixed model of age was used to characterise the growth curve of *T. v. hypoleucus* between 149 and 579 days old (i.e. approximately 5 months to 18 months). For these analyses ID was fitted as a random effect to account for within-possum variability.

4.4 Results

4.4.1 Capture data

There were 1056 captures of *T. v. hypoleucus* from 3308 trap-nights over 18 months (Table 4.1). Eighty-six *T. v. hypoleucus* (49M:37F) individuals were involved in this life history study. Individuals were trapped an average of 12 times each (range = 1-32 captures). The nature of the trapping data indicated that all adult resident individuals on the study site were trapped, given that the rate of accumulation in number of 'new' individuals trapped over time reached an asymptote after 12 months. Therefore, the total number of individuals known-to-be-alive (KTBA) provided a reliable estimate of population size on the study site. Based on KTBA at the end of the study (November 2003), the population density was 1.7 ha^{-1} (given a 100 m boundary strip around the trapping grid to estimate an effective trapping area of 36 ha).

4.4.2 Reproductive data

4.4.2.1 Breeding season

On the basis of the head length of pouch-young and observed growth rates (see below), the date of birth was estimated for 16 and 23 pouch-young for 2002 and 2003, respectively. In 2002, 63% were born in April and the remainder in May (median birth date was 29 April 2002). In 2003, 13% were born in February, 39% in March, 26% in April and 22% in May (median birth date was 23 March 2003). For both 2002 and 2003, births commenced in the same month in which the summer drought ended with > 50 mm rain (Figure 4.2). Although mean monthly maximum and minimum temperatures were negatively correlated with rainfall ($p < 0.001$, $r^2 = 0.66$ and $p = 0.004$, $r^2 = 0.31$, for max. and min. temperatures, respectively), their association with the timing of births was not as apparent (i.e. the timing of births were only roughly associated with the decline in mean monthly temperatures).

Most young remained in the pouch from April to August, but some remained as late as October. All mature females bred (one joey each) in both years (19 and 26 females for 2002 and 2003, respectively). Of the 19 pouch-young born in 2002, at least 16 (> 84.2%) survived beyond pouch emergence. One died when its mother was preyed on; and another was presumed to have died either as an advanced pouch-young or soon after pouch emergence – the mother did not breed again until the following breeding season. The fate of the remaining mother and pouch-young was unknown given that they were not recaptured. The fate of the young from 2003 was not determined.

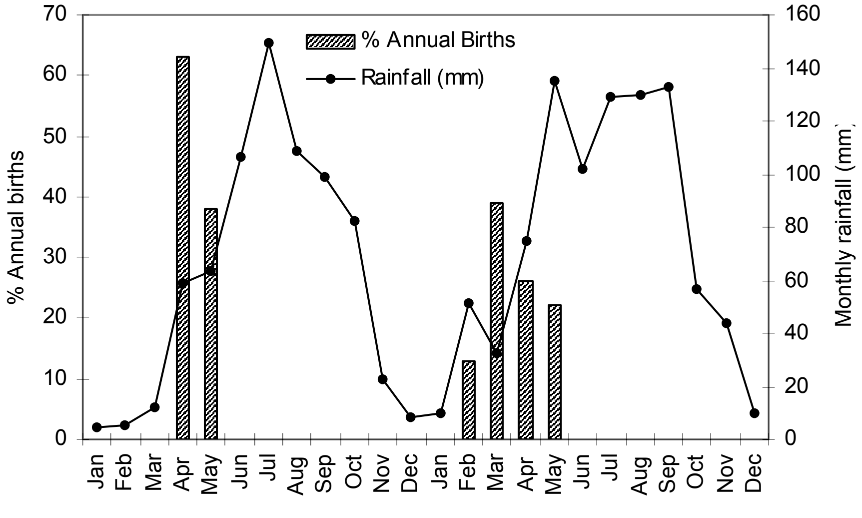

Figure 4.2. The percentage of annual births of *T. v. hypoleucus* per month in relation to total monthly rainfall at nearby Manjimup.

4.4.2.2 Offspring sex ratio

The sex ratio of *T. v. hypoleucus* pouch-young was 9M:9F in 2002 and 7M:6F in 2003 (sex unknown for one and 13 pouch-young for 2002 and 2003, respectively). The sex ratio of the pouch-young from known first time breeding mothers in 2003, was 2M:2F (sex unknown for two pouch-young).

4.4.2.3 Offspring growth rates

Ten pouch-young were first measured in 2002 with head lengths between 11.8 mm and 28.2 mm and then remeasured 21-78 days later. On the basis of these field observations, the average linear growth rate for early life was 0.3211 mm day^{-1} (SE = 0.048). Assuming a 7 mm head length at birth, the growth equation for neonates was:

Head length (mm) = 0.3211 x age (days) + 7.0

Twelve (5 male, 7 female) of the 16 pouch-young observed in 2002 had between four and ten repeat measurements over the 18-month study period. These measurements were used to model the growth of *T. v. hypoleucus* from 149 days old to adulthood (Figure 4.3). Given that the differences between the sexes and the interaction between sex and age were not significant, the final model was:

Head length (mm) = 698823.3 x (-1/age^2) + 85.7; ($p < 0.0001$).

A comparison between the two growth functions and their relation to the available possum data indicated that *T. v. hypoleucus* was best characterised by linear growth for the first 5 months and by a non-linear growth curve thereafter. The goodness of fit for these two growth functions was better than by various non-linear equations using the entire growth data.

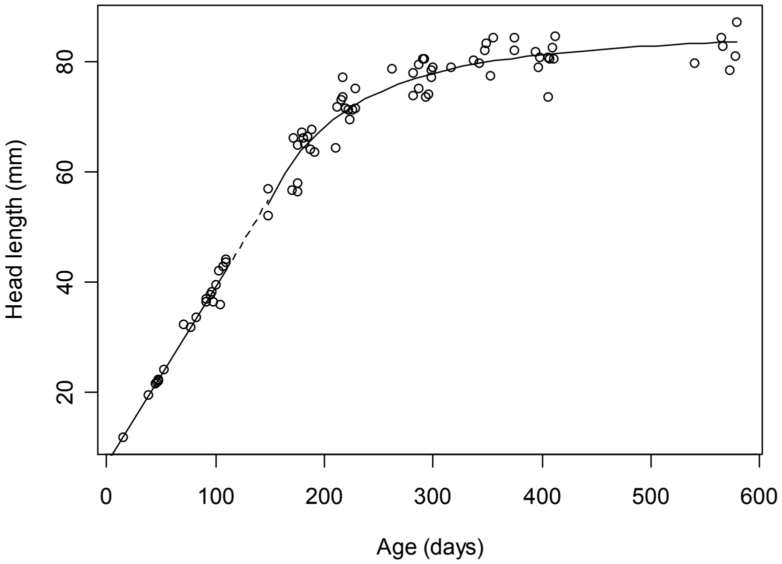

Figure 4.3. The relationship between head length and age of 12 *T. v. hypoleucus* at Chariup.

4.4.2.4 Age and size at maturity

Of the seven females born in 2002 and for which their ongoing life history was well known, six bred during 2003. The age at which they first gave birth was around 12 months (estimated range = 318-411 days, mean = 362 days, SD = 34). The mean weight at the time of first breeding was 1200 g (SD = 65). Similarly, the mean pes and mean head lengths were 57.8 mm (SD = 2.0) and 82.0 mm (SD = 5.1) respectively. The seventh female had not bred by the end of the study (20 November 2003) at 18 months of age.

Of the five sub-adult males known since early pouch life, two reached sexual maturity by 12 months of age (one at 342 days old, body mass 1280 g, head length 79.8 mm, pes 57.4 mm and the other by 352 days, body mass 1460 g, head length 77.5 mm, pes 64.6 mm). The other three males were not captured beyond February 2003 when they were around nine months old (i.e. either dead or dispersed).

4.4.3 Morphometric data

4.4.3.1 Adult size and body mass

Sub-adults were > 550 g and sexually matured at > 1000 g for both sexes. Sub-adult males were up to 1230 g and females were up to 1040 g before they matured. Adult males reached up to 2100 g and females up to 2000 g. There were no significant differences between the sexes with regard to the morphological measurements of juveniles and sub-adults. However, adult males were generally heavier ($p < 0.0001$), had longer heads ($p < 0.0033$) and larger pes ($p < 0.0049$) than adult females. There was no difference in tail length between adult males and females (Table 4.2).

Table 4.2. Summary of the morphometric measurements of *T. v. hypoleucus* at Chariup.

There were no significant differences between the sexes for juveniles or sub-adults. For adults, n.s. = not significant; *** = *p*-value < 0.005.

		JUVENILE	SUB-ADULT	FEMALE ADULT	MALE ADULT	P
Body mass (g)	**Mean**	**565**	**942**	**1470**	**1616**	***
	SE	38	36	28	38	
	#Observations	29	25	169	180	
	#Individuals	16	16	35	43	
Head length (mm)	**Mean**	**67**	**76.5**	**82.8**	**84.4**	***
	SE	1.0	0.7	0.4	0.5	
	#Observations	28	25	165	175	
	#Individuals	16	17	34	43	
Pes length (mm)	**Mean**	**50.4**	**57.5**	**59.7**	**61.1**	***
	SE	1.1	0.9	0.4	0.5	
	#Observations	28	24	158	166	
	#Individuals	16	17	35	43	
Tail length (mm)	**Mean**	**22.1**	**25.5**	**28.9**	**28.6**	n.s.
	SE	0.4	0.5	0.3	0.4	
	#Observations	24	18	57	90	
	#Individuals	15	14	27	40	
Left testis length (mm)	**Mean**		**11.2**		**22.6**	
	SE		0.8		0.3	
	#Observations		11		160	
	#Individuals		7		43	
Left testis width (mm)	**Mean**		**7.3**		**15.5**	
	SE		0.6		0.2	
	#Observations		11		160	
	#Individuals		7		43	

4.4.3.2 Coat colour

Of a subset of 30 male and 26 female *T. v. hypoleucus* for which their pelage was assessed using colour charts (Munsell 1954), 64% had various shades of grey coats with black tails, 25% had grey coats with some portion of white to the distal end of the tail (mean white tip tail length was 6 cm, range = 1-10 cm), 11% (3 male, 3 female) had black coats and black tails.

One of the males with predominantly grey coat and black tail had distinctly russet (reddish) shoulders and forehead.

4.4.4 Temporal changes in condition

4.4.4.1 Body condition

CI varied significantly over time and there was an interaction between month and sex ($F_{8, 313} = 7.9341$, $p < 0.001$). Male condition was poorest during the winter months (June, July and August 2002 and June 2003) and best in summer (December 2002, February 2003 and November 2003; Figure 4.4). A seasonal pattern in the variation in individual female condition was not statistically evident; however, condition tended to be better after April 2003 (Figure 4.4).

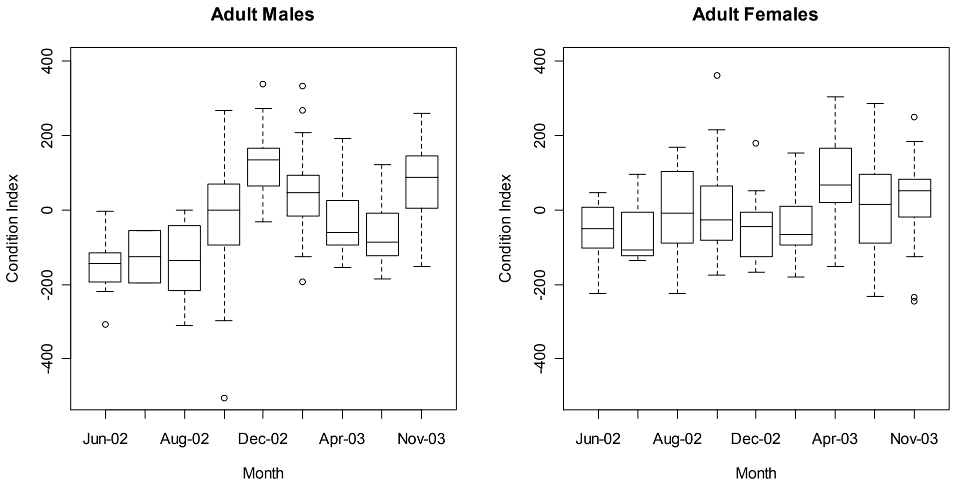

Figure 4.4. Box plots by survey month of the condition index of *T. v. hypoleucus* (a) adult males and (b) adult females at Chariup.

Survey months (and male, female sample sizes) are June (8, 11), July (2, 3), August (16, 17), October (27, 19) and December (21, 16) 2002; February (21, 18), April (28, 23), June (20, 30) and November (27, 24) 2003. Box plots: the horizontal line in the box indicates the sample median, the lower and upper extents of the box (i.e. ‘hinges’) indicate the 25th and 75th percentiles, the T-bar ‘whiskers’ indicate the maximum and minimum values, with the exception of sample outliers (symbolised by ‘o’).

4.4.4.2 Subjective assessments of body condition and coat condition

Coat condition was positively related to CI ($F_{1,\ 309} = 5.4218$, $p = 0.0205$), such that *T. v. hypoleucus* with good coats tended to have better CI values (independent of sex). This relationship was similar but weaker than that observed between the subjective assessment of body condition and CI ($F_{1,\ 325} = 34.979$, $p = < 0.001$).

4.4.4.3 Ectoparasites

Ectoparasites (Arachnida; Acarina, i.e. ticks and mites) as potential indicators of stress and/or fitness (Humphreys *et al.* 1984) were observed on 43% of possum captures with some counts being greater than 50 ticks per possum. Although there was a tendency for ectoparasites to be more frequently observed in autumn and winter, there was no significant difference between seasons. There also was no significant relationship between CI and ectoparasite load classes (none, moderate = 1-10, or high > 10 ticks or mites) or ectoparasite presence/absence.

4.4.4.4 Sternal gland activity

Sternal gland activity in males differed significantly between months ($F_{8,\ 148} = 3.132$, $p = 0.0027$); the sternal gland was most active in the summer and autumn months and least active during the winter months.

4.4.5 Longevity estimates and mortality

Based on the tooth wear index (Winter 1980), the average age at the time of last contact for 14 animals of each sex was 4.6 years. The oldest estimated ages were 5.5 years and 7.5 years for females and males, respectively.

Five individuals (3M, 2F) died, out of the 29 (14M, 15F) radio-collared adults, during the 18-month study. Three of these deaths were by predation (the two females in July 2002 and a male in May 2003), with the remains indicating that the same type of predator may have been responsible. Evidence of red foxes, feral cats (*Felis catus*), chuditch (*Dasyurus geoffroii*) and raptors including wedgetail eagles (*Aquila audax*) were found at the study site. Another male apparently died from misadventure, having been found impaled on a vertical, sharp, dead branch in the crown of a tree. The cause of the fifth observed death was unknown owing to an advanced state of decay.

4.5 Discussion

4.5.1 Reproduction

4.5.1.1 Breeding season and fecundity

The seasonality of breeding of *T. vulpecula* is highly variable throughout its range, from complete aseasonality to highly seasonal (e.g. Isaac and Johnson 2003). Populations typically breed in autumn and may have a second spring pulse that varies in magnitude between complete absence (e.g. *T. v. fuliginosus* in Tasmania, Tyndale-Biscoe 1973), to quite pronounced (Green 1984; Kerle 1984). The autumn breeding season in Australia and New Zealand often peaks in April and usually occurs between March and June (e.g. Dunnet 1956; Smith *et al.* 1969; Green 1984; Kerle 1984; Fletcher and Selwood 2000). Where they occur, spring births are between August and November and typically peak in September or October. Spring breeding results from individuals that (a) failed to breed or lost their young in autumn; or (b) are reproducing for a second time in the same year (i.e. 'double-breeding') (Kerle 1984; Isaac 2005). Breeding throughout the year also has been observed in some populations, typically with seasonal peaks (e.g. Tyndale-Biscoe 1955; Owen and Thomson 1965), while those of *T. v. arnhemensis* in northern Australian and *T. v. vulpecula* populations in Adelaide appear to be aseasonal (Kerle and Howe 1992).

The Chariup population clearly had a discrete single, autumn breeding season. The sternal gland activity of adult male *T. v. hypoleucus* at Chariup was greatest in summer and autumn (during the lead-up to mating), suggesting that sternal gland activity may be related to reproduction. All known mature females bred in both years and in all cases their litter size was one. No females were observed 'double-breeding' in either year. In the one case where a female's offspring died (about the time of pouch emergence), the mother did not breed again until the following autumn. More long-term data is required to confirm whether these trends and the reproductive potential of one young per year per adult female is representative of this and other jarrah forest populations.

The commencement of births coincided with the month in which the summer drought ended with the first substantial rains. Although ambient temperature was found to influence the onset of the breeding season in a captive *T. vulpecula* population in Brisbane (Gemmell 2004), such an association was not as apparent at Chariup as was the relationship with rainfall. Variation in the timing of the breeding season in the same habitat and between adjacent populations has been noted elsewhere (e.g. Bell 1981; Kerle 1984). For example, breeding has been earlier in recently burnt areas (Hocking 1981, cited in Kerle 1984). Some of the temporal variation in breeding also has been related to female body weight and body condition (Bell 1981). The influence of seasonal variation in nutrition and food supply on breeding is implicated in these and other examples (e.g. Humphreys *et al.*1984). While these factors may be modulators, day-length has been shown as the primary controlling factor for the onset of breeding by *T. vulpecula* in temperate eastern Australia (e.g. Gemmell *et al.* 1993; Gemmell and Sernia 1992, 1995).

The pronounced seasonality of the Mediterranean-type climate experienced in the south-west probably explains why such a trend was observed here and why it may not be so evident in temperate climates with less pronounced seasonality. It is possible that other *Trichosurus* populations that experience a similar Mediterranean-type climate also may have links between breeding and weather (e.g. South Australia and parts of Victoria). The factors relating to the onset of breeding within this and other Western Australian populations should be tested with larger and temporally more extensive datasets. Although the factors that initiate breeding remain poorly understood, they are likely to be complex and multifaceted (Gemmell 2004). Nonetheless, the evidence from this study and the examples above, indicate that seasonal food supply (i.e. quantity and/or quality) to support the nutrient requirements of reproduction is likely to be an important proximate link with the timing of breeding. For a general review of seasonal regulation of breeding in mammals see Bronson and Heideman (1994).

The single autumn breeding season observed at Chariup was similar to that observed for the relatively stable populations of *T. v. hypoleucus* at Abba River (How and Hillcox 2000) and Harry Waring Marsupial Reserve (Tan 1999). By contrast, ‘double-breeding’ and spring births have been observed at the Perth Zoo (Patt 1995) where food was abundant, and at Tutanning (Sampson 1971) where possum densities were very low and likely to be below potential carrying capacities. The variable breeding potential among *T. v. hypoleucus* populations is similar to variation among *T. vulpecula* populations elsewhere in Australia (e.g. How 1978; Hocking 1981 cited in Kerle 1984; Kerle 1998) and New Zealand (e.g. Bell 1981; Ramsey *et al.* 2002), where it has been associated with adult female body weight, food availability and population density.

4.5.1.2 Pouch-young survival

The survival of pouch-young beyond pouch emergence at Chariup (about 84.2%) was similar to the average survival rates reported by other studies in Western Australia (88.2%; Patt 1995), and elsewhere in Australia and New Zealand (87% and 85% respectively; Green 1984). Pouch-young survival can be highly variable between populations, between years and according to the mother’s age and condition – ranging between 52% and 100% (Bell 1981; Kerle 1984). Although other factors also may be related, Kerle (1984) suggested that the timing and availability of nutritious foods for lactating females and emerging pouch-young may be the most important proximate factor controlling the seasonal distribution of births, reproductive success and the proportion of the adult female population that is reproductively active. Similar relationships also have been found for many other species including mammals (e.g. Bronson and Heidman 1994), such as the common ringtail possum, *Pseudocheirus peregrinus* (e.g. Pahl and Lee 1988; Munks 1995).

4.5.1.3 Sex ratio

The sex ratio at Chariup did not differ significantly from parity for pouch-young (1.1 male bias) or adults (1.3 male bias). A long-term fauna-monitoring programme elsewhere in Perup Nature Reserve (Boyicup block and Yendicup block – approximately 1 km and 12 km respectively, from this study site), found a significant male bias in both the adults (1.6-1.8 male bias) and pouch-young (1.7-2.4 male bias) using data collected between 1974 and 1990 (Burrows and Christensen 2002). The differences between the methods and results of these two studies highlights the importance of potential sampling bias resulting from differences in behaviour and population turnover according to sex and age (e.g. Coleman and Green 1984; Efford 2000). In contrast to the frequently and densely trapped site used in our study, Burrows and Christensen (2002) used 15-20 km transects with ground traps spaced 200-300 m apart. Sparsely placed trap lines surveyed intermittently, such as these, are likely to selectively trap the most mobile animals, which in the case of *Trichosurus* are sub-adult and mature males (Coleman and Green 1984). Male bias is also likely in samples accumulated over time due to higher male turnover within a population (Efford 2000). Therefore, given the sampling methods used in our study, the adult sex ratio observed here is likely to be a more reliable representation of the population.

Within this context, variation in sex ratios between other *T. v. hypoleucus* populations also has been found. Parity ratios were found within all age classes at Abba River (How and Hillcox 2000) and for adults at Harry Waring Marsupial Reserve (Tan 1999). At the Perth Zoo, there was a significant male bias within the pouch-young (1.85 male bias; Patt 1995), but not within the adult population (1.2 to 1.6 male bias; Patt 1995; Tan 1999). Parity in pouch-young sex ratios are typical elsewhere in Australia and New Zealand, but data combined across several studies showed a significant male bias (Green 1984). Within the adult populations of *T. vulpecula*, the sex ratio has been observed from 0.4 to almost 3.0 males per female (Kerle 1984).

Populations with a strong adult male bias and greater proportion of immature individuals have been associated with re-colonising or increasing populations due to the differences in the dispersal patterns of immature males and females. Adult sex ratios are then suggested to reach parity as the population size stabilizes (Kerle 1984). Populations with an adult female bias (e.g. Dunnet 1964; How 1972; Winter 1976 cited in Green 1984) have been suggested to result from the higher mortality rates of males in relatively stable, high-density populations (Green 1984).

The sex ratio in the pouch-young is not subject to the same sampling bias as adults (Coleman and Green 1984). The sex ratio of offspring has been suggested to be adjustable within populations in response to the relative competition for resources (Johnson *et al.* 2001). When den availability is reduced due to relatively high population densities, females tend to produce more male offspring. Since male offspring disperse some distance beyond the range of their mother, they do not exacerbate competition for local den resources. Had they produced female offspring, which are philopatric, the mothers would be compounding the problem by having to compete directly with their daughter(s) (Johnson *et al.* 2001). The male bias in offspring at the Perth Zoo provides support to this theory given the high density of possums and the limitation in diurnal refuge sites relative to food availability.

4.5.1.4 Growth rates

The average growth rate (head length) of *T. v. hypoleucus* pouch-young (i.e. < 5 months old) in the jarrah forest at Chariup was 0.3211± 0.048 mm day^{-1} (n = 10). This tended to be less than *T. v. hypoleucus* at Abba River and in captivity (mean = 0.377± 0.049 mm day^{-1}, n = 4; and 0.363 mm day^{-1} respectively; How and Hillcox 2000 [p = 0.04 for a 1-tail t-test between Chariup and Abba growth rates], bearing in mind the small sample sizes), or *T. vulpecula* elsewhere in Australia (e.g. Lyne and Verhagen 1957). The growth rate for *T. v. arnhemensis* (0.33 mm day^{-1}; Kerle and Howe 1992) and *T. caninus* (0.338 mm day^{-1}; How 1976) was similar to that found in this study. The growth rates of the sympatric possum *Pseudocheirus occidentalis*, also were relatively slower at Chariup compared with conspecifics from Abba River (Wayne *et al.* 2005d [Chapter 5]). Nutritional differences between these populations may account for these differences, but remains to be tested.

The change from a linear growth rate to a non-linear growth curve approximately coincides with the expected age at pouch emergence and commencement of weaning at about 160 days (i.e. 5-6 months; e.g. Smith *et al.* 1969; Fletcher and Selwood 2000) and is similar to that observed for *T. v. arnhemensis* (Kerle and Howe 1992). Given the asymptotic nature of the growth curve, the accuracy of age estimation is expected to decrease with increasing head size. Caution is also required in the use of growth curves for estimating age given that growth rates can vary between populations and between years (Cowan 1990). Once *T. v. hypoleucus* mature, age may alternatively be estimated using tooth wear (e.g. Winter 1980) or more destructive methods such as the use of cementum layers from cross sections of molars (Clout 1982).

4.5.1.5 Age at maturity

While most female *T. vulpecula* sexually mature at 1-2 years of age, the proportion maturing at ages 1-4 years differs between populations (Dunnet 1956; Bell 1981; How 1981; Green 1984; Kerle 1984; Fletcher and Selwood 2000). According to Green (1984) maturation rates are generally faster in Australia than New Zealand and slower in established populations compared with increasing or colonising populations. Despite its relatively limited geographical range, *T. v. hypoleucus* exhibited the full range of maturation ages that have been observed across the entire range of the species. At Tutanning, females matured at the end of their first year (Sampson 1971). The age at first breeding at the Perth Zoo was established for only one female at an estimated 16 months (Patt 1995), and limited data at Abba River indicated that some females were not maturing until their third year (How and Hillcox 2000).

The body masses of breeding females at Chariup were similar to those observed at Abba River where the smallest female with pouch-young was 1220 g (How and Hillcox 2000). Males at Chariup matured from one year of age (> 1280 g), following a rapid growth in testes, but other older mature males were found with body masses as small as 1000 g. The age of male maturity at Chariup was similar to that at Abba River (How and Hillcox 2000) and that of *T. v. arnhemensis* in northern Australia (Kerle and How 1992). Within most other *T. vulpecula* populations, males mature during their second year (Kerle 1984). The age at which males successfully sire young at Chariup remains unknown.

4.5.2 Morphology

4.5.2.1 Coat colour

Variations in *Trichosurus* coat colour and fur length have been frequently noted in the literature. According to Kerle *et al.* (1991) the length and 'wooliness' of the fur and 'brushiness' of the tail increase with latitude. Grey coats with black tails are generally the most common colour form among populations. The incidence of black and russet (reddish) forms can vary but red shoulders tend to be more frequent in males (Kerle 1984; How and Kerle 1995). Troughton (1941 cited in Kerle 1984) associated red coat colouring with age, although red forms are considered more common in northern Australian populations for all ages (Kerle 1984). In Tasmania and New Zealand, there is apparently a distinct separation of colour forms according to habitat type with more black animals (up to 66%) occurring in regions of high rainfall (Kerle 1984; Cowan 1990). With respect to *T. v. hypoleucus*, Shortridge (1909) noted that there were more black females than males and that their incidence in the extreme south-west coastal populations (up to 20%) was greater than in inland populations. At the near-coastal population at Abba River, no males (n = 61) and only 8% of females (n = 72) were black (How and Hillcox 2000). In comparison, 10% of males (n = 30) and 11% of females (n = 26) in this study were black. The majority of *T. v. hypoleucus* in the Chariup population had grey coats (89%), while a quarter of them had white tipped tails. Shortridge (1909) noted that white-tipped tails in the south-west were more common than black tails in many areas. The incidence of white tipped tails in this population, despite being less than that observed by Shortridge (1909) was nonetheless greater than has been observed for *T. vulpecula* elsewhere (e.g. 5% in New Zealand, Cowan 1990). Although we have observed them elsewhere within the region, none of the black-furred animals in this study had white tipped tails.

4.5.2.2 Body size

The mean body mass and morphometrics of the Chariup population were similar to other south-west populations (Kerle *et al.* 1991; Patt 1995; How and Hillcox 2000; Burrows and Christensen 2002). *T. v. hypoleucus* along with *T. v. arnhemensis*, constitute the smallest forms of *Trichosurus* and are less than half the largest mean sizes of populations in Tasmania (e.g. Male = 3.4-3.8 kg, Female = 3.2 kg; Green 1973 and Hocking 1981 cited in Kerle *et al.* 1991), and less than a third the maximum weight of possums recorded in New Zealand (Cowan 1990). With the exception of *T. v. hypoleucus* and *T. v. arnhemensis* on Barrow Island, a general increase in *T. vulpecula* size occurs with increasing latitude (i.e. decreasing ambient temperature), consistent with Bergmann's rule (Yom-Tov *et al.* 1985; Yom-Tov and Nix 1986; Kerle *et al.* 1991; Taylor and Foulkes 2004). Australia-wide, body size also has been strongly associated with the moisture index of the driest quarter and air temperature, which is strongly associated with latitude (Yom-Tov and Nix 1986). Therefore, the relatively small size of *T. v. hypoleucus* is likely to be a response to the hot, dry summers and its influence on vegetation (i.e. habitat and food). The soils and trees of the south-west forests are some of the most nutrient impoverished in the world (Hingston *et al.* 1980; Dell and Havel 1989). It is, therefore, also possible that an evolutionary response of *T. v. hypoleucus* to these low nutrient environments has been smaller size.

4.5.2.3 Sexual dimorphism

Adult males in this study were significantly heavier, had longer heads and a longer pes than adult females. Tail lengths did not differ between the sexes. Sexual dimorphism was found at Abba River with respect to body mass but not head-length (How and Hillcox 2000). At the Perth Zoo there was no significant sexual dimorphism with respect to body mass, head length or pes length (Patt 1995; Table 4.3).

The extent of sexual dimorphism found in other *T. vulpecula* populations elsewhere in Australia and New Zealand is variable. For example, across nine studies in New Zealand, the body mass of females was on average 98.6% that of males (Cowan 1990), and in north-eastern New South Wales, there was evidence of sexual dimorphism only among older animals (Clinchy *et al.* 2004). The latter study also showed that male mating success was significantly greater for larger, older males. Sexual dimorphism irrespective of adult age was found in a *T. v. arnhemensis* population in which adult females were 86.0% the body mass of males, had a smaller head, arm and pes length and longer tail (Kerle and Howe 1992). Isaac and Johnson (2003) demonstrated that sexual dimorphism in *T. vulpecula* in Queensland and Northern Territory was related to the seasonality of breeding. The mechanism for this relationship was explained by the relative accessibility of oestrus females to males differing with the degree of breeding seasonality, thereby affecting the operational sex ratio and the potential extent of polygyny. Therefore, male-biased dimorphism should increase with the degree of polygyny, which for *T. vulpecula,* relates to a reduction in breeding seasonality.

Table 4.3. Summary of selected population parameters for *T. v. hypoleucus* at Tutanning (Sampson 1971), Perth Zoo (Patt 1995), Abba River (How and Hillcox 2000) and Chariup.

Sexual dimorphism values are adult male body mass / female body mass. * $p < 0.05$. Adult sex ratio did not differ significantly in any of the four populations. Note: population densities and sex ratios may not be strictly comparable given differences in sampling and calculation between the studies.

	Tutanning	Perth Zoo	Abba River	Chariup
Population Density (n/ha)	0.07	3.83	1.77	1.7
Spring Breeding (% total annual breeding)	37	4	0	0
Seasonality (% births in peak 2 months)	59	59	79	69
(No. births: peak 2 months)	(27: Apr/Oct)	(76:Mar/Apr)	(24: May/Jun)	(39: Apr/May)
Adult Sex Ratio (M:F)	42:31	97:80	41:49	49:37
Sexual Dimorphism	na	1.06	1.17*	1.10*
Mean Male Body Mass, g ± SD (n)	na	1619±346	1764±215.3 (39)	1616±166 (43)
Mean Female Body Mass, g ± SD (n)	na	1523±382	1509±171.5 (48)	1470±249 (35)
Pouch-young Growth, mm/day ± SD (n)	na	na	0.377±0.049 (4)	0.321±0.048 (10)

Furthermore, the degree of breeding seasonality was not related to latitudinal or climatic factors. Instead, it was suggested that the response to increasing population density was an increase in reproductive synchrony, and therefore a reduction in the degree of sexual dimorphism (Isaac and Johnson 2003). While this is an elegant series of relationships, and despite possum densities and population sample sizes being comparable to those observed in Queensland and Northern Territory (Isaac and Johnson 2003), they are somewhat contrary to the pattern observed for *T. v. hypoleucus* (Table 4.3). Therefore, while these relationships may be important in *T. v. hypoleucus* populations, they do not immediately explain the differences observed between south-west populations, suggesting that other factors also may be important. The artificial environment at the Perth Zoo may well be a confounding factor. Nonetheless, data from additional *T. v. hypoleucus* populations are required to test these relationships rigorously.

4.5.3 Temporal changes in condition

The condition index (CI) used in this study was considered a reasonable measure of body condition given that subjective assessments of body and coat condition, although less sensitive measures, were significantly related to CI. Despite parasites potentially affecting body condition and fitness (e.g. Humphreys *et al.* 1984), ectoparasites in this study did not vary significantly between seasons and did not relate to CI. Strong cyclical patterns in CI were apparent for male *T. v. hypoleucus* in which condition was poorest in winter and greatest in summer. Males were therefore generally at or close to their optimal condition leading into the autumn breeding season. The observed seasonal pattern of male condition coincides with plant productivity cycles and expected peaks in food availability during spring and summer. By indirect comparison, the body mass of both sexes of *T. v. hypoleucus* increased by up to 150 g during the breeding season at Abba River (How and Hillcox 2000). Seasonal variations in condition and body mass, and differences between the sexes, have been observed for *T. vulpecula* elsewhere in Australia and NZ (e.g. Crawley 1973; Bell, 1981; Clinchy *et al.* 2004; Isaac 2005). In contrast to the findings of other studies, the adult females at Chariup did not vary significantly in condition over time. It is possible that females in this population may be able to offset increased nutritional demands associated with breeding with the seasonal peak in food availability. Nonetheless, this finding is worth further detailed investigation. It is also noteworthy that given condition can vary seasonally and body mass is not independent of condition, skeletal measures such as head length, should be used as a more robust measure of size (e.g. to investigate sexual dimorphism).

4.5.4 Longevity estimates and mortality

The conservative estimate of the average age of adults at Chariup was 4.6 years, and the maximum age for an individual was conservatively estimated to be 7.5 years. There are, however, individuals in similar habitat ~30 km away that are known to be 10 or more years old (A. Wayne unpublished). These life spans are similar to those observed for other wild *T. vulpecula* (females tending to live longer than males) which have usually been less than 11 years, but may reach 15 years of age (Crawley 1970; How and Kerle 1995; Efford 2000; Fletcher and Selwood 2000). The approximate 12% annual mean mortality rate of *T. v. hypoleucus* in this study was similar to the 10-20% rates for *T. vulpecula* populations elsewhere in Australia and New Zealand (How 1978; Brockie *et al.* 1981; Efford 2000).

Three of five sub-adult males known from early pouch life in 2002 were no longer trapped beyond the age of 10 months and were presumed to have either dispersed or died. All seven young females that were well known since early pouch life in 2002 were still present within the study area at 12-18 months of age. *T. vulpecula* populations elsewhere have had high mortality rates for individuals 6-18 months of age, when they are dispersing from their natal range and endeavouring to establish their own home range (How 1981; How and Kerle 1995). Furthermore, the mortality rates of young males tend to be greater than those of females and may be as high as 80% (e.g. How 1978; Green 1984; Efford 1998). These differences in mortality rates are probably associated with differences in dispersal behaviour between the sexes. Females tend to establish their home ranges adjacent to, or within their mothers' home range (e.g. Tyndale-Biscoe 1973; Cowan and Clout 2000) – a behaviour generally supported by this study. Males, on the other hand, tend to disperse and establish themselves at least two to three home ranges away (Cowan and Clout 2000; Clinchy *et al.* 2004) and potentially as far as 41 km away (Cowan *et al.* 1996; Cowan *et al.* 1997;Cowan and Clout 2000). Without radio-collaring young sub-adults, it was not practical to discriminate between individuals that successfully dispersed and those that died.

4.6 Conclusion

The *T. v. hypoleucus* population within the jarrah forest at Chariup generally had similar life history attributes to those of other south-western populations that have been studied (Sampson 1971; Patt 1995; Tan 1999; How and Hillcox 2000). The population at Chariup was most like that at Abba River, which is geographically and climatically closest. The most striking variations between these south-west populations include age at maturity, the extent of a spring breeding pulse and female fecundity. These differences demonstrate the flexibility within the subspecies that is also evident within *T. vulpecula* throughout its Australian and New Zealand distribution. Superficially at least, *T. v. hypoleucus* shares similarities with *T. v. arnhemensis*, which are distinguishable from other *Trichosurus*, by their relatively smaller size and their less aggressive behaviour when handled.

This species is clearly highly adaptable and able to live within a wide range of habitats, climates and conditions. Despite this flexibility, *T. v. hypoleucus* and other subspecies have undergone a large contraction in their distribution and abundance within Australia. In conjunction with knowledge of their life history and breeding biology, an understanding of the relative importance and influence of ecological factors on their distribution and abundance will help to provide the necessary information required to ensure their long-term conservation within Australia and their control as a pest in New Zealand.

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4.8 References

Bailey, C. (1996). Western Shield: bringing wildlife back from the brink of extinction. *Landscope* **11**, 41-48.

Bamford, J. (1970). Estimating fat reserves in the brushtailed possum, *Trichosurus vulpecula* Kerr (Marsupialia: Phalangeridae). *Australian Journal of Zoology* **18**, 415-425.

Bell, B. D. (1981). Breeding and condition of possums *Trichosurus vulpecula* in the Orongorongo Valley, near Wellington, New Zealand, 1966-1975. In 'Proceedings of the first symposium on marsupials in New Zealand'. (Ed. B. D. Bell) No. 74 pp. 87-139. (Zoology Publications from Victoria University: Wellington)

Bradshaw, F. J. (1999). Trends in silvicultural practices in the native forests of Western Australia. *Australian Forestry* **62**, 255-264.

Brockie, R. E., Bell, B. D. and White, A. J. (1981). Age structure and mortality of possum *Trichosurus vulpecula* populations in New Zealand. In 'Proceedings of the first symposium on marsupials in New Zealand'. (Ed. B. D. Bell) No. 74 pp. 63-85. (Zoology Publications from Victoria University: Wellington)

Bronson, F. H. and Heideman, P. D. (1994). Seasonal regulation of reproduction in mammals. In 'The Physiology of Reproduction'. (Eds E. Knobil and J. D. Neill) Vol. 2 pp. 541-583. (Raven Press Ltd.: New York)

Burrows, N. D. and Christensen, P. E. S. (2002). Long-term trends in native mammal capture rates in a jarrah forest in south-western Australia. *Australian Forestry* **65**, 211-219.

CALM (1998). 'Draft Management Plan: Perup Forest and Lake Muir/Unicup Nature Reserves.' Western Australian Government Department of Conservation and Land Management, Perth.

CALM (2000). 'Western Shield Fauna Recovery Program Strategic Plan (July 1999 – June 2004).' Western Australian Government Department of Conservation and Land Management, Perth.

Clinchy, M., Taylor, A. C., Zanette, L. Y., Krebs, C. J. and Jarman, P. J. (2004). Body size, age and paternity in common brushtail possums (*Trichosurus vulpecula*). *Molecular Ecology* **13**, 195-202.

Clout, M. N. (1982). Determination of age in the brushtail possum using sections from decalcified molar teeth. *New Zealand Journal of Zoology* **9**, 405-408.

Coleman, J. D. and Green, W. Q. (1984). Variations in the sex and age distributions of brush-tailed possum populations. *New Zealand Journal of Zoology* **11**, 313-318.

Conservation Commission. (2004). 'Forest Management Plan 2004-2013.' Conservation Commission of Western Australia, Perth.

Cowan, P. E. (1990). Brushtail possum. In 'The Handbook of New Zealand Mammals'. (Ed. C. M. King) pp. 68-98. (Oxford University Press: Auckland)

Cowan, P. and Clout, M. (2000). Possums on the move: Activity patterns, home ranges and dispersal. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 24-34. (Manaaki Whenua Press: Lincoln, New Zealand)

Cowan, P. E., Brockie, R. E., Ward, G. D. and Efford, M. G. (1996). Long-distance movements of juvenile brushtail possums (*Trichosurus vulpecula*) on farmland, Hawke's Bay, New Zealand. *Wildlife Research* **23**, 237-244.

Cowan, P. E., Brockie, R. E., Smith, R. N. and Hearfield, M. E. (1997). Dispersal of juvenile brushtail possums, *Trichosurus vulpecula*, after a control operation. *Wildlife Research* **24**, 279-288.

Crawley, M. C. (1970). Longevity of Australian brush-tailed opossums (*Trichosurus vulpecula*) in indigenous forest in New Zealand. *New Zealand Journal of Science* **13**, 348-351.

Crawley, M. C. (1973). A live-trapping study of Australian brush-tailed possums, *Trichosurus vulpecula* (Kerr), in the Orongorongo Valley, Wellington, New Zealand. *Australian Journal of Zoology* **21**, 75-90.

Dell, B. and Havel, J. J. (1989). The jarrah forest, an introduction. In 'The Jarrah Forest: A Complex Mediterranean System'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 1-10. (Kluwer Academic Publishers: Dordrecht)

Dunnet, G. M. (1956). A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). *Wildlife Research* **1**, 1-18.

Dunnet, G. M. (1964). A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in eastern Australia. In 'Proceedings of the Zoological Society of London'. No. 142 pp. 665-695.

Efford, M. (1998). Demographic consequences of sex-biased dispersal in a population of brushtail possums. *Journal of Animal Ecology* **67**, 503-517.

Efford, M. (2000). Possum density, population structure and dynamics. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 47-61. (Manaaki Whenua Press: Lincoln, New Zealand)

Fletcher, T. and Selwood, L. (2000). Possum reproduction and development. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 62-81. (Manaaki Whenua Press: Lincoln, New Zealand)

Gemmell, R. T. (2004). The initiation of the breeding season of the common brushtail possum *Trichosurus vulpecula*. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 434-440. (Surrey Beatty and Sons: Sydney)

Gemmell, R. T. and Sernia, C. (1992). The role of photoperiod on the initiation of the breeding-season of the brushtail possum (*Trichosurus vulpecula*). *Journal of Reproduction and Fertility* **95**, 701-708.

Gemmell, R. T. and Sernia, C. (1995). Effect of changing from a short-day to long-day photoperiod on the breeding-season of the brushtail possum (*Trichosurus vulpecula*). *Journal of Experimental Zoology* **273**, 242-246.

Gemmell, R. T., Gepon, G. and Sernia, C. (1993). Effect of photoperiod on the breeding-season of the marsupial possum *Trichosurus vulpecula*. *Journal of Reproduction and Fertility* **98**, 515-520.

Goldingay, R. L. and Jackson, S. M. (2004). 'The Biology of Australian Possums and Gliders.' (Surrey Beatty and Sons: Sydney)

Green, W. Q. (1984). A review of ecological studies relevant to management of the common brushtail possum. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 483-499. (Australian Mammal Society: Sydney)

Herberle, G. (1997). Timber harvesting of Crown land in the south-west of Western Australia: An historical review with maps. *CALMScience* **2**, 203-224.

Hingston, F. J., Dimmock, G. M. and Turton, A. G. (1980). Nutrient distribution in a jarrah (*Eucalyptus marginata* Donn ex Sm.) ecosystem in south-west Western Australia. *Forest Ecology and Management.* **3**, 183-207.

Hocking, G. L. (1981). The population ecology of the brush-tailed possum, *Trichosurus vulpecula* (Kerr) in Tasmania. M.Sc. thesis, University of Tasmania.

How, R. A. (1972). The ecology and management of *Trichosurus* species (Marsupialia) in New South Wales. PhD thesis, University of New England.

How, R. A. (1976). Reproduction, growth and survival of young in the mountain possum, *Trichosurus caninus* (Marsupialia). *Australian Journal of Zoology* **24**, 189-199.

How, R. A. (1978). Population strategies of four species of Australian "possums". In 'Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery) pp. 305-313. (Smithsonian Institution Press: Washington)

How, R. A. (1981). Population parameters of two congeneric possums, *Trichosurus* spp., in north-eastern New South Wales. *Australian Journal of Zoology* **29(2)**, 205-215.

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

How, R. A. and Kerle, J. A. (1995). Common Brushtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan) pp. 273-275. (Reed Books: Chatswood)

Humphreys, W. F., Bradley, A. J., How, R. A. and Barnett, J. L. (1984). Indices of condition of phalanger populations: a review. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 59-77. (Australian Mammal Society: Sydney)

Hutchinson, M. F., Houlder, D. J., Nix, H. A. and McMahon, J. P. (1999). 'ANUCLIM User Guide, Version 5.0.' Centre for Resource and Environmental Studies, Australian National University, Canberra.

Inions, G. (1985). The interactions between possums, habitat trees and fire. Honours thesis, Australian National University.

Inions, G. B., Tanton, M. T. and Davey, S. M. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**, 449-458.

Isaac, J. L. (2005). Life history variation and reproductive success of the common brushtail possum *Trichosurus vulpecula*. PhD thesis, James Cook University.

Isaac, J. L. and Johnson, C. N. (2003). Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. *Behavioral Ecology* **14**, 818-822.

Johnson, C. N., Clinchy, M., Taylor, A. C., Krebs, C. J., Jarman, P. J., Payne, A. and Ritchie, E. G. (2001). Adjustment of offspring sex ratios in relation to the availability of resources for philopatric offspring in the common brushtail possum. *Proceedings of the Royal Society of London Series B - Biological Sciences* **268**, 2001-2005.

Kerle, J. A. (1984). Variation in the ecology of *Trichosurus:* its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 115-128. (Australian Mammal Society: Sydney)

Kerle, J. A. (1998). The population dynamics of a tropical possum, *Trichosurus vulpecula arnhemensis* Collett. *Wildlife Research* **25**, 171-181.

Kerle, J. A. (2001). 'Possums: the brushtails, ringtails and greater glider (First edn).' (University of New South Wales Press: Sydney)

Kerle, J. A. and Howe, C. J. (1992). The breeding biology of a tropical possum, *Trichosurus vulpecula arnhemensis* (Phalangeridae, Marsupialia). *Australian Journal of Zoology* **40**, 653-665.

Kerle, J. A., McKay, G. M. and Sharman, G. B. (1991). A systematic analysis of the brushtail possum, *Trichosurus vulpecula* (Kerr, 1792) (Marsupialia, Phalangeridae). *Australian Journal of Zoology* **39**, 313-331.

Kinnear, J. E., Sumner, N. R. and Onus, M. L. (2002). The red fox in Australia – an exotic predator turned biocontrol agent. *Biological Conservation* **108**, 335-359.

Lyne, A. G. and Verhagen, A. M. W. (1957). Growth of the marsupial *Trichosurus vulpecula* and a comparison with some higher mammals. *Growth* **21**, 167-195.

Maxwell, S., Burbidge, A. A. and Morris, K. (1996). 'The 1996 Action Plan for Australian Marsupials and Monotremes.' Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Project No. 500, Perth.

McArthur, W. M. and Clifton, A. L. (1975). 'Forestry and agriculture in relation to soils in the Pemberton area of Western Australia. Soils and Land Use Series No. 54 ' C.S.I.R.O., Melbourne.

McCaw, W. L. and Burrows, N. D. (1989). Fire management. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem.' (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 317-334. (Kluwer Academic Publishers: Dordrecht)

Montague, T. L. (2000). 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial.' (Manaaki Whenua Press: Lincoln, New Zealand)

Munks, S. A. (1995). The breeding biology of *Psedocheirus peregrinus viverrinus* on Flinders Island, Bass Strait. *Wildlife Research* **22**, 521-534.

Munsell (1954). 'Munsell Soil Color Charts.' (Munsell Color Company, Inc.: Baltimore, USA)

Orell, P. (2004). Fauna monitoring and staff training: Western Shield review – February 2003. *Conservation Science Western Australia* **5**, 51-95.

Owen, W. H. and Thomson, J. A. (1965). Notes on the comparative ecology of the common brushtail possum and mountain possums in eastern Australia. *Victorian Naturalist* **82**, 216-217.

Pahl, L. I. and Lee, A. K. (1988). Reproductive traits of two populations of the common ringtail possum, *Pseudocheirus peregrinus,* in Victoria. *Australian Journal of Zoology* **36**, 83-97.

Parker, A. K. and Krockenberger, A. K. (2002). Sometimes the simple way is best: an evaluation of total body electrical conductivity (TOBEC) and a morphological index as predictors of total body water in the northern brown bandicoot, *Isoodon macrourus*. *Wildlife Research* **29**, 135-140.

Patt, M. (1995). The free-ranging population of the brush-tail possum, *Trichosurus vulpecula* Kerr, in the urban environment of the Perth Zoo; population estimates and management implications. Honours thesis, Edith Cowan University.

Pilton, P. E. and Sharman, G. B. (1962). Reproduction in the marsupial *Trichosurus vulpecula*. *Journal of Endocrinology* **25**, 119-136.

Ramsey, D., Efford, M., Cowan, P. and Coleman, J. (2002). Factors influencing annual variation in breeding by common brushtail possums (*Trichosurus vulpecula)* in New Zealand. *Wildlife Research* **29**, 39-50.

Sampson, J. C. (1971). The biology of *Bettongia penicillata* Gray, 1837. PhD thesis, University of Western Australia.

Shortridge, G. C. (1909). An account of the geographical distribution of the marsupials and monotremes of south-west Australia, having special reference to the specimens collected during the Balston Expedition of 1904-1907. *Proceedings of the Zoological Society* **55**, 803-848.

Smith, M. J., Brown, B. K. and Firth, H. J. (1969). Breeding of the brush-tailed possum, *Trichosurus vulpecula* (Kerr), in New South Wales. *CSIRO Wildlife Research* **14**, 181-193.

Strelein, G. J. (1988). 'Site classification in the southern jarrah forest of Western Australia.' Western Australian Government Department of Conservation and Land Management, Perth.

Tan, P. (1999). Population parameters of two common brushtail possum, *Trichosurus vulpecula* (Kerr), populations. Honours thesis, University of Western Australia.

Taylor, A. C. and Foulkes, J. (2004). Molecules and morphology: a taxonomic analysis of the common brushtail possum *Trichosurus vulpecula* with an emphasis on the central Australian form. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 455-470. (Surrey Beatty and Sons: Sydney)

Troughton, E. L. (1941). 'Furred Animals of Australia.' (Angus and Robertson: Sydney)

Tyndale-Biscoe, C. H. (1955). Observations on the reproduction and ecology of the brush-tailed possum, *Trichosurus vulpecula* Kerr (Marsupialia), in New Zealand. *Australian Journal of Zoology* **3(2)**, 162-184.

Tyndale-Biscoe, H. C. (1973). Non-ruminant herbivores – the Phalangeridae. In 'Life of Marsupials'. pp. 146-169. (Edward Arnold: London)

Viggers, K. L., Lindenmayer, D. B., Cunningham, R. B. and Donnelly, C. F. (1998). Estimating body condition in the mountain brushtail possum, *Trichosurus caninus*. *Wildlife Research* **25**, 499-509.

Wayne, A. F., Cowling, A., Ward, C. G., Rooney, J. F., Vellios, C. V., Lindenmayer, D. B. and Donnelly, C. F. (2005b [Chapter 3]). A comparison of survey methods for arboreal possums in jarrah forest, Western Australia. *Wildlife Research* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005d [Chapter 5]). The life history of *Pseudocheirus occidentalis* (Pseudocheiridae) in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wayne, A. F., Knapp, S. O., Ward, C. G., Vellios, C. V., Rooney, J. F. and Lindenmayer, D. B. (in preparation-a [Chapter 6]). Habitat selection for diurnal refuges by arboreal marsupials in the Mediterranean jarrah (*Eucalyptus marginata*) forest, Western Australia.

Wilde, S. A. and Walker, I. W. (1984). Pemberton-Irwin Inlet, Western Australia. Geological Survey Series Explanation Notes. Geological Survey of Western Australia, Perth.

Winter, J. W. (1976). The behaviour and social organisation of the brushtail possum (*Trichosurus vulpecula* Kerr). PhD thesis, University of Queensland.

Winter, J. W. (1980). Tooth wear as an age index in a population of the brushtailed possum, *Trichosurus vulpecula* (Kerr). *Australian Wildlife Research* **7**, 359-363.

Yom-Tov, Y. and Nix, H. (1986). Climatology correlates for body size of five Australian mammals. *Biological Journal of the Linnean Society* **29**, 245-262.

Yom-Tov, Y., Green, W. Q. and Coleman, J. D. (1985). Morphological trends in the common brushtail possum, *Trichosurus vulpecula*, in New-Zealand. *Journal of Zoology* **33**, 583-593.

4.9 Appendix

Morphometric and life history data collected for *T. v. hypoleucus* individuals at Chariup.

ATTRIBUTES	DESCRIPTION
Dorsal, lateral and tail fur colour	Munsell Soil Colour Charts (Munsell 1954)
White tail length	Length of white tip tail (cm)
Body mass	Body mass (g), accuracy 10-20 g
Tooth wear	Scale 1-9 on M1 (Winter 1980)
Head length	Occipital protuberance to nose tip (mm)
Pes length	Hind foot length, from the heel to the tip of the longest toe, excluding the claw (mm)
Tail length	Ventral tail base to tail tip (mm)
Age	A = Adult (sexually mature), SA = Sub-adult (semi-independent, immature), J = Juvenile (dependant), PY = Infant, pouch-young.
Ectoparasites	Approximate count to the nearest 10, of visible ticks and mites around the ears and head
Body condition	Subjective score: 1 = very good, 2 = good, 3 = fair, 4 = poor, 5 = very poor
Coat condition	Subjective score: 1 = very good, 2 = good, 3 = fair, 4 = poor, 5 = very poor
Sternal gland condition	Subjective score: 1 = very active to 5 = not active
Testis Length	Left testis length (mm)
Testis Width	Left testis width (mm)
Pouch Condition	U = Undeveloped, P = Parous, not active, A = Active (moist, clean), no PY, S = Suckling young, L = Lactating but no PY
Lactating teat position	L = Left, R = Right
PY HL	Pouch-young head length (mm)
PY Sex	Pouch-young M = Male or F = Female

Chapter 5

LIFE HISTORY OF NGWAYIR

Citation: A. F. Wayne, J. F. Rooney, C. G. Ward, C. V. Vellios, and D. B. Lindenmayer (2005d) The life history of Pseudocheirus occidentalis *(Pseudocheiridae) in the jarrah forest of south-western Australia. Australian Journal of Zoology – revised manuscript in review*

Ngwayir,
Pseudocheirus occidentalis

5.1 Abstract

Life history attributes are described for the threatened ngwayir or western ringtail possum (*Pseudocheirus occidentalis*) in inland jarrah (*Eucalyptus marginata*) forest at Chariup (part of Perup Nature Reserve), east of Manjimup, south-western Australia. Data on 81 individuals were collected over 18 months. There was no sexual dimorphism and body size was similar to other *P. occidentalis* populations*,* but larger than the closely related *P. peregrinus* in eastern Australia. Breeding at Chariup was more strongly seasonal than that of coastal populations, with 77% of births in May – June and the remainder in October – November. All neonates were singletons except for one instance of non-viable twins. No females bred twice in the same year. Fecundity was lower than in other *P. occidentalis* populations or in *P. peregrinus*. The head length growth rate of pouch-young (0.245-0.362 mm per day) was slower than that observed for near-coastal populations, but similar to those of several other populations of *Pseudocheirus* in eastern Australia. Growth was curvilinear toward an asymptote after approximately 5-6 months of age. A condition index based on adult body mass varied seasonally in a similar manner for males and females, with condition being poorest in autumn and winter and best in late spring and early summer. Ectoparasites were most abundant in winter and spring. Coat condition was best in winter when it provides protection from the coolest and wettest weather. Eighty-four percent of observed deaths were between April and September and most deaths were caused by predation, predominantly by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). More effective and strategic control of introduced predators prior to and during autumn/winter, could lead to a substantial improvement in the population viability of *P. occidentalis* in the jarrah forest. Many of the life history traits of *P. occidentalis* in the jarrah forest appear to be influenced by nutrition. Compared with near-coastal populations in peppermint (*Agonis flexuosa*) woodland around Busselton, fecundity and growth rates were poorer in the jarrah forest. The more highly seasonal breeding and changes in body condition at Chariup also were associated with foliar nutrition and the phenology of staple food tree species. The differences in life history and conservation status between *P. occidentalis* and *P. peregrinus*, also may be partly explained by nutrition.

5.2 Introduction

A scientific understanding of biodiversity and of ecosystem processes is fundamental to their effective conservation and management. Knowledge of the biology and life history of a species is particularly important (Lindenmayer and Burgman 2005). Critical knowledge gaps in this understanding hamper the effective conservation management of ecosystems such as the jarrah forest (Wardell-Johnson *et al.* 2004; CALM 2004).

Pseudocheirus occidentalis (Pseudocheiridae, Thomas 1888; ngwayir or western ringtail possum) is endemic to south-western Australia and is a specialised arboreal folivore that feeds predominantly on the leaves of a few select species (Jones *et al.* 1994a, 1994b; Jones and Hillcox 1995; Jones 1995; Kerle 2001). Since the European settlement of south-western Australia in the 1820s, the distribution of *P. occidentalis* has been reduced by about 80-90% and the species is now absent from most of its former northern and inland range (Figure 5.1, de Tores 2000; Jones 2004). *P. occidentalis* is consequently classified as Vulnerable under the World Conservation Union (1994) criteria and as ‘fauna which is rare or likely to become extinct’ under the Western Australian *Wildlife Conservation Act 1950*. Only three large populations remain (de Tores 2000; Jones 2004). The densest population, located around Bunbury and Busselton, is in the southern extremity of the Swan Coastal Plain where the dominant peppermint tree (*Agonis flexuosa*) constitutes 90-95% of the species’ diet (Jones *et al.* 1994b). Similarly, the smaller south coast population around Albany is to be found mainly in near-coastal habitat where peppermint is common or dominant. The most extensive remnant population survives inland in the Upper Warren (in the IBRA Jarrah Forest Bioregion, Thackway and Creswell 1995), east of Manjimup. Here, the peppermint tree is effectively (naturally) absent and jarrah foliage constitutes the species’ staple diet (Jones *et al.* 1994b). Another conspicuous difference between the populations in coastal peppermint woodlands and in inland jarrah forest is the rare use of dreys (self-constructed nests) in inland areas, where tree hollows or hollow logs and balga (*Xanthorrhoea preissii*) constitute the main form of diurnal shelter (Inions *et al.* 1989; Jones *et al.* 1994b; Wayne *et al*. 2000; Wayne *et al.* in preparation-a [Chapter 6]).

The current understanding of the biology and ecology of *P. occidentalis* is largely derived from studies within the coastal peppermint woodlands and in the near-coastal tuart (*Eucalyptus gomphocephala*) and peppermint forest at Ludlow (both sites are near Busselton) (Ellis and Jones 1992; Jones *et al.*1994a, 1994b; Jones and Hillcox 1995). In contrast, detailed published knowledge of *P. occidentalis* in the jarrah forest is relatively limited (i.e. Inions *et al.* 1989; Jones *et al.* 1994b). More recent research found that *P. occidentalis* survivorship was substantially reduced during logging operations in the jarrah forest (Wayne *et al.* 2000, 2001). In response to these findings, more extensive research has sought to improve the detection efficiency of survey methods for this cryptic species (Wayne

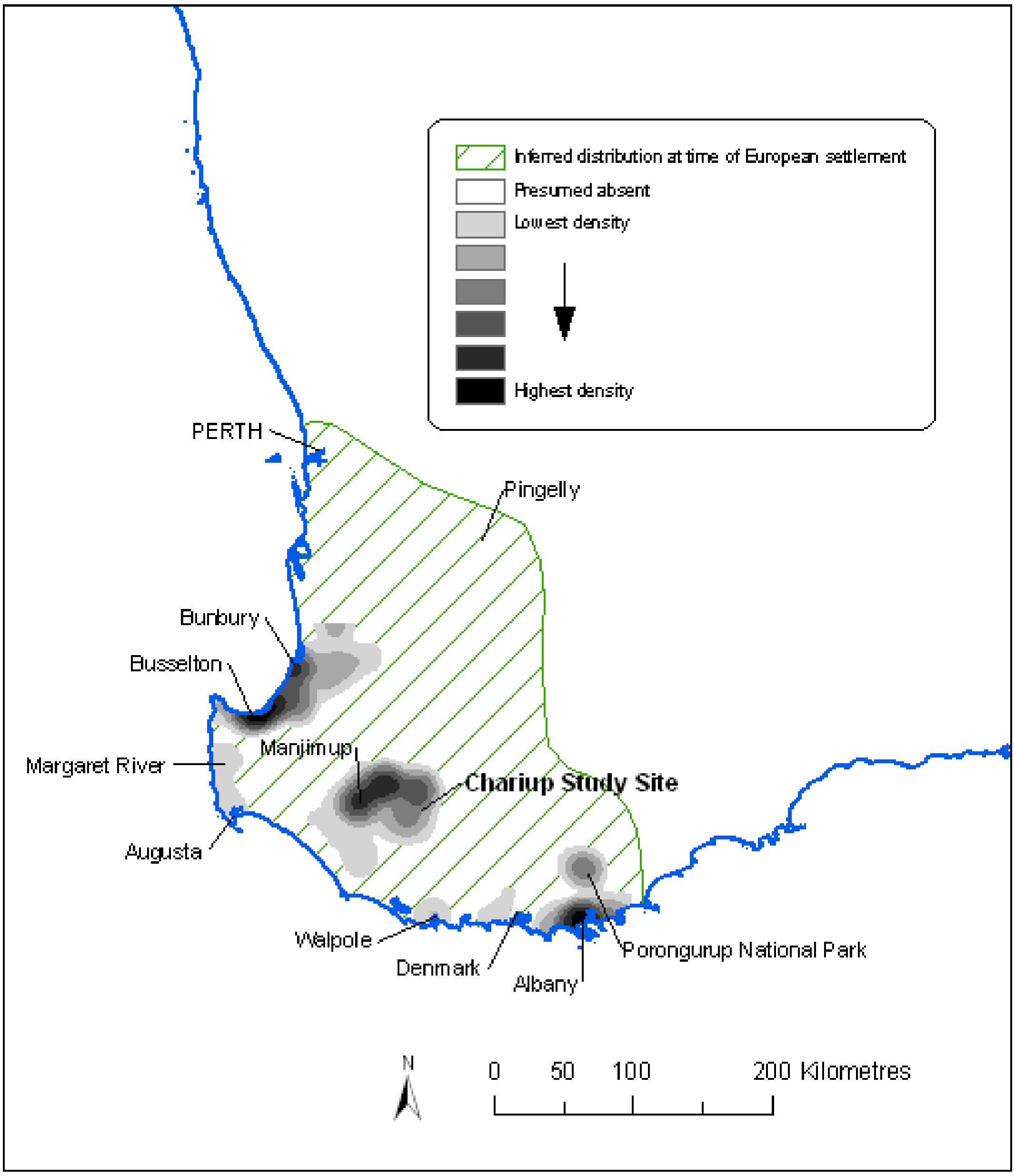

Figure 5.1. Historic and current distribution of *Pseudocheirus occidentalis* (exclusive of subfossil records) and the location of Chariup Study Site, south-western Australia. Source: P. de Tores.

Note: The density of location records reflects surveying effort, increased public awareness and proximity to major towns. It does not necessarily reflect the density of *P. occidentalis.*

Prior to the commencement of European settlement of the south-west in the 1820s, and based on sub-fossil evidence, *P. occidentalis* occurred between Geraldton on the mid-west coast and Eucla on the southern edge of the Nullarbor Plain, and up to 150 kilometres inland at Tutanning Nature Reserve, near Pingelly (de Tores 2000).

et al. 2005a, b [Chapters 2 and 3]). The findings of these studies facilitated investigations into the selection of diurnal refuges (Wayne *et al.* in preparation-a [Chapter 6]) and the anthropogenic factors related to the distribution and abundance of *P. occidentalis* at local and landscape scales within the Upper Warren (Wayne *et al.* 2005e [Chapter 7]). The purpose of these studies was to improve the biological and ecological understanding of the ngwayir within the jarrah forest as a means to improving their conservation and habitat management.

As part of the research programme, this study investigated aspects of the life history of *P. occidentalis* in an inland jarrah forest. We present data collected in 2002 and 2003 from individuals trapped, hand-captured and radio-collared in an area of 25 hectares within an extensive jarrah forest in Chariup (part of Perup Nature Reserve), in the Upper Warren. In particular, the morphology, reproduction, growth, temporal changes in condition and mortality of *P. occidentalis* individuals were investigated. A comparison of these results with other *P. occidentalis* populations and those of the closely related *P. peregrinus* is also presented.

5.3 Methods

5.3.1 Study area

The study area in Chariup forest block was within the southern portion of Perup Nature Reserve, 270 km south-south-east of Perth, 40 km east of Manjimup, south-western Australia (116^{o} 37’E, 34^{o} 16’S; Figure 5.1). Perup comprises 52,000 ha of dry sclerophyll forest with an overstorey dominated by jarrah and marri (*Corymbia calophylla*), and has been managed as a nature reserve since 1972 (CALM 1998). Prior to this the area was vested as State forest and commercially logged for timber. The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters. The local average annual rainfall is around 700 mm, and the monthly mean minimum and maximum temperature range is approximately 5 ^{o}C to 28 ^{o}C (ANUCLIM 2001 data, Hutchison *et al.* 1999). The topography is characterised by gently undulating plateaux tops, low lateritic ridges and broad valleys, 220-280 m above sea level. In recognition of the value of the remnant native fauna and the predation threat from the introduced red fox (*Vulpes vulpes*), irregular baiting using 1080 toxin began in some areas as early as 1977. Regular broad-scale aerial fox-baiting commenced in 1996 (CALM 2000). The Chariup study site had not been burnt for 18 years. More detailed management history and habitat attributes of the study area are described by McArthur and Clifton (1975), Wilde and Walker (1984), Strelein (1988), CALM (1998), and Burrows and Christensen (2002). The same study site was used for a number of other studies of *P. occidentalis* (Wayne *et al.* 2005b, in preparation-a [Chapters 3 and 6 respectively]) and the life history of *Trichosurus vulpecula hypoleucus* (koomal or common brushtail possum) (Wayne *et al.* 2005c [Chapter 4]).

5.3.2 Trapping and capture

Arboreal traps were shown in a previous study to capture more than nine times as many *P. occidentalis* as the same traps placed on the ground (Wayne *et al.* 2005b [Chapter 3]). Hence, a 500 m by 500 m grid of 121 arboreal trapping points spaced 50 m apart (i.e. 11 parallel transects with 11 points each) was used in this study. The arboreal platforms were constructed from a metal frame with a reinforced plywood decking (1200 mm x 200 mm x 10 mm) and were attached to trees approximately 1.8 m above ground. Sheffield wire mesh cages (220 mm x 220 mm x 590 mm) were secured to the platform using elastic hooks. A small straight bush stick was placed under the entrance of all traps to avoid tail injury to captured possums (i.e. to stop the tail potentially becoming wedged between the trap door and the platform decking). A thick hessian bag covered the traps to provide protection from the weather and exposure. Traps were baited with flour and vegetable oil dough scented with rose essence (12ml rose fragrance per kg of flour, Wayne *et al.* 2005b [Chapter 3]). During 18 months between June 2002 and November 2003, 10 trapping sessions were conducted, each for a duration of three or four consecutive days, and generally eight weeks apart (Table 5.1). Trapping was periodically supplemented with captures made either by hand (generally 0-4 m above ground), by a catch-pole (range = 2-8 m above ground), or by tranquilliser dart gun (range = 6-12 m above ground). The specially designed (B. Terrel) air gun was used to deliver custom darts developed by P. de Tores (personal communication) that contained Zoletil ™ sedative. Two trapping sessions were conducted in June 2002, at the commencement of the study and hand-capture methods were responsible for all captures made in November 2002, March 2003 and August 2003. Greater hand-capture effort was directed towards females.

Table 5.1. The number of *P. occidentalis* individuals captured per month by trapping or hand-capture at Chariup.

Note: J = Juvenile, S = Sub-adult, A = Adult

MONTH	TOTAL NO. INDIVIDUALS	MALES			FEMALES		
		J	S	A	J	S	A
Jun-02	16			7		1	8
Jul-02	8		1	3			4
Aug-02	16			5		1	10
Oct-02	18			8	1		9
Nov-02	11	1		3			7
Dec-02	17	1	1	6	1	1	7
Feb-03	5			1		1	3
Mar-03	9			1			8
Apr-03	13	1		3		1	8
Jun-03	7			4		1	2
Aug-03	2			1			1
Nov-03	13			4	1	1	7

5.3.3 Animal handling and data collection

During the initial phase of the study (June and July 2002), all adult possums captured for the first time were sedated using an intramuscular (quadricep) injection of Ketamine (20 mg/kg) and Xylazine (7 mg/kg), or Zoletil (10 mg/kg) to minimise handling stress and to facilitate the examination of tooth wear and pouch-young and, for some, the fitting of radio-collars. Sedation for examination was not used after July 2002 owing to the quiet nature of these animals and the ease with which they can be handled.

Individuals were considered to be pouch-young when suckling within the pouch, and juveniles when they had emerged from the pouch but were dependent on their mothers (i.e. back young). Sub-adults were at least semi-independent but were sexually immature. Adults were considered mature on the basis of testes size (> 10 mm wide, > 15 mm long) or the presence of a well-developed pouch.

The main morphological measurements collected from captured individuals are summarised in the Appendix at the end of this chapter. A relative and approximate measure of age was determined using an arbitrary nine-class system based on toothwear and the extent of exposed dentine (Thomson and Owen 1964). Coat condition was subjectively assessed on the extent of hair loss and matting, density, uniformity, and general appearance. Ectoparasites (Arachnida; Acarina) were counted on each animal's head.

5.3.4 Mortality events

Mortality-sensitive radio-transmitting collars (Biotrack, U.K.) were fitted to a subset of the adult population (21 males, 22 females) as part of a complementary study of habitat selection (Wayne *et al.* in preparation-a [Chapter 6]). Radio-collared individuals were scanned weekly to check whether they were still alive. When mortality radio-signals were detected, the collars were located and any possum remains examined. Where possible, necropsies and biopsies were conducted to assist with identifying factors contributing to the cause of death.

5.3.5 Condition index

Indices of 'body condition' attempt to quantify the general health and fitness of individuals (Humphreys *et al.* 1984; Viggers *et al.* 1998). An appropriate and meaningful condition index based on adult body mass and body size (head length or pes length) was not possible because of a lack of relationship between these factors. A condition index (CI) was therefore derived from the residuals of body mass from a linear mixed model, in which possum identity (ID) was fitted as a random effect. This produced a condition index that accounted for individual differences in body mass and was specific to each individual (see Wayne *et al.* 2005c [Chapter 4] for further details).

5.3.6 Data analysis

Morphometric measurements were tested for differences between the sexes using linear mixed models that accounted for multiple measurements of the same individual over time by including ID as a random effect. Analysis of variance (ANOVA) was used to identify differences between time classes (months or seasons) with respect to CI, body condition, coat condition and ectoparasites.

The growth rate of small pouch-young was determined for two individuals for which there were multiple measurements. Based on these two growth rates and assuming a head length at birth of 7 mm (Jones *et al.* 1994b) and linear growth within the pouch, the date of birth (month) was estimated for each pouch-young. The head length of pouch-young through to adulthood was characterised using multiple measurements of seven (4M:3F) young animals (2-3 measurements each). A linear mixed model of age was used to characterise the growth of individuals from approximately five months of age. ID was fitted as a random effect in this model to account for within-possum variability.

5.4 Results

5.4.1 Capture data

There were 96 trap captures of *P. occidentalis* from 3308 trap-nights, and an additional 50 hand-captures during the 18-month study (Table 5.1). Of the 81 individuals (31M:50F) involved in this study, the 34 (15M:19F) that were captured more than once were captured on average 2.9 times each (maximum seven captures each).

5.4.2 Morphometric data

The mean body mass and other morphological measurements (head length, pes or tail length) did not differ significantly between adult males and females (Table 5.2). Sub-adults of both sexes ranged between 600 g and 800 g. The body masses of mature males and females were greater than 800 g. The mean adult weight was 1080 g and individuals weighed up to 1330 g. All individuals were similar in colour with a very dark brown dorsal and lateral coat and were creamy white ventrally and immediately behind the ears. An albino was observed on a number of occasions 18 months prior to the commencement of this study but was not re-encountered during the study.

Table 5.2. Morphometric measures of *P. occidentalis* at Chariup: summarised according to sex and age, including body mass, head length, long pes length, and testis length and width.

There were no significant differences (at the 5% significance level) in the body mass, head length, pes length and tail length between adult male and adult female samples. Note: J = Juvenile, S = Sub-adult, A = Adult

		FEMALE			MALE		
		J	S	A	J	S	A
No. measurements		3	7	77	3	2	46
Body mass (g)	Mean	415.5	733.4	1086.1	421.7	728.0	1061.8
	s.e.	104.1	46.0	16.8	114.0	72.0	19.1
Head length (mm)	Mean	60.4	67.3	73.8	57.8	69.8	73.5
	s.e.	3.0	2.1	0.5	1.3	2.0	0.6
Long pes length (mm)	Mean	42.1	47.3	50.5	40.5	46.6	50.1
	s.e.	2.9	1.0	0.3	1.7	0.9	0.4
Tail length (cm)	Mean	28.0	34.9	37.3	28.9	31.3	36.9
	s.e.	2.6	1.0	0.3	2.9	0.8	0.5
Left testis length (mm)	Mean					10.5	23.2
	s.e.					0.5	0.4
Left testis width (mm)	Mean					5.8	16.5
	s.e.					0.2	0.3

5.4.3 Reproductive data

5.4.3.1 Breeding season and fecundity

Twenty-five female *P. occidentalis* were observed breeding during 2002. A further four adult females were caught during 2002 but exhibited no signs of breeding, however, their capture history was insufficient to be able to assess with certainty whether or not they bred in that year (i.e. captured 1-2 times each).

On the basis of the head length of 18 pouch-young and observed growth rates (see below), it was estimated that 77% were born in May and June 2002 (44% and 33% respectively), and the remainder were born in October and November 2002 (17% and 6% respectively). In 2003, only three autumn-winter births, and one November birth were recorded on account of sampling limitations. Only two females were observed throughout both the 2002 and 2003 breeding seasons and both individuals bred in both years. No females were observed to breed more than once per year.

In all but one case, females had single pouch-young. Twins less than a week old were observed on one occasion but when the mother was recaptured two months later, only a single pouch-young remained. The sex ratio of the 14 pouch-young for which sex was identified was 1:1.

5.4.3.2 Offspring growth rates and development

Repeat measurements of the head length of pouch-young were achieved in two cases; the head length of a male grew from 9.9 mm to 32.0 mm in 61 days (0.362mm per day) and that of a female grew from 19.1 mm to 24.0 mm in 20 days (0.245 mm per day). For the growth rates of individuals estimated to be greater than five months old, the relationship between head length and age (months) was made linear by transforming age to the negative reciprocal of age. A linear mixed model of this relationship was:

Head length (mm) = 77.98 + 109.04 x (-1/age); ($p < 0.0001$)

Because of the data limitations (i.e. the numbers of individuals and of repeat measurements) and the estimations of age in months, this growth model only provides a rough approximation (Figure 5.2). Nonetheless, *P. occidentalis* appear to mature and are capable of reproducing from about 12 months of age. Body mass at the commencement of adulthood was greater than 900 g and head length was greater than about 69 mm. Having matured, older adult body mass would range between 800 g and 1330 g, depending on the individual and over time.

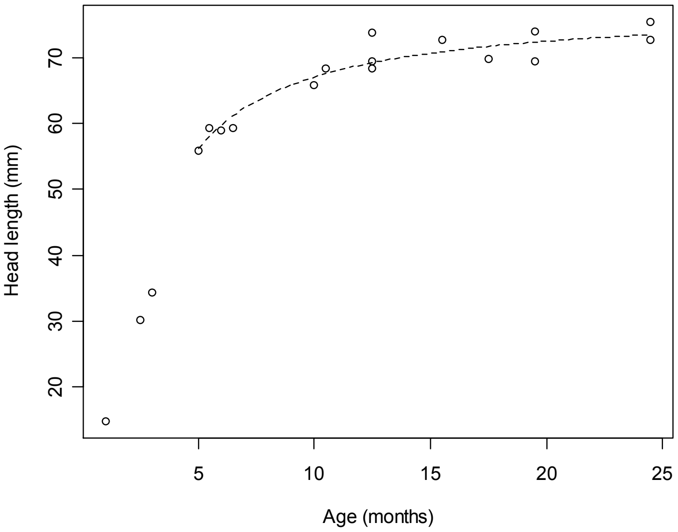

Figure 5.2. The relationship between head length and age of *P. occidentalis* pouch-young at Chariup.

5.4.4 Temporal changes in condition

To examine whether adult possum condition differed significantly over time, an ANOVA was modelled with month, sex and their two-way interaction as the factors, and the condition index (CI) as the response variable. The model found no significant difference in CI according to sex or the interaction between month and sex, but the CI did significantly vary between months ($F_{11,\ 107} = 3.0554$, $p = 0.0014$). The CI was poorest in autumn and winter (June and July 2002, March and June 2003) and greatest in late spring and summer (November and December 2002 and November 2003; Figure 5.3). There was insufficient data to test whether the cyclical patterns of the CI differed between females that bred in autumn, and those that bred in spring – the demands of lactation might affect condition.

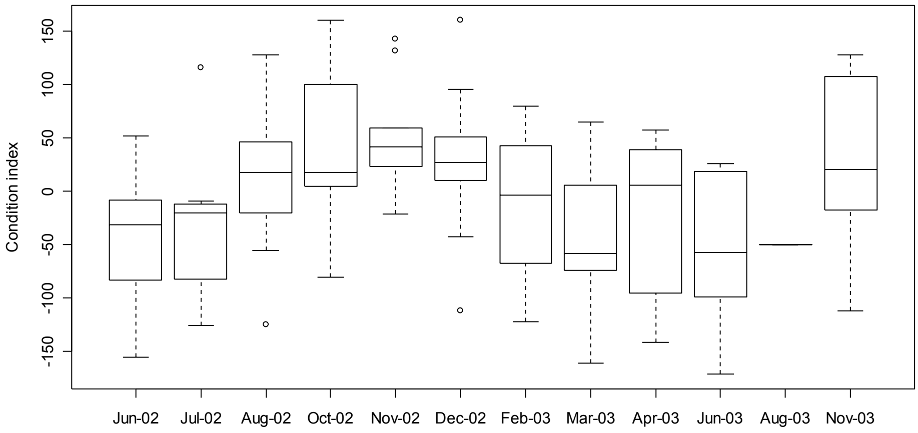

Figure 5.3. Box plots by survey month showing temporal variation in the condition index of adult P. occidentalis at Chariup.

Sample sizes for the 12 sample months were 15, 7, 14, 17, 10, 14, 4, 9, 12, 6, 1 and 10 respectively. Box plots: the horizontal line in the box indicates the sample median, the lower and upper extents of the box (i.e. ‘hinges’) indicate the 25th and 75th percentiles, the T-bar ‘whiskers’ indicate the maximum and minimum values, with the exception of sample outliers (symbolised by ‘o’).

Coat condition was highly variable between individuals and over time, including several cases of almost complete fur loss and superficial skin conditions (inconclusive results from skin biopsies) on the back and rump of some animals. Coat condition changed significantly with the seasons ($F_{3,\ 111} = 3.4961$, $p = 0.0180$) and was better in autumn and winter than in spring and summer (Figure 5.4). Coat condition also was significantly and negatively related to the condition index ($F_{1,\ 113} = 10.794$, $p = 0.0013$). The subjective assessment of body condition did not vary significantly between months. Furthermore, no relationship was found between the subjective body condition score and the condition index. Ectoparasites on *P. occidentalis* (mostly ticks) varied significantly with the seasons ($F_{3,\ 111} = 5.5744$, $p = 0.0013$), and were more abundant in winter and spring and least abundant in autumn (Figure 5.5).

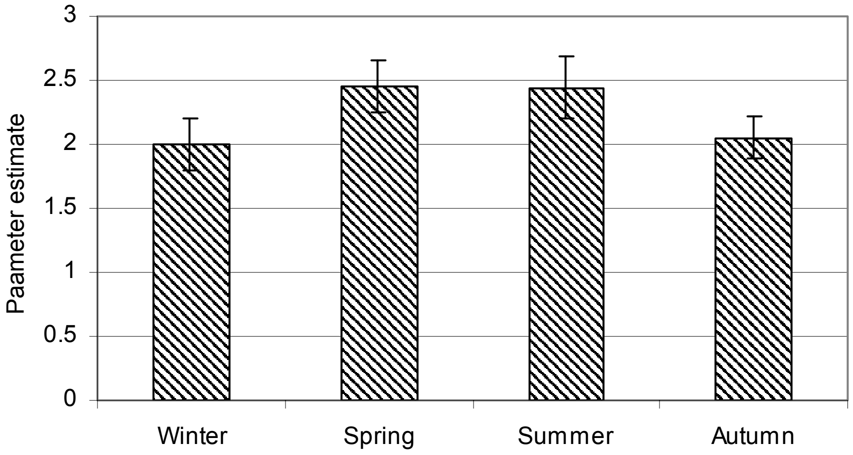

Figure 5.4. Seasonal variation in coat condition of *P. occidentalis* at Chariup, based on the mean and standard error of a subjectively derived score (1-5), where 1 = very good and 5 = very poor (i.e. the coat condition score decreases as coat condition improves).

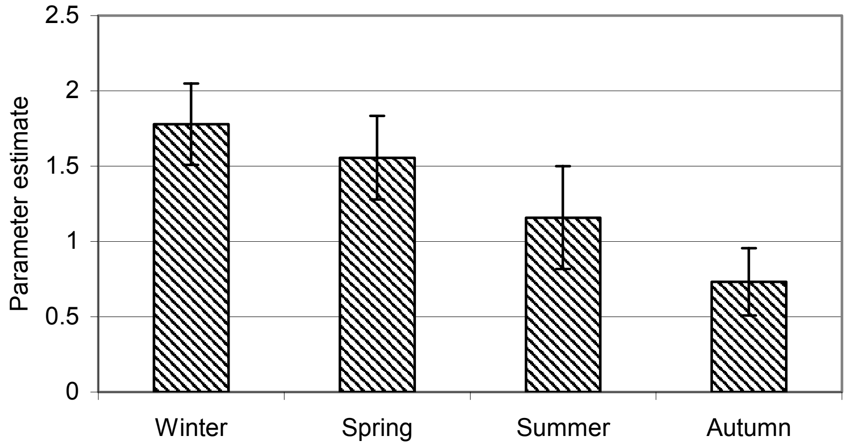

Figure 5.5. Seasonal variation in the abundance of ectoparasites found on *P. occidentalis* at Chariup, based on the mean and standard error of the log-transformed number of ticks and mites found on an individual's head.

5.4.5 Longevity estimates

Four of the *P. occidentalis* involved in this study were known as adults from a previous study conducted between November 2001 and March 2002 (Wayne *et al.* 2005b [Chapter 3]). Two of these individuals were radio-collared and were estimated to be at least 2.5 years of age when they died. The remaining two individuals were caught in this study only once or twice, at which time they were at least two years of age. Tooth wear was classified for 13 adult males and 15 adult females. The average tooth wear score was six for both sexes (i.e. approximately equivalent to a two to three-year-old *P. peregrinus* at Warramate Hills, Victoria; Thomson and Owen 1964). The highest scores were eight and nine for females and males respectively (i.e. approximately equivalent to a ≥4-year-old *P. peregrinus* at Warramate Hills, Victoria; Thomson and Owen 1964).

5.4.6 Mortality

Thirty-two out of 46 radio-collared individuals died during the 18-month study (i.e. a 46% annual adult mortality rate). Twenty-seven (84%) deaths were between April and September. Predation was the cause of 26 (81%) deaths, many of which occurred in ‘pulses’ where multiple mortalities were observed within periods of one or two weeks. Based on the animal signs associated with the possum remains, up to four of the predations may have been by a raptor (probably wedgetail eagle, *Aquila audax*) and up to six may have been by chuditch (*Dasyurus geoffroii*). It is likely that at least 16 animals were killed by either fox or cat (*Felis catus*). Evidence of red foxes, feral cats, chuditch and wedgetail eagles was found at the study site.

5.5 Discussion

5.5.1 Morphology

The lack of sexual dimorphism in adult *P. occidentalis* in the jarrah forest at Chariup was similar to that in the near-coastal populations in peppermint habitats around Busselton, Augusta and Albany (Ellis and Jones 1992; Jones *et al.* 1994b). Although this species is similar in size to *P. peregrinus viverrinus* on Flinders Island (which also is not sexually dimorphic; Munks 1995), *P. occidentalis* is slightly larger and darker than other populations of *P. peregrinus* (e.g. Hughes *et al.* 1965; How *et al.* 1984; Pahl and Lee 1988).

5.5.2 Reproduction

5.5.2.1 Breeding season

The seasonality of breeding at Chariup was more acute than in the near-coastal populations of *P. occidentalis,* where breeding occurs throughout most of the year (with peaks in April – June and October – December; Jones *et al.* 1994b). At Chariup, 77% of births occurred in May – June, and the remainder in October – November. As with other mammal species, seasonality of breeding is often a fundamental response to food availability (Bronson and Heideman 1994). Therefore, the difference in breeding seasonality between *P. occidentalis* populations probably reflects phenological and nutritional differences in the principal food species. For a number of arboreal marsupial species, including *P. peregrinus*, it has been suggested that predominantly autumn breeding ensures that the late stages of lactation and weaning of offspring (i.e. the period of highest nutritional demand for mothers, Munks and Green 1995) occur during late spring and early summer, when young foliage is most abundant (Pahl and Lee 1988; Munks 1995).

At Chariup, the period of late lactation by mothers and weaning of offspring (i.e. 5-6 months of age) born in autumn coincides with the emergence of young jarrah leaves (the preferred diet of *P. occidentalis*, Jones *et al.* 1994b; A. Wayne personal observation) between August and November. The young jarrah leaves mature between December and February (Abbott and Loneragan 1986; Abbott *et al.* 1989). In keeping with a bimodal seasonal pattern of plant productivity that occurs in south-western Australia, jarrah also may have a secondary leaf growth flush in autumn (Abbott and Loneragan 1986; Abbott *et al.* 1989). The secondary peak in *P. occidentalis* births in October – November results in the weaning of offspring coinciding with this secondary growth flush in jarrah.

In the peppermint woodlands near Busselton, young peppermint leaves are the preferred diet (Ellis and Jones 1992; Jones *et al.* 1994b). The winter and early spring leaf growth of peppermint trees would support the mothers and weaning offspring born in summer – early autumn. The mid-to-late-autumn peak of births (Jones *et al.* 1994b) results in the timing of weaning coinciding with the annual peak in nitrogen levels in peppermint leaves (i.e. October, Jones *et al.* 1994a). Furthermore, no or very few offspring are born in August – September that would subsequently be weaned when foliar nitrogen levels in peppermint trees are at their lowest (i.e. February, Jones *et al.* 1994a). Additional evidence for the influence of nutrition on the timing of *P. occidentalis* births is the aseasonality of breeding in a captive population where daily vitamin and mineral supplements were provided (Ellis and Jones 1992).

5.5.2.2 Fecundity and nutrition

Although no twins were successfully reared to pouch emergence at Chariup, the incidence of twins in coastal populations is not uncommon (17% of breeding mothers; Jones *et al.*

1994b). Double breeding was not observed for wild *P. occidentalis* either at Chariup or elsewhere (Jones *et al.* 1994b). However, a captive female *P. occidentalis* raised four single young in rapid succession within the first two years of maturity (Ellis and Jones 1992). The fecundity of *P. occidentalis* at Chariup of one young per adult female per year is, therefore, less than either its full potential or that of near-coastal conspecifics. Reproductive output at Chariup appears to be limited by environmental constraints. More longitudinal data from multiple sites are required to verify whether the observations at Chariup are representative of other jarrah forest populations.

Nonetheless, nutrition is a plausible key factor influencing fecundity (e.g. Norton 1987; Bronson and Heideman 1994). Preliminary measures of nitrogen (N), phosphorus (P), and potassium (K) levels in jarrah leaves at Chariup (mean = 0.86%, 0.01%, and 0.37% dry weight, respectively) appear approximately comparable to (P) or less than (N, K) the nutrient levels in peppermint tree leaves near Busselton (Jones *et al.* 1994a). However, nutrient levels within the same tree species do vary between individual trees and geographically. For individual trees nutrient levels vary seasonally with tree maturity, leaf maturity, and leaf position within the tree canopy (e.g. Hingston *et al.* 1980; Jones *et al* 1994a; A. Wayne unpublished data). Furthermore, an animal's ability to access foliar nutrients is dependent on its physiology (e.g. Chilcott 1984; Chilcott and Hume 1984a, 1984b; Hume *et al.* 1984; Pahl 1987a; Foley 1992) and the types and concentrations of secondary metabolites, such as formylated phloroglucinol compounds, to which *Pseudocheirus* are sensitive (e.g. Hume *et al.* 1996; Marsh *et al.* 2003a, 2003b). Therefore, determining the nutritional differences of tree species and the influences that these may have on *P. occidentalis* reproduction is complex and requires specific investigation.

Additional evidence for nutrient limitation in the jarrah forest is found in the larger home ranges and lower densities of *P. occidentalis* in this type of habitat (Wayne *et al.* 2000; A. Wayne unpublished data) compared with the near-coastal populations around Busselton (Jones *et al.* 1994a, 1994b). Furthermore, when compared with peppermint woodland around Busselton that was unoccupied by *P. occidentalis,* occupied peppermint woodland tended to have higher nutrient levels (particularly nitrogen) in late summer, when nitrogen and phosphorus levels were at an annual low (Jones *et al.* 1994a; see also Braithwaite *et al.* 1983, 1984 for nutritional influences on arboreal marsupial densities, etc).

When compared with *P. peregrinus* in eastern Australia, the reproduction and life history of *P. occidentalis* appear to be more constrained. For example, the average litter sizes of *P. peregrinus* range from 1.8 to 2 (e.g. Hughes *et al.* 1965; How 1978; How *et al.* 1984; Munks 1995; Smith *et al.* 2003) and litters of up to four young have been observed (e.g. Pahl and Lee 1988). Furthermore, up to 50% of female *P. peregrinus* may breed twice in the same year (e.g. Hughes *et al.* 1965; Pahl and Lee 1988). Fecundity at Chariup is, therefore, little more than half that of wild populations of *P. peregrinus* that have 1.8-2.4 young per adult female per year (Hughes *et al.* 1965; How 1978; Pahl and Lee 1988; Munks 1995). The more solitary nature of *P. occidentalis*, and its relatively larger body size also may reflect evolutionary responses to the poorer nutritional quality of its diet (Smith and Lee 1984; Ellis and Jones 1992; Jones *et al.* 2004). The lower fecundity of *P. peregrinus* on Flinders Island in comparison with other populations in eastern Australia also has been speculated to relate to the nutrient status and age of the forest habitat (Munks 1995). The soil fertility in south-western Australian forests and the nutrient concentrations in the dominant tree species of the region are recognised as some of the most impoverished in the world (Hingston *et al.* 1980, 1989; Dell and Havel 1989). Therefore, given that captive *P. occidentalis* are capable of reproductive outputs similar to *P. peregrinus*, it is plausible that the lower fecundity observed in wild *P. occidentalis* may be partly explained by nutritional constraints (e.g. Norton 1987; Bronson and Heideman 1994).

5.5.2.3 Offspring and adult sex ratios

The sex ratio of pouch-young at Chariup (7M:7F) was similar to that of *P. occidentalis* at Abba River, near Busselton (4M:3F, Jones *et al.* 1994b), in captivity (5M:6F, Ellis and Jones 1992), and for *P. peregrinus* elsewhere in Australia (e.g. Hughes *et al.* 1965; Munks 1995). *P. occidentalis* at Locke Estate near Busselton, on the other hand, had a significant female bias among the pouch-young (6M:14F) and adult populations (20M:43F, Jones *et al.* 1994b). Although there was an adult female bias in the animals captured at Chariup (31M:50F), this is not an accurate measure of the population because there was a greater hand-capture effort toward females. It has been speculated that equal sex ratios for *P. occidentalis* are indicative of stable populations, that female bias is indicative of an expanding population in a high quality habitat, and that a male bias is indicative of marginal or declining habitat conditions (Jones 2004; Jones *et al.* 2004). This remains to be verified. Nonetheless, relationships between population dynamics and sex ratios also have been suggested for *T. vulpecula* (e.g. Kerle 1984; Green 1984), including a tendency for mothers to produce more male offspring when competition for resources becomes intense (Johnson *et al.* 2001).

5.5.2.4 Offspring growth rates

The head length growth rates of pouch-young at Chariup (0.245-0.362 mm per day) were slower than those observed by Jones *et al.* (1994b) in coastal woodlands near Busselton (0.417 mm per day), but comparable to those observed for *P. peregrinus* in Victoria (0.229-0.307 mm per day; How *et al.* 1984), for captive *P. peregrinus* in Tasmania (approximately 0.302 mm per day; Munks and Green 1997), and for *P. herbertensis* in Queensland (0.329 mm per day; Haffenden 1984). The influence of maternal body mass and the nutritional quality of the maternal diet on the milk properties may explain differences in growth rates between populations (Munks *et al.* 1991; Munks 1995; Munks and Green 1997). Interestingly, the same tendency for slower head length growth rates at Chariup compared with those observed in the woodlands near Busselton was found for *Trichosurus vulpecula hypoleucus* (Wayne *et al.* 2005c [Chapter 4]).

A growth curve using the body mass of young *P. occidentalis* in captivity was developed by Ellis and Jones (1992). Caution is required when using either head length or body mass as an estimator of age because differences between populations and sexes have been observed for immature *P. peregrinus* (Pahl 1987b; Munks and Green 1997). Despite this, the use of head length when estimating age is considered more reliable than using body mass given the linear growth of head length until weaning (Munks and Green 1997), and the highly variable nature of body mass (e.g. Pahl 1987b). More comprehensive data for *P. occidentalis* would be required to provide a more reliable age estimator based on head length that accounted for potential differences between populations, sexes and seasons. Nonetheless, the results from this study indicate that after approximately the first 5-6 months, when weaning may commence (How 1978; Pahl and Lee 1988), head length growth is curvilinear toward an asymptote.

Females of known age at Chariup were first observed breeding at about 12 months. This is similar to the age observed for captive *P. occidentalis* (Ellis and Jones 1992), and wild *P. peregrinus* (Thomson and Owen 1964; How *et al.* 1984; Pahl and Lee 1988; Munks and Green 1995). The timing of breeding, litter size and the incidence of double breeding of *P. peregrinus* have been related to female age and body mass, with heavier, multiparous females likely to be more fecund than primiparous adults (Pahl and Lee 1988; Munks 1995). Female *P. peregrinus* that breed twice in the same year also wean their offspring sooner (5-6 months compared with 7-8 months; Pahl and Lee 1988; Munks 1995). Whether similar trends occur in *P. occidentalis* remains to be determined, but the accessibility and quality of nutrients are likely to be ultimate key factors (as has been observed for *T. vulpecula*; Kerle 1984) and should, therefore, be incorporated into any such investigation.

5.5.3 Temporal changes in condition

The seasonal variations in the condition index (CI) of *P. occidentalis* at Chariup were similar for males and females, with condition being poorest in autumn and winter and healthiest in late spring and early summer (Figure 5.3). Similar seasonal variations in body mass also have been observed for *P. peregrinus.* However, in these cases, the peaks and troughs were generally slightly out of phase between males and females (How *et al* 1984; Pahl 1987b; Munks 1995). The pronounced environmental seasonality (including jarrah phenology) experienced at Chariup may account for the synchrony in the condition index between the sexes observed there. Ectoparasite (ticks and mites) loads on *P. occidentalis* at Chariup also were most abundant in the wetter seasons of winter and spring, when body condition was generally poor, but also may coincide with the life cycle of the parasites. Whether ticks and mites significantly affect condition remains to be determined, but it has been suggested that relative ectoparasite loads may be an indicator of stress (e.g. Humphries *et al.* 1984).

Coat condition at Chariup also varied seasonally but inversely with the condition index. Having a good coat during winter, when the weather is wettest and coolest, may provide greater protection from climatic conditions. Good coat condition also coincided with the main breeding season.

5.5.4 Longevity and mortality patterns

The oldest observed age of *P. occidentalis* at Chariup of 2.5 years is an underestimate of longevity, given the limited duration of this study. The oldest observed age of *P. occidentalis* in the jarrah forest is four years (Wayne *et al.* 2000). Tooth wear may be another useful non-destructive means of estimating age. However, considerable care is required to ensure that variations according to sex, location and diet are appropriately accounted for (e.g. Pahl 1987b). Based on the available tooth wear data and adult survival rates, it is generally assumed that the average adult age of wild *P. occidentalis* in the jarrah forest is around three years and rarely exceeds four or five years. More extensive data on longevity are required to verify this. *P. peregrinus* have similar life expectancies (How 1978), but may live up to six years based on estimations from tooth wear (Pahl 1987b) or eight years in captivity (Thomson and Owen 1964).

As well as longevity, the viability of a population depends on the successful rearing of the next generation through to sexual maturity. With insufficient data for the survival of young *P. occidentalis* (Jones *et al.* 1994b), observations of *P. peregrinus* may give some indication. The average survivorship of young through to maturity is 30% across many of the *P. peregrinus* populations that have been studied, but may be as low as 2% during drought years – predation generally being the major cause of death (see Pahl 1987b). The population viability implications of anything significantly less than 100% survival of *P. occidentalis* young through to maturity in the jarrah forest may be profound, given an annual fecundity rate of one young per mature female and a relatively short life span. To maintain population size a female needs a minimum of two successful reproductive seasons (i.e. three years of age) and 100% offspring survival to maturity. Therefore, anything that reduces either offspring survival or the average life expectancy of a female to three years or less may threaten the viability of the population. Differences in the fecundity, offspring survivorship, and longevity between *P. occidentalis* and *P. peregrinus* will result in differences in the ability of populations to withstand and recover from negative population pressures, and may partly explain the differences in the conservation status between these species.

The deaths of adult *P. occidentalis* at Chariup were associated with the cooler, wetter months of the year (84% of deaths occurred between April and September), when body condition was poor. A similar mortality pattern was observed at Kingston (26 km to the north east of Chariup) where 89% (n = 9) and 93% (n = 14) of the deaths of radio-collared animals occurred between April and September in unlogged and logged jarrah forest, respectively (Wayne *et al.* 2000).

The seasonal patterns of mortality and body condition of *P. occidentalis* at Chariup are associated with temporal cycles in food quality and quantity (see above). For example, the increase in body condition coincides with the emergence of young jarrah leaves (August – November). Seasonal periods of poor condition and high mortality coincide with periods of little or no new leaf growth on jarrah (i.e. winter). Higher rates of mortality in winter also have been observed for *T. vulpecula* (particularly males) in New Zealand, following the loss of fat reserves during autumn (e.g. Efford 2000).

The seasonal commencement of the decline in condition of *P. occidentalis* at Chariup also coincides with the hottest and driest months of the year (December – March). Sensitivity to heat and drought-induced stress has been observed in *P. occidentalis* around Busselton (Jones *et al* 1994b). Furthermore, weight loss and deaths of *P. peregrinus* in Victoria in late summer were associated with excessive heat and drought (Thomson and Owen 1964; Pahl 1987b). However, there were only two out of 32 deaths (both apparent predations) at Chariup between December 2002 and March 2003, in similar temperatures to those experienced by the population studied by Pahl (1987b). Manjimup, which has a milder climate than Chariup, had 33 days with maximum temperatures of 30-34 ^{o}C, and 10 days with maxima of 35-39 ^{o}C (CALM weather records). Therefore, although the hot summer drought may be contributing to the stress and poorer condition of *P. occidentalis* at Chariup, it does not account for the high mortality rates in the cooler and wetter months between April and September.

It is possible that protection from the weather by diurnal refuges may help to reduce summer mortality of *P. occidentalis* in jarrah forest. The preference for deeper hollows by *P. occidentalis* and *T. v. hypoleucus* in the jarrah forest (Inions *et al.* 1989) led to speculation that the use of dreys was rare in these forests because of the need for added insulation in inland regions where the seasonal and diurnal variations in temperature, and the severity of summer drought are greater (Jones *et al.* 1994a, 1994b): similar speculation has been made for *P. peregrinus* in eastern Australia (e.g. Kerle 2004). However, dreys are used in some dense habitats within the jarrah forest, which are capable of supporting dense populations (see Chapter 6). It therefore seems more likely that the differences in types of diurnal refuge between coastal and inland populations are mainly a response to habitat structure, rather than habitat selection being determined simply by physiological limitations (see Chapter 6). Specific physiological studies would more precisely quantify when and to what extent *P. occidentalis* may be physiologically stressed, and hence to what extent they may be susceptible to heat and drought stress in summer and/or malnutrition in winter.

Predation was the cause of most deaths at Chariup, and is expected to be a major determinant of the demographic characteristics and viability of jarrah forest populations. The apparent predation pulses observed at Chariup also are indicative of so-called 'rogue predators' (Dickman 1996), whereby the impact of individuals with hunting skills developed for particular prey may have a major impact on populations.

Most predations at Chariup appeared to be by foxes or cats. These also are major predators of other *Pseudocheirus* populations (Thomson and Owen 1964; Jones *et al.* 1994b, 2004; Dickman 1996; Russell *et al.* 2003). At Chariup, most deaths occurred (i.e. April – September) when other prey, such as reptiles and invertebrates, were scarce (see also Molsher 1999; Molsher *et al.* 1999, 2000). Winter is the breeding season for foxes (e.g. Saunders *et al.* 1995) and is the period when adult fox densities and mobility are potentially at their greatest. The capture rates and lethal baiting of feral cats also are higher in late autumn and winter, which is thought to be due to the scarcity of food, increased energy needs and/or increased dispersal of young adult cats (e.g. Molsher 2001; Burrows *et al.* 2003).

The abundance of ngwayir (which are particularly predator-naïve, A. Wayne personal observation) in the Upper Warren was positively associated with sustained and intensive fox-baiting (Wayne *et al.* 2005e [Chapter 7]) over and above the four standard fox-baiting sessions per year (CALM 2000) in operation in the Chariup site and in most publicly-managed jarrah forests. Although the standard level of fox-baiting is sufficient to allow population recovery of other native jarrah forest fauna species (CALM 2000; Orell 2004), the results from this study suggest that predation may still be a problem for the long-term viability of *P. occidentalis* populations in jarrah forest. Based on the seasonal pattern of *P. occidentalis* mortality and of fox and cat activity, it is highly likely that strategically timed and increased control of introduced predators prior to and during autumn/winter could be particularly effective in reducing the rate of deaths during this period. The extent to which predators cause the premature death of potentially physiologically stressed *P. occidentalis* in autumn/winter remains to be determined. Such knowledge could help determine the effectiveness of more intensive baiting at this time.

5.6 Conclusions

This study has substantially increased the knowledge of the life history of *P. occidentalis* in the jarrah forest, about which very little was known. In comparison with the near-coastal populations in peppermint habitat, the population at Chariup exhibited lower fecundity with smaller litter sizes, slower offspring growth rates, larger home ranges, and lower densities. The higher fecundity of *P. occidentalis* in captivity further demonstrates the extent of the environmentally-limited reproductive potential of the Chariup population. Furthermore, differences in the seasonality of breeding appear to be associated with the seasonal variations in foliar nutrients and in the phenology of the trees that constitute the staple diet of the Busselton and Chariup populations (peppermint and jarrah respectively). Seasonal variations in adult body condition also were associated with food quantity and quality (i.e. availability of young jarrah leaves). The high incidence of mortality (principally by predation) between April and September corresponds with periods when body condition is poor. A strategic approach to reducing the numbers of predators immediately prior to and during this period would probably be particularly beneficial to conservation efforts for *P. occidentalis*. In summary, several of the demographic and reproductive patterns of the *P. occidentalis* population in the jarrah forest at Chariup, appear to be influenced by nutrition.

At a species level, *P. occidentalis* has a lower reproductive potential than that of *P. peregrinus* in eastern Australia. Other evidence suggesting that *P. occidentalis* may be nutritionally constrained includes its more solitary nature, larger body size, and the fact that the soils and dominant tree species in south-western Australia are among the most nutrient-impoverished in the world. Differences in life history and conservation status between *P. occidentalis* and *P. peregrinus* may thus be partly explained by nutrition.

These findings together provide some clear directions for future research such as (1) investigating the role and importance of nutrients; (2) developing a deeper understanding of the processes behind biological patterns (e.g. seasonal differences in breeding, causes of mortality, and physiology of heat stress); (3) population viability modelling based on our improved understanding; and (4) determining what implications these findings may have for the conservation and management of *P. occidentalis* and its habitat.

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5.8 References

Abbott, I. and Loneragan, O. (1986). 'Ecology of jarrah (*Eucalyptus marginata*) in the northern jarrah forest of Western Australia.' Western Australian Government Department of Conservation and Land Management, Perth.

Abbott, I., Dell, B. and Loneragan, O. (1989). The jarrah plant. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem.' (Eds B. Dell, J. J. Havel and N. Malajczuk). (Kluwer Academic Publishers: Dordrecht)

Braithwaite, L. W., Dudzinski, M. L. and Turner, J. (1983). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales: II Relationship between the fauna density, richness and diversity, and measured variables of the habitat. *Australian Wildlife Research* **10**, 231-247.

Braithwaite, L. W., Turner, J. and Kelly, J. (1984). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales: III Relationships between fauna densities, eucalypt occurrence and foliage nutrients, and soil parent materials. *Australian Wildlife Research* **11**, 41-48.

Bronson, F. H. and Heideman, P. D. (1994). Seasonal regulation of reproduction in mammals. In 'The Physiology of Reproduction'. (Eds E. Knobil and J. D. Neill) Vol. 2 pp. 541-583. (Raven Press Ltd.: New York)

Burrows, N. D., Algar, D., Robinson, A. D., Sinagra, J., Ward, B. and Liddelow, G. (2003). Controlling introduced predators in the Gibson Desert of Western Australia. *Journal of Arid Environments* **55**, 691-713.

Burrows, N. D. and Christensen, P. E. S. (2002). Long-term trends in native mammal capture rates in a jarrah forest in south-western Australia. *Australian Forestry* **65**, 211-219.

CALM (1998). 'Draft Management Plan: Perup Forest and Lake Muir/Unicup Nature Reserves.' Western Australian Government Department of Conservation and Land Management, Perth.

CALM (2000). 'Western Shield Fauna Recovery Program Strategic Plan (July 1999 – June 2004).' Western Australian Government Department of Conservation and Land Management, Perth.

CALM (2004). 'Towards a biodiversity conservation strategy for Western Australia: discussion paper.' Western Australian Government Department of Conservation and Land Management, Perth.

Chilcott, M. J. (1984). Coprophagy in the common ringtail possum, *Pseudocheirus peregrinus* (Marsupialia: Petauridae). *Australian Mammalogy* **7**, 107-110.

Chilcott, M. J. and Hume, I. D. (1984a). Digestion of *Eucalyptus andrewsii* foliage by the common ringtail possum, *Pseudocheirus peregrinus*. *Australian Journal of Zoology* **32**, 605-613.

Chilcott, M. J. and Hume, I. D. (1984b). Nitrogen and urea metabolism and nitrogen requirements of the common ringtail possum, *Pseudocheirus peregrinus*, fed *Eucalyptus andrewsii* foliage. *Australian Journal of Zoology* **32**, 615-622.

Dell, B. and Havel, J. J. (1989). The jarrah forest, an introduction. In 'The Jarrah Forest: A Complex Mediterranean System'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 1-10. (Kluwer Academic Publishers: Dordrecht)

de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

Dickman, C. R. (1996). 'Overview of the impacts of feral cats on Australian native fauna.' Australian Nature Conservation Agency, Canberra.

Efford, M. (2000). Possum density, population structure and dynamics. In 'The Brushtail Possum: Biology, impact, and management of an introduced marsupial'. (Ed. T. L. Montague) pp. 47-61. (Manaaki Whenua Press: Lincoln, New Zealand)

Ellis, M. and Jones, B. (1992). Observations of captive and wild western ringtail possums *Pseudocheirus occidentalis*. *Western Australian Naturalist* **19**, 1-10.

Foley, W. J. (1992). Nitrogen and energy retention and acid-base status in the common ringtail possum (*Pseudocheirus peregrinus*) – Evidence of the effects of absorbed allelochemicals. *Physiological Zoology* **65**, 403-421.

Green, W. Q. (1984). A review of ecological studies relevant to management of the common brushtail possum. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 483-499. (Australian Mammal Society: Sydney)

Haffenden, A. (1984). Breeding, growth and development in the Herbert River ringtail possum, *Pseudocheirus herbertensis* (Marsupialia : Petauridae). In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 277-281. (Australian Mammal Society: Sydney)

Hingston, F. J., Dimmock, G. M. and Turton, A. G. (1980). Nutrient distribution in a jarrah (*Eucalyptus marginata* Donn ex Sm.) ecosystem in south-west Western Australia. *Forest Ecology and Management.* **3**, 183-207.

Hingston, F. J., O'Connell, A. M. and Grove, T. S. (1989). Nutrient cycling in jarrah forest. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 155-177. (Kluwer Academic Publishers: Dordrecht)

How, R. A. (1978). Population strategies of four species of Australian "possums". In 'Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery) pp. 305-313. (Smithsonian Institution Press: Washington)

How, R. A., Barnett, J. L., Bradley, A. J., Humphreys, W. F. and Martin, K. J. (1984). Population biology of *Pseudocheirus peregrinus* in a *Leptospermum laevigatum* thicket. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 261-268. (Australian Mammal Society: Sydney)

Hughes, R. L., Thomson, J. A. and Owen, W. H. (1965). Reproduction in natural populations of the Australian ringtail possum, *Pseudocheirus peregrinus* (Marsupialia: Phalangeridae), in Victoria. *Australian Journal of Zoology* **13**, 383-406.

Hume, I. D., Bladon, R. V. and Soran, N. (1996). Seasonal changes in digestive performance of common ringtail possums (*Pseudocheirus peregrinus*) fed *Eucalyptus* foliage. *Australian Journal of Zoology* **44**, 327-336.

Hume, I. D., Foley, W. J. and Chilcott, M. J. (1984). Physiological mechanisms of foliage digestion in the greater glider and ringtail possum (Marsupialia: Pseudocheiridae). In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 247-251. (Australian Mammal Society: Sydney)

Humphreys, W. F., Bradley, A. J., How, R. A. and Barnett, J. L. (1984). Indices of condition of phalanger populations: a review. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 59-77. (Australian Mammal Society: Sydney)

Hutchinson, M. F., Houlder, D. J., Nix, H. A. and McMahon, J. P. (1999). 'ANUCLIM User Guide, Version 5.0.' Centre for Resource and Environmental Studies, Australian National University, Canberra.

Inions, G. B., Tanton, M. T. and Davey, S. M. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**, 449-458.

World Conservation Union (1994). 'IUCN Red List Categories.' Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Johnson, C. N., Clinchy, M., Taylor, A. C., Krebs, C. J., Jarman, P. J., Payne, A. and Ritchie, E. G. (2001). Adjustment of offspring sex ratios in relation to the availability of resources for philopatric offspring in the common brushtail possum. *Proceedings of the Royal Society of London Series B - Biological Sciences* **268**, 2001-2005.

Jones, B. (1995). Western Ringtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan) pp. 252-254. (Reed Books: Chatswood)

Jones, B. (2004). The possum fauna of Western Australia: decline, persistence and status. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 149-160. (Surrey Beatty and Sons: Sydney)

Jones, B. and Hillcox, S. (1995). A survey of the possums *Trichosurus vulpecula* and *Pseudocheirus occidentalis* and their habitats in forest at Ludlow, Western Australia. *Western Australian Naturalist* **20**, 139-150.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994a). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175-187.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994b). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Jones, B. A., Meathrel, C. E. and Calver, M. C. (2004). Hypotheses arising from a population recovery of the western ringtail possum *Pseudocheirus occidentalis* in fire regrowth patches in a stand of *Agonis flexuosa* trees in south-western Australia. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 656-662. (Royal Zoological Society of New South Wales: Sydney)

Kerle, J. A. (1984). Variation in the ecology of *Trichosurus:* its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 115-128. (Australian Mammal Society: Sydney)

Kerle, J. A. (2001). 'Possums: the brushtails, ringtails and greater glider (First edn).' (University of New South Wales Press: Sydney)

Kerle, J. A. (2004). A cautionary tale: decline of the common brushtail possum *Trichosurus vulpecula* and common ringtail possum *Pseudocheirus peregrinus* in the woodlands of the western slopes and plains of New South Wales. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 71-84. (Surrey Beatty and Sons: Sydney)

Lindenmayer, D. B. and Burgman, M. A. (2005). 'Practical Conservation Biology.' (CSIRO Publishing: Melbourne)

Marsh, K. J., Foley, W. J., Cowling, A. and Wallis, I. R. (2003a). Differential susceptibility to *Eucalyptus* secondary compounds explains feeding by the common ringtail (*Pseudocheirus peregrinus*) and common brushtail possum (*Trichosurus vulpecula*). *Journal of Comparative Physiology B - Biochemical Systemic and Environmental Physiology* **173**, 69-78.

Marsh, K. J., Wallis, I. R. and Foley, W. J. (2003b). The effect of inactivating tannins on the intake of *Eucalyptus* foliage by a specialist *Eucalyptus* folivore (*Pseudocheirus *peregrinus*) and a generalist herbivore (*Trichosurus vulpecula*). *Australian Journal of Zoology* **51**, 31-42.

McArthur, W. M. and Clifton, A. L. (1975). 'Forestry and agriculture in relation to soils in the Pemberton area of Western Australia. Soils and Land Use Series No. 54 ' C.S.I.R.O., Melbourne.

Molsher, R. (1999). The ecology of feral cats, *Felis catus*, in open forest in New South Wales: Interactions with food resources and foxes. PhD thesis, University of Sydney.

Molsher, R. L. (2001). Trapping and demographics of feral cats (*Felis catus*) in central New South Wales. *Wildlife Research* **28**, 631-636.

Molsher, R., Newsome, A. and Dickman, C. (1999). Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research* **26**, 593-607.

Molsher, R. L., Gifford, E. J. and McIlroy, J. C. (2000). Temporal, spatial and individual variation in the diet of red foxes (*Vulpes vulpes*) in central New South Wales. *Wildlife Research* **27**, 593-601.

Munks, S. (1995). The breeding biology of *Pseudocheirus peregrinus viverrinus* on Flinders Island, Bass Strait. *Wildlife Research* **22**, 521-534.

Munks, S. A. and Green, B. (1995). Energy allocation for reproduction in a marsupial arboreal folivore, the common ringtail possum (*Pseudocheirus peregrinus*). *Oecologia* **101**, 94-104.

Munks, S. and Green, B. (1997). Milk consumption and growth in a marsupial arboreal folivore, the common ringtail possum, *Pseudocheirus peregrinus*. *Physiological Zoology* **70**, 691-700.

Munks, S. A., Green, B., Newgrain, K. and Messer, M. (1991). Milk-composition in the common ringtail possum, *Pseudocheirus peregrinus* (Petauridae, Marsupialia) *Australian Journal of Zoology* **39**, 403-416.

Munsell (1954). 'Munsell Soil Color Charts.' (Munsell Color Company, Inc.: Baltimore, USA)

Norton, T. W. (1987). Ecology of greater gliders, *Petauroides volans* Kerr 1792, in relation to variations in habitat quality in eucalypt forests in south-east New South Wales. PhD thesis, The Australian National University.

Orell, P. (2004). Fauna monitoring and staff training: Western Shield review – Feb 2003. *Conservation Science Western Australia* **5**, 51-95.

Pahl, L. I. (1987a). Feeding behaviour and diet of the common ringtail possum, *Pseudocheirus peregrinus*, in *Eucalyptus* woodlands and *Leptospermum* thickets in southern Victoria. *Australian Journal of Zoology* **35**, 487-506.

Pahl, L. I. (1987b). Survival, age determination and population age structure of the common ringtail possum, *Pseudocheirus peregrinus*, in a *Eucalyptus* woodland and a *Leptospermum* thicket in southern Victoria. *Australian Journal of Zoology* **35**, 625-639.

Pahl, L. I. and Lee, A. K. (1988). Reproductive traits of two populations of the common ringtail possum, *Pseudocheirus peregrinus,* in Victoria. *Australian Journal of Zoology* **36**, 83-97.

Russell, B. G., Smith, B. and Augee, M. L. (2003). Changes to a population of common ringtail possums (*Pseudocheirus peregrinus)* after bushfire. *Wildlife Research* **30**, 389-396.

Saunders, G., Coman, B. J., Kinnear, J. E. and Braysher, M. L. (1995). 'Managing Vertebrate Pests: Foxes.' (Australian Government Publishing Service: Canberra)

Smith, A. and Lee, A. K. (1984). The evolution of strategies for survival and reproduction in possums and gliders. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 17-33. (Australian Mammal Society: Sydney)

Smith, B., Augee, M. and Rose, S. (2003). Radio-tracking studies of common ringtail possums, *Pseudocheirus peregrinus*, in Manly Dam Reserve, Sydney. *Proceedings of the Linnean Society of New South Wales* **124**, 183-194.

Strelein, G. J. (1988). 'Site classification in the southern jarrah forest of Western Australia.' Western Australian Government Department of Conservation and Land Management, Perth.

Thackway, R. and Cresswell, I. D. (1995). 'An interim biogeographic regionalisation for Australia: a framework for setting priorities in the National Reserves System Cooperative Program, Version 4.0.' Australian Nature Conservation Agency, Canberra.

Thomson, J. A. and Owen, W. H. (1964). A field study of the Australian ringtail possum *Pseudocheirus peregrinus* (Marsupialia : Phalangeridae). *Ecological Monographs* **34**, 27-52.

Viggers, K. L., Lindenmayer, D. B., Cunningham, R. B. and Donnelly, C. F. (1998). Estimating body condition in the mountain brushtail possum, *Trichosurus caninus*. *Wildlife Research* **25**, 499-509.

Wardell-Johnson, G., Calver, M. C., Saunders, D. A., Conroy, S. and Jones, B. (2004). Why integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 394-417. (Royal Zoological Society of New South Wales: Sydney)

Wayne, A. F., Ward, C., Rooney, J. and Wheeler, I. (2000). 'The immediate impacts of timber harvesting and associated activities on the ngwayir (*Pseudocheirus occidentalis*) in the jarrah forest of Kingston State Forest Block. Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Rooney, J., Ward, C., Wheeler, I. and Mellican, A. (2001). 'Spotlight surveys to investigate the impacts of timber harvesting and associated activities within the jarrah forest of Kingston State Forest, with particular reference to the koomal (*Trichosurus vulpecula*) and ngwayir (*Pseudocheirus occidentalis*). Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Cowling, A., Rooney, J. F., Ward, C. G., Wheeler, I. B., Lindenmayer, D. B. and Donnelly, C. F. (2005a [Chapter 2]). Factors affecting the detection of possums by spotlighting in Western Australia. *Wildlife Research* – revised manuscript in review.

Wayne, A. F., Cowling, A., Ward, C. G., Rooney, J. F., Vellios, C. V., Lindenmayer, D. B. and Donnelly, C. F. (2005b [Chapter 3]). A comparison of survey methods for arboreal possums in jarrah forest, Western Australia. *Wildlife Research* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005c [Chapter 4]). The life history of *Trichosurus vulpecula hypoleucus* (Phalangeridae), in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wayne, A. F., Cowling, A., Lindenmayer, D. B., Ward, C. G., Vellios, C. V. and Donnelly, C. F. (2005e [Chapter 7]). The abundance of a threatened arboreal marsupial in relation to anthropogenic disturbances at local and landscape scales in Mediterranean-type forest in south-western Australia. *Biological Conservation* – revised manuscript in review.

Wayne, A. F., Knapp, S. O., Ward, C. G., Vellios, C. V., Rooney, J. F. and Lindenmayer, D. B. (in preparation-a [Chapter 6]). Habitat selection for diurnal refuges by arboreal marsupials in the Mediterranean jarrah (*Eucalyptus marginata*) forest, Western Australia.

Wilde, S. A. and Walker, I. W. (1984). Pemberton-Irwin Inlet, Western Australia. Geological Survey Series Explanation Notes. Geological Survey of Western Australia, Perth.

5.9 Appendix

Morphometric and life history data collected for *P. occidentalis* individuals at Chariup.

ATTRIBUTES	DESCRIPTION
Dorsal, lateral and tail fur colour	Munsell Soil Colour Charts (Munsell 1954)
White tail length	Length of white tail tip (cm)
Body mass	Body Mass (g), accuracy 10-20 g
Tooth wear	Scale 1-9 (Thomson and Owen 1964)
Head length	Occipital protuberance to nose tip (mm)
Pes length	Hind foot length, from the heel to the tip of the longest toe, excluding the claw (mm)
Tail length	Ventral tail base to tail tip (mm)
Age	A = Adult (sexually mature), SA = Sub-adult (semi-independent, immature), J = Juvenile (dependant), PY = Infant, pouch-young.
Ectoparasites	Approximate count to the nearest 10, of visible ticks and mites around the ears and head
Body condition	Subjective score: 1 = very good, 2 = good, 3 = fair, 4 = poor, 5 = very poor
Coat condition	Subjective score: 1 = very good, 2 = good, 3 = fair, 4 = poor, 5 = very poor
Testis Length	Left testis length (mm)
Testis Width	Left testis width (mm)
Pouch Condition	U = Undeveloped, P = Parous but not active, A = Active (moist, clean), no PY, S = Suckling young, L = Lactating but no PY
Lactating teat position	L = Left, R = Right
PY HL	Pouch-young head length (mm)
PY Sex	Pouch-young M = Male or F = Female

SECTION C

POSSUM ECOLOGY IN JARRAH FOREST

This section comprises Chapters 6 and 7 and focuses on aspects of the ecology of koomal and ngwayir in the jarrah forest. Habitat selection is examined at multiple spatial scales in recognition that different ecological patterns and processes operate at different spatial scales. Chapter 6 presents a study on the habitat selection for diurnal refuges by both possum species. At the 'micro-scale', the attributes of habitat units, such as single trees or logs that were used as diurnal refuge, were related to what was available. Similarly, characteristics of the habitat surrounding these units also were incorporated into logistic regression models to identify important aspects of the 'meso-habitat' that relates to habitat selection for diurnal refuges. The models developed in this chapter can be used to predict the likelihood that the koomal or ngwayir use a particular tree as shelter, based on key attributes of the tree and surrounding habitat. This information is particularly useful for identifying important habitat that may need protection for the purposes of possum conservation and ecologically sustainable forest management.

Chapter 7 describes a study that investigated how ngwayir distribution and abundance related to anthropogenic disturbance factors at both the local (3 ha) and landscape scales (> 300 ha). Concentrating on the jarrah forest in the Upper Warren, east of Manjimup, the study focussed on ngwayir associations with logging, fire, fox control and forest fragmentation. The scat survey method tested in Section A Chapter 3, was used to measure the relative abundance of ngwayir at the 90 stratified sites involved in this study.

Chapter 6

HABITAT SELECTION FOR DIURNAL REFUGE BY KOOMAL AND NGWAYIR

*Citation: A.F. Wayne, S.O. Knapp, C.G. Ward, C.V. Vellios, J.F. Rooney, and D.B. Lindenmayer (in preparation-a). Habitat selection for diurnal refuge by arboreal marsupials in the Mediterranean-type jarrah (*Eucalyptus marginata*) forest, Western Australia.*

Note: this chapter will be submitted for publication as two manuscripts

Radio-telemetry for diurnal refuges (above)

Diurnal refuge, R36 – the most frequently used tree at Chariup (left and below)

6.1 Abstract

Diurnal refuge use and selection by koomal (common brushtail possum, *Trichosurus vulpecula hypoleucus*) and ngwayir (western ringtail possum, *Pseudocheirus occidentalis*) were investigated in the jarrah (*Eucalyptus marginata*) forest at Chariup (part of Perup Nature Reserve), south-western Australia. Twenty-nine koomal and 43 ngwayir within a 25 ha area of forest were radio-collared for up to 18-months. Each individual was observed for up to 96 days, resulting in a total of 3338 records of diurnal refuge use by all collared animals of both species. Of the 238 refuges recorded, 204 were hollow-bearing trees and 21 were hollow logs. Forest debris, root cavities (burrows), balga (*Xanthorrhoea preissii*), a hollow stump and a drey (self-constructed ngwayir nest) also were used. Hollow-bearing trees were occupied by koomal and ngwayir 98% and 96% of the time, respectively. Koomal occupied up to 23 different refuges each (mean = 7.3 ± 4.7 and 10.8 ± 5.6 for females and males, respectively). Ngwayir individuals occupied up to 16 different refuges each (mean = 5.4 ± 3.3 and 6.1 ± 4.2 for females and males, respectively). Most refuges were visited rarely and a few were visited frequently, indicating that some refuges were more important than others. For both possum species, approximately 60% of refuges were occupied by only one individual. The remainder were co-used (i.e. temporally discrete use) by up to five conspecifics and up to nine individuals of both species. Concurrent sharing of the same refuge (but not necessarily the same hollow) between koomal occurred 11% of the time, and 2% of the time between ngwayir. Most sharing was between male-female pairs. Interspecific sharing occurred 3% of the time.

Logistic regression modelling of the morphological characteristics of standing trees occupied by both species of arboreal marsupial indicated that tree diameter was the single best predictor of tree use. Crown senescence, canopy connectivity, tree species and possum signs also were significant predictors of tree use. Elements of the meso-habitat, such as vegetation strata heights and percentage cover also were significantly related to diurnal refuge use, thus emphasising that habitat selection occurs at multiple spatial scales. The importance of canopy connectivity and habitat context on the selection of shelter sites has implications for conservation and sustainable forest management for these tree-dependent species. This is particularly relevant to ‘habitat tree’ retention practices within forests available for logging. Differences between suitable habitats that are physically available and those that are actually occupied demonstrate that habitat selection is a complex process that is influenced by biological factors (e.g. competition, predation, etc) that need to be considered when identifying important habitats for the purposes of conservation and forest management.

6.2 Introduction

Habitat selection is one of the most poorly understood ecological processes, yet it is fundamental to understanding the distribution and abundance of animals (Krebs 1985). Habitat selection occurs when the resources used by an animal are disproportionate to those available (Johnson 1980). The ‘choice’ as to where an animal lives can differ between individuals and may be influenced by many factors, including vegetation structure, floristics, food availability, weather, conspecifics, interspecific competition, predation risk and/or parasites (e.g. Luck 2002; Kerr *et al.* 2003; and references therein). It also is important to recognise that habitat selection functions at different spatial scales (e.g. Johnson 1980; Holling 1992; Mackey and Lindenmayer 2001; Mitchell *et al.* 2001) and different temporal scales (e.g. Schooley 1994; Schmidt *et al.* 2000; Bos and Carthew 2003).

Understanding habitat selection has particularly important implications for the management of endangered species (e.g. Chambers and Dickman 2002; Bos and Carthew 2003; Vernes 2003), because it helps to evaluate the potential responses of these species to environmental changes (Pulliam and Danielson 1991; Dunning *et al.* 1995; Dasgupta and Alldredge 2000). Some examples where this has been effective include the spotted owl (*Strix occidentalis,* e.g. Ganey *et al.* 1999; Herter *et al.* 2002; McComb *et al.* 2002) and the red-cockaded woodpecker (*Picoides borealis*, e.g. Rudolph and Conner 1996) in North America, and large owls (e.g. Loyn *et al.* 2001) and arboreal marsupials (e.g. Lindenmayer 2000) in eastern Australia.

This paper explores habitat selection by two possum species found in the jarrah (*Eucalyptus marginata*) forest in south-western Australia. These species are the koomal (common brushtail possum, *Trichosurus vulpecula hypoleucus*) and the ngwayir (western ringtail possum, *Pseudocheirus occidentalis*). Both have declined substantially since the settlement of Western Australia by Europeans (de Tores 2000; How and Hillcox 2000), and are conservation-listed taxa at risk of further decline (Maxwell *et al.* 1996; de Tores 2000). These species are also likely to be highly susceptible to logging (Calver *et al.* 1999; Wayne *et al.* 2000). The abundance of tree hollows has been associated with the abundance of both koomal (Sampson 1971; Jones 2004; see also Kerle 1984) and ngwayir (Jones *et al.* 1994a; Jones and Hillcox 1995), as well as the closely-related common brushtail possum (*T. vulpecula*) and common ringtail possum (*P. peregrinus*), and other arboreal marsupials in eastern Australia (e.g. Mackowski 1984; Merredith 1984; Traill 1991). Whitford and Williams (2002) used relationships between tree attributes and the abundance of hollows to develop predictions for the occurrence of hollows potentially suitable for 10 vertebrate species in the jarrah forest (see also Whitford 2001, 2002). On the basis of their findings, they recommended refinements to silvicultural guidelines in order to improve the selection criteria of ‘habitat trees’ to be retained during jarrah forest logging operations to conserve key habitat required by hollow-dependent fauna. A strategic risk assessment based on a similar process also was used to determine the potential impacts of a decline in hollow abundance on 42 hollow-dependent vertebrate taxa in south-western Australian forests (Abbott and Whitford 2002). In the absence of sufficient direct biological data, these studies used a physical, mechanistic approach based on the assumption that animals occupied hollows on the basis of size alone. It was recognised by the authors of these studies and by others (e.g. Wardell-Johnson *et al.* 2004) that there is a need for more detailed ecological studies that directly examine habitat selection by various species. Such studies would also verify the results of these general models based on indirect approaches.

The present study addresses this need by directly investigating the selection of diurnal refuges (dens) by koomal and ngwayir within the jarrah forest at Chariup (part of Perup Nature Reserve), Western Australia (i.e. at the home range spatial scale, Johnson's [1980] third order of selection). In conjunction with an understanding of the life histories of these animals (Wayne *et al.* 2005c, 2005d [Chapters 4 and 5]) and factors that relate to their distribution and abundance at local and landscape scales (Wayne *et al.* 2005e [Chapter 7], in preparation-b), an understanding of their finer-scale habitat selection can be used to evaluate better their responses to management and environmental change (e.g. McComb 1994). We asked four specific questions: (1) What types of habitat are occupied as day refuges? (2) Are all refuge sites occupied with the same frequency? (3) To what extent do individuals simultaneously 'share' or 'co-use' day refuges, and are there sex-related or temporal patterns to sharing and co-use? (4) Which morphological characteristics of the day refuges affect their probability of use? The implications of this research for conservation, especially in forests available for logging, are discussed.

6.3 Methods

6.3.1 Study area

The study area was in the Chariup forest block, part of Perup Nature Reserve, 270 km south-south-east of Perth, and 40 km east of Manjimup, in south-western Australia (116^{o} 37'E, 34^{o} 16'S). Perup comprises 52,000 hectares of dry sclerophyll forest dominated by jarrah and marri (*Corymbia calophylla*), which has been managed as a Nature Reserve since 1971 (CALM 1998). The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters and a local long-term average annual rainfall of around 700 mm. The topography is characterised by gently undulating plateaux tops, low lateritic ridges and broad valleys, 220-280 m above sea level.

6.3.2 Possum Capture

The study site was a 500 m x 500 m grid with trap and reference points spaced 50 m apart. Individuals for radio-telemetry were captured from within the core of the study grid in an attempt to collar all adult individuals within this area. Based on intensive and extensive trapping and capture efforts at the study site (Wayne *et al.* 2005c, 2005d [Chapters 4 and 5]), we are confident that all resident adult koomal within the core of the study area were radio-collared. Given the difficulty of catching ngwayir, we estimate that at least 80% of the adult individuals were collared in the core of the study area (based on all available trapping and spotlight data available for this period, Wayne *et al.* 2005c, 2005d [Chapters 4 and 5]; A. Wayne unpublished data). Cohort sample sizes of radio-collared animals aimed to satisfy the recommendations of Aebischer *et al.* (1993), particularly, that more than 10 individuals per category are required and that at least 10 (and preferably more than 30 animals) are needed to represent a population adequately. Twenty-nine koomal (14 male, 15 female) and 43 ngwayir (22 female and 21 male) were radio-collared in this study.

Given the difficulty of trapping ngwayir (Wayne *et al.* 2005b [Chapter 3]), handcaptures (Wayne *et al.* 2005d [Chapter 5]) were used to supplement the individuals that were trapped. Mortality-sensitive radio-collars (Biotrack, U.K.) were used with either 6-month or 12-month batteries (i.e. 17-25 g), constituting less than 3% of an animal's body weight. When radio-collared possums were found dead, alternative possums for radio-collaring were sought.

6.3.3 Radio-telemetry

Koomal and ngwayir were radio-tracked every fourth week for five consecutive days over a period of 18 months between June 2002 and November 2003. During each session, the daytime location of each individual was recorded once each day. Animal locations were directly pin-pointed to avoid triangulation error (e.g. White and Garrot 1986; Nams 1989). The possums at the study site were not trapped or spotlighted for at least two weeks prior to the week of radio-tracking to avoid any potential influence on habitat use.

6.3.4 Diurnal refuge habitat

Diurnal refuges were assigned to one of seven types: (1) 'Standing Tree' – hollow-bearing tree; (2) Hollow Log – fallen trees, either natural or created by previous logging; (3) 'Balga' – *Xanthorrhoea preissii* grass tree (mid-storey species), in which animals seek refuge within the thick skirt or thatch created by dead leaves; (4) 'Above Ground Nest' – any non-hollow, non-balga position off the ground including dreys (nests) constructed by ngwayir; (5) 'Forest Debris' – refuge site within vegetative debris on the forest floor; (6) 'Burrow' – created by other animals (e.g. rabbit, *Oryctolagus cuniculus*) or root cavity created by fallen trees or fire; and (7) ‘Hollow Stump’ – tree stump (natural or created from logging).

For conservation management purposes it was not necessary to identify the attributes of specific hollows or nesting sites. Rather, it was more useful to identify the attributes of the trees or logs, etc, that host these refuge sites, given that it is more practical to manage important habitats at the scale of trees or logs. Hence, depending on the refuge type, up to 11 microhabitat attributes were recorded for each refuge. The attributes measured for standing trees and hollow logs are summarised in Table 6.1. Tree height and height to lowest hollows were measured using a clinometer; diameter at breast height over bark (DBHob) was measured using a diameter tape; the Whitford (2002) senescence and decay (dead branch order) scales were used to characterise crown condition; the number of visible hollows from the ground was a count of all cavities greater than 5 cm in diameter and potentially deeper than 10 cm; possum signs were scored on a scale zero to five to describe the amount of bark wear (‘tracks’) on the tree bole indicating the level of possum ‘traffic’; the amount of tree lean was measured using a protractor and plumb line; canopy connectivity was a count of the number of contacts and near contacts (< 2 m) by which a possum could potentially access the subject tree above ground. The probability that the tree contained potentially suitable hollows for koomal and ngwayir was calculated using the predictive models of Whitford and Williams (2002). For hollow logs, the origin was categorised as either natural or cut (i.e. logging residue). Log diameter was measured at the larger end, and hollow diameters were measured horizontally and vertically (i.e. x and y hollow diameters, respectively).

The location of each refuge was recorded using a GPS (< 10 m accuracy) and ‘tied-in’ to the closest of the 50 m x 50 m grid reference points (GPS accuracy < 1m) using a compass and distance to the nearest metre. Meso-habitat data (vegetation floristics and structure within 20 m radius) recorded for each refuge included the dominant species, maximum height and estimated percentage cover for the upper, middle and lower storeys (i.e. vegetation strata). Canopy cover also was measured using a convex spherical densiometer (Lemmon 1956) and the basal area for each tree species was measured using a basal area optical prism or ‘wedge’.

Table 6.1. Day refuge habitat attribute variables measured for standing trees and hollow logs occupied by possums in jarrah forest at Chariup.

See text for an explanation of these variables.

STANDING TREE	RANGE	TYPE	HOLLOW LOG	RANGE	TYPE
Tree Species	3 Species	Categorical	Species	2 Species	Categorical
Dead/Alive	2 Categories	Categorical	Origin	2 Categories	Categorical
Tree Lean (degrees)	0-44	Continuous	Length (m)	2.5-15	Continuous
Height (m)	4-36	Continuous	Log Diameter (cm)	25-130	Continuous
DBHob (cm)	25-143	Continuous	Hollow Diameter X (cm)	6-80	Continuous
Senescence Scale	0-10	Ordinal	Hollow Diameter Y (cm)	7-50	Continuous
Decay Scale	0-10	Ordinal	No. of Entrances	1 or 2	Categorical
Hollows Visible	0-12	Continuous			
Ht. to lowest hollow (m)	0-24	Continuous			
Possum Signs	0-5	Ordinal			
Canopy Connectivity	0-8	Continuous			

6.3.5 Quantifying available habitat

Habitat data were collected using 121 plots at the trap and reference points spaced 50 m apart in grid formation within the study area. Within each circular plot (0.04ha), the same micro- and meso-habitat data recorded for diurnal refuges were collected for all trees (> 15 cm DBHob), balga (> 1 m tall), logs (> 20cm diameter) and stumps (> 20cm diameter) located within these plots.

6.3.6 Data Analysis

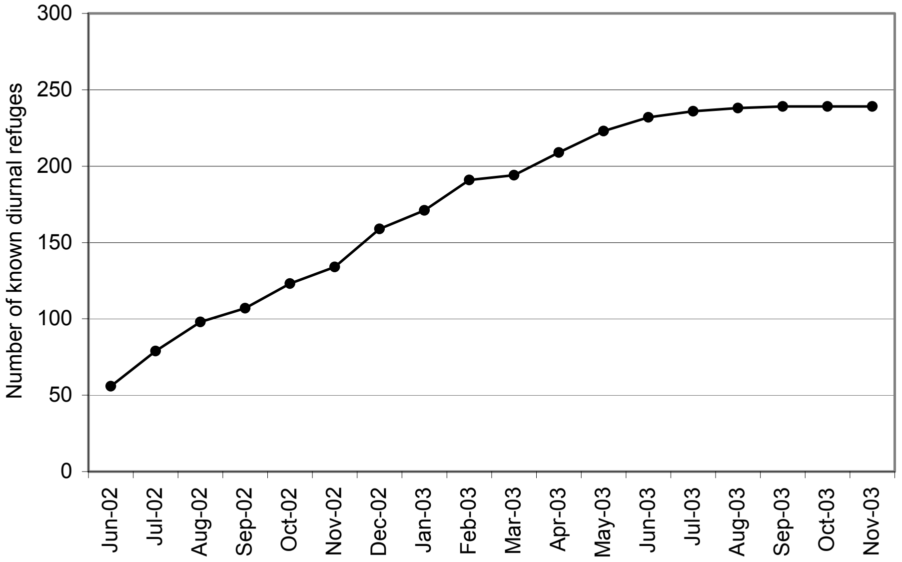
6.3.6.1 Modelling habitat selection

Considerable variation exists in the methods used to examine habitat selection (e.g. Thomas and Taylor 1990; Cooper and Millspaugh 1999). Given the complexity and array of methods, particular care is required to determine the most appropriate approach to avoid drawing incorrect conclusions. Common problems in habitat selection studies include inadequately addressing model assumptions (e.g. Schooley 1994; Bos and Carthew 2003) and insufficient recognition of the limitations of the methods used (e.g. White and Garrot 1986; Porter and Church 1987; Nams 1989; Aebischer *et al.* 1993). Several techniques have been reviewed (Thomas and Taylor 1990; Alldredge and Ratti 1986, 1992; Alldredge *et al.* 1998; Alldredge and Dasgupta 2003) and solutions for many technical issues have been suggested (e.g. Porter and Church 1987; Wilson *et al.* 1998; Dunning *et al.* 1992; Hjermann 2000).

Having considered these issues, we used logistic regression to develop models that described which factors affected the probability of use of a given tree. Standard logistic regression requires that a random sample of all trees be taken; it is then determined whether the tree is occupied (i.e. positive) or unoccupied (i.e. negative). A different sampling approach was used in this study; the 'positives' were sampled by tracking radio-collared possums and the 'negatives' were a sample of trees from the population (i.e. using 'available habitat' plots). Two approaches are commonly used for dealing with these differences in sampling method. The first is to estimate the parameters in the standard fashion, in which case the intercept term is not identified, and then interpret the results in terms of odds ratios. The second approach is to adjust the intercept term, which requires knowledge of the sampling rates for both the 'positives' and the 'negatives' (see Keating and Cherry 2004). These sampling rates can be estimated as follows:

Let n_1 and n_0 be the number of 'positives' and 'negatives' respectively, let a_0 and A_0 be the areas of the sample from the population and the area of the study site respectively, let N_1 and N_0 be the total number of 'positives' and the total number of trees in the study site, let n_{01} be the number of 'positives' that occurred in the sample from the population. We can estimate P_1 / P_0 as required (Keating and Cherry 2004) with $P_1/P_0 = (n_1/N_1)/(n_0/N_0) \approx n_1/n_{01}$. It is implicit in this calculation that most of the trees in which possums ever reside have been sampled. This was assumed to be valid, given that the accumulation of previously unrecorded diurnal refuges reached an asymptote after 12 months of data collection (Figure 6.1).

Figure 6.1. The cumulation of different diurnal refuges observed being used by koomal and ngwayir by radio-tracking over the duration of the study at Chariup.



6.3.6.2 Logistic regression considerations and model development

Since the sample of 'negative' trees from the available population may include occupied trees (i.e. 'positives'), there is also the issue of 'contamination'. This is addressed by Lancaster and Imbens (1996), who give an algorithm that can deal with this issue. However, they note that this algorithm seems to become unstable when contamination is < 20%. From the number of known 'positives' in the sample of the population, and noting that conservatively at least 80% of the possums in the region were tracked, we estimated the rate of contamination to be around 2.2%. Since this rate is low, we chose to leave the contaminants in the sample of 'negatives' so as not to introduce any bias due to non-uniform sampling effort across the study site.

Due to limitations in the number of radio collars available, more effort was spent capturing and collaring possums near the centre of the study area. No account was taken of this in the modelling, where it is hence implicitly assumed that the forest is uniform enough for the effect of this to be negligible.

Each observation of a possum in a tree was used in the modelling: hence the probabilities from the models should be interpreted as 'the probability that a given tree contains a possum on a given day'. This modelling approach was used because it was considered the most relevant for applied conservation and management.

Models were manually selected by starting with overparameterised models and then deleting variables until only those that were highly significant ($p < 0.001$) were left. This level of significance was used because the data were expected to include some pseudoreplications derived from multiple observations per animal (Hurlbert 1984). This model development approach resulted in several equally plausible models. For demonstrative purposes, it was necessary to select a 'best model'. The selection criteria for this process were based on cross-validation values, biological plausibility and the AIC (Akaike's Information Criterion) (these three criteria generally ranked models similarly). As a result, two general types of model were developed for each species: (1) those containing only micro-habitat variables (i.e. characteristics of the tree only); and (2) those containing both micro- and meso-habitat variables (e.g. including habitat context within a radius of 20 m).

6.3.6.3 Logistic plots

For the development of the logistic plots of the highly significant parameters in the micro-habitat models, we used the mean values of all parameters for trees greater than 70 cm DBHob and the most common level of the factor 'Species' (i.e. jarrah). These arbitrary values were selected for demonstrative purposes and were used for two main reasons: (1) tree diameter was found to be the best-fitting single variable to predict the probability of use by a possum (see Results below); and (2) the selection criteria for primary 'habitat trees' in the current silvicultural guidelines specify for trees greater than 70 cm DBHob (CALM 1995).

Interpretation of these plots should be considered in this context and as being indicative only.

6.3.6.4 Alternative models for comparison

Poisson regression modelling was used to examine whether the characteristics of occupied trees related to the extent of use. The diagnostic analyses for these models indicated that there were violations of the model assumptions, particularly in the case of the most frequently occupied trees, which could not be explained by the attribute data available. It was, therefore, not appropriate to develop these models any further without more information on other factors that might affect the extent of tree use, such as behaviour and social interactions between possums, which are also thought to influence habitat selection.

Logistic regression models based on the number of different possums that occupied each tree also were developed for comparative purposes. These models were not used as the primary approach because the interpretation of the resulting probabilities was not considered as relevant to conservation and management. Potential issues of pseudoreplication are not so great in these models, which can thus be used to assess to what extent the models developed on all of the available data may be influenced by pseudoreplication. A comparison of the models using these different data indicated that they were generally similar, and that potential problems with pseudoreplication do not seem to affect the ability to choose the best models. However, pseudoreplication will still affect the statistical properties of the models and hence the confidence regions shown here may be narrower than they would be without pseudoreplication. These factors should be considered when interpreting the plots presented below.

6.4 Results

6.4.1 The possums

During 109 days of radio-tracking between May 2002 and November 2003, 3338 day fixes were recorded (1768 and 1570 records for the 29 koomal and 43 ngwayir respectively). Diurnal refuge use was recorded on up to 92 occasions for each radio-collared koomal, resulting in the recorded use of up to 14 and 23 different refuges each for females and males respectively (Table 6.2, Table 6.3a). With up to 96 observations per individual, female ngwayir were observed using up to 12 different refuges. Male ngwayir were found occupying up to 16 different refuges each from up to 67 observations per animal (Table 6.2, Table 6.3b).

The number of different refuges occupied by an individual was a function of the number of observations (i.e. as observations increased, the number of different refuges occupied increased; Figure 6.2) for all except one female koomal. The female koomal concerned did not accumulate any more than the three refuges occupied in the first 30 out of 91 observations. For koomal, the relationship between the logarithmic transformations of the number of observations and the number of different refuges occupied by an individual was highly significant ($F_{1,\ 27} = 44.7$, $p < 0.001$; Figure 6.3a), and when sex was added to the model, it was marginal but statistically insignificant ($F_{1,\ 26} = 3.9$, $p = 0.0589$). For ngwayir, the relationship between the number of observations and the number of different refuges occupied by an individual was highly significant ($F_{1,\ 39} = 70.5$, $p < 0.001$) and differed significantly according to sex ($F_{1,\ 39} = 10.9$, $p = 0.029$; Figure 6.3b).

Table 6.2. The mean number (and standard deviation) of day refuges and observations recorded for each radio-collared koomal and ngwayir in the jarrah forest at Chariup.

	KOOMAL		**NGWAYIR**	
	FEMALE	**MALE**	**FEMALE**	**MALE**
Number of Individuals (n)	15	14	22	21
Number of Refuges	7.3 (4.7)	10.8 (5.6)	5.4 (3.3)	6.1 (4.2)
Number of Observations	58.3 (37.2)	64.1 (29.7)	43.4 (30.2)	29.6 (22.2)

Table 6.3a. The number of observations and the number of different refuges occupied by koomal at Chariup; classified by refuge type.

BU = Burrow, HL = Hollow log, HS = Hollow stump, ST = Standing tree (hollow-bearing).
* Female koomal ID 11 was also found resting on the ground, usually at the base of two ST, on six occasions before being predated within two weeks.
# Male koomal ID 109 also found active on the ground during the day on one occasion.

		NO. OBSERVATIONS					**NO. REFUGES**				
Sex	ID	BU	HL	HS	ST	**Tot**	BU	HL	HS	ST	**Tot**
F	5				91	**91**				10	**10**
F	9				92	**92**				14	**14**
F	11				1*	**1**				1	**1**
F	13				13	**13**				1	**1**
F	14				89	**89**				7	**7**
F	15				91	**91**				3	**3**
F	22				92	**92**				12	**12**
F	24				34	**34**				4	**4**
F	25				49	**49**				5	**5**
F	33		1		85	**86**		1		12	**13**
F	34				1	**1**				1	**1**
F	35	1	1		89	**91**	1	1		9	**12**
F	39				92	**92**				13	**13**
F	81				23	**23**				4	**4**
F	83				24	**24**				7	**7**
M	2		1		60	**61**		1		16	**17**
M	6		14		70	**84**		5		18	**23**
M	7		2		87	**89**		1		11	**12**
M	8		2		64	**66**		2		12	**14**
M	10				92	**92**				10	**10**
M	12				92	**92**				6	**6**
M	16				81	**81**				9	**9**
M	18		4		86	**90**		1		17	**18**
M	26				87	**87**				11	**11**
M	31				68	**68**				8	**8**
M	32				10	**10**				3	**3**
M	59			1	20	**21**			1	4	**5**
M	109				24#	**24**				7	**7**
M	148				33	**33**				8	**8**
Percent (%)		0.1	1.4	0.1	98.5		0.4	4.6	0.4	94.2	

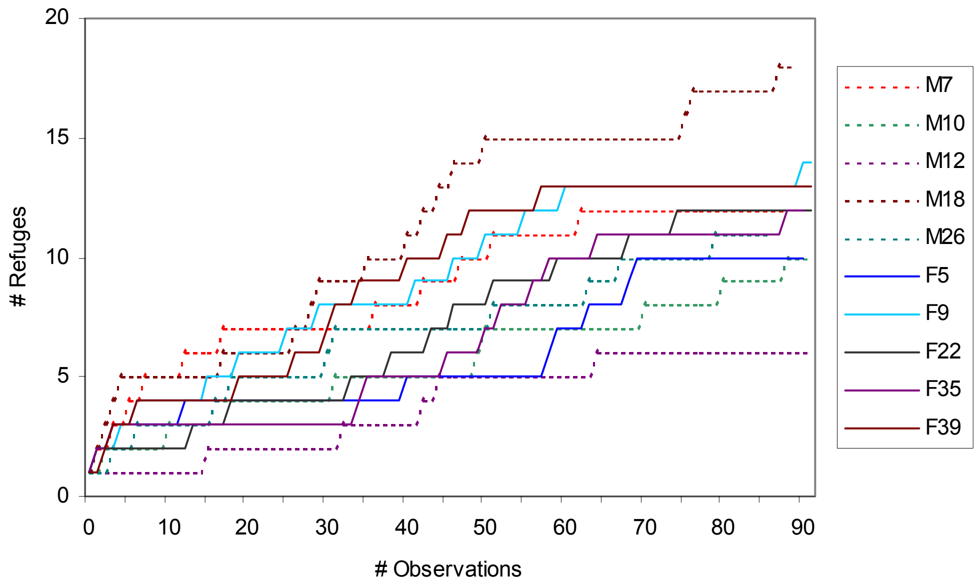
Table 6.3b. The number of observations and the number of different refuges occupied by ngwayir at Chariup; classified by refuge type.

AG = Above-ground nest (drey), BB = Balga, BU = Burrow, FD = Forest Debris, HL = Hollow log, ST = Standing tree (hollow-bearing).

		NO. OBSERVATIONS							**NO. REFUGES**						
Sex	ID	AG	BB	BU	FD	HL	ST	**Tot**	AG	BB	BU	FD	HL	ST	**Tot**
F	17					6	82	**88**					2	9	**11**
F	19	8		1		8	51	**68**	1		1		3	4	**9**
F	20						91	**91**						8	**8**
F	28						25	**25**						4	**4**
F	36						66	**66**						3	**3**
F	38						70	**70**						7	**7**
F	43						96	**96**						12	**12**
F	46						83	**83**						9	**9**
F	47						16	**16**						2	**2**
F	49						76	**76**						10	**10**
F	51						21	**21**						2	**2**
F	52						16	**16**						2	**2**
F	56						19	**19**						5	**5**
F	58						12	**12**						2	**2**
F	90						55	**55**						6	**6**
F	91						31	**31**						2	**2**
F	93					3	13	**16**					1	3	**4**
F	116						10	**10**						2	**2**
F	130						20	**20**						2	**2**
F	141						25	**25**						7	**7**
F	157				4		22	**26**				1		3	**4**
F	159					1	23	**24**					1	4	**5**
M	21						1	**1**						1	**1**
M	29			1	3	1	62	**67**			1	1	1	8	**11**
M	40						37	**37**						3	**3**
M	42						1	**1**						1	**1**
M	44						67	**67**						8	**8**
M	45						64	**64**						11	**11**
M	48						10	**10**						3	**3**
M	53		2				9	**11**		1				5	**6**
M	54		4		1	3	51	**59**		1		1	1	11	**14**
M	55						16	**16**						5	**5**
M	57					3	60	**63**					1	15	**16**
M	82			3		1	27	**31**			1		1	6	**8**
M	94				2		33	**35**				1		6	**7**
M	121						10	**10**						3	**3**
M	122					1	12	**13**					1	3	**4**
M	129					4	21	**25**					2	6	**8**
M	132						24	**24**						6	**6**
M	145						34	**34**						2	**2**
M	146		1				10	**11**		1				2	**3**
M	147						20	**20**						5	**5**
M	156						22	**22**						2	**2**
Percent (%)		0.5	0.4	0.3	0.6	2.0	96.1		0.4	1.2	1.2	1.6	5.7	89.8	

Figure 6.2. The cumulation of the number of different day refuges used by individuals in relation to the number of observations for a subset of male and female (a) koomal and (b) ngwayir at Chariup.

a) Koomal



b) Ngwayir

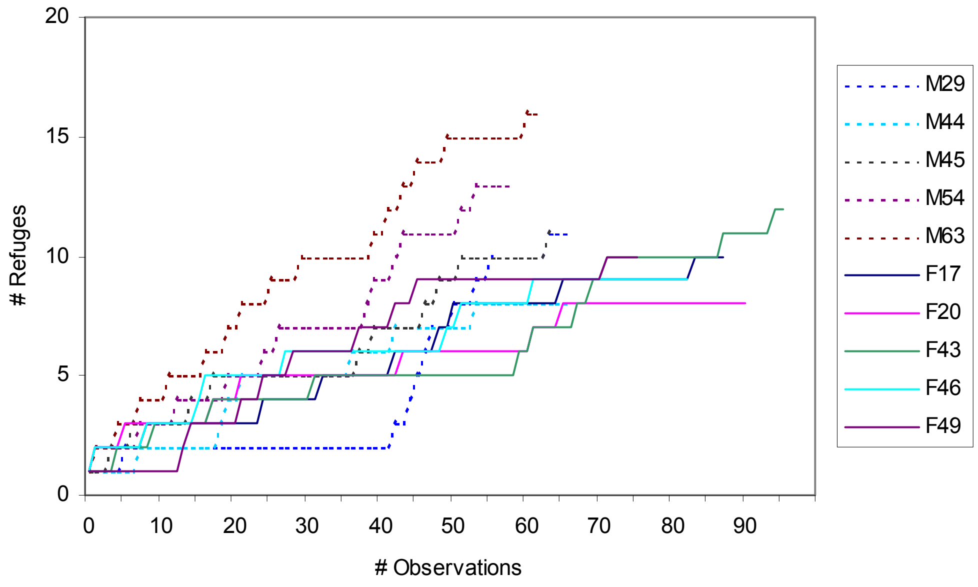
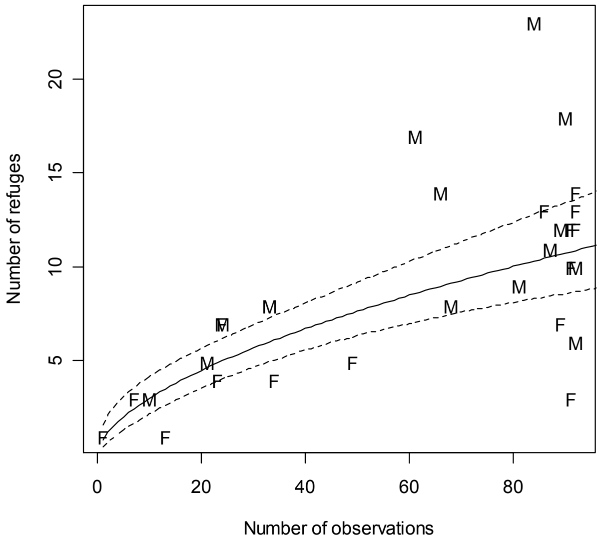


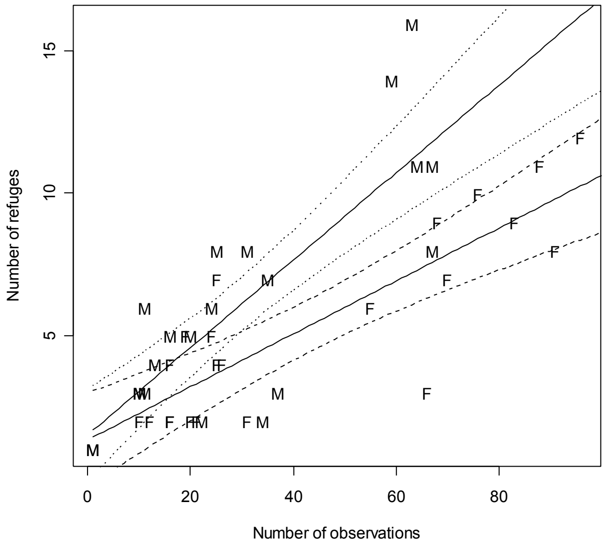
Figure 6.3. The relationship between the number of observations and the number of different refuges occupied by individual (a) koomal and (b) ngwayir at Chariup.

Note: M = male, F = female; Solid line = predicted relationship based on a linear regression model, Dashed lines = 95% confidence intervals for the predicted relationship.

a) Koomal



b) Ngwayir



6.4.2 Types of refuge occupied

Of the 238 different diurnal refuges recorded, 204 were in standing (hollow-bearing) trees, 21 in hollow logs, four in forest debris, four in burrows, three in balga, one in a hollow stump and one was a drey. Sixty-two refuges were occupied by both koomal and ngwayir (26%), 61 of which were hollow-bearing trees and one was a hollow log. The remaining 175 refuges were occupied by one species only.

Of the 147 refuges visited by koomal, 134 were standing trees, 10 were hollow logs, one was a burrow and one a hollow stump. Of the 154 refuges visited by ngwayir, there were 131 standing trees, 12 were hollow logs, four were in forest debris, three were in balga, three were in burrows and one was a drey.

For both koomal and ngwayir, 55% of occupancies were recorded in the 62 co-used refuges. These refuges also were visited by more individuals of each species (mean = 2.1 koomal and 1.9 ngwayir individuals) than those occupied by only one of the species (mean = 1.5 and 1.4 individuals, respectively).

On average, 94.2% of the refuges used by individual koomal and 98.5% of the total koomal occupancy records were within hollow-bearing trees. Hollow logs accounted for 4.6% of the refuges occupied by koomal and 1.4% of the occupancy records. Burrows and hollow stumps each constituted 0.4% of the refuges occupied by koomal and 0.1% of the total koomal occupancy records (Table 6.3a). One radio-collared individual (female ID 11) was found on six occasions resting on the ground, relatively exposed (usually in one of two hollow-butts at the base of hollow-bearing refuge trees). This animal was in poor condition and within two weeks was predated. On one occasion a male koomal (ID 109) was found active and travelling on the ground in the middle of the day.

On average, 90% of the refuges used by individual ngwayir and 96% of the total ngwayir occupancy records were in hollow-bearing trees. Hollow logs accounted for 6% of the refuges occupied by ngwayir and 2% of the total ngwayir occupancy records. Forest debris, balga, burrows and a drey were rarely occupied (Table 6.3b).

6.4.3 Frequency of visits to different refuges

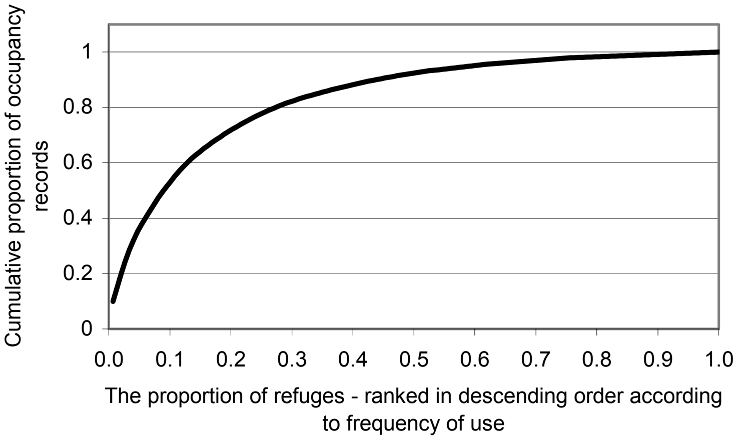
Most refuges were visited infrequently, only a few refuges being visited frequently (i.e. a few refuges were occupied disproportionately more often than others; Figure 6.4). For instance, the 40 most frequently-used refuges (i.e. 27% of total refuges) were occupied by koomal 80% of the time, and the 70 least-used refuges (i.e. 47% of total refuges, each visited on no more than 3 occasions) were collectively occupied by koomal 7% of the time. For a comparable example for ngwayir, the 53 most frequently-used refuges (i.e. 34% of total refuges) were occupied by ngwayir 80% of the time and the 65 least-used refuges (i.e. 42%

of total refuges, each visited on no more than 3 occasions) were collectively occupied by ngwayir 7% of the time. There were no sex differences for either species in the proportion or number of refuges that were occupied once by individuals.

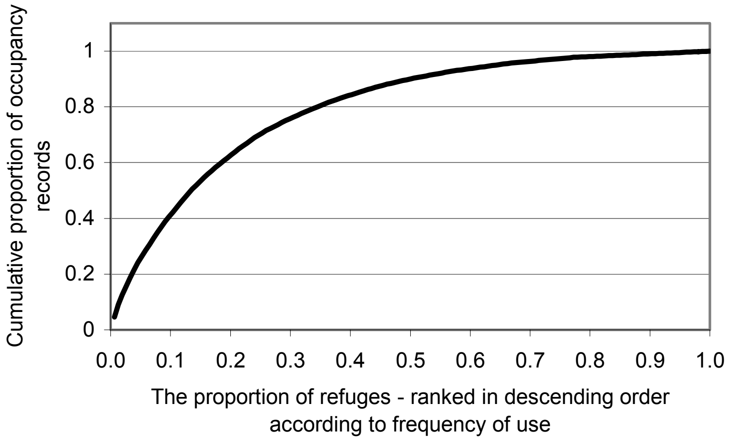
Figure 6.4. Relationships between refuges and their extent of use by (a) koomal and (b) ngwayir at Chariup.

Note: Refuges are ranked from the most frequently used to the least used, so that as the proportion of refuges increases the number of occupancy records per extra refuge diminishes (i.e. the most frequently used refuges were collectively occupied most of the time).

a) Koomal



b) Ngwayir



6.4.4 Refuge sharing and co-use

Sharing is defined as the simultaneous use of a specific refuge by more than one radio-collared possum. Co-use of the same refuge is temporally discrete (i.e. not simultaneous) (Lindenmayer *et al.* 2004).

Results for sharing and co-use are underestimates and conservative approximations for actual occurrence. Not all possums in the area were radio-tracked and those that were radio-tracked were not tracked every day. Furthermore, radio-collared animals on the periphery of the study area may have co-used or shared refuges with other uncollared possums. Similarly, co-use and sharing with sub-adults was not recorded because only adult possums were collared.

6.4.4.1 Co-use

Most refuges were occupied by only one individual (60% and 62% of the refuges occupied by koomal and ngwayir, respectively); a few refuges were co-used by multiple adults (Figure 6.5). Refuges hosted up to five different adults of the same species for both koomal and ngwayir (Figure 6.5) and up to nine different possums, irrespective of species. Those refuges that were occupied by more individuals also were visited more frequently ($F_{1,\ 146} = 134.9$, $p < 0.0001$ and $F_{1,\ 152} = 118.6$, $p < 0.0001$ for koomal and ngwayir respectively, both modelled with log-transformed x and y data; Figure 6.6).

Of the 147 refuges occupied by koomal, males occupied 111, females occupied 86, and both sexes co-used 50 of these (i.e. 45% of male refuges and 58% of female refuges were co-used with at least one other conspecific of the opposite sex). Of the 154 refuges occupied by ngwayir, males occupied 113, females occupied 91, and both sexes co-used 50 of these (i.e. 44% of male refuges and 55% of female refuges were co-used with at least one other conspecific of the opposite sex).

Figure 6.5. The proportion of refuges visited by one or multiple conspecific individuals of koomal (148 refuges) and ngwayir (154 refuges) at Chariup.

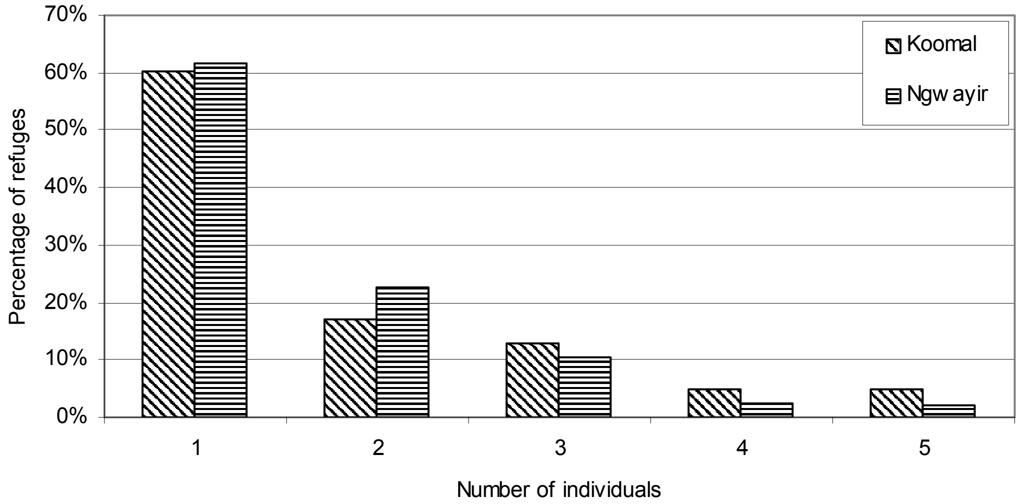
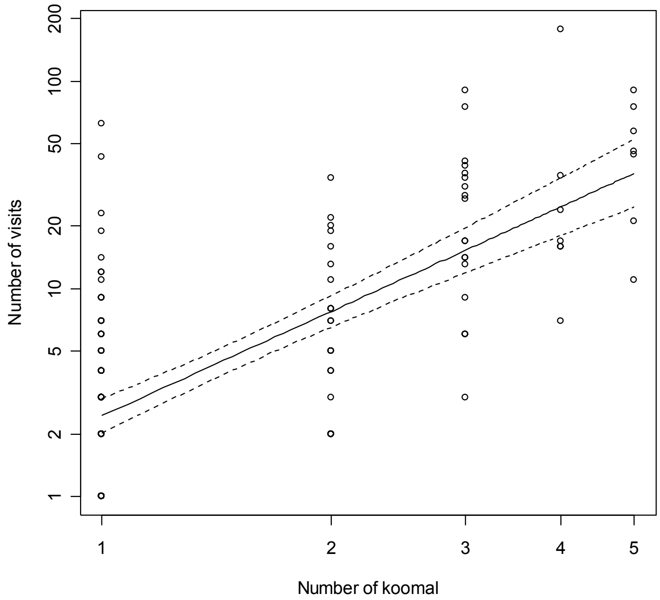


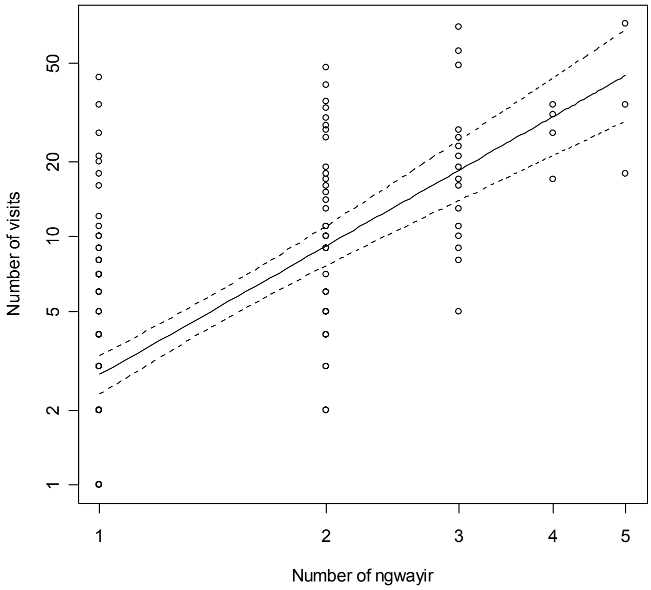
Figure 6.6. The relationship between the number of visits and the number of individuals using each refuge for (a) koomal and (b) ngwayir at Chariup.

Note: Solid line = predicted relationship based on a linear regression model, Dashed lines = 95% confidence intervals for the predicted relationship.

a) Koomal



b) Ngwayir



6.4.4.2 Sharing

Koomal shared with one other radio-collared koomal on 8.4% of recorded occasions of refuge use and with two other radio-collared koomal on 2.2% of occasions. When two individuals shared the same refuge, 90% of cases were accounted for by male and female pairs, 8% were by female pairs and 2% by male pairs (Table 6.4). Of the 34 occasions when three animals shared the same refuge in all but one case, the trio was comprised of two females and one male; two males and one female were observed sharing the same refuge once. A total of 12 females and nine males were observed sharing. Most of these individuals (13) shared with 2-5 others over the course of the study (mean = 2.2 individuals, SD = 1.0 and 2.8 individuals, SD = 1.8 for females and males, respectively). Of the 12 females, seven shared with at least one male and eight shared with at least one other female. Of the nine males, eight shared with at least one female and six shared with another male (Table 6.4). Sharing between male and female pairs occurred throughout the year, concurrent sharing by three koomal, however, only occurred between June and September (Figure 6.7a).

Radio-collared ngwayir were observed sharing with other radio-collared ngwayir on only 2% of occasions. Of the 34 instances of sharing, 79% were between male and female pairs, 18% between two females, and on one occasion (3%) between two males (Table 6.4). On no occasion were more than two ngwayir observed simultaneously sharing a refuge. Twelve females and 11 males were observed sharing. Most individuals shared with only one other, but two individuals shared at different times with two other ngwayir. Three individuals shared at different times with three other ngwayir. For those that did share, the mean number of individuals with which a ngwayir shared was 1.4 (SD = 0.8) and 1.3 (SD = 0.6), for females and males respectively. Of the 12 females, 10 shared with at least one male and five shared with at least one other female (Table 6.4). Of the 11 males, 10 shared with at least one female and 2 shared with another male. Sharing between male and female pairs occurred predominantly in summer (67%) and autumn (15%) (Figure 6.7b).

Twenty-two refuges, all of which were hollow-bearing trees, hosted concurrent sharing by koomal and ngwayir individuals on 114 occasions (3% of observations). Sharing by one individual of each species occurred on 73% of these occasions, by two koomal and one ngwayir on 26% of occasions, and by four individuals (one of each sex for both species) on one occasion (i.e. 1%).

Table 6.4a. Summary of refuge sharing by koomal at Chariup.

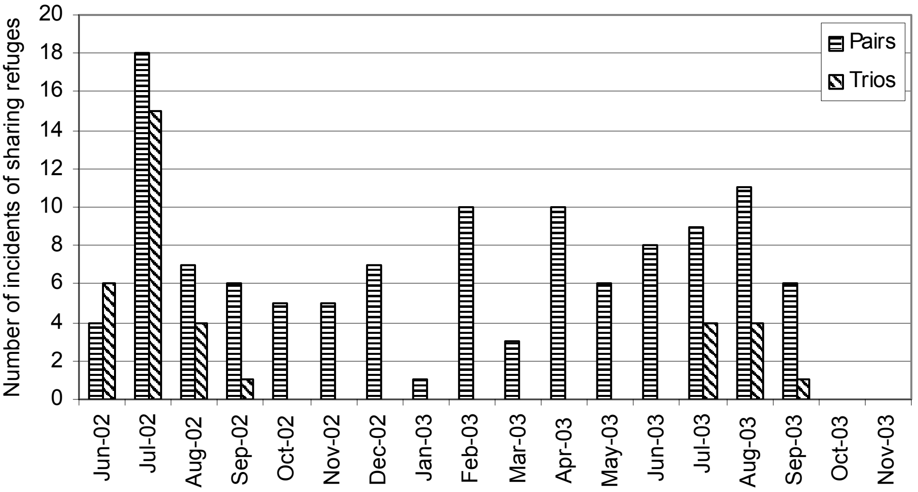
NO. SHARING	FEMALE 1 (ID)	FEMALE 2 (ID)	MALE 1 (ID)	MALE 2 (ID)	REFUGE NUMBER	NO. SHARING OCCASIONS
Pair	5		6		R048, R052	3
Pair	9		8		R015, R029, R033	7
Pair	9		18		R015, R029	3
Pair	13		12		R036	1
Pair	14		18		R021	8
Pair	15		12		R036	58
Pair	22		8		R033	1
Pair	22		18		R030, R033	3
Pair	24		26		R034	8
Pair	33		7		R013	3
Pair	33		26		R019	1
Pair	35		12		R037	1
Pair	39		2		R129	3
Pair	39		26		R019	6
Pair	81		109		R006	9
Pair	9	22			R033	3
Pair	24	25			R050	3
Pair	33	39			R019. R035, R084	4
Pair			8	18	R103	1
Pair			26	148	R035	1
Trio	9	22	18		R033	1
Trio	9	22	2		R033	1
Trio	9	22	8		R033	8
Trio	13	15	12		R036	12
Trio	24	25	26		R050	3
Trio	33	39	26		R019	8
Trio	15		2	12	R036	1

Table 6.4b. Summary of refuge sharing by ngwayir at Chariup.

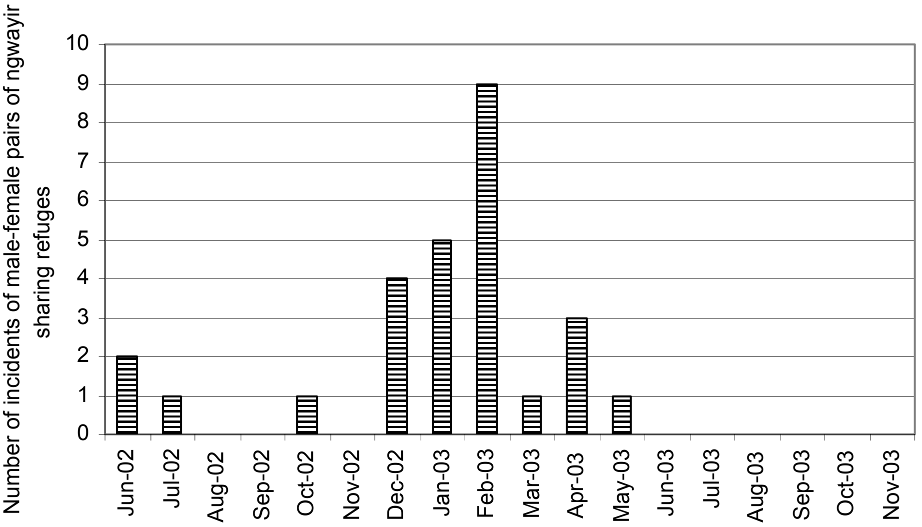
FEMALE 1 (ID)	FEMALE 2 (ID)	MALE 1 (ID)	MALE 2 (ID)	REFUGE NUMBER	NO. SHARING OCCASIONS
17		45		R003	2
19		94		R001	10
28		21		R009	1
36		45		R015	1
38		129		R013	1
43		45		R029	1
43		147		R036, R060	2
49		122		R063, R106	3
51		55		R081	1
90		82		R126	2
93		29		R062	1
141		44		R076	2
36	38			R015	1
36	43			R015, R029	4
51	56			R081	1
		29	57	R010	1

Figure 6.7. The incidence of refuge sharing by (a) koomal and (b) ngwayir at Chariup.

a) Koomal



b) Ngwayir



6.4.5 Comparisons between the attributes of available and occupied habitats

Habitats were characterised from measurements of structural, floristic and other attributes on 121 plots (0.04 ha each). As a result, attribute data comparable to that collected for day refuges was recorded for 1123 trees, 157 logs and 15 balga.

6.4.5.1 Standing Trees

Table 6.5 summarises some of the key physical attributes of the available tree habitats compared with trees occupied as diurnal refuges by koomal and ngwayir. Jarrah constituted 56%, marri 41% and wandoo (*Eucalyptus wandoo*) 3% of the trees available at the Chariup study site. Koomal occupied significantly fewer jarrah (40%), more marri (52%) and more wandoo (8%) than were proportionally available ($X^2_2 = 14.1$, $p < 0.001$). Ngwayir occupied jarrah (55%) and marri (39%) approximately in proportion to availability, but tended to use slightly (but insignificantly) more wandoo (6%) in proportion to availability. The tendency to use a larger number of dead trees than were proportionately available was highly significant ($X^2_1 = 21.2$, $p < 0.001$) for koomal and marginally so for ngwayir ($X^2_1 = 3.5$, $p = 0.0598$). In proportion to availability, the trees occupied by both possum species were on average taller, had a larger diameter, greater canopy connectivity (except wandoo), more advanced stage of crown senescence and decay, more visible and predicted hollows (using the models by Whitford and Williams, 2002) and higher possum sign values (Table 6.5). The diameters of occupied trees were 25-143 cm.

Table 6.5. Summary of tree attributes from a sample of available habitat compared with trees occupied by koomal and ngwayir at Chariup.

Note: Figures in parentheses are not averages but counts or percentages as indicated.

	AVAILABLE		KOOMAL		NGWAYIR	
	Ave	SD	**Ave**	SD	**Ave**	SD
JARRAH						
Sample size (n)	**(624)**		**(54)**		**(72)**	
Proportion dead (%)	**(5.3)**		**(14.8)**		**(9.7)**	
Height, m	**16.8**	5.1	**21.8**	3.4	**21.9**	4.1
DBHob, cm	**39.1**	19.4	**77.9**	19.6	**76.4**	22.7
Canopy connectivity	**1.6**	1.2	**2.0**	1.6	**2.2**	1.5
Senescence scale	**3.2**	1.9	**5.5**	2.0	**5.0**	2.0
Decay scale	**3.3**	1.6	**4.9**	1.3	**4.8**	1.4
No. Hollows visible	**0.3**	0.9	**3.1**	1.5	**3.4**	2.2
Predicted ngwayir hollows	**0.1**	0.1	**0.2**	0.2	**0.3**	0.9
Predicted koomal hollows	**0.0**	0.0	**0.1**	0.1	**0.1**	0.2
Possum signs	**1.3**	1.2	**3.1**	1.6	**2.5**	1.7
MARRI						
Sample size (n)	**(458)**		**(70)**		**(51)**	
Proportion dead (%)	**(2.8)**		**(11.4)**		**(3.9)**	
Height, m	**13.7**	5.3	**20.5**	5.8	**21.0**	5.6
DBHob, cm	**32.8**	19.5	**81.3**	20.3	**86.0**	20.5
Canopy connectivity	**1.9**	1.2	**2.3**	1.6	**2.4**	1.5
Senescence scale	**2.4**	1.7	**5.5**	2.0	**5.1**	2.1
Decay scale	**2.6**	1.7	**5.3**	1.6	**5.0**	1.7
No. Hollows visible	**0.2**	0.6	**2.2**	1.2	**2.0**	1.2
Predicted ngwayir hollows	**0.1**	0.2	**0.6**	0.3	**0.6**	0.4
Predicted koomal hollows	**0.1**	0.1	**0.3**	0.3	**0.3**	0.3
Possum signs	**1.3**	1.0	**2.8**	1.2	**2.4**	1.4
WANDOO						
Sample size (n)	**(38)**		**(10)**		**(8)**	
Proportion dead (%)	**(5.3)**		**(30.0)**		**(25.0)**	
Height, m	**14.6**	4.9	**18.2**	8.0	**17.2**	6.7
DBHob, cm	**28.7**	11.8	**59.2**	20.6	**55.2**	18.2
Canopy connectivity	**2.1**	1.0	**2.1**	1.5	**1.9**	1.0
Senescence scale	**1.9**	0.8	**5.8**	2.2	**5.3**	2.6
Decay scale	**2.0**	0.9	**4.5**	1.3	**4.4**	0.9
No. Hollows visible	**0.0**	0.2	**2.9**	1.9	**2.3**	1.5
Predicted ngwayir hollows	**0.1**	0.1	**0.5**	0.2	**0.4**	0.2
Predicted koomal hollows	**0.0**	0.0	**0.3**	0.2	**0.2**	0.2
Possum signs	**0.6**	0.8	**2.5**	1.4	**2.1**	1.1

6.4.5.2 Hollow Logs

There were 32.4 logs per hectare on the study site, of which 16% contained hollows (i.e. 5.2 hollow logs ha^{-1}). Eighty-five percent of logs without hollows were jarrah, 14% were marri and 1% were wandoo. Of the available logs with hollows, 72% were jarrah and 28% were marri. Of the 21 hollow logs occupied by koomal and ngwayir (10 and 11 respectively), each was visited up to six times by either one or two different individuals of the same species. Hollow logs occupied by koomal were predominantly jarrah (7 jarrah, 3 marri) and those occupied by ngwayir were predominantly marri (3 jarrah, 8 marri). There were no significant physical differences between hollow logs occupied by koomal and ngwayir with regard to the log length and diameter or the diameter of the hollows. Hollow logs occupied by either possum species were 2.5-15 m in length (mean = 8.7 m), 25-130 cm in external diameter (mean = 62 cm), and with a 6-80 cm (x-mean = 19.6 y-mean = 24.1 cm) hollow diameter (Table 6.6). The physical attributes of the hollow logs occupied by possums did not differ significantly from those that were available (Table 6.6). Hollow logs (both occupied and available) were of similar length but had significantly larger external diameters than available logs without hollows (t-test, $p < 0.0001$).

Table 6.6. Summary of the attributes from a sample of available habitat logs without hollows (n = 132) and with hollows (n = 25), compared with hollow logs (n = 21) occupied by koomal and ngwayir at Chariup.

	AVAILABLE LOGS				**OCCUPIED**	
	NO HOLLOW		**HOLLOW**			
	Ave	SD	**Ave**	SD	**Ave**	SD
Length (m)	**8.49**	5.35	**8.68**	5.06	**8.67**	3.78
Log Diameter (cm)	**43.73**	16.25	**56.36**	25.48	**61.60**	26.85
Hollow Diameter X (cm)	-	-	**18.92**	10.92	**24.14**	18.75
Hollow Diameter Y (cm)	-	-	**15.52**	7.07	**19.62**	11.71

6.4.5.3 Balga

Three balga were occupied (each balga by a different ngwayir): they measured 0.5 m, 0.75 m, and 2.4 m in height (height to the apical meristem), had one, six and four grass heads respectively, and were visited four, one and two times, respectively. Of the 15 sampled available balga taller than 1 m in height (3.1 ha^{-1}), 10 had a single grass head, five had two heads, and each balga was up to 1.8 m tall (mean = 1.4 m, SD = 0.25).

6.4.5.4 Other Refuge Types

The hollow stump occupied by a koomal was created in a tree cut during the last cycle of logging in the area in the early 1970s. The hollow jarrah stump had a 106 cm diameter, with a 13 to 15 cm x-y hollow diameter to a depth of 70 cm. Of the available 5.0 stumps ha^{-1}, at least half were formed as a result of previous logging, while the remaining stumps appeared to have been created naturally. All but one stump (a marri) was jarrah. Five of the 24 sampled stumps had hollows (i.e. 1.0 hollow stump ha^{-1}). Four of the hollow stumps were cut, the mean internal x and y hollow diameters were 18 and 22 cm (range = 7-35 cm) and the mean hollow depth was 39 cm (range = 22-70 cm). The external diameters of the hollow stumps (mean = 61 cm, range = 54-76 cm, n = 5) were slightly smaller than those without hollows (mean = 70 cm, range = 21-116 cm, n = 19).

The burrows occupied by both possum species were cavities created by burnt out and/or rotten tree roots, or by trees that had fallen over. The forest debris occupied by ngwayir consisted of naturally fallen branches, under the leaves of which the ngwayir sheltered. The drey occupied by a ngwayir was 8 m above ground, within the crown of a marri (31.1 cm DBHob). No comparable availability data were collected for these locally uncommon types of refuge.

6.4.6 Morphological characteristics of standing trees that affect the probability of use as a diurnal refuge

Logistic regression modelling, with a logit transformation ($Logit(p) = \ln[p/(1-p)]$ where p is the probability of the tree being occupied), examined tree attributes that related to the probability that a tree was occupied as a diurnal refuge. Of the many models developed, most of the better models consistently included the same variables. For demonstrative purposes, it was necessary to select a ‘best model’. We based this choice on cross-validation values (i.e. predictive ability) and biological plausibility. Although model selection for each possum species was conducted separately, the final models for koomal and ngwayir included the same five highly significant ($p < 0.001$) explanatory variables. For both koomal and ngwayir, the probability that a tree was occupied increased with the square-root of tree diameter, crown senescence, canopy connectivity and possum signs. Tree species also affected the probability of occupancy, but the effect was different for the two possum species. Wandoo and marri trees were significantly more likely to be occupied by koomal than jarrah. For ngwayir, wandoo and jarrah were significantly more likely to be occupied than marri (Table 6.7).

The linear term of the micro-habitat model for koomal was;

$$\begin{aligned}\text{Logit}(\text{p}) = {} & -17.82958 + 1.30466\sqrt{\text{Tree Diameter}} + 0.63454(\text{Crown senescence}) + \\ & 0.62965(\text{Canopy connectivity}) + 0.75717(\text{Species; Marri}) + \\ & 2.94844(\text{Species; Wandoo}) + 0.83525(\text{Possum sign})\end{aligned}$$

and for ngwayir it was;

$$\begin{aligned}\text{Logit}(\text{p}) = {} & \text{-}15.53263 + 1.25819\sqrt{\text{Tree Diameter}} + 0.51080(\text{Crown senescence}) + \\ & 0.57798(\text{Canopy connectivity}) \text{ - } 0.80482\ (\text{Species; Marri}) + \\ & 2.16096(\text{Species; Wandoo}) + 0.73475(\text{Possum sign})\end{aligned}$$

where values for marri and wandoo are indicator variables (e.g. Species;Marri = 1 if the tree is a marri).

Tree diameter was the single most reliable predictor of tree occupancy for both possum species – based on single variate logistic regression models and cross-validation values. Figure 6.8 provides an example of how the probability of tree use varies by tree diameter for the three different tree species, jarrah, marri and wandoo. The probability of use was substantially higher for a given diameter in wandoo trees compared with jarrah and marri.

For demonstrative purposes, Figure 6.9 provides an example of the probability relationships of koomal and ngwayir use of trees for diurnal refuge for three parameters: crown senescence, canopy connectivity and possum signs. The parameter values at equivalent probabilities tended to be higher for koomal than for ngwayir (i.e. koomal occupied larger, more senescent, and better connected trees than ngwayir).

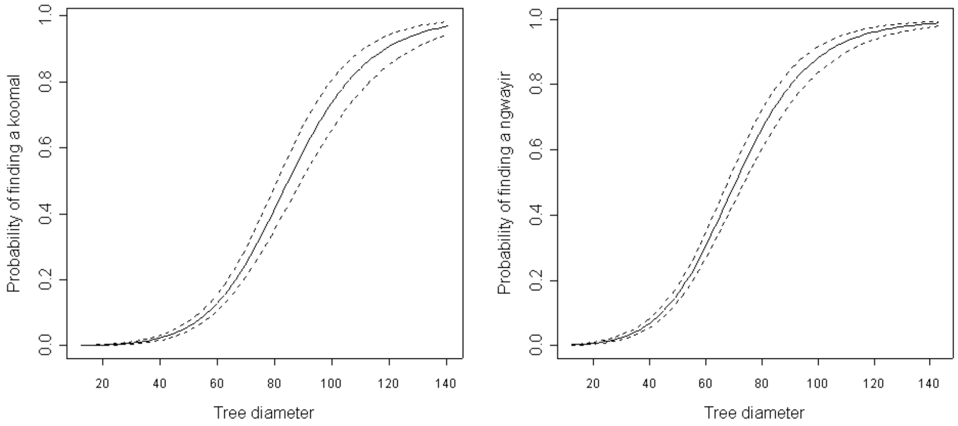
Table 6.7. A relative comparison of probabilities (including the lower and upper 95% confidence intervals, CI) that a tree was used as a diurnal refuge by koomal or ngwayir based on the tree species at Chariup.

KOOMAL	LOWER 95% CI	MEAN PROBABILITY	UPPER 95% CI
Jarrah	0.39	0.46	0.53
Marri	0.57	0.65	0.72
Wandoo	0.87	0.94	0.98
NGWAYIR			
Jarrah	0.64	0.70	0.76
Marri	0.44	0.51	0.58
Wandoo	0.90	0.95	0.98

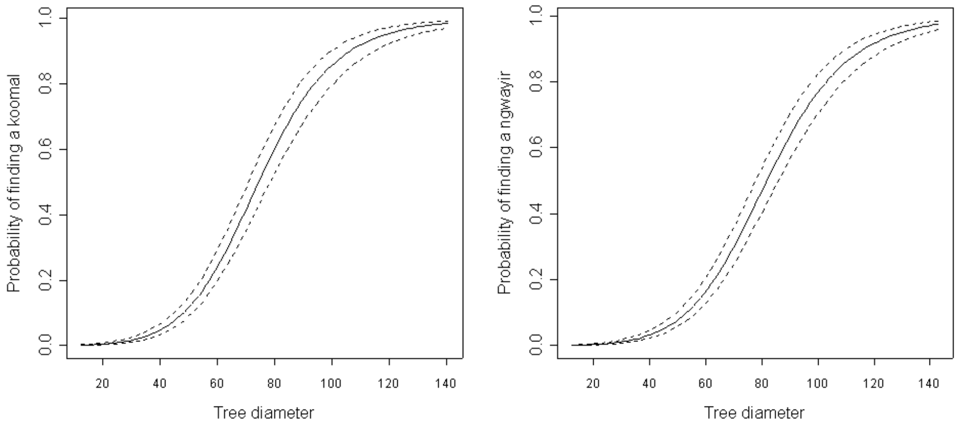
Figure 6.8. The probability that a tree was occupied as a diurnal refuge by koomal (left) or ngwayir (right) in relation to tree diameter (cm) for (a) jarrah, (b) marri and (c) wandoo trees, at Chariup.

The 95% confidence limits are included. Note: these figures have been developed with arbitrarily set values for the other parameters in the micro-habitat models and are intended for demonstrative purposes only (see Methods for details).

(a) Jarrah



(b) Marri



(c) Wandoo

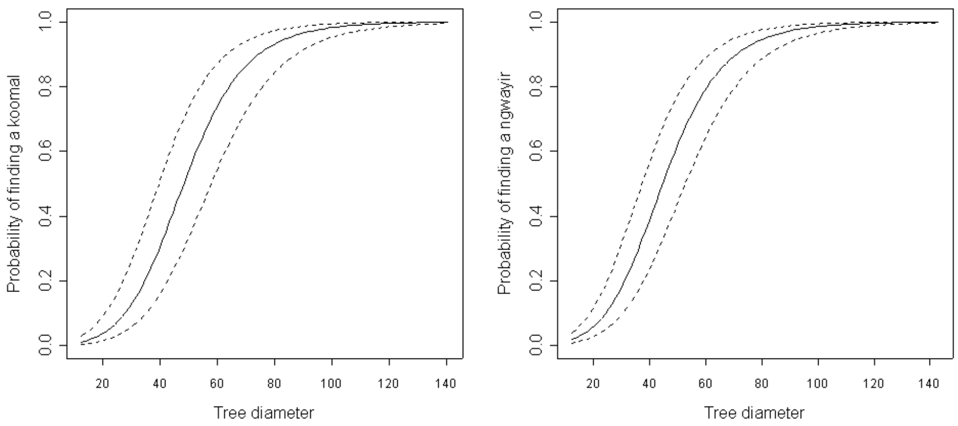
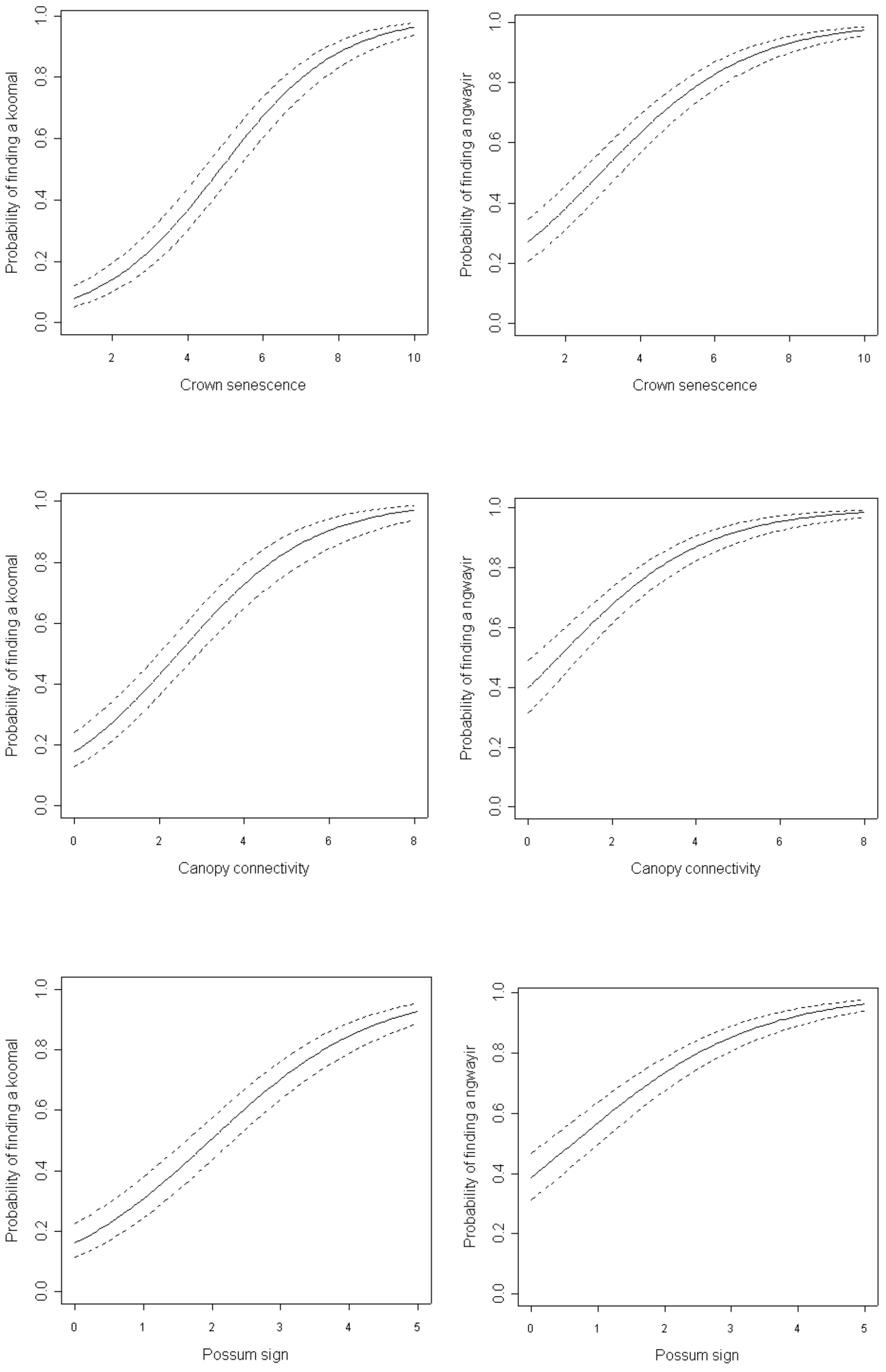


Figure 6.9. The probability that a tree was occupied as a diurnal refuge by koomal (left) or ngwayir (right) in relation to crown senescence, canopy connectivity and possum signs, at Chariup.

The 95% confidence limits are included. Note: these figures have been developed with arbitrarily set values for the other parameters in the micro-habitat models and are intended for demonstrative purposes only (see Methods for details).



6.4.7 The effect of a meso-habitat context on the probability of refuge use

When contextual variables were included in the logistic regression models to capture some of the meso-scale habitat of standing trees, the cross-validation values improved, indicating that aspects of the meso-habitat were contributing to the probability that possums might use a tree. The final models selected for koomal and ngwayir were different.

For koomal, the probability that a tree was occupied as a diurnal refuge was negatively related to upper- and mid-storey height, and positively related to canopy cover and the basal area of jarrah. Koomal also were more likely to be found in dead trees than live trees.

The linear term of the micro- and meso-habitat model for koomal was;

$$\begin{aligned}\mathrm{Logit}(p) = {} & -24.649863 - 0.635114(\text{US height}) - 1.110293(\text{MS height}) + \\ & 0.127942(\text{Canopy Cover}) + 0.123478(\text{Basal area jarrah}) + \\ & 4.114412(\text{Tree; Dead}) + 0.661925(\text{Species; Marri}) + \\ & 5.136683(\text{Species; Wandoo}) + 3.014059\sqrt{\text{Tree Diameter}} + \\ & 0.694085(\text{Canopy connectivity}) + 1.126619(\text{Crown senescence}) + \\ & 1.485117(\text{Possum sign}) - 0.015434(\text{Crown senescence * Diameter})\end{aligned}$$

where ‘Tree; Dead’ and Species;Marri/Wandoo are indicator variables (e.g. Tree;Dead = 1 if the tree is dead), ‘US height’ is upper-storey height (m), ‘MS height’ is mid-storey height (m), and ‘Basal area jarrah’ is expressed per hectare.

For ngwayir, the probability that a tree was occupied as a diurnal refuge was negatively related to mid- and lower-storey height. Ngwayir were more likely to use a tree if the surrounding lower storey cover was sparse (i.e. 2-10% ground cover). The likelihood that ngwayir occupied a tree also decreased with increasing tree height.

The linear term of the micro- and meso-habitat model for ngwayir was;

$$\begin{aligned}\mathrm{Logit}(p) = {} & -6.6312986 - 0.5754350(\text{MS height}) - 4.5515920(\text{LS height}) + \\ & 3.7187415(\text{LS cover 2 - 10\%}) + 1.6747700(\text{LS cover 30 - 70\%}) - \\ & 0.3284649(\text{LS cover 70 - 100\%}) - 0.0798991(\text{Tree height}) + \\ & 1.1305477\sqrt{\text{Tree Diameter}} + 0.3916497(\text{Canopy connectivity}) + \\ & 0.6102142(\text{Possum sign}) + 0.0047956(\text{Crown senescence * Diameter})\end{aligned}$$

where ‘MS height’ is mid-storey height (m), ‘LS height’ is lower-storey height (m), and the ‘LS cover’ factors are indicator variables.

6.4.8 Sex related differences in day refuge selection

For both koomal and ngwayir the rankings of the models were very similar for males and females, though the cross-validation scores were lower when the sexes were estimated separately than when they were estimated together. It was not possible to test for differences in the parameter sets between these models because the sex of a possum could not be made an attribute of the tree (because many trees were occupied by both sexes), and hence the models could not be nested. Furthermore, if there were competition or other limitations for available habitat, then there will be complicated dependencies between the two parameter datasets that would be very difficult to overcome.

6.5 Discussion

Other studies have quantified the physical attributes of tree hollows most likely to be occupied by various fauna and then developed models to predict the likelihood that a tree contains these hollows (e.g. McComb *et al.* 1994; Gibbons *et al.* 2002; Whitford and Williams 2002). Similarly, other studies have made predictions of which hollow logs might be occupied by selected fauna (e.g. Faunt 1992; McComb *et al.* 1994; Williams and Faunt 1997). The advantages of this physical approach are principally efficiency of data collection (e.g. time, effort, resources) and the ability to use this method simultaneously for a large number of species. However, these model approaches are not based on extensive data derived from direct observation of habitat use by animals. The advantage of the approach used in this study is that refuge use is observed *directly*. It therefore examines *actual* habitat selection because it includes the biological context of ‘choice’, and not just the physical factors of hollows. The use of the direct approach is, however, constrained by the difficulties of observing habitat use of some particularly cryptic species, and by the physical and financial resources required (e.g. radio-collars are costly, data collection takes time and is labour-intensive).

This study, therefore, provides the biological and ecological context of habitat selection necessary to verify the accuracy of the indirect approach in predicting important habitat (e.g. McComb *et al.* 1994; Faunt 1992; Williams and Faunt 1997; Whitford 2002; Whitford and Williams 2002). This comparison also has implications for models developed for other hollow-dependent species for which the indirect approach has been used and for which data from direct observation of habitat use is unavailable and/or more difficult to collect. This study provides direct empirical data necessary to improve population viability models (PVA) and other models that may be used to assess the conservation status of these species and their potential responses to alternative forest management scenarios (e.g. McComb 1994).

6.5.1 The number of refuges occupied

The number of refuges occupied by an individual koomal or ngwayir was a function of the number of observations for that individual. This also was observed within the nearby Kingston populations, some 20 km from the Chariup study site (Wayne *et al.* 2000 and A. Wayne unpublished data). The same phenomenon has been observed for other Australian arboreal marsupials (e.g. Lindenmayer *et al.* 1996, 2004). Given that these animals were sedentary and that the number of available refuges must be finite, the cumulative number of refuges occupied by an individual might be expected eventually to reach an asymptote (Lindenmayer *et al.* 2004). The fact that the number of refuges occupied by an animal accumulates with time suggests that refuge choice and refuge use are dynamic. Although there may be a number of reasons for this, such as competition (e.g. Maitz and Dickman 2001; Gibbons and Lindenmayer 2002; Ginger *et al.* 2003; Kokko *et al.* 2004), this nonetheless implies that most individuals are open to new refuge opportunities throughout their adult life, and are therefore, likely to exploit new refuges as they become available. This behaviour contrasts with that of other species that exhibit relatively high levels of nest-site fidelity such as some fish (e.g. King and Withler 2005), sea turtles (e.g. Wang and Cheng 1999; Nordmoe *et al.* 2004), birds such as the mallee fowl, *Leipoa ocellata*, in eastern Australia (Priddel and Wheeler 2003), the eastern bluebird, *Sialia sialis* (Stanback and Rockwell 2003) and wood duck, *Air sponsa* (Semel and Sherman 2001) in North America, and roost sites for some bats (Storz *et al.* 2000; Young 2001).

6.5.2 Types of refuge occupied

Both the koomal and the ngwayir at Chariup were similarly dependent on hollow-bearing trees as the principal form of day refuge (98% and 96% of all occupancy records, respectively; Table 6.3). Hollow logs, burrows and hollow stumps were rarely occupied by koomal. For ngwayir, hollow logs, forest debris, balga, burrows and dreys were rarely occupied. For hollow-bearing trees, details of the hollow type and attributes were not examined because of the difficulty of detecting hollows (Whitford 2002), identifying which hollows were occupied and assessing their characteristics from the ground (Gibbons and Lindenmayer 2002; Lindenmayer *et al.* 2004). This also was not a level of detail required by this study.

6.5.2.1 Koomal

Extensive use of tree hollows is common to all populations of common brushtail possum studied in Australian forests. Similar types of refuge use have been observed for other koomal populations in south-western Australia (e.g. Sampson 1971; Inions 1985; Tan 1999; How and Hillcox 2000; Abbott 2005) and elsewhere for common brushtail possums (e.g. Wood Jones 1924; Tyndale-Biscoe 1955; Dunnet 1956; Kerle 2001, 2004; Paull and Kerle

2004). For example, in the (contemporarily unlogged) jarrah forest at Kingston (approximately 20 km from Chariup), averages for the proportion of refuges that were hollow-bearing trees ranged from 68% to 96%. Similarly, the average proportions of refuges that were hollow logs ranged from 0-23%, hollow stumps 0-9%, burrows 0-6% and above-ground roosts (i.e. including dreys) 0-1% (A. Wayne unpublished data). On one occasion, Sampson (1971) observed koomal at Tutanning using the fork of a balga under the 'skirt' of leaves as a diurnal refuge site. This was not observed at Chariup or at Kingston (A. Wayne unpublished data) where balga were present at a range of densities.

6.5.2.2 Ngwayir

The ngwayir and the closely-related common ringtail possum (*Pseudocheirus peregrinus*) exhibit diversity in the types of habitat used for diurnal refuge (e.g. Thomson and Owen 1964; Kerle 2001; Smith *et al.* 2003; Munks *et al.* 2004). The main types of refuge occupied also may differ substantially between populations. For example, at nearby Kingston, the average proportions of refuges in the form of hollow-bearing trees used by three cohorts (5-18 individuals each) in different areas ranged between 2-65%. Similarly, the average proportions of refuges in balga were between 8-35%, in dreys 6-49%, forest debris 1-19%, and in burrows and hollows stumps 0-1% each (Wayne *et al.* 2000).

Differences in the relative use of various types of refuge are probably related to variations in habitat structure and availability of shelter resources in different areas. Both the ngwayir and the common ringtail possum use mainly arboreal dreys (self constructed nests) in areas where vegetation is dense (e.g. in coastal areas; e.g. Thomson and Owen 1964; How *et al.* 1984; Pahl 1987; Ellis and Jones 1992; Jones *et al.* 1994a, 1994b; Smith *et al.* 2003), and tree hollows may be scarce. In contrast, populations in more open forest areas tend to use tree hollows predominantly (e.g. in inland areas; see Meredith 1984; Bennett *et al.* 1991; Traill 1991; Jones *et al.* 1994a, 1994b; Augee *et al.* 1996; Lindenmayer *et al.* 2001; Kerle 2004; this study). An untested hypothesis to explain differences in the main refuge types used in different areas is that hollows may provide better insulation during hotter inland summers than dreys (e.g. Pahl 1987; Jones *et al.* 1994b; Kerle 2004). Alternatively, drey use may be directly related to habitat structure *per se.* Supporting evidence for this includes the extent of drey use in response to vegetation succession after intense fire (Russell *et al.* 2003). Similarly, dreys were used extensively by some individuals in inland jarrah forest at Kingston, in an area with dense riparian vegetation and few large trees, while ngwayir in adjacent, more open forest, predominantly used tree hollows (Wayne *et al.* 2000). The use of dreys by ngwayir also has been observed in dense stump coppice regrowth in recently logged areas of Kingston (A. Wayne personal observation).

At Chariup, few balga were used for diurnal refuge by ngwayir, though their use by this species has been observed elsewhere (e.g. Abbott 2005; and P. de Tores personal communication). At Kingston the use of balga was particularly extensive, accounting for 35%

of refuges in some areas, and some individuals occupied balga almost exclusively (Wayne *et al.* 2000). The differences in the extent of balga use between areas are probably related to its availability, which is very patchy (A. Wayne personal observation).

Given the open nature of much of the eastern jarrah forest, the dependence on hollows by ngwayir may be substantially greater than in areas where dense mid-stories provide more suitable habitat that is conducive to the construction and use of dreys. Dreys in more open habitat also would be more conspicuous and their occupants would potentially be more vulnerable to predation, especially by raptors. The dependence on tree hollows by common ringtail possums in forest with an open understorey has been found elsewhere (e.g. Traill 1991).

The difference in reliance on particular habitat elements for diurnal refuges has conservation implications. For example, the strategic risk assessment of south-western Australian forest fauna dependent on tree hollows (Abbott and Whitford 2002) assumed that a species' reliance on hollows in standing trees was the most important criterion by which to assess susceptibility to changes in hollow abundance. On this basis, the ngwayir was not considered at risk of a reduction in the abundance of tree hollows, given the moderate ranking of its reliance on hollows and its ability to build dreys and to use a broad array of other types of habitat for diurnal refuge. However, the reliance of ngwayir on tree hollows in eastern jarrah and in more open forests and woodlands may be substantially greater than in other areas in which it is found, given the lack of suitable alternative refuge sites (e.g. dense vegetation for dreys and an abundance of large, multi-head balga). The conservation risk for ngwayir populations in some areas may therefore have been underestimated.

Burrows and hollow stumps, as well as rock crevices and other oddities such as an active sea eagle nest, an arboreal termite nest and mistletoe clumps (e.g. Thomson and Owen 1964; Kerle 2001; Smith *et al.* 2003; Munks *et al.* 2004), are recorded among rarely-used diurnal refuges in populations that have been studied. Terrestrial refuge sites within dense vegetation or debris, while generally rarely used (e.g. Smith *et al.* 2003; Munks *et al.* 2004), have been used more substantially in active logging coupes (e.g. 44% of refuges and 29% of occupancy records at Kingston, Wayne *et al.* 2000). The susceptibility of possums in these terrestrial refuge sites to predation and fire (e.g. post-silvicultural burns within logged areas) in particular, suggests that these forms of refuge are neither preferred nor optimal choices of habitat.

6.5.3 Frequency of visits to different refuges

For both koomal and ngwayir, a few refuges were occupied extensively, while most were occupied infrequently (Figure 6.4). As well as the similarities of both species' behaviour at Chariup, very similar trends were also observed for both species at Kingston. For example, for ngwayir at Kingston, the 20% of refuges most extensively occupied were occupied 65%

of the time (A. Wayne unpublished data), compared with 63% of the time at Chariup. Similar phenomena have been observed for arboreal mammals elsewhere in Australia (e.g. Lindenmayer *et al.* 1996, 2004) and New Zealand (e.g. Ward 1978). The more frequently-visited refuges at Chariup also were occupied by more conspecifics (Figure 6.6). Both species had similar preferences: the 63 refuges occupied by both koomal and ngwayir (i.e. 26% of all refuges) accounted for 55% of occupancy records for both species. For koomal and ngwayir, hollow-bearing trees were revisited more frequently than other refuge types.

The relatively high importance of a few select refuges has important conservation implications. Management of these habitat elements will afford the greatest benefit in terms of shelter resources for these species. For example, guidelines for selecting ‘habitat trees’ to be retained within logging coupes can be improved to ensure that the most suitable trees are protected. This study provides the first published and the most comprehensive information of koomal and ngwayir habitat use that can be put to this purpose.

6.5.4 Refuge co-use and sharing

The conservative estimates of co-use and sharing indicate that about 60% of refuges were occupied by only one radio-collared individual, while some refuges were occupied by up to five koomal and ngwayir conspecifics (Figure 6.5). Up to nine radio-collared individuals of both species were recorded using the same refuge. It was not possible to determine if these individuals occupied the same hollow in a single tree. This was because of the limited ability to observe hollows from the ground (Whitford 2002; Harper *et al.* 2004) and the difficulty for observers to access arboreal refuges. Inter-specific sharing always occurred in hollow-bearing trees (n = 22) with multiple hollows. In those cases where both koomal and ngwayir shared the same refuge, it is extremely unlikely that individuals of different species would simultaneously share the same hollow given that ngwayir have been observed being evicted by the more aggressive koomal (How and Hillcox 2000; A. Wayne personal observation).

6.5.4.1 Koomal

Concurrent conspecific sharing by koomal occurred only 10.6% of the time. This highlights the fact that the species is primarily solitary. Sharing by two adult koomal was principally between members of the opposite sex, although same-sex sharing also occurred. The reason for the seasonal pattern of sharing between three koomal (almost always two females and one male) is unclear (Figure 6.7a), but given that it occurred only in the coldest months of the year (June to September), it may serve to keep individuals warm (if they were in fact sharing the same hollow and not just the same tree). The minor winter peaks of paired male-female sharing (Figure 6.7a) may be for the same reason. The minor peak of paired sharing between February and April coincides with the breeding season for this species (Wayne *et al.* 2005c [Chapter 4]). Although the genetic and social relationships between sharing individuals were unknown, it is expected that most different-sex sharing events involved reproductive mates.

6.5.4.2 Ngwayir

Paired sharing by ngwayir was rare (only 2% of the time), and predominantly between males and females. The summer (67%) and autumn (15%) peaks in sharing did not relate strongly to the main seasonal breeding peak in May – June or to the minor peak in October – November (Wayne *et al.* 2005d [Chapter 5]). The rarity and seasonality of sharing may result from female aggression toward males, as the female common ringtail possums in South Australia apparently do not permit males to come near them for most of the year (Wood Jones 1924). By comparison, common ringtail possums in Victoria displayed no seasonal trends in sharing, with males and females being found together throughout the year (Thomson and Owen 1964). At Chariup, no more than pairs of adults were observed sharing, though up to five individuals co-used the same refuge. Near Sydney, up to 11 common ringtail possums were recorded using the same refuge and, in contrast to our study, female-female pairs were never observed sharing (Smith *et al.* 2003). Nonetheless, the low incidence of refuge sharing by ngwayir provides supporting evidence that this species is more solitary than the koomal and less social than the common ringtail possum (e.g. Jones 1995; McKay and Ong 1995).

6.5.5 Comparisons between the attributes of available and occupied habitat

6.5.5.1 Hollow logs

At Chariup, 16% of logs contained hollows potentially large enough for occupancy by a possum (i.e. 5.2 logs with hollows $\geq$ 50 mm internal diameter and $\geq$ 100 mm deep per hectare). A similar proportion (16%) of 1272 logs also was found to have hollows (> 20 mm internal diameter) potentially suitable for vertebrate fauna in 10 northern jarrah forest sites (Faunt 1992; Williams and Faunt 1997). However, the average densities of logs and hollow logs in northern jarrah forest were four times greater than those observed at Chariup. External log diameter was the most important factor positively associated with hollows in logs, followed by evidence of low-to-moderate fire damage, intermediate stages of decomposition and termite attack (Williams and Faunt 1997).

Although sample sizes were too small to test for statistical differences, the tree species of hollow logs occupied by koomal approximated those generally available. Ngwayir tended to use disproportionately more hollow marri logs than were generally available. There were no other significant differences (length, external diameter or hollow diameter) between the hollow logs occupied by koomal and those occupied by ngwayir, or between the hollow logs that were occupied by either species and those that were available.

6.5.5.2 Balga

The limited use of balga by ngwayir at Chariup was largely attributed to their limited availability (see above). However, the suitability of balga as diurnal refuge sites also is related to their physical attributes. Most of the balga occupied by ngwayir in Kingston were taller than two metres, and their use is positively and significantly related with the number of grass heads per plant (Wayne *et al.* 2000). All of the balga occupied at Kingston and Chariup had thick, long (≥ 1 m) skirts (thatch) of dead leaves in which the ngwayir nested. The concealed forks between multiple heads provide a commonly used roost. The insulation properties of balga refuges are the same as those of occupied tree hollows (Driscoll 2000).

6.5.5.3 Standing trees

Previous research near Chariup, based on the extent of possum signs on tree boles, suggested that tree hollows suitable for koomal and ngwayir were occupied regardless of tree species, condition, height or size, and that the depth of the hollow was the only parameter that significantly related to occupancy (Inions *et al.* 1989). Research on other subspecies of the common brushtail possum in other parts of Australia suggests that several types of large hollow are occupied (e.g. Traill 1991; Paull and Kerle 2004), but that the type and location of the hollow are important, and that hollows close to the ground are suboptimal (Winter 1976, cited in Kerle 2004). Common ringtail possums in Victoria predominantly use crown hollows (Traill 1991) and prefer hollows at least 40 cm deep (Thomson and Owen 1964; Calder *et al.* 1983, cited in Paull and Kerle 2004).

Research in the northern jarrah forest found that the probability of a tree containing a hollow suitable for koomal increased with tree diameter (McComb *et al.* 1994). The influence of tree species, bole length and internal defects was not significant (McComb *et al.* 1994). In a separate study, the occurrence of hollows suitable for koomal and ngwayir was principally related to tree size and crown condition (Whitford and Williams 2002). The health status of a tree (alive, dying or dead), its lean (relevant to koomal), and height also were related (Whitford and Williams 2002). Using the predictive models of Whitford and Williams (2002), the trees occupied by possums at Chariup were on average more likely to contain suitable hollows than were available trees in general. This suggests that the models developed by Whitford and Williams (2002) relate to the trees that are actually occupied by koomal and ngwayir. However, in our investigation tree diameter alone was better at predicting whether or not a tree might be occupied than were these models. Other differences between the Whitford and Williams (2002) models for predicting tree occupancy and our studies concern the use of estimations of what makes a physically suitable hollow (i.e. the Whitford and Williams [2002] approach), and observations of what was actually occupied (the approach used here). These differences are discussed below.

Tree species:

The preference by koomal for marri over jarrah probably reflects the likelihood of this species to contain suitable hollows. Whitford (2002) demonstrated that although a larger number of jarrah have a larger number of hollows, the hollows in marri are significantly larger and deeper and may therefore, be more important for birds and mammals (including possums) that depend on larger hollows. For seven species, including koomal and ngwayir, marri trees were predicted to contain 2-3 times more useable hollows than jarrah (Whitford and Williams 2002). The disproportionate use of marri over jarrah by koomal at Chariup supports these findings, though this preference does not seem to be as marked as the predictions of Whitford and Williams (2002) would suggest.

In contrast to the Whitford and Williams (2002) predictions, ngwayir at Chariup preferred jarrah to marri. This preference and its contradiction with Whitford and Williams (2002) may result not from a lack of suitable hollows, but from competition and avoidance by ngwayir of hollows occupied by koomal. Nonetheless, this highlights the importance of direct observations of habitat use in order to incorporate the biological context of selection, which cannot be captured using models based only on the physical attributes of what might be available.

Compared with jarrah and marri, there was an even stronger preference for wandoo by both koomal and ngwayir at Chariup (Table 6.5 and 6.7). The average diameter of wandoo occupied by the possums also was smaller than that of occupied jarrah or marri. The disproportionate use of smaller wandoo is very probably a result of the greater availability of suitable hollows. Wandoo are particularly susceptible to termite infestation and are therefore highly likely to contain hollows. Furthermore, the hollows in wandoo tend to have substantially thinner walls than hollows in marri or jarrah, thus providing larger hollows in smaller branches (A. Wayne personal observation). In contrast, fire and decay by rot are the major factors in the development of hollows in jarrah and marri (McComb *et al.* 1994).

Tree diameter and crown condition:

Tree diameter was the single variable most likely to predict the use of a tree by either koomal or ngwayir. The diameter of trees occupied by possums at Chariup was similar to that found 2 km away at Boyicup (Inions *et al.* 1989) and in the northern jarrah forest (McComb *et al.* 1994). The findings at Chariup that trees with larger diameters were more likely to be occupied by possums concurs with the findings of others that this variable is the most reliable predictor of the presence of hollows suitable for these species (McComb *et al.* 1994; Whitford and Williams 2002). These findings also support other studies that have found a similar preference for larger trees by other hollow-dependent species (e.g. Gibbons and Lindenmayer 2002; Lindenmayer *et al.* 1991a; 2004).

The increased probability of use by koomal and ngwayir of trees with an increasing extent of crown senescence (i.e. generally older trees) also generally concurs with previous research (Whitford and Williams 2002). According to Whitford and Williams (2002), trees with intermediate senescence values (3-8, maximum likelihood at 5) were most likely to bear hollows suitable for a number of species, including ngwayir. For koomal, trees with senescence values of 7-9 were most likely to contain suitable hollows (Whitford and Williams 2002).

Dead trees:

The finding at Chariup that koomal (but not ngwayir) occupied disproportionately more dead trees than were generally available supports the finding of Whitford and Williams (2002) that this variable can be an important predictor of potentially suitable hollows. Dead trees of some species are more likely to bear hollows, and other hollow-using fauna have been shown to prefer dead trees (e.g. Saunders *et al.* 1982; Whitford and Williams 2002). Univariate analyses in this study showed that dead trees were significantly more likely to be used as diurnal refuges by koomal and ngwayir than live trees. In the other plausible but larger models developed in this study, this variable was frequently included for koomal. However, in the model finally selected, the addition of this variable did not improve the cross-validation value. It is therefore likely that other variables in the final models, such as crown senescence, were correlated and largely explained this preference. The inclusion of the 'Dead/Alive' variable in the final koomal model with meso-habitat variables suggested that there might be a relationship between this tree attribute and the meso-habitat that influences the probability of possum use.

Tree lean and tree height:

Tree lean and tree height were not selected in the final models for koomal or ngwayir at Chariup, but were present in many of the more reliable models. The addition of these variables to the final models did not improve the cross-validation value. Therefore, while these factors may be associated with the possible presence of suitable hollows (Whitford and Williams 2002), they are not necessary for the development of a model that predicts what is actually occupied by possums. The inclusion of tree height in the final meso-habitat model for ngwayir suggested that there might be a relationship between this tree attribute and the meso-habitat that influences the probability of possum use.

Canopy connectivity:

With the exception of wandoo, trees occupied by possums had a greater number of canopy connections with adjacent trees. The logistic regression models also demonstrated that increased canopy connectivity was an important predictor of the usefulness of trees to both koomal and ngwayir, indicating that arboreal access to trees is an important determinant of the use of standing trees for diurnal refuge. The degree of canopy continuity in coastal woodlands has been associated with the abundance of ngwayir (Jones *et al.* 1994a; Jones and Hillcox 1995) and as being important to common ringtail possums in Tasmania (Munks *et al.* 2004). The importance of arboreal access via adjacent vegetation as a criterion for the selection of hollow-bearing trees as diurnal refuge also has been demonstrated for Leadbeater's possum (*Gymnobelideus leadbeateri*) (Lindenmayer *et al.* 1991a).

The preference of both koomal and ngwayir for trees with extensive canopy connectivity has implications for management, particularly within forests available for logging. Our results imply that greater connectivity around retained habitat trees in logged areas will increase the probability of these trees being used as diurnal refuges by possums. The creation of 'habitat islands' and/or corridors within logging areas, by protecting vegetation (including trees) adjacent to retained habitat trees should, therefore, provide greater habitat value than isolated trees (analogous in some respects to the concept of 'understorey islands' for some plant species, Ough and Murphy 1998; Lindenmayer 2003).

Possum signs:
The extent of possum signs was a significant variable in the logistic regression models for both species (Table 6.7, Figure 6.9) and thus provides a useful indicator of trees occupied for shelter in the jarrah forest. It is important to note that the presence of signs may alternatively be indicative of other important habitat, such as food and access routes to other resources. Possum signs will be dependent also on possum densities and the relative availability of other arboreal access routes. Thus, while the presence of obvious possum signs is an indicator of important possum habitat, the absence of signs should not be interpreted to the contrary.

6.5.6 The influence of meso-habitat on diurnal refuge selection

The importance of canopy connectivity demonstrates the influence of habitat context on diurnal refuge selection. The inclusion of other significant meso-habitat variables in the predictive models shows that habitat selection is a complex phenomenon influenced by a number of factors at multiple spatial scales (e.g. Johnson 1980; Holling 1992; Mackey and Lindenmayer 2001). The details of these results provide a robust and reliable predictive model of the meso-habitat variables that affect habitat selection for diurnal refuge by koomal and ngwayir. However, given that the Chariup study site does not encapsulate the full range of habitat conditions found in the jarrah forest, the details of these results should not be applied indiscriminately across the entire jarrah forest bioregion. This point is important in view of the flexibility of these possums and their responsiveness to the types of refuge available in various habitats (e.g. dreys versus hollows; see above).

At Chariup the preferred arboreal diurnal refuges of koomal were trees in areas with higher jarrah basal areas (i.e. areas more densely forested with jarrah) and more extensive canopy cover but with shorter upper- and lower-storey heights (Table 6.8). The diurnal refuge selection of ngwayir on the other hand, was negatively related to mid- and lower-storey height and lower storey cover. These relationships with lower- and mid-storey variables are particularly interesting in view of the highly arboreal nature of the ngwayir. Structural complexity and/or floristics in the understorey have been related to habitat selection by near-coastal populations of koomal and ngwayir (Jones and Hillcox 1995; How and Hillcox 2000) and by other arboreal species (e.g. Davey 1984; Pahl 1984; Lindenmayer *et al.* 1990, 1991a, 1991b; Kerle 2004).

Habitat structure in the jarrah forest is the result of numerous factors – including logging and fire history, soil nutrients and soil moisture – functioning at multiple scales. It is not yet clear as to what extent possums are responding (1) directly to these physical factors, (2) to the vegetation (biological) responses to these factors, or (3) to other factors that have not been measured but are correlated with the significant habitat variables. A combination of all three factors is most likely.

6.5.7 Biological factors affecting habitat selection

6.5.7.1 Potential competition

The logistic regression models for koomal and ngwayir were independently very similar, particularly those based on tree attributes alone. The findings of the present study clearly indicate that, at Chariup, both possum species are using very similar habitat for diurnal refuge. Given the more aggressive nature of koomal, combined with observations of ngwayir being readily evicted from tree hollows by koomal (How and Hillcox 2000; A. Wayne personal observation), it is likely that koomal will prevail in the event of competitive interaction between the two species. Conspecific competition for diurnal refuges is also to be expected (e.g. Smith *et al.* 2003).

There were, nonetheless, differences between the two species in the use of diurnal refuges. The more extensive use of jarrah than of marri trees by ngwayir contrasts with the preference for marri by koomal and with the predicted availability of suitable hollows based on size (Whitford and Williams 2002). The bias by ngwayir for jarrah, which contain larger numbers of smaller hollows than marri (Whitford and Williams 2002), and the use of smaller trees than koomal probably reflect this species' ability to use smaller hollows than those required by the larger koomal. The logistic regression models that incorporated a meso-habitat context in diurnal refuge selection also show that there may be some spatial differentiation or resource partitioning between the possum species based on habitat structure and floristics. Exclusion experiments would be required to determine how much these species effectively compete for resources. Resource partitioning also has been observed for other arboreal marsupials elsewhere in Australia (e.g. Davey 1984; Lindenmayer *et al.* 1991a; Lindenmayer 1997).

Competition for hollow resources with other hollow-dependent fauna, such as birds (e.g. Saunders *et al.*1982; Mawson and Long 1994; Abbott 1998), is also possible. The exclusion from some hollows by hives of feral European honeybees, *Apis mellifera,* is also to be expected (e.g. Wood and Wallis 1998). For example, common brushtail possums in Victoria occupied only 74% of the suitable hollow-bearing trees and 48% of the suitable hollows, partly as a result of competition with feral honeybees (Wood and Wallis 1998).

6.5.7.2 Predation, habitat structure, food, temporal variations etc.

Other biological factors not examined here also may affect the use of habitat for diurnal refuge. The risk of predation may affect habitat use by possums (e.g. Russell *et al.* 2003; Pickett *et al.* 2005), while food availability and foraging behaviour (e.g. Goldingay and Kavanagh 1995; Eyre and Smith 1997), may both influence and be influenced by the selection of diurnal refuges (e.g. Ward 1978). Temporal variations in the selection of habitat in relation to food availability have been observed for a number of arboreal species (e.g. Kavanagh 1984; 1987; Goldingay and Kavanagh 1995). Seasonal variations in diurnal refuge habitat selection may similarly be a response to factors such as food availability, climate and reproduction. The presence of parasites is another biological factor that may affect habitat use (e.g. Gibbons and Lindenmayer 2002). Some of these aspects of koomal and ngwayir ecology in the jarrah forest will be addressed in subsequent studies (A. Wayne unpublished data).

6.6 Conclusions

Koomal and ngwayir use a diversity of habitat elements to provide diurnal shelter. The types of refuge selected, and their relative importance, apparently depend on the resources that are physically and biologically available. In the jarrah forest at Chariup, hollow-bearing trees were the most important form of diurnal refuge for both koomal and ngwayir. The use of such trees and the dependency on them and on other types of refuge by both species of possum are different elsewhere (e.g. Jones and Hillcox 1995; Wayne *et al.* 2000). This study showed that the trees selected for diurnal refuge by both species are significantly related to crown senescence, canopy connectivity, tree species, possum signs and, in particular tree diameter. The importance of canopy connectivity has special implications for habitat tree retention practices in the jarrah forest and canopy access and/or continuity also may be significant in other systems and for other species, especially hollow-users and arboreal mammals. The significant relationships between elements of the meso-habitat and the selection of diurnal refuges provide supporting evidence that habitat selection functions at different spatial scales (e.g. Johnson 1980; Holling 1992; Mackey and Lindenmayer 2001; Mitchell *et al.* 2001).

As well as emphasising the importance of recognising the influence of scale, this study also demonstrates the value of effective integration of the biological context into research aimed at conservation and management. A more holistic approach to understanding the koomal and ngwayir in the jarrah forest could be developed by integrating the ecological understanding of habitat selection developed here, with complementary studies of habitat selection at larger spatial scales (Wayne *et al.* 2005e [Chapter 7], in preparation-b) and with information on the life histories of these possums (Wayne *et al.* 2005c, 2005d [Chapters 4 and 5]). The results of such an exercise could be particularly relevant and helpful to both the conservation of these species and to sustainable forest management.

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6.8 References

Abbott, I. (1998). Conservation of the forest red-tailed black cockatoo, a hollow-dependent species, in the eucalypt forests of Western Australia. *Forest Ecology and Management* **109**, 175-185.

Abbott, I. (2005). Historical perspectives of the ecology of some conspicuous vertebrate species in south-west Western Australia. Manuscript (in preparation to be submitted for publication to *Conservation Science Western Australia*).

Abbott, I. and Whitford, K. (2002). Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: strategic risk assessment in relation to ecology, policy, planning, and operations management. *Pacific Conservation Biology* **7**, 240-255.

Aebischer, N. J., Robertson, P. A. and Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313-1325.

Alldredge, J. R. and Dasgupta, N. (2003). Multiple comparisons in resource selection using logistic regression. *Journal of Agricultural, Biological and Environmental Statistics* **8**, 356-366.

Alldredge, J. R. and Ratti, J. T. (1986). Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management.* **50**, 157-165.

Alldredge, J. R. and Ratti, J. T. (1992). Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **56**, 1-9.

Alldredge, J. R., Thomas, D. L. and McDonald, L. L. (1998). Survey and comparison of methods for study of resource selection. *Journal of Agricultural, Biological, and Environmental Statistics* **3**, 237-253.

Augee, M. L., Smith, B. and Rose, S. (1996). Survival of wild and hand-reared ringtail possums (*Pseudocheirus peregrinus*) in bushland near Sydney. *Wildlife Research* **23**, 99-108.

Bennett, A. F., Lumsden, L. F., Alexander, J. S. A., Duncan, P. E., Johnson, P. G., Robertson, P. and Silveira, C. E. (1991). Habitat use by arboreal mammals along an environmental gradient in north-eastern Victoria. *Wildlife Research* **18**, 125-146.

Bos, D. G. and Carthew, S. M. (2003). The influence of behaviour and season on habitat selection by a small mammal. *Ecography* **26**, 810-820.

Calder, T. G., Golding, B. G. and Manderson, A. D. (1983). 'Management of arboreal species in Wombat State Forest. Environmental Report No. 16.' Graduate School of Environmental Science, Monash University, Melbourne.

CALM (1995). 'Silvicultural Guidelines 1/95: Silvicultural Practice in Jarrah Forest.' Western Australian Government Department of Conservation and Land Management, Perth.

CALM (1998). 'Draft Management Plan: Perup Forest and Lake Muir/Unicup Nature Reserves.' Western Australian Government Department of Conservation and Land Management, Perth.

Calver, M. C., Bradley, J. S. and Wright, I. W. (1999). Towards scientific contributions in applying the precautionary principle: an example from southwestern Australia. *Pacific Conservation Biology* **5**, 63-72.

Chambers, L. K. and Dickman, C. R. (2002). Habitat selection of the long-nosed bandicoot, *Perameles nausuta* (Mammalia, Peramelidae), in a patchy urban environment. *Austral Ecology* **27**, 334-342.

Cooper, A. B. and Millspaugh, J. J. (1999). The application of discrete choice models to wildlife resource selection studies. *Ecology* **80**, 566-575.

Dasgupta, N. and Alldredge, J. R. (2000). A chi-square goodness-of-fit analysis of dependent resource selection data. *Biometrics* **56**, 402-408.

Davey, S. M. (1984). Habitat preferences of arboreal marsupials within a coastal forest in southern New South Wales. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 509-516. (Australian Mammal Society: Sydney)

de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

Driscoll, A. W. (2000). A comparison between the insulation qualities of hollows in trees and nests in balga (*Xanthorrhoea preissii*): A study relating to habitat used by the western ringtail possum (*Pseudocheirus occidentalis*). Honours thesis, Australian National University.

Dunnet, G. M. (1956). A live-trapping study of the brush-tailed possum *Trichosurus vulpecula* Kerr (Marsupialia). *Wildlife Research* **1**, 1-18.

Dunning, J. B., Danielson, B. J. and Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos* **65**, 169-175.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. and Stevens, E. E. (1995). Spatially-explicit population models – current forms and future uses. *Ecological Applications* **5**, 3-11.

Ellis, M. and Jones, B. (1992). Observations of captive and wild western ringtail possums *Pseudocheirus occidentalis*. *Western Australian Naturalist* **19**, 1-10.

Eyre, T. J. and Smith, A. P. (1997). Floristic and structural habitat preferences of yellow-bellied gliders (*Petaurus australis*) and selective logging impacts in southeast Queensland, Australia. *Forest Ecology and Management* **98**, 281-295.

Faunt, K. (1992). 'Formation, frequency and longevity of hollows in jarrah.' Western Australian Government Department of Conservation and Land Management, Perth.

Ganey, J. L., Block, W. M., Jenness, J. S. and Wilson, R. A. (1999). Mexican spotted owl home range and habitat use in pine-oak forest: Implications for forest management. *Forest Science* **45**, 127-135.

Gibbons, P. and Lindenmayer, D. B. (2002). ' Tree Hollows and Wildlife Conservation in Australia.' (CSIRO Publishing: Melbourne)

Gibbons, P., Lindenmayer, D. B., Barry, S. C. and Tanton, M. T. (2002). Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation* **103**, 1-12.

Ginger, S. M., Hellgren, E. C., Kasparian, M. A., Levesque, L. P., Engle, D. M. and Leslie, D. M. (2003). Niche shift by Virginia opossum following reduction of a putative competitor, the raccoon. *Journal of Mammalogy* **84**, 1279-1291.

Goldingay, R. L. and Kavanagh, R. P. (1995). Foraging behavior and habitat use of the feathertail glider (*Acrobates pygmaeus*) at Waratah Creek, New South Wales. *Wildlife Research* **22**, 457-470.

Harper, M. J., McCarthy, M. A., van der Ree, R. and Fox, J. C. (2004). Overcoming bias in ground-based surveys of hollow-bearing trees using double-sampling. *Forest Ecology and Management* **190**, 291-300.

Herter, D. R., Hicks, L. L., Stabins, H. C., Millspaugh, J. J., Stabins, A. J. and Melampy, L. D. (2002). Roost site characteristics of northern spotted owls in the nonbreeding season in central Washington. *Forest Science* **48**, 437-444.

Hjermann, D. O. (2000). Analysing habitat selection in animals without well-defined home ranges. *Ecology* **8**, 1462-1468.

Holling, C. S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* **62**, 447-502.

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

How, R. A., Barnett, J. L., Bradley, A. J., Humphreys, W. F. and Martin, K. J. (1984). Population biology of *Pseudocheirus peregrinus* in a *Leptospermum laevigatum* thicket. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 261-268. (Australian Mammal Society: Sydney)

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187-211.

Inions, G. (1985). The interactions between possums, habitat trees and fire. Honours thesis, Australian National University.

Inions, G. B., Tanton, M. T. and Davey, S. M. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**, 449-458.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **6**, 65-71.

Jones, B. (1995). Western Ringtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan) pp. 252-254. (Reed Books: Chatswood)

Jones, B. (2004). The possum fauna of Western Australia: decline, persistence and status. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 149-160. (Surrey Beatty and Sons: Sydney)

Jones, B. and Hillcox, S. (1995). A survey of the possums *Trichosurus vulpecula* and *Pseudocheirus occidentalis* and their habitats in forest at Ludlow, Western Australia. *Western Australian Naturalist* **20**, 139-150.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994a). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175-187.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994b). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Kavanagh, R. P. (1984). Seasonal changes in habitat use by gliders and possums in south eastern New South Wales. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 527-543. (Australian Mammal Society: Sydney)

Kavanagh, R. P. (1987). Forest phenology and its effect on foraging behaviour and selection of habitat by the yellow-bellied glider, *Peturus australis* Shaw. *Australian Wildlife Research* **14**, 371-384.

Keating, A. K., and Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *Wildlife Management* **68**, 774-789.

Kerle, J. A. (1984). Variation in the ecology of *Trichosurus:* its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 115-128. (Australian Mammal Society: Sydney)

Kerle, J. A. (2001). 'Possums: the brushtails, ringtails and greater glider (First edn).' (University of New South Wales Press: Sydney)

Kerle, J. A. (2004). A cautionary tale: decline of the common brushtail possum *Trichosurus vulpecula* and common ringtail possum *Pseudocheirus peregrinus* in the woodlands of the western slopes and plains of New South Wales. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 71-84. (Surrey Beatty and Sons: Sydney)

Kerr, G. D., Bull, C. M. and Burzacott, D. (2003). Refuge sites used by the scincid lizard *Tiliqua rugosa*. *Austral Ecology* **28**, 152-160.

King, J. R. and Withler, R. E. (2005). Male nest site fidelity and female serial polyandry in lingcod (*Ophiodon elongatus*, Hexagrammidae). *Molecular Ecology* **14**, 653-660.

Kokko, H., Harris, M. P. and Wanless, S. (2004). Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology* **73**, 367-376.

Krebs, C. J. (1985). 'Ecology: The Experimental Analysis of Distribution and Abundance (Third edn).' (Harper Collins Publishers: New York)

Lancaster, T. and Imbens, G. (1996). Case-control studies with contaminated controls. *Journal of Econometrics* **71**, 145-160.

Lemmon, P. E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science* **2**, 314-320.

Lindenmayer, D. B. (1997). Differences in the biology and ecology of arboreal marsupials in forests of southeastern Australia. *Journal of Mammalogy* **78**, 1117-1127.

Lindenmayer, D. B. (2000). Factors at multiple scales affecting distribution patterns and their implications for animal conservation – Leadbeater's possum as a case study. *Biodiversity and Conservation* **9**, 15-35.

Lindenmayer, D. B. (2003). Integrating wildlife conservation and wood production in Victorian montane ash forests. In 'Towards Forest Sustainability'. (Eds D. B. Lindenmayer and J. F. Franklin) pp. 47-72. (CSIRO Publishing: Melbourne)

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P. and Nix, H. A. (1990). The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, southeast Australia: I. Factors influencing the occupancy of trees with hollows. *Biological Conservation* **54**, 111-131.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P. and Nix, H. A. (1991a). Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. *Forest Ecology and Management* **40**, 289-308.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Nix, H. A. and Smith, A. P. (1991b). The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia: III. The habitat requirements of Leadbeater’s possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. *Biological Conservation* **56**, 295-315.

Lindenmayer, D. B., Welsh, A., Donnelly, C. F. and Meggs, R. A. (1996). Use of nest trees by mountain brushtail possum (*Trichosurus caninus*) (Phalangeridae: Marsupialia). I. Number of occupied trees and frequency of tree use. *Wildlife Research* **23**, 343-361.

Lindenmayer, D. B., Cunningham, R. B., MacGregor, C., Tribolet, C. and Donnelly, C. F. (2001). A prospective longitudinal study of landscape matrix effects on fauna in woodland remnants: experimental design and baseline data. *Biological Conservation* **101**, 157-169.

Lindenmayer, D. B., Pope, M. L. and Cunningham, R. B. (2004). Patch use by the greater glider (*Petauroides volans*) in a fragmented forest ecosystem. II. Characteristics of den trees and preliminary data on den-use patterns. *Wildlife Research* **31**, 569-577.

Loyn, R. H., McNabb, E. G., Volodina, L. and Willig, R. (2001). Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. *Biological Conservation* **97**, 361-376.

Luck, G. W. (2002). The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation* **105**, 383-394.

Mackey, B. G. and Lindenmayer, D. B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography* **28**, 1-21.

Mackowski, C. M. (1984). The ontogeny of hollows in blackbutt (*Eucalyptus pilularis*) and its relevance to the management of forests for possums, gliders and timber. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 553-567. (Australian Mammal Society: Sydney)

Maitz, W. E. and Dickman, C. R. (2001). Competition and habitat use in native Australian *Rattus*: is competition intense, or important? *Oecologia* **128**, 526-538.

Mawson, P. R. and 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.

Maxwell, S., Burbidge, A. A. and Morris, K. (1996). 'The 1996 Action Plan for Australian Marsupials and Monotremes.' Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Project No. 500, Perth.

McComb, B. (1994). 'Mapping potential habitat for vertebrates in forests of Western Australia – Final Report.' Department of Forest Science, Oregon State University, Oregon.

McComb, W. C., Faunt, K., Bradshaw, F. J. and Biggs, P. (1994). 'Hollow availability for selected vertebrates in jarrah forests, Western Australia.' Western Australian Government Department of Conservation and Land Management, Perth.

McComb, W. C., McGrath, M. T., Spies, T. A. and Vesely, D. (2002). Models for mapping potential habitat at landscape scales: An example using northern spotted owls. *Forest Science* **48**, 203-227.

McKay, G. M. and Ong, P. (1995). Common Ringtail Possum. In 'The Australian Museum Complete Book of Australian Mammals'. (Ed. R. Strahan) pp. 254-256. (Reed Books: Chatswood)

Meredith, C. W. (1984). Possums or poles? The effects of silvicultural management on possums of Chiltern State Park, north-east Victoria. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 575-577. (Australian Mammal Society: Sydney)

Mitchell, M. S., Lancia, R. A. and Gerwin, J. A. (2001). Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications* **11**, 1692-1708.

Munks, S. A., Mooney, N., Pemberton, D. and Gales, R. (2004). An update on the distribution and status of possums and gliders in Tasmania, including off-shore islands. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 111-129. (Surrey Beatty and Sons: Sydney)

Nams, V. O. (1989). Effects of radiotelemetry error on sample-size and bias when testing for habitat selection. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **67**, 1631-1636.

Nordmoe, E. D., Sieg, A. E., Sotherland, P. R., Spotila, J. R., Paladino, F. V. and Reina, R. D. (2004). Nest site fidelity of leatherback turtles at Playa Grande, Costa Rica. *Animal Behaviour* **68**, 387-394.

Ough, K. and Murphy, A. (1998). 'Understorey Islands: a method of protecting understorey flora during clearfelling operations.' Department of Natural Resources and Environment. Agriculture Resources Conservation Land Management, No. 29, Victoria.

Pahl, L. I. (1984). Diet preference, diet composition and population density of the ringtail possum (*Pseudocheirus peregrinus cooki*) in several plant communities in southern Victoria. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume) pp. 253-260. (Australian Mammal Society: Sydney)

Pahl, L. I. (1987). Survival, age determination and population age structure of the common ringtail possum, *Pseudocheirus peregrinus*, in a *Eucalyptus* woodland and a *Leptospermum* thicket in southern Victoria. *Australian Journal of Zoology* **35**, 625-639.

Paull, D. and Kerle, J. A. (2004). Recent decline of common brushtail and common ringtail possums in the Pilliga forests, New South Wales? In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 85-90. (Surrey Beatty and Sons: Sydney)

Pickett, K. N., Hik, D., Newsome, A. and Pech, R. P. (2005). The influence of predation risk on foraging behaviour of brushtail possums in Australian woodlands. *Wildlife Research* **32**, 121-130.

Porter, W. F. and Church, K. E. (1987). Effects of environmental pattern on habitat preference analysis. *Journal of Wildlife Management* **51**, 681-685.

Priddel, D. and Wheeler, R. (2003). Nesting activity and demography of an isolated population of malleefowl (*Leipoa ocellata*). *Wildlife Research* **30**, 451-464.

Pulliam, H. R. and Danielson, B. J. (1991). Sources, sinks, and habitat selection – a landscape perspective on population-dynamics. *American Naturalist* **137**, S50-S66.

Rudolph, D. C. and Conner, R. N. (1996). Red-cockaded woodpeckers and silvicultural practice: Is uneven-aged silviculture preferable to even-aged? *Wildlife Society Bulletin* **24**, 330-333.

Russell, B. G., Smith, B. and Augee, M. L. (2003). Changes to a population of common ringtail possums (*Pseudocheirus peregrinus)* after bushfire. *Wildlife Research* **30**, 389-396.

Sampson, J. C. (1971). The biology of *Bettongia penicillata* Gray, 1837. PhD thesis, University of Western Australia.

Saunders, D. A., Smith, G. T. and Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research* **9**, 541-556.

Schmidt, K. A., Earnhardt, J. M., Brown, J. S. and Holt, R. D. (2000). Habitat selection under temporal heterogeneity: exorcising the ghost of competition past. *Ecology* **81**, 2622-2630.

Schooley, R. L. (1994). Annual variation in habitat selection – patterns concealed by pooled data. *Journal of Wildlife Management* **58**, 367-374.

Semel, B. and Sherman, P. W. (2001). Intraspecific parasitism and nest-site competition in wood ducks. *Animal Behaviour* **61**, 787-803.

Smith, B., Augee, M. and Rose, S. (2003). Radio-tracking studies of common ringtail possums, *Pseudocheirus peregrinus*, in Manly Dam Reserve, Sydney. *Proceedings of the Linnean Society of New South Wales* **124**, 183-194.

Stanback, M. T. and Rockwell, E. K. (2003). Nest-site fidelity in eastern bluebirds (*Sialia sialis*) depends on the quality of alternate cavities. *Auk* **120**, 1029-1032.

Storz, J. F., Balasingh, J., Nathan, P. T., Emmanuel, K. and Kunz, T. H. (2000). Dispersion and site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*) in southern India. *Journal of Tropical Ecology* **16**, 117-131.

Tan, P. (1999). Population parameters of two common brushtail possum, *Trichosurus vulpecula* (Kerr), populations. Honours thesis, University of Western Australia.

Thomas, D. L. and Taylor, E. J. (1990). Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* **54**, 322-330.

Thomson, J. A. and Owen, W. H. (1964). A field study of the Australian ringtail possum *Pseudocheirus peregrinus* (Marsupialia : Phalangeridae). *Ecological Monographs* **34**, 27-52.

Traill, B. J. (1991). Box-ironbark forests: tree hollows, wildlife and management. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 119-123. (Royal Zoological Society of NSW: Sydney)

Tyndale-Biscoe, C. H. (1955). Observations on the reproduction and ecology of the brush-tailed possum, *Trichosurus vulpecula* Kerr (Marsupialia), in New Zealand. *Australian Journal of Zoology* **3**, 162-184.

Vernes, K. (2003). Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, north-eastern Australia. *Austral Ecology* **28**, 471-479.

Wang, H. C. and Cheng, I. J. (1999). Breeding biology of the green turtle, *Chelonia mydas* (Reptilia : Cheloniidae), on Wan-An Island, Penghu archipelago. II. Nest site selection. *Marine Biology* **133**, 603-609.

Ward, G. D. (1978). Habitat use and home range of radio-tagged opossums *Trichosurus vulpecula* (Kerr) in New Zealand lowland forest. In 'Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery) pp. 267-287. (Smithsonian Institution Press: Washington)

Wardell-Johnson, G., Calver, M. C., Saunders, D. A., Conroy, S. and Jones, B. (2004). Why integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 394-417. (Royal Zoological Society of New South Wales: Sydney)

Wayne, A. F., Ward, C., Rooney, J. and Wheeler, I. (2000). 'The immediate impacts of timber harvesting and associated activities on the ngwayir (*Pseudocheirus occidentalis*) in the jarrah forest of Kingston State Forest Block. Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Cowling, A., Ward, C. G., Rooney, J. F., Vellios, C. V., Lindenmayer, D. B. and Donnelly, C. F. (2005b [Chapter 3]). A comparison of survey methods for arboreal possums in jarrah forest, Western Australia. *Wildlife Research* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005c [Chapter 4]). The life history of *Trichosurus vulpecula hypoleucus* (Phalangeridae), in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wayne, A. F., Ward, C. G., Rooney, J. F., Vellios, C. V. and Lindenmayer, D. B. (2005d [Chapter 5]). The life history of *Pseudocheirus occidentalis* (Pseudocheiridae) in the jarrah forest of south-western Australia. *Australian Journal of Zoology* – revised manuscript in review.

Wayne, A. F., Cowling, A., Lindenmayer, D. B., Ward, C. G., Vellios, C. V. and Donnelly, C. F. (2005e [Chapter 7]). The abundance of a threatened arboreal marsupial in relation to anthropogenic disturbances at local and landscape scales in Mediterranean-type forest in south-western Australia. *Biological Conservation* – revised manuscript in review.

Wayne, A. F., Cowling, A., Lindenmayer, D. B., Ward, C. G., Vellios, C. V. and Donnelly, C. F. (in preparation-b). The abundance of koomal, *Trichosurus vulpecula hypoleucus* in relation to anthropogenic disturbances at local and landscape scales in Mediterranean forest in Western Australia.

White, G. C. and Garrott, R. A. (1986). Effects of biotelemetry triangulation error on detecting habitat selection. *Journal of Wildlife Management* **50**, 509-513.

Whitford, K. R. (2001). Dimensions of tree hollows used by fauna in the jarrah forest: improving the dimensional description of potentially usable hollows. *CALMScience* **3**, 499-511.

Whitford, K. R. (2002). Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees: I. Hollow sizes, tree attributes and ages. *Forest Ecology and Management* **160**, 201-214.

Whitford, K. R. and Williams, M. R. (2002). Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees – II. Selecting trees to retain for hollow dependent fauna. *Forest Ecology and Management* **160**, 215-232.

Williams, M. R. and Faunt, K. (1997). Factors affecting the abundance of hollows in logs in jarrah forest of south-western Australia. *Forest Ecology and Management* **95**, 153-160.

Wilson, S. F., Shackleton, D. M. and Campbell, K. L. (1998). Making habitat-availability estimates spatially explicit. *Wildlife Society Bulletin* **26**, 626-631.

Winter, J. W. (1976). The behaviour and social organisation of the brushtail possum (*Trichosurus vulpecula* Kerr). PhD thesis, University of Queensland.

Wood Jones, F. (1924). South Australian ring-tailed possum. In 'The Mammals of South Australia'. pp. 175-180. (Government Printer: Adelaide)

Wood, M. S. and Wallis, R. L. (1998). Potential competition for nest sites between feral European honeybees (*Apis mellifera*) and common brushtail possums (*Trichosurus vulpecula*). *Australian Mammalogy* **20**, 377-381.

Young, R. A. (2001). The eastern horseshoe bat, *Rhinolophus megaphyllus*, in south-east Queensland, Australia: colony demography and dynamics, activity levels, seasonal weight changes, and capture-recapture analyses. *Wildlife Research* **28**, 425-434.

Chapter 7

THE ABUNDANCE OF NGWAYIR IN RELATION TO ANTHROPOGENIC DISTURBANCES AT LOCAL AND LANDSCAPE SCALES

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Six-year-old regrowth jarrah forest (Dudijup)

Old-growth jarrah forest (Curtin), immediately after a prescribed fuel-reduction burn

7.1 Abstract

This study investigated associations between the relative abundance of the threatened ngwayir (western ringtail possum, *Pseudocheirus occidentalis*) and anthropogenic disturbances at local and landscape scales within the publicly-managed jarrah (*Eucalyptus marginata*) forests of south-western Australia. Logging, fire, fox (*Vulpes vulpes*) control and forest fragmentation were investigated in relation to the relative abundance of ngwayir at 90 sites within an area of 285,000 ha east of Manjimup; the location of the last remaining substantial population of ngwayir in jarrah forest. Overall, ngwayir abundance was greatest in areas with limited anthropogenic disturbance. At the local scale, ngwayir abundance was negatively associated with greater fire intensity. At the landscape scale, it was positively associated with fox control and negatively associated with forest fragmentation and distance from non-remnant vegetation (i.e. agriculture and tree plantations). Abundance was also greatest in predominantly unlogged landscapes and in forests that had been regrowing for an average of 40 years since the landscape was most recently logged, in other words, where logging was historically least intense. Interactions between fox control efforts and forest fragmentation were also important. This study emphasises the importance of conducting research at appropriate spatial scales and to account for the synergistic effects of the causes of decline. An adaptive management approach to the mitigation of the agents of decline is recommended.

Indirect evidence indicates that high value habitat for ngwayir has in all likelihood been selectively cleared for agriculture, owing to its fertile and productive nature. Habitat loss is, therefore, also likely to be a major cause of the modern decline of the species. While many jarrah forest areas that support remaining high abundances of the ngwayir have been incorporated into reserves, conservation of ngwayir habitat and populations outside reserves also will be essential for the recovery and long-term viability of the species.

7.2 Introduction

Understanding the processes that shape the distribution and abundance patterns of species is fundamental for the study of ecology (Elton, 1927) and for effective biodiversity conservation (Caughley and Gunn, 1996; Lindenmayer and Burgman, 2005). Most modern population declines and extinctions are principally caused by anthropogenic factors, including the loss, degradation and fragmentation of habitats, and introduced species (Primack, 2001; Gaston and Spicer, 2004). Given the complexity and synergistic effects of threatening processes (Hobbs, 2001) and potential confounding factors, the need for large sample sizes means that it is more tractable to study declining populations *before* they become too scarce (Norton et al., 1995). Greater understanding of the threatening processes enables more effective and efficient mitigation. Linking the threatening processes with the patterns of distribution and abundance in a timely manner is therefore fundamental to creating successful conservation strategies.

The decline and extinction of mammals in modern times have been greatest in Australia (Burbidge and McKenzie, 1989; Maxwell et al., 1996). Of 305 mammal species present prior to European settlement, 27 are extinct and 86 are threatened (World Wildlife Fund, 2004). Although forests cover only 5% of Australia's landmass, they are an important habitat for 77% of its mammal species (Lamb and Smyth, 2003). The jarrah (*Eucalyptus marginata*) forests of south-western Australia support a particularly high level of biodiversity (Wardell-Johnson and Horwitz, 1996). The jarrah forest bioregion is one of the most important Australian bioregions for the conservation of numerous species that have disappeared from much of their former ranges (National Land and Water Resources Audit, 2002). Although considerable research into disturbance ecology has been carried out in the region (Wardell-Johnson and Nichols, 1991), the lack of appropriate studies of the causes of declining populations of native species seriously hampers the effective conservation of local biodiversity (Christensen and Abbott, 1989; Nichols and Muir, 1989; Christensen, 1997; Calver and Dell, 1998a, b; Friend and Wayne, 2003; Wardell-Johnson et al., 2004).

One such species is the ngwayir (pronounced 'n-waar-ear') or western ringtail possum (*Pseudocheirus occidentalis*), a specialist arboreal folivore endemic to south-western Australia. Having undergone a substantial reduction in distribution since European settlement (Jones, 2004; P. de Tores, unpublished data), the ngwayir is currently considered 'vulnerable' (World Conservation Union, 1994) and 'fauna which is rare or likely to become extinct' (Western Australian *Wildlife Conservation Act, 1950*). Mainly on account of the difficulties associated with detecting this rare species (Jones et al., 1994a; Wayne et al., 2005b [Chapter 3]), no previous study has explicitly quantified the factors underpinning its distribution and abundance patterns or the causes for its decline. There also are differences of opinion regarding the response of ngwayir to logging (Calver and Dell, 1998a, b; Abbott and Whitford, 2002), fire (Christensen and Abbott, 1989; Friend and Wayne, 2003) and fox control (Jones, 2004; Wardell-Johnson et al., 2004).

The purpose of this study was to increase the ecological knowledge of the ngwayir relevant to its conservation within the publicly owned and managed jarrah forest of the Upper Warren region of south-western Australia. More specifically and within this context, this study examined ngwayir distribution and abundance in relation to logging, fire, fox control and native forest fragmentation at both local and landscape scales. In so doing, this paper serves to resolve some of the contentions regarding ngwayir responses to selected anthropogenic factors. As such, this study constitutes the first extensive and detailed ecological research into the last substantial ngwayir population in the jarrah forests.

7.3 Methods

7.3.1 Study area

Jarrah occurs in the Mediterranean-type forest ecosystems confined to south-western Australia (Dell and Havel, 1989). Within the main forest belt, 65% remains of the distribution of jarrah forests present at the time of European settlement (2.8 million ha). Of the present extent, 87% (1.6 million ha) is managed by the Western Australian Government Department of Conservation and Land Management (Conservation Commission, 2004). Historically, jarrah has been one of the most important native timbers in Australia and most of what remains has therefore been subject to recurrent logging (Jarvis, 1979; Herberle, 1997). Currently, 52% of the jarrah forests vested in the Conservation Commission and managed by the Department of Conservation and Land Management are formally or informally reserved. The remainder are available for logging (Conservation Commission, 2004).

The study area (Figure 7.1), termed the Upper Warren, consists of 285,000 ha of publicly-managed jarrah forest (managed by the Department of Conservation and Land Management) within the upper catchment area of the Warren River, east of Manjimup. Further details on the region are provided by McArthur and Clifton (1975), Wilde and Walker (1984), Strelein (1988) and Department of Conservation and Land Management (1998).

7.3.1.1 Logging history

After unregulated logging in many jarrah forests between the 1870s and 1920, controls were imposed and silvicultural practices have evolved (Bradshaw, 1999; Calver and Wardell-Johnson, 2004;Wardell-Johnson and Calver, 2004, 2005; Stoneman et al., 2005). Between 1920 and 1940, some parts of the jarrah forest were intensively treated as part of a group selection system of logging. More extensive but less intensive logging practices occurred between 1940 and 1960s. From about 1970, more intensive cutting aimed to reduce the area logged each year (Bradshaw, 1999; Stoneman et al., 2005; Wardell-Johnson and Calver 2005). Recent (i.e. 1984 - 2003) silvicultural practices most closely resemble the group selection system used in the 1920s and 1930s. These practices included the intensive ‘Gap release’ treatment of patches up to 10 ha in stands with acceptable lignotuber stocking rates that would be released from suppression by almost complete overstorey removal. Designated ‘habitat’ trees (4-5 ha^{-1} primary and 6-8 ha^{-1} potential habitat trees) were retained and protected to provide shelter for hollow-dependent fauna. Where lignotuber densities were insufficient or inadequately developed for immediate release, a less intensive ‘Shelterwood’ system was adopted (Department of Conservation and Land Management, 1995). These areas retained an overstorey as a seed source, together with some of the structural habitat, while establishing lignotubers in preparation for the next cycle of logging.

This study was conducted prior to the commencement of new timber-harvesting practices that began in 2004 (Conservation Commission, 2004).

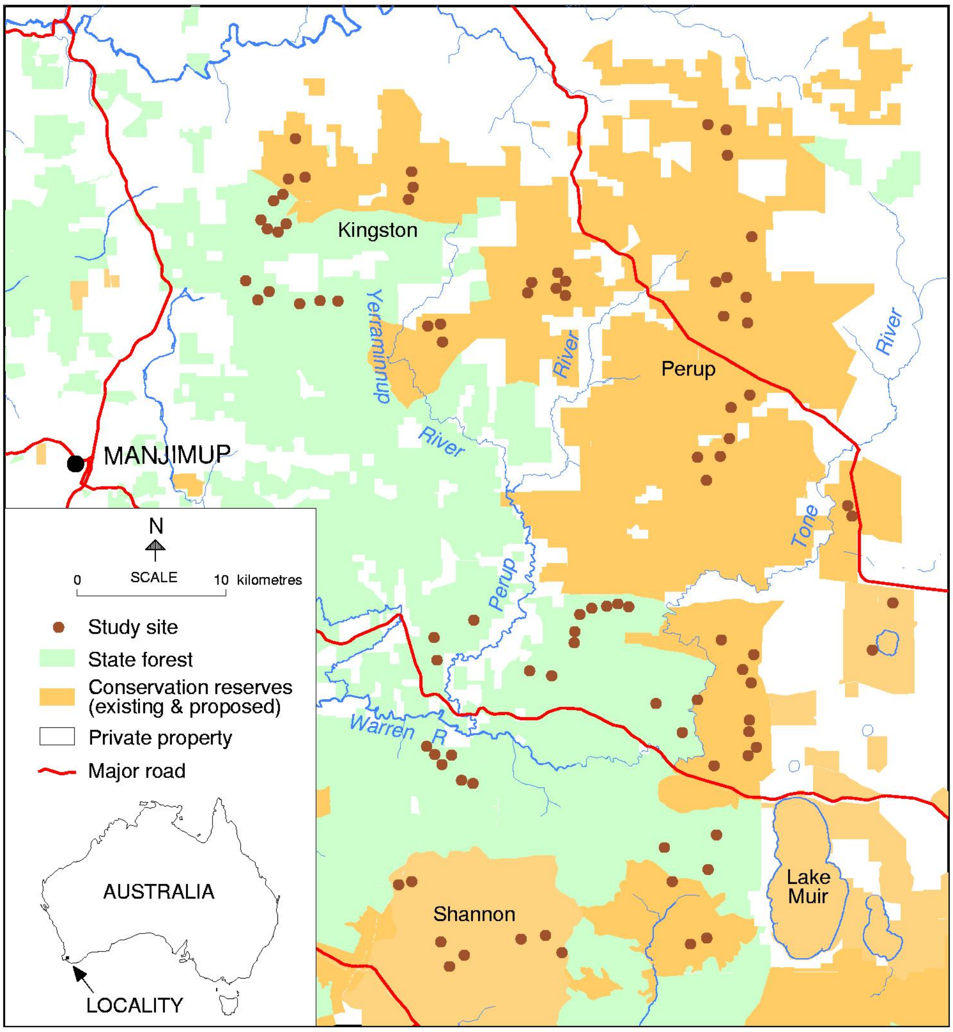

Figure 7.1. Location of the 90 study sites selected on the basis of logging history, fire history and topographic position in the publicly managed jarrah forests of the Upper Warren, south-western Australia.

7.3.1.2 Fire history

Fire scars on balga (X*anthorrhoea preissii*) grass trees suggest that the Noongar (south-west Australian Aborigines) activities prior to European settlement resulted in much of the jarrah forests being burnt about three times per decade. Since European settlement, fire frequency has declined (Ward et al., 2001; Lamont et al., 2003). Detailed fire history records for the study area since 1938 indicate that most forest stands have experienced one or more wildfires over the past 70 years (Burrows and Christensen, 2002). Since the 1950s, most of these forests have been subject to low-to-moderate-intensity fires every 7-12 years as part of a prescribed fuel-reduction burning programme (Department of Conservation and Land Management, 1998). Some areas have remained unburnt, since as long ago as 1954, as part of this programme. Silvicultural burns are generally applied to logging coupes after timber extraction has been completed. These are generally high intensity fires used to remove heavy fuel loads created by the logging debris and to stimulate regeneration. The regrowth is then protected from fire for the next 15-20 years to facilitate tree regeneration.

7.3.1.3 History of fox control

Predation by introduced red foxes has been identified as a key threat for many of Australia's small and medium-sized mammals (Burbidge and McKenzie, 1989; Kinnear et al., 2002). Native south-western Australian fauna have evolved a resistance to sodium monofluoroacetate (1080), which is naturally found in the endemic legume genus *Gastrolobium* (Twigg et al., 2003). The use of this toxin in meat baits to reduce fox numbers (Thomson et al., 2000) without adversely affecting native fauna has resulted in a strong recovery of many native mammal populations (Kinnear et al., 1998, 2002; Orell, 2004) and has improved the conservation status of several previously threatened species including the woylie (*Bettongia penicillata*), quenda (*Isoodon obesulus fusciventer*), tammar (*Macropus eugenii*) and chuditch (*Dasyurus geoffroii*) (Start et al., 1998; Morris et al., 2003).

Fox control in the Upper Warren has varied substantially between areas. Fox-baiting for the conservation of native fauna and research occurred in two areas of Perup Nature Reserve between 1977 and 1990 (Burrows and Christensen, 2002). Some areas, particularly in the northern part of the Upper Warren, also were occasionally ground-baited to reduce wild dogs (*Canis familiaris*) and foxes and protect nearby livestock between 1986 and 1992. Between 1992 and 1998, a strategy was introduced to ground-bait selected areas for conservation purposes, the selection being based partly on the existing diversity and abundance of native medium-sized mammals (I. Wilson, unpublished data). Extensive aerial fox-baiting (four baitings per year) within most of the publicly-managed forests of the Upper Warren (including all 90 study sites) began in 1996 as part of the 'Western Shield' conservation programme (Department of Conservation and Land Management, 2000; Orell, 2004).

7.3.2 Study design

Ninety sites within the Upper Warren were chosen as representative samples of logging histories, fire histories and topographic positions. Combinations of five logging classes and four fire history classes were included in an unbalanced experimental design, with 2-3 replicates per combination, resulting in 28 landscape units (Table 7.1). Most landscape units comprised three sites, one in each of three topographic positions: ‘Depression’, ‘Valley’ and ‘Upland’. Only two topographic positions were available in three of the long-unburnt landscape units. Landscape units in areas logged after 1985 had six sites, rather than three, to account for modern logging practices, which produce relatively small logged patches in a network of contemporarily unlogged forest. In these cases, paired sites were selected in each of the three topographic positions; one in an area intensively logged under the ‘Gap Release’ guidelines (Department of Conservation and Land Management, 1991, 1995), and one located in immediately adjacent, contemporarily unlogged forest within the same logging coupe.

Table 7.1. The logging history and fire history stratification matrix used to examine factors explaining the distribution and abundance of possums in publicly managed jarrah forests of the Upper Warren.

For each stratification combination there were either two or three replicate landscape units. Each landscape unit generally contained three sites, one in each of three topographic positions (depression, valley, upland). Variations on this design are described in further detail in the text. They are indicated here as follows:
* = A ‘depression’ position was unavailable for one of the landscape units;
** = A ‘depression’ or ‘valley’ position was absent for two of the landscape units;
^ = For each of the three replicate landscape units there were a total of six sites, comprising paired sites in each of the three topographic positions, one within a recently logged area, the other in immediately adjacent contemporarily unlogged forest.

		LOGGING HISTORY				
FIRE HISTORY	**FIRE INTENSITY**	**> 1985**	**1970-1984**	**1960-1969**	**< 1960**	**UNCUT**
Long Unburnt			2	2	2*	3**
Recent Burnt	Low to Mild intensity		2	2	2	2
Recent Burnt	High intensity		2	2	2	2
Silvicultural		3^				

7.3.2.1 Logging, fire and topographic classes for site selection

Using a Geographic Information System (GIS), all candidate study areas were selected from public jarrah forests managed by the Department of Conservation and Land Management. On the basis of evolving logging practices (Bradshaw, 1999), and after consultation with senior forest managers (Department of Conservation and Land Management), logging history was classified in five classes: uncut, last logged prior to 1960 (< 1960), last logged 1960-69, last logged 1970-1984 and last logged after 1985 (> 1985) (Table 7.2).

With regard to fire, it was considered more appropriate to distinguish sites based on fire intensity rather than distinguish between prescribed burns and wildfires. This was because fire intensity is likely to be more relevant to ngwayir response than whether or not the fire was planned and initiated by forest managers. Thus, fire history was classified in four classes: (1) long unburnt areas (last burnt before 1985); (2) recent, mild-intensity fire between 1995/1996 and 2003/2004); (3) recent, high-intensity fire between 1995/1996 and 2003/2004; and (4) silvicultural burn (which applies only to the post-1985 logging class).

The definition of the three topographic positions used to select sites within a given landscape unit was derived from the aggregation of vegetation associations by Havel and Mattiske (2000). The three topographic classes reflect an interaction between landscape position, landform, substrate, drainage and, consequently, the vegetative responses to these factors. They are defined as follows;

Depressions are generally flat, convex or very gently sloping sites located anywhere throughout the landscape. The soils are predominantly sedimentary, ranging from pale grey to yellow sandy (quartzose) surfaces, usually over clay. These sites are characteristically infertile, with poor lateral and internal drainage, and are usually seasonally waterlogged.

Valleys are sloping or terraced sites that may be broadly to moderately incised. The yellow, red-brown or brown soils generally contain some loam. Fertility is moderate-to-good. The slopes are water-shedding and the terraces water-gaining. They generally have moderate to good water infiltration and storage capacities. Some valleys may contain intermittent streams, but rarely have any permanent water.

Uplands are generally low hills, broadly convex crests, and smooth slopes of granite and/or laterite. They typically have gravely yellow duplex or shallow soils. Fertility is low-to-moderate. These are generally water-shedding sites with poor-to-moderate water infiltration and storage capacities.

Table 7.2. The five logging history classes used in the stratification matrix and selection of study sites for the investigation into which factors explain the distribution and abundance of ngwayir in the jarrah forests of the Upper Warren.

CLASS	DESCRIPTION
Uncut	No record of official logging activities. Some areas may have experienced some minimal or non-commercial timber removal
Pre-1960	Generally light selective harvests for premium jarrah sawlog. Logged areas were limited in extent and concentrated around the mills. Commercial activity began in the 1920s and expanded steadily, except during the First and Second World Wars.
1960-1969	Some variability in logging intensity, frequency and treatment, but generally selective harvesting for premium jarrah sawlogs. Extensive areas remain representative of this class, reflecting the high level of activity during this period.
1970-1984	Some variability in logging intensity, frequency and treatment, but generally selective harvesting for premium jarrah sawlogs. Extensive areas remain representative of this class, reflecting the high level of activity during this period.
Post-1985	Areas are either intensively logged (‘Gap Release’), moderately logged (‘Shelterwood’) or thinned, depending on the forest structure and potential for rapid regeneration (Department of Conservation and Land Management, 1991, 1995). Only Gap Release areas were included in this study.

7.3.2.2 Study sites

Sites were selected as centrally as possible within the larger available treatment areas to reduce potential edge effects. Within each landscape unit, the three sites for each topographic position were generally spaced > 1000 m apart. The recently-logged topographic site pairs were 200 m to 600 m apart. The distance between different landscape units and replicates was maximised where possible, and an even spread of sites over the entire study region was obtained where possible. The location of sites was nonetheless strongly influenced by the limited options available and the uneven spatial distribution of logging histories. At each of the 90 field survey sites, two 300 m parallel transects were spaced 50 m apart to fit within the ‘Gap Release’ logging cells (< 10 ha) and narrow linear valley systems.

7.3.3 Relative measure of ngwayir abundance

The incidence of scats was used as an index of abundance (Jones et al., 1994a). Ngwayir are difficult to trap, and the incidence of scats is robust to inter-observer variability and has a strong correlation with estimates from more direct and intensive spotlight survey methods (Wayne et al., 2005b [Chapter 3]). Scat counts thus provide a reliable and practical means of assessing a wide range of sites and habitats (Wayne et al., 2005b [Chapter 3]). At each site, the presence or absence of ngwayir scats was assessed within 42 circular scat plots (1 m diameter each), spaced 15 m apart along the two 300 m parallel transects. Plots were located under a tree canopy and away from tracks and areas of recent ground disturbance. All scat surveys were conducted during January and February 2004, towards the end of the summer drought, when moisture-driven scat decay was minimal (Chapman 2002).

7.3.4 Covariate data

Habitat surveys at six regularly spaced circular plots (0.04 ha) per site provided data on local-scale covariates such as logging intensity (basal area of cut stumps) and fire intensity (average jarrah char height). Other covariates relating to logging, fire, fox control and native forest fragmentation were derived from GIS data. These covariates are described in Appendix 1. While we acknowledge that interactions will occur between anthropogenic and environmental variables (e.g. nutrients, climate, topography and vegetation), a similar pragmatic approach to that of Catling *et al.* (2000, 2002) was used, in which anthropogenic factors were modelled separately from environmental factors. Potential historical legacies, such as disease and hunting, may also influence the current distribution and abundance of ngwayir. These have not been incorporated into our analyses as few data are available.

7.3.5 Data analysis

Binomial generalised linear models were used: (1) to describe the general spatial pattern of possum abundance; and (2) to examine how anthropogenic factors related to the abundance of possums at (a) the local scale, and (b) the landscape scale. The response variable for all models was the number of plots in which scats were detected at each site. The explanatory variables for the spatial pattern were one-knot regression splines in latitude, longitude and their interaction. To examine whether the response to each of the anthropogenic covariates could be approximated by linear terms in the generalised linear models, generalised additive models (GAMs) were used. In generalised additive models, the usual linear functions of the covariates are replaced by unspecified smooth functions, revealing the appropriate shape of each covariate effect (Hastie and Tibshirani, 1990). Forward selection of anthropogenic covariates was used both with and without the spatial terms included in the models.

7.4 Results

At each site ngwayir scats were detected on an average of nine out of 42 plots (data range = 0-41 plots). No ngwayir scats were recorded on any plots at 22 of the 90 sites.

7.4.1 Overall distribution and abundance patterns

A general spatial pattern to ngwayir abundance was evident from the raw data (Figure 7.2a), and was described using a generalised linear model and regression splines (Figure 7.2b). Abundance was generally greatest in the north-eastern quarter of the Upper Warren (i.e. Perup Nature Reserve), with a smaller secondary peak in the north-west (around Kingston forest). The abundance of ngwayir tended to be low or absent at the southern sites. The generalised additive models revealed that linear relationships between the response variable and covariates were appropriate for all except ‘average logging age’ at the landscape scale. A regression spline with one knot was used for this covariate. When spatial terms were fitted first in generalised linear models examining the relationship between ngwayir abundance and local-scale or landscape-scale anthropogenic factors, no other covariates had a significant effect, showing that there was no additional information in these variables that had not already been accounted for in the spatial terms. Therefore, only the anthropogenic factors were entered in generalised linear models using a forward fitting procedure.

7.4.2 Local-scale associations with ngwayir abundance

When the covariates were included in the models one at a time, fire intensity, fire age and fire frequency were significantly related to ngwayir abundance. When these terms were entered using a forward stepwise succession procedure, fire intensity was the only significant term ($F_{1, 88} = 25.9166$, $p < 0.001$; Table 7.3; Figure 7.3). When the spatial terms were added to this model after fire intensity, the residual deviance was significantly ($p = < 0.001$) reduced from 1597 in the null model, to 1252 with fire intensity included. Residual deviance was further reduced to 180 after the spatial terms had been added.

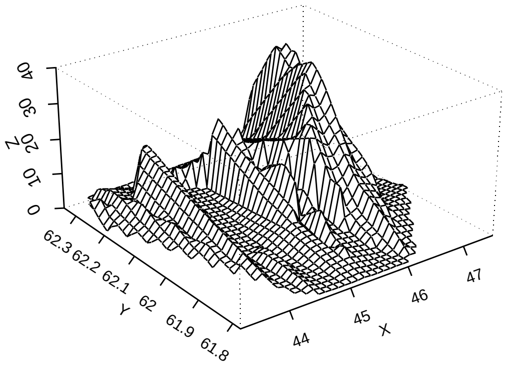

Figure 7.2a. Abundance of ngwayir throughout the Upper Warren based on the raw data of the incidence of scats at a given study site (90 sites, each containing 42 scat plots). The Eastings (x-axis) and Northings (y-axis), based on the Map Grid of Australia (MGA), provide the spatial distribution of sites, while the relative index of abundance of ngwayir (number of plots with scats out of 42) is represented on the z-axis.

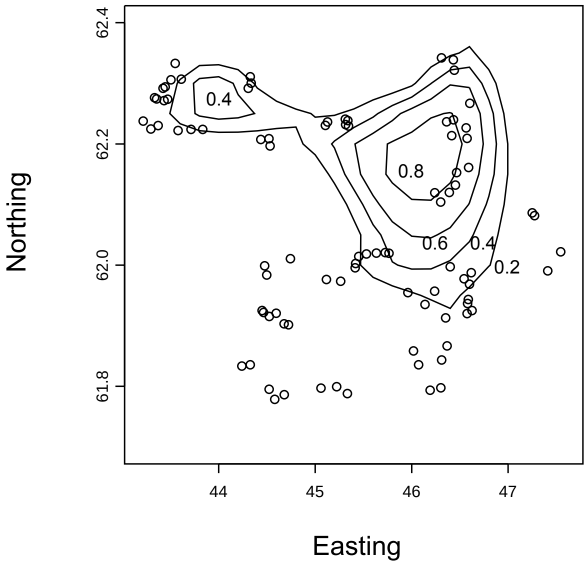

Figure 7.2b. Spatial pattern of the relative abundance of ngwayir throughout the Upper Warren using a generalised linear model with regression splines. The x- and y-axes are coordinates based on the Map Grid of Australia (MGA). The circles indicate the location and spatial distribution of the 90 study sites. The contours provide an index of relative abundance of ngwayir (0-1) based on scat surveys.

Table 7.3. Parameter estimates for the generalised linear model of the relative abundance of ngwayir in relation to local-scale anthropogenic factors in the Upper Warren.

Significant Terms	df	F-value	*p*-value
Fire Intensity	1	25.91652	<0.0001

Significant Terms	Coefficient	SE
Intercept	-0.6365387	0.0517
Fire Intensity	-0.5709233	0.0375

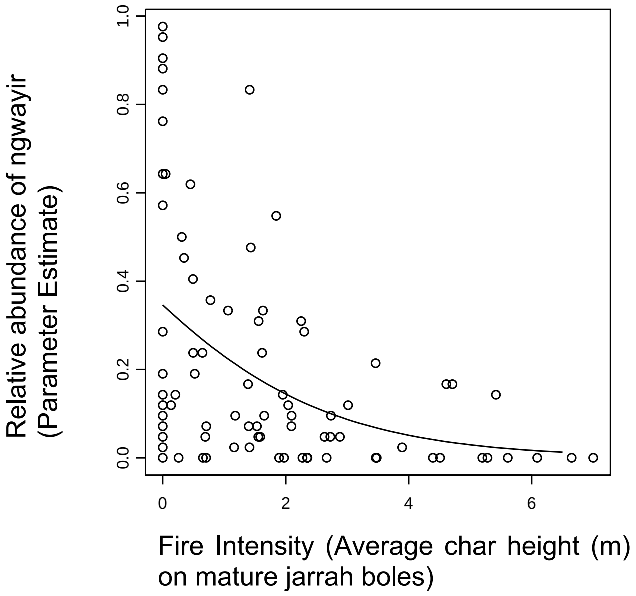

Figure 7.3. The relationship between fire intensity and the predicted relative abundance of ngwayir at each of the 90 study sites in the Upper Warren based on a generalised linear model.

7.4.3 Landscape-scale associations with ngwayir abundance

In the final model that excluded spatial terms at the landscape scale, there were four significant covariates and a single two-way interaction (Table 7.4). Relatively higher abundances of ngwayir were associated with areas that (1) had a high level of fox control effort; (2) were predominantly unlogged, or areas that on average were last logged in the 1960s (i.e. non-linear association); (3) had less non-remnant vegetation within a 5 km radius of the site; and (4) were closer to non-remnant vegetation. There also was an interaction between fox control effort and non-remnant vegetation. In areas with high fox control effort, ngwayir abundance decreased in conjunction with an increase in the area of non-remnant vegetation within a 5 km radius of sites. In areas of low and moderate fox control effort, the already relatively lower ngwayir abundances did not vary substantially with increased areas of non-remnant vegetation.

Table 7.4. Parameter estimates for the generalised linear model of the relative abundance of ngwayir in relation to landscape-scale anthropogenic factors. Only the significant terms for the linear coefficients are presented (i.e. average logging age is not included).

Significant Terms	df	F-value	*p*-value
Fox control effort	2	23.7449	<0.001
Non-remnant vegetation (5 km radius)	1	26.7681	<0.001
Distance to non-remnant vegetation	1	12.8868	<0.001
Average logging age (non-linear) (1 km radius)	4	7.1823	<0.001
Fox control : Non-remnant vegetation interaction	2	10.6949	<0.001

Significant Terms	Coefficient	SE
Intercept	2.36230	0.23065
Fox control LOW	-4.19021	0.25306
Fox control MODERATE	-5.03366	0.41024
Non-remnant vegetation within 5 km radius	-0.00227	0.00015
Distance to non-remnant vegetation	-0.00003	0.00005
Fox control LOW : Non-remnant vegetation < 5 km	0.00213	0.00024
Fox control MODERATE : Non-remnant vegetation < 5 km	0.00361	0.00033

7.5 Discussion

This study focused on the distribution and abundance of ngwayir in relation to selected anthropogenic factors within the publicly owned and managed jarrah forests that encompass the last remaining substantial inland population of this threatened species. The findings of this study can directly inform conservation and forest management of these and other similar jarrah forests that currently or potentially will support ngwayir populations. The improved ecological understanding derived from this study also will be indirectly helpful in refining research and conservation priorities of ngwayir populations elsewhere (e.g. free-hold land and in coastal and near coastal habitats; Jones, 2004; Wayne et al., 2005d [Chapter 5]; P. de Tores unpublished data) and for the species as a whole.

7.5.1 Spatial patterns of abundance

Within the public jarrah forests of the Upper Warren region, ngwayir abundance was highest in Perup Nature Reserve, with a secondary peak around Kingston (Figure 7.2). These are the most substantial remaining inland populations of ngwayir. Most of the public forests in which ngwayir survive in relatively high densities have been incorporated in proposed changes to the forest reservation system (Figure 7.1; i.e. National Parks, Nature Reserves, and 'Fauna Habitat Zones' within areas remaining available for logging, Conservation Commission, 2004). Nonetheless, other important populations remain in areas not formally protected. While reserves are important, all suitable forest habitats, irrespective of tenure, need to be managed in a way that ensures the long-term viability and recovery of biota, including the ngwayir (Lindenmayer and Franklin, 2002).

7.5.2 Anthropogenic factors associated with ngwayir distribution and abundance

7.5.2.1 Logging

Despite several studies of faunal responses to logging in jarrah forests (Rhind, 1996a, b; Christensen, 1997; Morris et al., 2001), concerns remain regarding the accuracy of assessments of the conservation status of some species, including the ngwayir, and the sustainability of current forestry practices (Calver and Dell, 1998a, b; Wardell-Johnson et al., 2004). A number of studies have used information on the general biology and ecology of jarrah forest fauna to predict how each species may respond to logging. One study suggested that the ngwayir was the most sensitive of three potentially suitable mammalian sustainability indicators for logging in jarrah forests (Calver et al., 1999). This is in contrast to other studies, which did not consider the ngwayir to be at high risk of being negatively impacted by current jarrah forestry practices (Nichols and Muir, 1989; Abbott and Whitford, 2002). One of these used a detailed risk assessment based predominantly on a species' reliance on tree hollows and their availability (Abbott and Whitford, 2002).

Our study indicates that the ngwayir is indeed sensitive to logging intensity, the effects of which may last for several decades. Specifically, ngwayir abundances were greater in predominantly unlogged forests, and in landscapes with an average logging age in the 1960s (Table 7.4) when logging practices were historically least intense (i.e. between 1940 and 1970; Bradshaw, 1999; Stoneman et al., 2005). These findings are consistent with results from a radio-telemetry study in Kingston, which found that logging operations reduced ngwayir survivorship (Wayne et al., 2000). In addition, ten years of spotlight monitoring in Kingston showed declines since 1998 that may be a delayed response to logging activities that occurred between 1995 and 1997 (Wayne et al. 2001, 2005a [Chapter 2]). In Kingston, changes in the forest structure from logging resulted in ngwayir travelling and denning more frequently on or near to the ground. As a consequence, ngwayir were more vulnerable to predation by foxes and cats (Wayne et al., 2000). In comparison, much of Perup Nature Reserve was selectively logged for jarrah in the 1960s and 1970s. Ngwayir were fairly rare in these forests in the 1970s when logging ceased and research, fox control and long-term monitoring activities commenced (Christensen, 1980a; Burrows and Christensen, 2002). Their numbers subsequently increased during the 1980s and have maintained relatively high levels since then (N. Burrows, P. Christensen and G. Liddelow personal communications). The positive relationship between the abundance of ngwayir in peppermint (*Agonis flexuosa*) coastal woodlands and the extent of canopy cover also has been related to the species' ability to avoid terrestrial predators (Jones and Hillcox, 1995; Jones et al., 2004). Other arboreal marsupials also have been shown to be sensitive to logging intensity (Kavanagh and Bamkin 1995; Laurance and Laurance 1996; Lindenmayer *et al.* 1999; Lindenmayer 2000).

Our findings demonstrate that it is simplistic to assess the vulnerability of a species to logging only on the basis of its reliance on structural elements of forests that are modified by logging (e.g. availability of tree hollows). This is because substantial impacts may result from interactions between multiple factors (Wardell-Johnson and Horwitz, 1996; Calver et al., 1998) that may or may not be apparent prior to the collection of empirical data (e.g. interaction between logging disturbance and predation). This emphasises the importance of regarding predictions based on a species' general ecology as no more than hypotheses that need to be appropriately tested empirically.

7.5.2.2 Fire

Ngwayir abundance was positively associated with sites subject to very low fire intensity or those that had not experienced fire for at least 20 years (Figure 7.3, Table 7.3). This suggests that ngwayir may be more sensitive to fire than previously thought (Christensen and Abbott, 1989), but supports the previous predictions by Friend and Wayne (2003) that this species might prefer forests that have been unburnt for a relatively long time (other reviews of fauna responses to fire include Nichols and Muir, 1989; Wardell-Johnson and Nichols, 1991; Calver and Dell, 1998a, b; Abbott and Burrows, 2003; Wardell-Johnson et al., 2004).

Increase in fire intensity may affect ngwayir in three key ways: (1) by reducing the availability of food resources; (2) through the loss of shelter sites; and/or (3) by directly or indirectly killing individuals. With regard to food, ngwayir feed on the leaves of a limited number of plant species (Ellis and Jones, 1992; Jones et al., 1994b). In the short-to-medium term, intense fires can remove suitable forage by scorching or defoliating the vegetation. As a consequence, if an intense fire is extensive, ngwayir may starve during the three to four months that it takes for sufficient epicormic resprouting to provide a replacement food source. Full canopy replacement may take 1-3 years depending on fire intensity (N. Burrows personal communication). In the longer term, intense fires may decrease the abundance of jarrah saplings (Abbott and Loneragan, 1986; Bell et al., 1989), which are a particularly important food source (A. Wayne, unpublished data). Given that ngwayir favour young leaves (Ellis and Jones, 1992), patchy, low intensity fires may, on the other hand, be nutritionally beneficial. For instance, in the peppermint woodlands near Busselton, a mosaic regrowth from a patch-fire was hypothesised as providing localised, high quality browse habitat that supported a vibrant population recovery within a decade (Jones et al., 2004). With regard to loss of shelter sites, while many large trees with hollows may remain or be replaced (Inions et al., 1989), the ngwayir also rely heavily on other habitat attributes. These include the dead grass skirts of balga (Wayne et al., 2000) and dense mid-storey vegetation where dreys are constructed. It may be some years after an intense fire before such refuge sites become suitable for habitation (Russell et al., 2003). Increased fire intensity also may kill larger numbers of individuals directly, as well as increase the vulnerability of survivors to predation on account of (a) a reduction in vegetation density (i.e. potentially more travelling on the ground as a result of fewer opportunities for arboreal travel and reduced food and shelter resources, as well as reduced ability to avoid detection and capture by a predator); and (b) the potential attraction of predators to areas of disturbance (Christensen, 1980a, b; Russell et al., 2003).

As with many other Mediterranean-type systems, jarrah forests are fire-prone (Bell et al., 1989; McCaw and Hanstrum, 2003). The use or exclusion of fire can be valuable and/or essential for conserving biota (Christensen and Maisey, 1987; Jones et al., 2004), but needs to be actively managed to reduce the negative effects of intense, large-scale wildfires. Prescribed burning can mitigate the impact of wildfires through the use of low intensity fire. The reasons for prescribed burning are varied (e.g. legislation, protection of life, property, community and environmental values, commercial considerations, legal liability, and risk management; McCaw and Burrows, 1989). A sound understanding of the ecological processes associated with fire is critical for developing sustainable fire regimes and management strategies to meet all these demands (Bradstock et al., 2002). Because the fire-associated needs of the many fauna and flora present in any landscape are different, it is necessary to deliver a range of appropriate fire regimes (e.g. a mosaic of temporal and spatial scales), with particular consideration of species at risk (Woinarski and Recher, 1997; Burrows and Wardell-Johnson, 2003; Friend and Wayne, 2003; Wardell-Johnson et al., 2004).

7.5.2.3 Fox control

A particularly strong and important finding in our study was the ngwayir's association with areas of increased fox control effort (Table 7.4). However, there have been concerns as to whether fox-baiting has detrimental or beneficial consequences for ngwayir because of the potential for changes in predator dynamics or intra-specific competition (Jones, 2004). For example, in some areas, reduced fox numbers can result in an increase in the numbers of feral cats (Christensen and Burrows, 1995; Risbey et al., 2000; Read and Bowen, 2001; Burrows et al., 2003), which are potentially major predators of the ngwayir (Dickman, 1996). Fox control also leads to increases in the numbers of koomal (*Trichosurus vulpecula hypoleucus*) (Orell, 2004), which may be an aggressive sympatric competitor of the ngwayir. Nonetheless, the findings of this study and long-term monitoring in some areas of Perup Nature Reserve (which have been baited for foxes since 1977; N. Burrows, P. Christensen and G. Liddelow personal communications) suggest that concerns regarding the possible disadvantages associated with fox control are far outweighed by the net benefits to ngwayir and many other species. More detailed research is required to test this observation, with a view to improving these putative benefits. For instance, if predation by rising numbers of feral cats is an issue, efforts can be directed to neutralise this threat. Nevertheless, the interactions between fox predation and other factors, such as logging, fire and forest fragmentation (see below) need to be considered fully in conservation and research efforts. This is particularly important on account of the potential synergisms between interactive factors (Hobbs, 2001).

7.5.2.4 Native forest fragmentation

The abundance of ngwayir was negatively associated with increased forest fragmentation, but it was also positively related with the proximity to cleared land (agricultural or exotic tree plantations). Increased abundance associated with forest edges has been observed in a number of species including raccoons (*Procyon lotor*) in North America (Pedlar et al., 1997), the green woodpecker (*Picus viridis*) in Scandinavia (Rolstad et al., 2000) and raptors in Spain (Sanchez-Zapata and Calvo, 1999). In our study, this relationship is most likely explained by the patchy distribution of nutrients and the highly selective nature of agricultural development (McArthur and Clifton, 1975; Ahern et al., 1994; Dargavel, 1995; Norton et al., 1995). The cleared land in the study region (32% of the region) generally coincided with more fertile and productive land near watercourses (Figure 7.1). The importance of foliage nutrients and forest productivity in determining abundance has been demonstrated for ngwayir in south-western Australian coastal woodlands (Jones et al., 1994a), and for other arboreal marsupials in eastern Australia (Braithwaite, 1984, 1991; Braithwaite et al., 1984, 1988, 1993; Pausas et al., 1995; Cork and Catling, 1996; Soderquist and Mac Nally, 2000; Wormington et al., 2002; Kanowski, 2004).

The interaction between fox control and forest fragmentation in this study also was important in relation to ngwayir abundance. While areas of high fox control generally supported more ngwayir, their abundance declined as fragmentation increased, i.e. fox control appears to be less effective in more fragmented landscapes. An association between increased fox numbers and their preying on native Australian fauna and increasing forest fragmentation has been observed elsewhere (Catling and Burt, 1995; May and Norton, 1996). Our findings also are supported by research in jarrah forests, which found that areas near to forest edges (i.e. < 5 km from forest edges) required more frequent baiting than core forest areas to maintain similar levels of abundance of medium-sized mammals (P. de Tores, unpublished data). Enhanced control measures along forest edges adjacent to agricultural land and plantations may increase ngwayir densities and also may have a beneficial buffering effect on ngwayir densities in core habitat.

7.6 Conclusions

The assessment of the putative causes of the decline of the ngwayir at both local and landscape scales within the Upper Warren demonstrated a negative association with anthropogenic disturbance. The preference of many forest mammals for undisturbed forest also has been observed elsewhere (Lunney, 1987; Catling et al., 2000). In summary, ngwayir were most abundant in areas with relatively low intensities of logging and fire and increased fox control. They were more abundant in less fragmented forest (where there may be less predation by foxes), but also in forest close to cleared land (which is likely to be more productive). Although an experimental approach is required to demonstrate causality, these results can immediately be used to improve the conservation of this threatened species. An ‘active’ adaptive management approach (Walters and Holling, 1990; Lee, 1999) is recommended. Such a ‘learning-by-doing’ approach enables immediate precautionary action aimed at preventing further declines while recognising the inherent uncertainty within complex systems (Walters and Holling, 1990). It also tests these activities through rigorous experimentation, which serves to refine our understanding and further improve management practices.

Key conservation recommendations for ngwayir within public jarrah forests include (1) both unprotected and reserved areas of high habitat value should be actively managed for conservation; (2) the intensity and scale of disturbance (e.g. fire and logging) should be minimised throughout the ngwayir’s forest habitat; (3) forest fragmentation by land clearance should cease; and (4) fox control should continue. Fox control may be more effective with the more strategic use of this powerful conservation tool, such as greater fox-baiting effort in areas of high habitat value, highly disturbed areas and forest edges.

Priorities for further research within public jarrah forests include (1) refinement of the ‘diagnosis of decline’ by testing specific hypotheses for the processes responsible for the species’ decline (Caughley and Gunn, 1996); (2) more detailed assessment of the ngwayir’s vulnerability to predation, especially in disturbed landscapes and forest edges; and (3) examination of environmental factors that may be related to the distribution and abundance of ngwayir.

At the species level, the conservation implications of this research principally include the recognition that much of the high value habitat for ngwayir has in all likelihood been selectively captured within freehold land tenure and subsequently cleared for agriculture and urbanisation, owing to its more fertile soils and productive nature. Although the extent of this phenomenon remains to be specifically and rigorously verified, the selective loss of high-quality habitat and the fragmentation of generally poorer quality remnants has in all likelihood been a major cause for the modern decline of the ngwayir throughout its distribution. It is therefore possible that protecting and restoring native vegetation in these areas could achieve substantial conservation outcomes for the ngwayir as with other species (Fischer and Lindenmayer, 2002; Lindenmayer and Hobbs, 2004; Mbora and Meikle, 2004; Fischer et al., 2005a, b).

This study also highlights a number of broader implications for research and conservation in general. First, this research exemplifies the importance of studying the ecology of threatened species at appropriate multiple spatial scales to avoid incomplete or erroneous inferences (Johnson, 1980; Wiens, 1989; Mackey and Lindenmayer, 2001; Luck 2002; Sergio et al., 2003; Wardell-Johnson, et al. 2004). Second, organisms respond to many different factors, some of which may synergistically interact. For example, ngwayir abundance was associated with an interaction between forest fragmentation and fox control. The study of causal factors in isolation may thus over-simplify our understanding of all the ecological processes involved. It is important that factors be investigated together with others that may be operating in concert, either simultaneously or sequentially (Caughley and Gunn, 1996). Third, effective conservation and management need a holistic approach that considers the conservation requirements of all the constituents of an ecosystem, but particularly those that are of conservation concern. For example, sustainable fire management and forestry need to account for the diversity of responses by a range of species. Finally, conservation objectives need to be managed within the socio-economic context of other values and competing demands (e.g. fire management and forestry). Therefore, the success of achieving effective conservation outcomes depends on the effective exchanges between researchers, land managers, local communities, other stakeholders and society in general.

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7.8 References

Abbott, I., Burrows, N.D., 2003. Fire in Ecosystems of South-West Western Australia: Impacts and Management. Backhuys Publishers, Leiden.

Abbott, I., Loneragan, O., 1986. Ecology of jarrah (*Eucalyptus marginata*) in the northern jarrah forest of Western Australia. In Research Bulletin No. 1. Western Australian Government Department of Conservation and Land Management, Perth.

Abbott, I., Whitford, K., 2002. Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: strategic risk assessment in relation to ecology, policy, planning, and operations management. Pacific Conservation Biology 7, 240-255.

Ahern, C.R., Shields, P.G., Enderlin, N.G., Baker, D.E., 1994. The soil fertility of central and north-east Queensland grazing lands. Meat Research Corporation and Department of Primary Industry, Queensland.

Bell, D.T., McCaw, W.L., Burrows, N.D., 1989. Influence of fire on jarrah forest vegetation. In The Jarrah Forest: A Complex Mediterranean System, eds. B. Dell, J.J. Havel, N. Malajczuk, pp. 203-215. Kluwer Academic Publishers, Dordrecht.

Bradshaw, F.J., 1999. Trends in silvicultural practices in the native forests of Western Australia. Australian Forestry 62, 255-264.

Bradstock, R.A., Williams, J.E., Gill, A.M., 2002. Flammable Australia: The fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge.

Braithwaite, L.W., 1984. The identification of conservation areas for possums and gliders in the Eden Woodpulp Concession District. In Possums and Gliders, eds. A.P. Smith, I.D. Hume, pp. 501-508. Australian Mammal Society, Sydney.

Braithwaite, L.W., 1991. Arboreal mammals of the Eden (New South Wales) woodchip forests: a regional survey. In Nature conservation: cost effective survey methods and data analysis, eds. C.R. Margules, M.P. Austin, pp. 127-133. CSIRO, Melbourne.

Braithwaite, L.W., Belbin, L., Ive, I., Austin, M.P., 1993. Land use allocation and biological conservation in the Batemans Bay forests of New South Wales. Australian Forestry 56, 4-21.

Braithwaite, L.W., Binns, D.L., Nowlan, R.D., 1988. The distribution of arboreal marsupials in relation to eucalypt forest types in the Eden (NSW) Woodchip Concession Area. Australian Wildlife Research 15, 363-373.

Braithwaite, L.W., Turner, J., Kelly, J., 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales: III. Relationships between faunal densities, eucalypt occurrence and foliage nutrients and soil parent materials. Australian Wildlife Research 11, 41-48.

Burbidge, A.A., McKenzie, N.L., 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological Conservation 50, 143-198.

Burrows, N.D., Algar, D., Robinson, A.D., Sinagra, J., Ward, B., Liddelow, G., 2003. Controlling introduced predators in the Gibson Desert of Western Australia. Journal of Arid Environments 55, 691-713.

Burrows, N.D., Christensen, P.E.S., 2002. Long-term trends in native mammal capture rates in a jarrah forest in south-western Australia. Australian Forestry 65, 211-219.

Burrows, N.D., Wardell-Johnson, G., 2003. Fire and plant interactions in forested ecosystems of south-west Western Australia. In Fire in Ecosystems of South-West Western Australia: Impacts and Management, eds. I. Abbott, N.D. Burrows, pp. 225-268. Backhuys Publishers, Leiden.

Calver, M.C., Bradley, J.S., Wright, I.W., 1999. Towards scientific contributions in applying the precautionary principle: an example from southwestern Australia. Pacific Conservation Biology 5, 63-72.

Calver, M.C., Dell, J., 1998a. Conservation status of mammals and birds in southwestern Australian forests. I. Is there evidence of direct links between forestry practices and species decline and extinction? Pacific Conservation Biology 4, 296-314.

Calver, M.C., Dell, J., 1998b. Conservation status of mammals and birds in southwestern Australian forests. II. Are there unstudied, indirect or long-term links between forestry practices and species decline and extinction? Pacific Conservation Biology 4, 315-325.

Calver, M.C., Dickman, C.R., Feller, M.C., Hobbs, R.J., Horwitz, R.J., Horwitz, P., Recher, H.F., Wardell-Johnson, G., 1998. Towards resolving conflict between forestry and conservation in Western Australia. Australian Forestry 61, 258-266.

Calver, M.C., Wardell-Johnson, G., 2004. Sustained unsustainability? An evaluation of evidence for a history of overcutting in the jarrah forests of Western Australia and its consequences for fauna conservation. In Conservation of Australia's Forest Fauna, ed. D. Lunney, pp. 94-114. Royal Zoological Society of New South Wales, Sydney.

Catling, P.C., Burt, R.J., 1995. Why are red foxes absent from some eucalypt forests in eastern New South Wales. Wildlife Research 22, 535-546.

Catling, P.C., Burt, R.J., Forrester, R.I., 2000. Models of the distribution and abundance of ground-dwelling mammals in the eucalypt forests of north-eastern New South Wales in relation to habitat variables. Wildlife Research 27, 639-654.

Catling, P.C., Burt, R.J., Forrester, R.I., 2002. Models of the distribution and abundance of ground-dwelling mammals in the eucalypt forests of north-eastern New South Wales in relation to environmental variables. Wildlife Research 29, 313-322.

Caughley, G.C., Gunn, A., 1996. Conservation Biology in Theory and Practice. Blackwell Science, Cambridge.

Chapman, K., 2002. Differential decay rates of brushtail possum (*Trichosorus vulpecula*) and Western Ringtail Possum (*Pseudocheirus occidentalis*) scats. Honours thesis, University of Western Australia.

Christensen, P.E.S., 1980a. The biology of *Bettongia penicillata* Gray 1837, and *Macropus eugenii* Desmarest 1817, in relation to fire. Bulletin 91. In Bulletin 91. Western Australian Government Forests Department, Perth.

Christensen, P.E.S., 1980b. A sad day for native fauna. Forest Focus 23, 1-12.

Christensen, P.E.S., 1997. A review of the knowledge of the effects of key disturbances on fauna in the south-west forest region. Western Australian Government Department of Conservation of Land Management, Perth.

Christensen, P.E.S., Abbott, I., 1989. Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. Australian Forestry 52, 103-121.

Christensen, P.E.S., Burrows, N.D., 1995. Project Desert Dreaming: experimental reintroduction of mammals to the Gibson Desert, Western Australia. In Reintroduction Biology of Australia and New Zealand Fauna, ed. M. Serena, pp. 199-207. Surrey Beatty and Sons, Sydney.

Christensen, P.E.S., Maisey, K., 1987. The use of fire as a management tool in fauna conservation reserves. In Nature Conservation: The Role of Remnants of Native Vegetation, eds. D.A. Saunders, G.W. Arnold, A.A. Burbidge, A.J.M. Hopkins, pp. 323-329. Surrey Beatty and Sons, Sydney.

Conservation Commission, 2004. Forest Management Plan 2004-2013. pp. 1-144. Conservation Commission of Western Australia, Perth.

Cork, S.J., Catling, P.C., 1996. Modelling distributions of arboreal and ground-dwelling mammals in relation to climate, nutrients, plant chemical defences and vegetation structure in the eucalypt forest of southeastern Australia. Forest Ecology and Management 85, 163-175.

Dargavel, J., 1995. Fashioning Australia's Forests. Oxford University Press, Melbourne.

Dell, B., Havel, J.J., 1989. The jarrah forest, an introduction. In The Jarrah Forest: A Complex Mediterranean System, eds. B. Dell, J.J. Havel, N. Malajczuk, pp. 1-10. Kluwer Academic Publishers, Dordrecht.

Department of Conservation and Land Management, 1991. Silvicultural Specification 2/91: Treemarking and Silvicultural Treatment in the Jarrah Forest. Western Australian Government Department of Conservation and Land Management, Perth.

Department of Conservation and Land Management, 1995. Silvicultural Guidelines 1/95: Silvicultural Practice in Jarrah Forest. Western Australian Government Department of Conservation and Land Management, Perth.

Department of Conservation and Land Management, 1998. Draft Management Plan: Perup Forest and Lake Muir/Unicup Nature Reserves. pp. 1-59. Western Australian Government Department of Conservation and Land Management, Perth.

Department of Conservation and Land Management, 2000. Western Shield Fauna Recovery Program Strategic Plan (July 1999 - June 2004). Western Australian Government Department of Conservation and Land Management, Perth.

Dickman, C.R., 1996. Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency, Canberra.

Ellis, M., Jones, B., 1992. Observations of captive and wild western ringtail possums *Pseudocheirus occidentalis.* Western Australian Naturalist 19, 1-10.

Elton, C.S., 1927. Animal Ecology. Methuen, London.

Fischer, J., Fazey, I., Briese, R., Lindenmayer, D.B., 2005b. Making the matrix matter: challenges in Australian grazing landscapes. Biodiversity and Conservation 14, 561-578.

Fischer, J., Lindenmayer, D.B., 2002. Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. Biological Conservation 106, 129-136.

Fischer, J., Lindenmayer, D.B., Barry, S.C., Flowers, E., 2005a. Lizard distribution patterns in the Tumut fragmentation "natural experiment" in south-eastern Australia. Biological Conservation 123, 301-315.

Friend, G.R., Wayne, A.F., 2003. Relationships between mammals and fire in south-west Western Australian ecosystems: what we know and what we need to know. In Fire in Ecosystems of South-West Western Australia: Impacts and Management, eds. I. Abbott, N.D. Burrows, pp. 363-380. Backhuys Publishers, Leiden.

Gaston, K.J., Spicer, J.I., 2004. Biodiversity: An introduction. Blackwell Publishing, Melbourne.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman and Hall, New York.

Havel, J.J., Mattiske, E.M., 2000. Vegetation mapping of southwest forest regions of Western Australia. Mattiske Consulting Pty. Ltd.

Herberle, G., 1997. Timber harvesting of Crown land in the south-west of Western Australia: An historical review with maps. CALMScience 2, 203-224.

Hobbs, R.J., 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conservation Biology 15, 1522-1528.

Inions, G.B., Tanton, M.T., Davey, S.M., 1989. Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. Australian Wildlife Research 16, 449-458.

Jarvis, N.T., 1979. Western Australia: an atlas of human endeavour, 1829-1979. Education and Lands and Surveys Departments of Western Australia, Perth.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 6, 65-71.

Jones, B., 2004. The possum fauna of Western Australia: decline, persistence and status. In The Biology of Australian Possums and Gliders, eds. R.L. Goldingay, S.M. Jackson, pp. 149-160. Surrey Beatty and Sons, Sydney.

Jones, B., Hillcox, S., 1995. A survey of the possums *Trichosurus vulpecula* and *Pseudocheirus occidentalis* and their habitats in forest at Ludlow, Western Australia. Western Australian Naturalist 20, 139-150.

Jones, B.A., How, R.A., Kitchener, D.J., 1994a. A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. Wildlife Research 21, 175-187.

Jones, B.A., How, R.A., Kitchener, D.J., 1994b. A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. Wildlife Research 21, 189-201.

Jones, B.A., Meathrel, C.E., Calver, M.C., 2004. Hypotheses arising from a population recovery of the western ringtail possum *Pseudocheirus occidentalis* in fire regrowth patches in a stand of *Agonis flexuosa* trees in south-western Australia. In Conservation of Australia's Forest Fauna, ed. D. Lunney, pp. 656-662. Royal Zoological Society of New South Wales, Sydney.

Kanowski, J., 2004. What factors control the distribution and abundance of folivorous possums inhabiting rainforests of the Atherton Tableland in north-east Queensland. In The Biology of Australian Possums and Gliders, eds. R.L. Goldingay, S.M. Jackson, pp. 539-547. Surrey Beatty and Sons, 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, Australia. Biological Conservation 71, 41-53.

Kinnear, J.E., Onus, M.L., Sumner, N.R., 1998. Fox control and rock-wallaby population dynamics - II. An update. Wildlife Research 25, 81-88.

Kinnear, J.E., Sumner, N.R., Onus, M.L., 2002. The red fox in Australia - an exotic predator turned biocontrol agent. Biological Conservation 108, 335-359.

Lamb, D., Smyth, A., 2003. Forests. In Ecology: An Australian Perspective, eds. I. Attiwill, B. Wilson, pp. 331-351. Oxford University Press, Melbourne.

Lamont, B.B., Ward, D.J., Eldridge, J., Korczynskyj, D., Colangelo, W.I., Fordham, C., Clements, E., Wittkuhn, R., 2003. Believing the balga: a new method for gauging the fire history of vegetation using grasstrees. In Fire in Ecosystems of South-West Western Australia: Impacts and Management, eds. I. Abbott, N.D. Burrows, pp. 147-169. Backhuys Publishers, Leiden.

Laurance, W.F., Laurance, S.G.W., 1996. Responses of five arboreal marsupials to recent selective logging in tropical Australia. Biotropica 28, 310-322.

Lee, K.N., 1999. Appraising adaptive management. Conservation Ecology 3, 3.

Lindenmayer, D.B., 2000. Factors at multiple scales affecting distribution patterns and their implications for animal conservation - Leadbeater's possum as a case study. Biodiversity and Conservation 9, 15-35.

Lindenmayer, D.B., Burgman, M.A., 2005. Practical Conservation Biology. CSIRO Publishing, Melbourne.

Lindenmayer, D.B., Cunningham, R.B., McCarthy, M.A., 1999. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-eastern Australia. VIII. Landscape analysis of the occurence of arboreal marsupials. Biological Conservation 89, 83-92.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington.

Lindenmayer, D.B., Hobbs, R.J., 2004. Fauna conservation in Australian plantation forests - a review. Biological Conservation 119, 151-168.

Luck, G.W., 2002. The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105, 383-394.

Lunney, D., 1987. Effects of logging, fire and drought on possums and gliders in the coastal forests near Bega, N.S.W. Australian Wildlife Research 14, 263-274.

Mackey, B.G., Lindenmayer, D.B., 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. Journal of Biogeography 28, 1-21.

Maxwell, S., Burbidge, A.A., Morris, K., 1996. The 1996 Action Plan for Australian Marsupials and Monotremes. In Endangered Species Program, Project No. 500. pp. 133-134. Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Perth.

May, S.A., Norton, T.W., 1996. Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in Australian forest ecosystems. Wildlife Research 23, 387-400.

Mbora, D.N.M., Meikle, D.B., 2004. The value of unprotected habitat in conserving the critically endangered Tana River red colobus (*Procolobus rufomitratus*). Biological Conservation 120, 91-99.

McArthur, W.M., Clifton, A.L., 1975. Forestry and agriculture in relation to soils in the Pemberton area of Western Australia. Soils and Land Use Series No. 54. C.S.I.R.O., Melbourne.

McCaw, L., Hanstrum, B., 2003. Fire environment of Mediterranean south-west Western Australia. In Fire in Ecosystems of South-West Western Australia: Impacts and Management, eds. I. Abbott, N.D. Burrows, pp. 87-106. Backhuys Publishers, Leiden.

McCaw, W.L., Burrows, N.D., 1989. Fire management. In The Jarrah Forest: A Complex Mediterranean System, eds. B. Dell, J.J. Havel, N. Malajczuk, pp. 317-334. Kluwer Academic Publishers, Dordrecht.

Morris, K., Johnson, B., Orell, P., Gaikhorst, G., Wayne, A., Moro, D., 2003. Recovery of the threatened chuditch (*Dasyurus geoffroii):* A case study. In Predators with Pouches: The Biology of Carnivorous Marsupials, eds. M. Archer, M.E. Jones, C.R. Dickman, pp. 435-451. CSIRO Publishing, Melbourne.

Morris, K., Johnson, B., Rooney, J., Ward, C., 2001. The short-term impacts of timber harvesting and associated activities on the abundance of medium-sized mammals in the jarrah forest of Western Australia. In Nature Conservation 5: Conservation in the Production Environments: Managing the Matrix, eds. J.L. Craig, N. Mitchell, D.A. Saunders, pp. 60-70. Surrey Beatty and Sons, Sydney.

National Land and Water Resources Audit, 2002. Australian Terrestrial Biodiversity Assessment 2002. National Land and Water Resources Audit, Canberra.

Nichols, O.G., Muir, B., 1989. Vertebrates of the jarrah forest. In The Jarrah Forest: A Complex Mediterranean System, eds. B. Dell, J.J. Havel, N. Malajczuk, pp. 133-153. Kluwer Academic Publishers, Dordrecht.

Norton, D.A., Hobbs, R.J., Atkins, L., 1995. Fragmentation, disturbance, and plant distribution - mistletoes in woodland remnants in the Western Australian Wheatbelt. Conservation Biology 9, 426-438.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H., Graham, R.L., 1988. Indices of landscape pattern. Landscape Ecology 1, 153-162.

Orell, P., 2004. Fauna monitoring and staff training: Western Shield review - February 2003. Conservation Science 5, 51-95.

Pausas, J.G., Braithwaite, L.W., Austin, M.P., 1995. Modelling habitat quality for arboreal marsupials in the south coastal forests of New South Wales, Australia. Forest Ecology and Management 78, 39-49.

Pedlar, J.H., Fahrig, L., Merriam, H.G., 1997. Raccoon habitat use at two spatial scales. Journal of Wildlife Management 61(1), 102-112.

Primack, R., 2001. Causes of extinction. In Encyclopedia of Biodiversity. Volume 2., ed. S.A. Levin, pp. 697-713. Academic Press, San Diego.

Read, J., Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildlife Research 28, 195-203.

Rhind, S.G., 1996a. Habitat tree requirements and the effects of removal during logging on the marsupial brush-tailed phascogale (*Phascogale tapoatafa tapoatafa*) in Western Australia. Western Australian Naturalist 21, 1-22.

Rhind, S.G., 1996b. Addendum - Errata: Habitat tree requirements and the effects of removal during logging on the marsupial brush-tailed phascogale (*Phascogale tapoatafa tapoatafa*) in Western Australia. Western Australian Naturalist 21, 1.

Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S., Wright, I.W., 2000. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. Wildlife Research 27, 223-235.

Rolstad, J., Loken, B., Rolstad, E., 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. Oecologia 124, 116-129.

Russell, B.G., Smith, B., Augee, M.L., 2003. Changes to a population of common ringtail possums (*Pseudocheirus peregrinus)* after bushfire. Wildlife Research 30, 389-396.

Sanchez-Zapata, J.A., Calvo, J.F., 1999. Raptor distribution in relation to landscape composition in semi-arid Mediterranean habitats. Journal of Applied Ecology 36, 254-262.

Sergio, F., Pedrini, P., Marchesi, L., 2003. Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. Biological Conservation 112, 351-362.

Soderquist, T.R., Mac Nally, R., 2000. The conservation value of mesic gullies in dry forest landscapes: mammal populations in the box-ironbark ecosystem of southern Australia. Biological Conservation 93, 281-291.

Start, T., Burbidge, A., Armstrong, D., 1998. A review of the conservation status of the woylie, *Bettongia penicillata ogilbyi* (Marsupialia: Potoroidae) using IUCN criteria. CALMScience 2, 277-289.

Stoneman, G.L., Hagan, R., Rayner, M.E., 2005. Evolution of silvicultural practices in the jarrah forest of Western Australia. In 6th National Conference of the Australian Forest History Society. eds. M.C. Calver, H. Bigler-Cole, G. Bolton, J. Dargavel, A. Gaynor, P. Horwitz, J. Mills, G. Wardell-Johnson. pp. 693-706. Millpress Science Publishers, Rotterdam.

Strelein, G.J., 1988. Site classification in the southern jarrah forest of Western Australia. In Research Bulletin 2. Western Australian Government Department of Conservation and Land Management, Perth.

Thomson, P.C., Marlow, N.J., Rose, K., Kok, N.E., 2000. The effectiveness of a large-scale baiting campaign and an evaluation of a buffer zone strategy for fox control. Wildlife Research 27, 465-472.

Twigg, L.E., Martin, G.R., Eastman, A.F., King, D.R., Kirkpatrick, W.E., 2003. Sensitivity of some Australian animals to sodium fluoroacetate (1080): additional species and populations, and some ecological considerations. Australian Journal of Zoology 51, 515-531.

Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. Ecology 71, 2060-2068.

Ward, D.J., Lamont, B.B., Burrows, C.L., 2001. Grasstrees reveal contrasting fire regimes in eucalypt forest before and after European settlement of southwestern Australia. Forest Ecology and Management 150, 323-329.

Wardell-Johnson, G., Calver, M.C., 2004. Resolving historical sustainability in Western Australia's jarrah forests. In Ecology, Conservation and Management of Mediterranean Climate Ecosystems. eds. M. Arianoutsou, V. Papanastasis. pp. 1-12. Millpress Science Publishers, Rotterdam.

Wardell-Johnson, G., Calver, M.C., 2005. Toward sustainable management: southern Africa's Afromontane, and Western Australia's jarrah forests. In 6th National Conference of the Australian Forest History Society. eds. M.C. Calver, H. Bigler-Cole, G. Bolton, J. Dargavel, A. Gaynor, P. Horwitz, J. Mills, G. Wardell-Johnson. pp. 729-739. Millpress Science Publishers, Rotterdam.

Wardell-Johnson, G., Calver, M.C., Saunders, D.A., Conroy, S., Jones, B., 2004. Why integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. In Conservation of Australia's Forest Fauna, ed. D. Lunney, pp. 394-417. Royal Zoological Society of New South Wales, Sydney.

Wardell-Johnson, G., Horwitz, P., 1996. Conserving biodiversity and the recognition of heterogeneity in ancient landscapes: a case study from south-western Australia. Forest Ecology and Management 85, 219-238.

Wardell-Johnson, G., Nichols, O., 1991. Forest wildlife and habitat management in southwestern Australia: knowledge, research and direction. In Conservation of Australia's Forest Fauna, ed. D. Lunney, pp. 161-192. Royal Zoological Society of New South Wales, Sydney.

Wayne, A.F., Cowling, A., Rooney, J.F., Ward, C.G., Wheeler, I.B., Lindenmayer, D.B., Donnelly, C.F., 2005a [Chapter 2]. Factors affecting the detection of possums by spotlighting in Western Australia. Wildlife Research – revised manuscript in review.

Wayne, A.F., Cowling, A., Ward, C.G., Rooney, J.F., Vellios, C.V., Lindenmayer, D.B., Donnelly, C.F., 2005b [Chapter 3]. A comparison of survey methods for arboreal possums in jarrah forest, Western Australia. Wildlife Research – revised manuscript in review.

Wayne, A.F., Rooney, J., Ward, C., Wheeler, I., Mellican, A., 2001. 'Spotlight surveys to investigate the impacts of timber harvesting and associated activities within the jarrah forest of Kingston State Forest, with particular reference to the koomal (*Trichosurus vulpecula*) and ngwayir (*Pseudocheirus occidentalis*). Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A.F., Ward, C.G., Rooney, J.F., Vellios, C.V., Lindenmayer, D.B., 2005d [Chapter 5]. The life history of *Pseudocheirus occidentalis* (Pseudocheiridae) in the jarrah forest of south-western Australia. Australian Journal of Zoology – revised manuscript in review.

Wayne, A.F., Ward, C., Rooney, J., Wheeler, I., 2000. 'The immediate impacts of timber harvesting and associated activities on the ngwayir (*Pseudocheirus occidentalis*) in the jarrah forest of Kingston State Forest Block. Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 385-397.

Wilde, S.A., Walker, I.W., 1984. Pemberton-Irwin Inlet, Western Australia. Geological Survey Series Explanation Notes. In Geological Survey Series Explanation Notes. Geological Survey of Western Australia, Perth.

Woinarski, J.C.Z., Recher, H.F., 1997. Impact and response: a review of the effects of fire on the Australian avifauna. Pacific Conservation Biology 3, 183-205.

World Conservation Union, 1994. IUCN Red List Categories. Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

World Wildlife Fund, 2004. The current status of threatened species in Australia. World Wildlife Fund.

Wormington, K.R., Lamb, D., McCallum, H.I., Moloney, D.J., 2002. Habitat requirements for the conservation of arboreal marsupials in dry sclerophyll forests of southeast Queensland, Australia. Forest Science 48, 217-227.

7.9 Appendix

The covariates used to examine which anthropogenic factors are associated with the distribution and abundance of ngwayir at 90 sites within the publicly managed jarrah forests of Upper Warren, south-western Australia.

Local-scale	
Logging age	Number of years since the site was last logged
Logging intensity	Basal area (m^2) of cut stumps per hectare
Logging frequency	Number of times the site has been logged since the 1920's
Fire age	Number of years since the site was last burnt
Last fire intensity	Average char height on jarrah trees (> 15 cm DBHOB). Note, char ht = 0 for long unburnt sites (i.e. > 20 years)
Fire frequency	Number of fires (prescribed or wildfire) recorded on site from 1953/54 to 2002/03

Landscape-Scale	
Fox control ground effort	3 Classes; Low = Relatively low frequency or short duration of fox-baiting effort (i.e. little or no ground-baiting), Moderate = some ground-baiting, High = irregular ground-baiting since 1986, regular since 1992.
Non-remnant vegetation	The area (ha) of non-remnant vegetation within a 5000 m radius (7854Ha) of each site (includes agricultural and plantation uses).
Distance to non-remnant	The shortest distance (m) from each site to an area of non-remnant vegetation greater than 1ha in size.
Roads	The length (m) of all sealed roads and unsealed roads within a 1000 m radius (312 ha) of each site
Fire extent	The extent (ha) of the last fire at each site.
Distance to Fire boundary	The shortest distance (m) from each site to the nearest boundary of the most recent fire.
Average logging age	Average year when last logged, of the forest within a 1000 m radius
Logging age diversity	*Index of the diversity of logging age classes within 1000 m radius of each site.

*Logging age diversity incorporated the number and relative contribution of forest logging age classes, *sensu* O’Neill *et al.* (1988);

$$\text{Logging Age Diversity } (H) = -\sum_{k=1}^{s} (P_k)\log(P_k)$$

where P_k = the proportion of the landscape (1000 m radius) in logging age class k

s = number of logging age classes (i.e. 5, same as the design variable)

Given that there are five logging age classes, the values for logging diversity range from 0 to 0.699

SECTION D

SYNTHESIS

This section synthesises the information presented in the earlier sections and concludes this thesis. In particular, it integrates some of the new insights of the biology and ecology of the koomal and the ngwayir. This new understanding is then used to explain the pattern of decline of ngwayir observed since European settlement in south-western Australia. The value of these findings to conservation and management is discussed, and this thesis is presented in the context of ongoing and future research.

Chapter 8

THESIS SYNTHESIS

This thesis aimed to improve the biological and ecological understanding of the koomal (*Trichosurus vulpecula hypoleucus*) and the ngwayir (*Pseudocheirus occidentalis*) within the jarrah (*Eucalyptus marginata*) forest to provide essential information for their conservation and ecologically sustainable forest management. Particular emphasis was placed on the ngwayir, because it is a threatened species (Maxwell *et al.* 1996; de Tores 2000; Jones 2004). This chapter has five sections. The first part summarises the improvements in the survey methodology that facilitated subsequent ecological research. In the second, insights acquired from ecological studies on koomal and ngwayir are outlined. Third, the distributions of both species are discussed in relation to their ecology. Fourth, the applied value of this research to conservation and management is discussed. And finally, future research priorities are addressed.

8.1 Improvements to survey methodology

To achieve the aim of the thesis, it was necessary first to improve the survey methods to reliably detect koomal and ngwayir. For ngwayir, in particular, no reliable trapping methods existed prior to this research. The improvements to survey methods described in Chapters 2 and 3 were integral to the success of subsequent studies. Arboreal trapping increased capture rates by factors of 2.3 and 9.3 for koomal and ngwayir, respectively. Arboreal trapping was, therefore, used at the Chariup study site to investigate the life history of koomal and ngwayir (Chapters 4 and 5, respectively) and as the principal means of capturing individuals for radio-telemetry to investigate possum selection of diurnal refuges (Chapter 6). In addition, the use of the scat survey method tested in Chapter 3 provided a robust and efficient abundance index to examine the anthropogenic factors associated with ngwayir distribution and abundance (Chapter 7).

Furthermore, improved pedestrian-based spotlight methods identified in Chapter 3 facilitated 50 ngwayir hand-captures to supplement possums caught by trapping as part of the life history studies (Chapters 5 and 6). The results of the study of environmental and procedural factors relating to the spotlight detection of possums (Chapter 2) also proved useful for other research and monitoring efforts. For example, the Western Australian Government Department of Conservation and Land Management (CALM) has already incorporated key parts of the methods developed in this thesis into several long-term spotlight-monitoring programmes (e.g. Kingston Study – A. Wayne; Western Shield Conservation Programme – I. Wilson personal communication).

The findings described in Chapters 2 and 3 have helped to overcome one of the key factors limiting the acquisition of biological and ecological knowledge concerning the koomal and the ngwayir, by improving methods for studying these species. They are also relevant to other research and monitoring of arboreal mammals in other parts of Australasia and elsewhere (e.g. Lemurs in Madagascar, and some primates in Africa, Asia and South America).

8.2 Biological and ecological insights

8.2.1 Koomal

The information on the life history of the koomal presented in Chapter 4 substantially enhanced existing knowledge about this subspecies. The jarrah forest population at Chariup exhibited sexual dimorphism, with a single autumn breeding season timed to coincide with the end of the summer drought. Unlike many other koomal and brushtail possum populations, no spring breeding or 'double breeding' events were observed, resulting in adult females producing one young per year. At least 83% of pouch-young survived to pouch-emergence and sexually matured at 1 year of age. Body condition in adult males, but not females, varied significantly with the seasons, with condition being poorest in winter and healthiest in summer. The south-western Australian populations of this brushtail subspecies display much of the variations in life history and adaptability of the species across its range.

The study of habitat selection for diurnal refuges showed that koomal had a strong preference for hollow-bearing trees (Chapter 6). The likelihood of a tree being used by a koomal increased substantially with tree diameter. Koomal used wandoo (*Eucalyptus wandoo*) and marri (*Corymbia calophylla*) proportionately more than jarrah, and the probability of use increased with crown senescence and canopy connectivity. The extent of possum signs on a tree and the structure of surrounding habitat also were good predictors of tree use. The understanding of the ecology of koomal in the jarrah forest will be improved further on the completion of several ongoing studies to examine nocturnal habitat selection, spatial patterns of habitat use, and the relationships between abundance and anthropogenic and environmental factors in the Upper Warren (Wayne *et al.* in preparation-b; A. Wayne unpublished data).

8.2.2 Ngwayir

The study of the life history of the threatened ngwayir in jarrah forest at Chariup highlighted the reduced capacity of this population to withstand further exogenous pressures. Chapter 5 showed that populations at Chariup were less fecund (about one young per adult female per year) than coastal populations. At the species level, ngwayir was shown to be less fecund than the closely-related common ringtail possum in eastern Australia. The proportion of wild ngwayir young surviving through to maturity is unknown. Nevertheless, with an oldest recorded age in the jarrah forest of four years, the life expectancy of adult ngwayir is short. Given that females become sexually mature at about one year of age, and assuming a 100% survival rate of offspring, the average life expectancy of females would need to be greater than three years to maintain a stable population size (i.e. to ensure population turnover). Given the low reproductive potential of ngwayir and their relatively short life span, any factors that affect female fecundity, offspring survival rates, longevity, or any negative population pressure sustained over several years could have profound effects on population viability and increase the likelihood of local extinction. More longitudinal data from multiple sites would be needed to verify whether the findings at Chariup are representative, both in space and time, of other remnant ngwayir populations in jarrah forest. Beyond the Upper Warren, however, ngwayir populations in the jarrah forest are rare and small, such that study replication elsewhere would be exceptionally difficult. Nonetheless, current findings alone present a plausible hypothesis as to why ngwayir (and inland forest populations, in particular) have declined dramatically, while populations of the common ringtail possum in eastern Australia are more stable (Jones 2004). It is also plausible that nutrition may be a key factor in explaining at least some of the differences in fecundity between populations. The timing of breeding, body condition and mortality appear to be related to the seasonal quality and quantity of food, principally young jarrah leaves.

The susceptibility of the ngwayir to population decline is further explained by its relationship with anthropogenic factors in the Upper Warren (Chapter 7). The relationships between ngwayir abundance and logging, fire and forest fragmentation indicate that the species is sensitive to disturbance, especially intensive logging and fire events. A strong association with fox (*Vulpes vulpes*) control also was found, suggesting that the introduced fox exerts major negative pressure on ngwayir populations, which can be reduced by increased fox control efforts.

8.2.3 Timing, intensity, frequency and scale of disturbance

The significantly poorer body condition of ngwayir in autumn/winter and the fact that 84% of deaths occurred between April and September suggest that individuals are probably particularly susceptible to disturbance and predation during this period (Chapter 5). The investigation into the habitat selection for diurnal refuges revealed that the ngwayir was particularly reliant on large hollow-bearing trees in the eastern jarrah forest (Chapter 6). The intensity, scale and frequency of logging and fire will affect the availability of suitable shelter resources.

8.2.4 Ecological processes and patterns

Ecological patterns are the result of underlying ecological processes that function at multiple spatial and temporal scales (e.g. Wiens 1992). Key processes broadly relate to food, shelter, reproduction, competition and predation (Fischer *et al.* 2004, 2005). Some ecological patterns were examined in relation to habitat selection for diurnal refuges at micro- and meso-scales (Chapter 6), as were the associations between possum abundance and anthropogenic factors at the local and landscape scales (Chapter 7). Although the work in Chapters 6 and 7 did not directly investigate ecological processes, they should form the basis of more detailed research into these aspects.

8.2.5 Interactions between ecological factors

Synergistic interactions between several processes probably elicit stronger responses than the same process acting alone. The potential for powerful interactions between predation and other disturbance factors provides such an example. Despite the fact that fewer than 18% of ngwayir deaths were directly attributed to logging activity, the life expectancy of ngwayir within the “Kingston 4” logging coupe was 40% lower than that of control cohorts in adjacent unlogged areas. The reduced survivorship was apparently due to an increased vulnerability to predation, predominantly by foxes and cats (*Felis catus*) (Wayne *et al.* 2000). Similarly, at the regional scale, the abundance of ngwayir was associated with the interaction between forest fragmentation and fox control effort (Chapter 7). Possible effects, generated by interactions between fire and introduced predators, on the abundance of native mammals in the jarrah forest also have been identified in other studies (e.g. Friend and Wayne 2003; Wardell-Johnson *et al.* 2004). Improved awareness and more responsive management of potentially detrimental interactions between several threatening processes should be a high conservation priority.

Better understanding of the biology and ecology of koomal and ngwayir and of the processes underlying the patterns of their decline in south-western Australia also can directly contribute to more effective conservation and sustainable land management practices, as well as provide direction for more focused future research.

8.3 A hypothesis for the pattern of ngwayir decline

The ngwayir has declined dramatically since European settlement, and is now distributed patchily in south-western Australia (de Tores 2000; Jones 2004). This pattern may have resulted from historical and ecological differences affecting birth and death rates, and the level of interaction between populations (i.e. metapopulation dynamics; e.g. Caughley and Gunn 1996). Although unequivocally identifying the historical causes for the decline of the ngwayir may be impossible, the improved understanding of its ecology presented in this thesis provides clues.

The ngwayir's decline has been most substantial in northern and inland areas of its former distribution (de Tores 2000; Jones 2004). Given the reliance of ngwayir on trees for food, shelter and avoidance of predators, habitat loss is expected to be the main cause of its local extinction within extensively cleared agricultural landscapes. However, large areas of jarrah forest remain in which the ngwayir no longer persist (de Tores 2000; Jones 2004). If the species' fecundity as observed at Chariup was similar to that of former jarrah forest populations, then its capacity to withstand and recover from negative population pressures would be expected to be substantially lower than that of coastal populations where birth rates are higher (Jones *et al.* 1994a). Thus, low fecundity (and possibly shorter generation lengths) was probably a factor in the disappearance of the ngwayir from parts of its former distribution.

Since European settlement, anthropogenic pressures on ngwayir populations have included bycatch from a lucrative fur trade in koomal (~1890-1940), exotic diseases and the establishment of introduced predators (~1830-1940) (Abbott 2002, 2005); altered fire regimes (e.g. Wardell-Johnson *et al.* 2004); habitat modification such as logging (Wayne *et al.* 2000); and habitat loss and fragmentation by agriculture and urbanisation (e.g. Jones 2004; Chapter 7). These factors are broadly recognised as constituting the principal threats to the ngwayir (e.g. Maxwell *et al.* 1996; de Tores 2000; Jones 2004).

Chapter 6 demonstrated the sensitivity of ngwayir populations in jarrah forest to anthropogenic disturbance. While anthropogenic disturbances are likely proximate causes for ngwayir decline (*sensu* Simberloff 1986), ultimately, climate and nutrient availability have probably contributed to a higher extinction proneness of ngwayir in parts of its range. Geographic differences in temperature and rainfall affect the ngwayir's access to nutrients (i.e. climatic influence on plant food species and productivity affects seasonal food availability and quality). Nutrition, in turn, is likely to affect animal fecundity and longevity (Norton 1987; Bronson and Heideman 1994). Seasonal variations in climate also may impose physiological stress on the ngwayir (e.g. summer drought). Climate also affects vegetation structure (Specht and Morgan 1981), which determines the habitat resources available for shelter and avoidance of predators. For instance, in drier areas, the reduced height and density of the forest result in reduced canopy connectivity, which in turn means ngwayir need to travel more on the ground in order to access more widely-dispersed resources, thus increasing ngwayir susceptibility to predation (e.g. Paull and Kerle 2004; Kerle 2004). The greater dependence of ngwayir on hollows in more open forest also renders the species more susceptible to logging operations that remove the large trees upon which they depend (Chapter 6).

Soil fertility and foliar nutrients in south-western Australian forests are recognised as some of the most impoverished in the world (Hingston *et al.* 1980, 1989; Dell and Havel 1989). The lower species diversity of arboreal marsupials in the south-west than in eastern Australia also may be explained by the combined effects of a number of factors including (1) reduced availability of nutrients; (2) the geographic isolation of the forests from similar habitat; and (3) the relatively lower overstorey species diversity within the south-west forests.

8.3.1 Why have ngwayir persisted in the Upper Warren but not elsewhere in the jarrah forest?

An obvious exception to the general pattern of decline has been the persistence of the ngwayir population in the Upper Warren, particularly in Perup Nature Reserve, which includes Chariup (de Tores 2000; Jones 2004). This is particularly interesting because Perup Nature Reserve has retained much mammalian fauna no longer found in other areas. Christensen (1980a) suggested that predation pressure from introduced foxes has historically been relatively low around Perup Nature Reserve. The area is characterised by a relatively high density of *Gastrolobium*, which contain sodium monofluoroacetate (1080 poison). Unlike native fauna, introduced mammals lack the co-evolved resistance to this poison (Twigg *et al.* 2003). By preying on native fauna that have recently fed on *Gastrolobium*, foxes may suffer lethal poisoning, thereby keeping their numbers relatively low (Christensen 1980). In addition, the apparently low frequency of intense wildfires in the Upper Warren may explain why this area has retained more marsupial species than other south-western Australian forests (Wardell-Johnson *et al.* 2004). Based on the findings in this thesis (namely the vulnerability of ngwayir to predation and sensitivity to fire intensity), both theories are plausible explanations for the persistence of ngwayir in the Upper Warren.

8.3.2 Why have ngwayir declined more dramatically than koomal in south-western Australia?

The koomal and ngwayir have respectively been lost from ~50% and ~80-90% of their former habitat in south-western Australia (de Tores 2000; How and Hillcox 2000; Jones 2004). Five factors may account for the different declines observed for these two largely sympatric possum species.

First, although the birth rates at Chariup were similar for both species, it is likely that inland populations of koomal have greater reproductive potential than inland populations of ngwayir. Multiple successful births by the same female within the same year have been observed for koomal in inland forests (Sampson 1971) but not for ngwayir (Chapter 5). This is despite the potential for twinning and/or double breeding by ngwayir (Ellis and Jones 1992; Jones *et al.* 1994a).

Second, the life expectancy of the koomal is longer than that of the ngwayir (10 years versus 4 years; Chapters 4 and 5). This means that koomal individuals produce more offspring during their lifetime and are better placed to withstand and recover from acute disturbances (e.g. drought, logging; see above).

Third, the koomal has a more generalist diet and exhibits greater biological and ecological variability across its range than the ngwayir. It therefore adapts more easily to differing habitats than the ngwayir, which is a specialised arboreal folivore.

Fourth, the koomal appears less susceptible to predation than the ngwayir. At almost twice the size, the koomal is substantially more active and aggressive than the ngwayir; it also appears to be more responsive to potential danger. If on the ground, it will run either through the ground vegetation or, more often up a nearby tree. The defence strategy of the ngwayir is generally to remain stationary. Compared with the koomal, the ngwayir is slower-moving and remarkably predator-naïve (A. Wayne personal observation).

Finally, given its more aggressive nature and larger size, the koomal is more likely to prevail in the event of direct competition with the ngwayir (see below).

8.3.2.1 Potential competition and resource partitioning between koomal and ngwayir

Chapter 6 briefly discusses the similarities and differences in the habitat selection of diurnal refuges by koomal and ngwayir. Both species used hollow-bearing trees > 96% of the time, and the characteristics of the trees that they used were very similar. The main differences between the two species, with respect to diurnal refuge use, included the more extensive use of marri (compared with jarrah) by koomal and of jarrah (compared with marri) by ngwayir. Ngwayir are able to use smaller trees (i.e. smaller hollows) than koomal, because of their smaller body size. Given the aggressive nature of koomal, it is likely that koomal would prevail in competitive interactions between the two species. Further studies will be needed to confirm whether or not the differences in diurnal refuge use between these species are the result of competition or of preference alone.

Differences in the meso-habitat context of diurnal refuge selection between koomal and ngwayir potentially reflect spatial differentiation or resource partitioning. Other ongoing studies by the author will examine the extent of spatial and habitat differences between the two species (see ‘8.5 Future research’ below). Whatever the extent of competition between the two species, there is evidently sufficient niche differentiation for sympatric co-existence in the Upper Warren.

8.4 Value of this research to conservation and land management

This study has substantially improved the understanding of the biology and ecology of the koomal and ngwayir in jarrah forests of south-western Australia. Conservation and land management activities need to make the best possible use of all the available ecological information if they are to be effective in maintaining viable populations of both species. The improved knowledge presented in this thesis will contribute to the pursuit of this objective. Some of the key considerations for conservation and land management derived from this research are briefly presented below. Given that research on the koomal and ngwayir continues (see '8.5 Future research' below), these principles will be subject to further refinement as new insights emerge.

1. Consider animal responses in terms of ecological processes. The objective of mitigating the impact of disturbance on koomal and ngwayir is best approached from an understanding of how disturbance affects biological and ecological processes such as access to food and shelter, competition, predation and reproductive fitness. A process-based perspective is also more likely to identify effective solutions that might not otherwise become apparent. For example, the temporal associations between seasonal food supply, ngwayir condition and mortality indicate that strategic timing of fox and cat control when ngwayir are most vulnerable is highly likely to be substantially more effective than current practices (see Chapter 5 and below). Effective conservation and sustainable forest management strategies also should consider other means to improve fecundity and/or life expectancy as a means to maintaining population viability.

2. Consider intensity, scale, timing and frequency of disturbance. The intensity of disturbances such as logging and fire appear to be particularly important determinants of ngwayir abundance (Chapter 7). The scale of such events also is important and will influence the responses by ngwayir given their small home-ranges, limited dispersal ability (Wayne *et al.* 2000; A. Wayne unpublished data) and their association with anthropogenic disturbance factors at multiple spatial scales (Chapter 7). The patchiness and extent of disturbance can affect the ability for individuals to access resources within their home-ranges (MacArthur and Levins 1964), as well as the potential for metapopulation dynamics to facilitate recruitment from outside affected areas. Given the seasonal variation in koomal and ngwayir body condition and mortality of the latter (Chapters 4 and 5), the timing of disturbances also is likely to influence the magnitude and type of response by possums. For example, the timing of logging or fire events may directly affect the survival outcome of ngwayir, as well as their breeding cycles and reproductive success. For instance, disturbance between April and September, when ngwayir condition is poor and vulnerability to predation is high, may have a greater impact on survivorship rates than at other times of the year. The loss of food (including young jarrah leaves) to fire between August and November, when offspring are weaned and becoming independent, may affect the survivorship of mother and young of both possum species. The frequency and duration of disturbances also will affect the ability of populations to recover. For example, sufficient time is required for the formation of new tree hollows to replace aging 'habitat trees' retained in the last cycle of logging before the next cycle of logging commences (Gibbons and Lindenmayer 2002). Possum populations also need sufficient time to recover from previous disturbance events to improve the chances of surviving subsequent perturbations.

3. Different management strategies are required for different populations. Inland populations of ngwayir are less fecund (Chapter 5) and more reliant on tree hollows (Chapter 6) than coastal populations. These differences probably result from habitat differences, and highlight the need to consider conservation management in this context (Jones et al. 1994a). In particular, the maintenance of tree hollows in the more open inland habitats will be more important than in coastal woodlands where ngwayir predominantly use dreys (Chapter 5). Similarly, predator control may need to be more effective in (1) more open inland habitats where movement through the canopy is limited; (2) along forest edges where predation pressure may be greater; and (3) in areas where fecundity is relatively low and life expectancy shorter. It also is important to recognise that the major threatening processes may differ between populations. Habitat loss and fragmentation from agriculture, urbanisation and mining are particularly important threats to the survival of many coastal populations around Busselton (Jones 2004), whereas predation, logging and altered fire regimes are key management issues for populations within publicly-owned jarrah forest (Chapter 7).

4. Identification and protection of key habitat. Integral to the success of conservation efforts is the identification and adequate protection of high value habitat. Understanding the relationships between koomal and ngwayir abundance, anthropogenic disturbance (Chapter 7) and environmental factors (ongoing research, see '8.5 Future research' below) will contribute substantially to the identification of suitable habitat. Although the reservation and protection of these areas should be a high priority, the long-term conservation of koomal and ngwayir also will depend on appropriate conservation strategies outside of reserves (e.g. Recher 1985; Lindenmayer and Franklin 2002).

Within a landscape, some areas may be more valuable as habitat than others (e.g. Soderquist and Mac Nally 2000), such as riparian and more mesic vegetation for ngwayir (e.g. Jones 1994b; Abbott 2005). Such key areas should be managed differently from other parts of the jarrah forest (e.g. fire frequency and intensity). More generally, managing and maintaining the heterogeneity of jarrah forests is fundamentally important to ensure biodiversity conservation (e.g. Law and Dickman 1998; Wardell-Johnson *et al.* 2004).

5. Climate change may impose additional pressure on possum populations. The ~20% decline in rainfall in the south-west over the last 30 years and anticipated further reductions in rainfall and increased temperatures associated with global climate changes (e.g. Timbal 2004) are expected to impose additional pressure on the biodiversity of the region. This is particularly the case for the ngwayir, for which already low reproductive rates may be further compromised. Remnant ngwayir populations, particularly those in inland and northern areas, may be especially vulnerable. Further contraction in animal distributions to the most fertile and mesic forest remnants might occur if other causal factors of decline are not adequately addressed.

6. Fox and cat control. Extensive fox control conducted over nearly 3.5 million hectares of native vegetation in south-western Australia has been extremely successful in promoting the recovery of many native animals (part of the Western Shield Conservation Programme, CALM 2000; Orell 2004). The abundance of ngwayir in the jarrah forest of the Upper Warren also has been positively associated with above-average fox control efforts (Chapter 7). Strategic and effective predator control is thus fundamental to the conservation of ngwayir, and an increase in the frequency to more than four fox-baitings per year may be required to protect ngwayir effectively in some areas. Integrated predator control also provides an excellent example of how the management of key interactions between multiple factors may be an extremely effective means of limiting the negative impacts of potential synergisms between different threatening processes. For example, integration of effective predator control with the management of logging, fire and fragmentation should achieve substantially better conservation outcomes than the isolated implementation of the same management strategies (Chapter 7). Identifying the role of feral cats in fox-baited forests should be a priority, in order to determine to what extent cat control (as distinct from fox control) may further enhance wildlife conservation.

Insights into the biology and ecology of ngwayir and other mammals (e.g. de Tores *et al.* 2004; de Tores personal communication) indicate that substantial improvements to the effectiveness of predator control can be achieved through a more strategic spatial and temporal delivery of control efforts. For example, reduced abundance of ngwayir within fragmented landscapes indicates that fox control may not be as effective as it is in unfragmented landscapes (Chapter 7), thus supporting similar findings for other species in the jarrah forest (e.g. de Tores *et al.* 2004; de Tores personal communication). Conservation outcomes may be improved by augmenting predator control efforts in high quality habitats where vulnerability to predation may be greater, such as forest peripheries and more open habitats (see above). The highly seasonal pattern of mortality of ngwayir (84% April – September) suggests that substantial gains could be ensured by keeping predator numbers particularly low when the ngwayir is most vulnerable (see Chapter 5).

7. Logging. The ngwayir is particularly sensitive to jarrah forest logging (Wayne *et al.* 2000) and its abundance has been associated with the post-logging age of forests and logging intensity at the landscape scale (Chapter 7). Briefly, recommendations for sustaining ngwayir populations within forests available for logging include (1) keeping logging intensity to a minimum; (2) effective predator control during and after logging to reduce vulnerability to predation (the main cause of death); (3) at the landscape scale (i.e. ~1000 ha – within the dispersal range of ngwayir), maintain habitat diversity (structure and floristics) in order to provide sufficient accessible mature forest for the species to persist and to function as a source of recruitment for regrowth areas (e.g. Recher *et al.* 1987; Burrows *et al.* 2002); and (4) at the ngwayir home-range scale (~3 ha), maintain important food and shelter resources in order to support individuals and their offspring. Chapter 6 describes how to identify the trees most likely to be used by koomal and ngwayir as diurnal refuges. Tree diameter was the single best predictor of tree use by both species. Crown senescence, canopy connectivity, tree species and possum signs also were included in a composite model that can be used to predict which trees are most likely to be used by both possum species. In addition to connectivity with adjacent trees, other elements of the habitat immediately around trees also were related to refuge use and should be taken into consideration when selecting 'habitat trees' for protection within logging coupes (i.e. 'habitat islands' and/or corridors). Balga (*Xanthorrhoea preissii*) and hollow logs are among other important diurnal refuges that also should be protected within forest areas (Chapter 6).

8. Fire. Ecologically sustainable fire management can benefit from the findings that both koomal (Friend and Wayne 2003; A. Wayne unpublished data) and ngwayir (Chapter 7) abundances are sensitive to fire intensity. Intense wildfires are expected to be particularly devastating to possum populations. Koomal were more abundant in frequently burnt forest (A. Wayne unpublished data), while ngwayir tended to be more abundant in forests left unburnt for longer periods (Chapter 7). Furthermore, the scale (patchiness and extent) and timing of fire will also influence possum responses and population viability (see above). Like timber harvesting, ecologically sustainable fire management is a complex issue that is further complicated by the spatial and temporal heterogeneity of the jarrah forest (e.g. Wardell-Johnson *et al.* 2004). Given the fire-prone nature of the jarrah forest (e.g. Bell *et al.* 1989; McCaw and Hanstrum 2003), active fire management involving controlled burning is necessary for conservation purposes (Chapter 7). The challenge is managing the complexity of these biological systems. For example, it is probably better to burn some habitats that are more suitable for ngwayir, such as riparian zones and more mesic forest patches (Jones *et al.* 1994a), less frequently than adjacent forest which may provide more suitable habitat for koomal. Variations in fire intensities also will be necessary, based on the vegetation responses to fire and the habitat requirements for the diversity of wildlife that depend on these forests. Ecologically informed fire management for the maintenance of fine-grain mosaics, while challenging, should help to conserve biodiversity (Law and Dickman 1998). Research in progress (see '8.5 Future research' below) will provide further information on koomal and ngwayir and lead to more specific recommendations for their conservation.

9. Forest fragmentation. The finding that ngwayir abundance was negatively associated with forest fragmentation at the landscape scale also has implications for the conservation and management of remnant forest and for habitat restoration on both privately- and publicly-owned land. Conservation of native vegetation and fauna in agricultural landscapes is particularly important given that the most fertile and productive areas tend to be selected for agriculture and human settlement (e.g. McArthur and Clifton 1975; Braithwaite *et al.* 1984, 1988; Dargavel 1995; Norton *et al.* 1995) and are also particularly valuable habitat for many species such as the ngwayir (Chapter 7), and some arthropods and birds (Recher *et al*. 1996). Given the extent of decline by ngwayir since the European settlement of Western Australia (de Tores 2000; Jones 2004), no further land clearing should occur in or adjacent to high-value habitat that may threaten the long-term viability of remnant populations of ngwayir or other native species (e.g. Recher 1999). Habitat connectivity within fragmented landscapes also is particularly important, especially in the context of rapid or major environmental change (e.g. Peters and Darling 1985; Lindenmayer and Franklin 2002; Soule *et al.* 2004).

10. Use 'active' adaptive management for efficient and effective conservation progress. An 'active' adaptive management approach (Walters and Holling 1990; Lee 1999) can provide an efficient and potentially optimal model whereby applied ecological research and effective conservation are achieved conjointly (Chapter 7). Particular strengths of this approach include the explicit recognition by research and management that knowledge is incomplete, and with co-ordinated and collaborative interaction between the disciplines, the 'learning by doing' approach can provide efficient and timely improvement to conservation outcomes. The 'active' adaptive management approach is highly relevant and applicable to all of the major management implications and recommendations presented in this section.

8.5 Future research

Several aspects of the research programme, of which this thesis is a part, remain to be completed (i.e. analysis and publication). These include further study of the following:

(1) The home-ranges, movement and spatial patterns of habitat use by koomal and ngwayir at the Chariup study site.

(2) Nocturnal habitat selection by koomal and ngwayir to complement research into diurnal refuge selection. This includes examining the spatial relationships between diurnal refuges and nocturnal habitats.

(3) The distribution and abundance of ngwayir in the Upper Warren in relation to environmental factors (e.g. nutrients, climate, water, vegetation structure, floristics etc) at local and landscape scales.

(4) The distribution and abundance of koomal in the Upper Warren in relation to (a) anthropogenic factors and (b) environmental factors at local and landscape scales.

Additional future research should include (1) bioclimatic and population viability studies of the ngwayir's former and current distribution to identify the potential processes underlying its decline, and to explore potential future scenarios within the context of climate change and alternative management scenarios; (2) the impact of cat predation in fox-baited forest on the populations of threatened species such as the ngwayir and phascogales (*Phascogale tapoatafa* and *P. calura*); (3) the role of nutrition on ngwayir fecundity, seasonality of breeding, and seasonal variation in body condition; (4) integration of knowledge of life history and demographics (e.g. fecundity) with an understanding of the anthropogenic and environmental factors that relate to possum abundance, with a view to identifying possible metapopulation dynamics, the location of source and sink populations and, therefore, which habitat elements within the landscape are particularly important to protect and manage; and (5) the use of active adaptive management approaches to improve the ecological sustainability of forest management. Examples of areas in which these approaches can be particularly useful include (a) predator control regimes in disturbed areas, along forest edges and in fragmented forest; (b) prescribed burning practices; and (c) jarrah forest timber harvesting. Other relevant subjects for future research have been presented in context elsewhere in this and other chapters.

8.6 References

Abbott, I. (2002). Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research* **29**, 51-74.

Abbott, I. (2005). Historical perspectives of the ecology of some conspicuous vertebrate species in south-west Western Australia. Manuscript (in preparation to be submitted for publication to *Conservation Science Western Australia*).

Bell, D. T., McCaw, W. L. and Burrows, N. D. (1989). Influence of fire on jarrah forest vegetation. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 203-215. (Kluwer Academic Publishers: Dordrecht)

Braithwaite, L. W., Turner, J. and Kelly, J. (1984). Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales: III Relationships between fauna densities, eucalypt occurrence and foliage nutrients, and soil parent materials. *Australian Wildlife Research* **11**, 41-48.

Braithwaite, L. W., Binns, D. L. and Nowlan, R. D. (1988). The distribution of arboreal marsupials in relation to eucalypt forest types in the Eden (NSW) Woodchip Concession Area. *Australian Wildlife Research* **15**, 363-373.

Bronson, F. H. and Heideman, P. D. (1994). Seasonal regulation of reproduction in mammals. In 'The Physiology of Reproduction'. (Eds E. Knobil and J. D. Neill) Volume 2 pp. 541-583. (Raven Press Ltd.: New York)

Burrows, N. D., Christensen, P. E. S., Hopper, S. D., Ruprecht, J. and Young, J. (2002). 'Towards ecologically sustainable forest management in Western Australia: A review of Draft Silviculture Guideline 1/02.' Conservation Commission of Western Australia, Perth.

CALM (2000). 'Western Shield Fauna Recovery Program Strategic Plan (July 1999 – June 2004).' Western Australian Government Department of Conservation and Land Management, Perth.

Caughley, G. C. and Gunn, A. (1996). 'Conservation Biology in Theory and Practice.' (Blackwell Science: Cambridge)

Christensen, P. E. S. (1980a). 'The biology of *Bettongia penicillata* Gray 1837, and *Macropus eugenii* Desmarest 1817, in relation to fire. Bulletin 91.' Western Australian Forests Department, Perth.

Dargavel, J. (1995). 'Fashioning Australia's Forests.' (Oxford University Press: Melbourne) de Tores, P. (2000). 'Review of the distribution and conservation status of the western ringtail possum, *Pseudocheirus occidentalis*, and recommendations for management.' Unpublished Report. Western Australian Government Department of Conservation and Land Management, Perth.

de Tores, P. J., Hayward, M. W. and Rosier, S. M. (2004). The western ringtail possum, *Pseudocheirus occidentalis*, and the quokka, *Setonix brachyurus*. Case studies for the February 2003 review of Western Shield. *Conservation Science Western Australia* **5**, 235-257.

Dell, B. and Havel, J. J. (1989). The jarrah forest, an introduction. In 'The Jarrah Forest: A Complex Mediterranean System'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 1-10. (Kluwer Academic Publishers: Dordrecht)

Ellis, M. and Jones, B. (1992). Observations of captive and wild western ringtail possums *Pseudocheirus occidentalis*. *Western Australian Naturalist* **19**, 1-10.

Fischer, J., Lindenmayer, D. B. and Fazey, I. (2004). Appreciating ecological complexity: Habitat contours as a conceptual landscape model. *Conservation Biology* **18**, 1245-1253.

Fischer, J., Lindenmayer, D. B., Barry, S. C. and Flowers, E. (2005). Lizard distribution patterns in the Tumut fragmentation "natural experiment" in south-eastern Australia. *Biological Conservation* **123**, 301-315.

Friend, G. R. and Wayne, A. F. (2003). Relationships between mammals and fire in south-west Western Australian ecosystems: what we know and what we need to know. In 'Fire in Ecosystems of South-West Western Australia: Impacts and Management'. (Eds I. Abbott and N. D. Burrows) pp. 363-380. (Backhuys: Leiden)

Gibbons, P. and Lindenmayer, D. B. (2002). 'Tree Hollows and Wildlife Conservation in Australia.' (CSIRO Publishing: Melbourne)

Hingston, F. J., Dimmock, G. M. and Turton, A. G. (1980). Nutrient distribution in a jarrah (*Eucalyptus marginata* Donn ex Sm.) ecosystem in south-west Western Australia. *Forest Ecology and Management.* **3**, 183-207.

Hingston, F. J., O'Connell, A. M. and Grove, T. S. (1989). Nutrient cycling in jarrah forest. In 'The Jarrah Forest: A Complex Mediterranean Ecosystem'. (Eds B. Dell, J. J. Havel and N. Malajczuk) pp. 155-177. (Kluwer Academic Publishers: Dordrecht)

How, R. A. and Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81-89.

Jones, B. (2004). The possum fauna of Western Australia: decline, persistence and status. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 149-160. (Surrey Beatty and Sons: Sydney)

Jones, B. A., How, R. A. and Kitchener, D. J. (1994a). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). II. Population studies. *Wildlife Research* **21**, 189-201.

Jones, B. A., How, R. A. and Kitchener, D. J. (1994b). A field study of *Pseudocheirus occidentalis* (Marsupialia: Petauridae). I. Distribution and habitat. *Wildlife Research* **21**, 175-187.

Kerle, J. A. (2004). A cautionary tale: decline of the common brushtail possum *Trichosurus vulpecula* and common ringtail possum *Pseudocheirus peregrinus* in the woodlands of the western slopes and plains of New South Wales. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 71-84. (Surrey Beatty and Sons: Sydney)

Law, B. S. and Dickman, C. R. (1998). The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity and Conservation* **7**, 323-333.

Lee, K. N. (1999). Appraising adaptive management. *Conservation Ecology* **3**, 3.

Lindenmayer, D. B. and Franklin, J. F. (2002). 'Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach.' (Island Press: Washington)

MacArthur, R. H. and Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. In 'Proceedings of the National Academy of Science in the USA'. 51 pp. 1207-1210.

Maxwell, S., Burbidge, A. A. and Morris, K. (1996). 'The 1996 Action Plan for Australian Marsupials and Monotremes.' Wildlife Australia - Endangered Species Program - Australasian Marsupial and Monotreme Specialist Group, Species Survival Commission, International Union for the Conservation of Nature and Natural Resources, Project No. 500, Perth.

McArthur, W. M. and Clifton, A. L. (1975). 'Forestry and agriculture in relation to soils in the Pemberton area of Western Australia. Soils and Land Use Series No. 54 ' C.S.I.R.O., Melbourne.

McCaw, L. and Hanstrum, B. (2003). Fire environment of Mediterranean south-west Western Australia. In 'Fire in Ecosystems of South-West Western Australia: Impacts and Management'. (Eds I. Abbott and N. D. Burrows), pp. 87-106. (Backhuys: Leiden)

Norton, D. A., Hobbs, R. J. and Atkins, L. (1995). Fragmentation, disturbance, and plant distribution – mistletoes in woodland remnants in the Western Australian Wheatbelt. *Conservation Biology* **9**, 426-438.

Norton, T. W. (1987). Ecology of greater gliders, *Petauroides volans* Kerr 1792, in relation to variations in habitat quality in eucalypt forests in south-east New South Wales. PhD thesis, The Australian National University.

Orell, P. (2004). Fauna monitoring and staff training: Western Shield review – February 2003. *Conservation Science Western Australia* **5**, 51-95.

Paull, D. and Kerle, J. A. (2004). Recent decline of common brushtail and common ringtail possums in the Pilliga forests, New South Wales? In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson) pp. 85-90. (Surrey Beatty and Sons: Sydney)

Peters, R. L. and Darling, J. D. S. (1985). The greenhouse-effect and nature reserves. *Bioscience* **35**, 707-717.

Recher, H. F. (1985). A diminishing resource: Mature forest and its role in forest management. In 'Wildlife management in the forests and forest-controlled lands in the tropics and southern hemisphere'. (Ed. J. Kikkawa) pp. 28-33. (IUFRO and University of Queensland: Brisbane)

Recher, H. F. (1999). The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Australian Zoologist* **31**, 11-27.

Recher, H. F., Shields, J., Kavanagh, R. P. and Webb, G. (1987). Retaining remnant mature forest for nature conservation at New South Wales. In 'Nature Conservation: The Role of Remnants of Native Vegetation'. (Eds D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. Hopkins) pp. 177-194. (Surrey Beatty and Sons: Sydney)

Recher, H. F., Majer, J. D. and Ganesh, S. (1996). Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. *Forest Ecology and Management* **85**, 177-195.

Sampson, J. C. (1971). The biology of *Bettongia penicillata* Gray, 1837. PhD thesis, University of Western Australia.

Simberloff, D. (1986). The proximate causes of extinction. In 'Patterns and Processes in the History of Life'. (Eds D. M. Raup and D. Jablonski) pp. 259-276. (Springer-Verlag Berlin: Heidelberg)

Soderquist, T. R. and Mac Nally, R. (2000). The conservation value of mesic gullies in dry forest landscapes: mammal populations in the box-ironbark ecosystem of southern Australia. *Biological Conservation* **93**, 281-291.

Soule, M. E., Mackey, B. G., Recher, H. F., Williams, J. E., Woinarski, J. C. Z., Driscoll, D., Dennison, W. C. and Jones, M. E. (2004). The role of connectivity in Australian conservation. *Pacific Conservation Biology* **10**, 266-279.

Specht, R. L. and Morgan, D. G. (1981). The balance between the foliage projective covers of overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology* **6**, 193-202.

Timbal, B. (2004). Southwest Australia past and future rainfall trends. *Climate Research* **26**, 233-249.

Twigg, L. E., Martin, G. R., Eastman, A. F., King, D. R. and Kirkpatrick, W. E. (2003). Sensitivity of some Australian animals to sodium fluoroacetate (1080): additional species and populations, and some ecological considerations. *Australian Journal of Zoology* **51**, 515-531.

Walters, C. J. and Holling, C. S. (1990). Large-scale management experiments and learning by doing. *Ecology* **71**, 2060-2068.

Wardell-Johnson, G., Calver, M. C., Saunders, D. A., Conroy, S. and Jones, B. (2004). Why integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 394-417. (Royal Zoological Society of New South Wales: Sydney)

Wayne, A. F., Ward, C., Rooney, J. and Wheeler, I. (2000). 'The immediate impacts of timber harvesting and associated activities on the ngwayir (*Pseudocheirus occidentalis*) in the jarrah forest of Kingston State Forest Block. Unpublished Progress Report.' Western Australian Government Department of Conservation and Land Management, Manjimup.

Wayne, A. F., Cowling, A., Lindenmayer, D. B., Ward, C. G., Vellios, C. V. and Donnelly, C. F. (in preparation-b). The abundance of koomal, *Trichosurus vulpecula hypoleucus* in relation to anthropogenic disturbances at local and landscape scales in Mediterranean forest in Western Australia.

Wiens, J. A. (1992). Ecology 2000: An essay on future directions in ecology. *Ecological Society of America Bulletin* **73**, 165-170.

APPENDICES

This section comprises three appendices. The first two are the abstracts for the honours theses of Driscoll (2000) and Chapman (2002). These honours theses are directly relevant to the research of koomal and ngwayir in the jarrah forest and were co-supervised by the author of this thesis. Allison Driscoll completed her Honours at the School of Resource and Environmental Management, Australian National University and was principally supervised by Mick Tanton. Her study on the insulative properties of diurnal refuges used by ngwayir is particularly relevant to Chapter 6. Kristy Chapman completed her Honours thesis at the Faculty of Natural and Agricultural Sciences, University of Western Australia and was principally supervised by Harriet Mills. Her study on the differential decay rates of koomal and ngwayir scats is particularly relevant to Chapter 3 and to the scat survey method used for ngwayir in Chapter 7.

Appendix 3 is a review of the relationships between the mammals and fire in south-western Australia. Co-authored with Gordon Friend, it includes as one of its case studies, a discussion of the responses of koomal to autumn and spring prescribed burns in the jarrah forest. The ngwayir also is briefly discussed. This work provides a useful background to the thesis on fire ecology in relation to mammals in the jarrah forest, and also is directly relevant to Chapter 7.

Appendix 1

NGWAYIR DIURNAL REFUGES: A COMPARISON BETWEEN THE INSULATION QUALITIES OF HOLLOWS IN TREES AND NESTS IN BALGA

*Citation: Driscoll, A. W. (2000). A comparison between the insulation qualities of hollows in trees and nests in balga (*Xanthorrhoea preissii*): A study relating to habitat used by the western ringtail possum (*Pseudocheirus occidentalis*). Honours thesis, Australian National University.*

Abstract

This study, in Jarrah forest in the south-west of Western Australia, set out to determine a reason for the use of Balga (*Xanthorrhoea preissii*) as nesting sites by the Western Ringtail Possum (*Pseudocheirus occidentalis*). It also aimed to increase the limited knowledge about the habitat requirements of the Western Ringtail Possum.

Thirteen Balga and twelve trees were tested for insulation quality by measuring minimum and maximum temperatures inside and outside nests or hollows. A general linear mixed model was fitted by restricted maximum likelihood to a subset of the data. Hourly maximum temperatures were analysed visually.

Statistical results showed that Balga nests has slightly lower insulation qualities than hardwood hollows, but in biological terms, there was no difference in suitability between a nest in Balga and a hollow in hardwood. Ambient temperatures would need to reach 53 ^{o}C and 47 ^{o}C before a Western Ringtail Possum would become heat stressed inside a Balga or tree hollow respectively. Temperatures of this degree have never been recorded on the vicinity of the study site.

This study indicated the need for silvicultural guidelines that include the protection and retention of Balga as a valuable resource for the Western Ringtail Possum during harvesting and other silvicultural activities such as prescribed burning. It should also encourage continued research into habitat requirements of the Western Ringtail Possum and provide a basis for further investigation into the use of Balga as a commonly used refuge type.

Appendix 2

DIFFERENTIAL DECAY RATES OF KOOMAL AND NGWAYIR SCATS

*Citation: Chapman, K. (2002). Differential decay rates of brushtail possum (*Trichosurus vulpecula*) and Western Ringtail Possum (*Pseudocheirus occidentalis*) scats. Honours thesis, University of Western Australia.*

Abstract

Scat counts are a useful tool to indirectly measure animal abundance. In particular it may be useful in assessing the populations of the brushtail possum (*Trichosurus vulpecula*) and the western ringtail possum (*Pseudocheirus occidentalis*) because they are tree-dwelling and nocturnal feeding animal, and it is difficult to count them directly. To get an accurate measure of abundance through the use of scat counting methods, the defecation rate and the decay rate of scats must be known.

Precipitation has been identified as the major factor affecting the rate of scat decay, along with temperature. However, these elements tend to interact with other factors such as canopy cover, litter, wind speed and insect activity to affect the final rate of decay. The decay rate of brushtail possum and western ringtail possum scats was investigated in the laboratory, under different levels of rainfall and temperature; and in the field at four locations within the jarrah forest of Western Australia, either in the presence or absence of litter. Also, the effect of a peppermint (*Agonis flexuosa*) leaf diet, and a jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) leaf diet were compared for western ringtail possums.

Under different temperature and rainfall treatments, there was little sign of decay of either brushtail possum or western ringtail possum scats after an 8 week period. However, in the field, brushtail possum scats tended to decay faster than western ringtail possum scats. Also, in the field, the interaction between the presence and absence of litter with climate varied between locations. There seemed to be no difference in the decay rate of scats between the two diets of the western ringtail possum.

Scat counts may not be compared across different locations, or between these two possum species without some correction for the rate of decay. It may be suitable to measure western ringtail possum abundance during winter or early spring. If scat counts are used to count

brushtail possums at this time, they need to be completed within 2 weeks to avoid error associated with the decay of scats.

Appendix 3

RELATIONSHIPS BETWEEN MAMMALS AND FIRE IN SOUTH-WESTERN AUSTRALIAN ECOSYSTEMS: WHAT WE KNOW AND WHAT WE NEED TO KNOW

Citation: Friend, G. R. and Wayne, A. F. (2003). Relationships between mammals and fire in south-western Australian ecosystems: what we know and what we need to know. In 'Fire in Ecosystems of South-West Western Australia: Impacts and Management'. (Eds I. Abbott and N. D. Burrows) pp. 363-380. (Backhuys: Leiden)

A3.1 Abstract

A brief overview is provided of past research and reviews addressing the relationships between fire and mammals in the forests, woodlands and shrublands of south-west Western Australia. Several frameworks and approaches used by various researchers to help understand Australian fire ecology are described in order to place current knowledge in perspective and to highlight gaps in understanding. Elements addressed in our review include the component characteristics of a disturbance such as fire (eg. scale, timing, frequency and season), patterns of post-fire succession for species and their abundances within a community, the use of species life histories and development of a “fire response index” to predict responses to fire, and the realisation that mammal responses are primarily determined by vegetation density and structure rather than time-since-fire *per se*. To further illustrate fire responses, case histories are provided for a range of species representative of early, middle and late successional stages (*viz*. the introduced House Mouse *Mus domesticus,* Ash-grey Mouse *Pseudomys albocinereus,* Little Long-tailed Dunnart *Sminthopsis dolichura,* Common Brushtail Possum *Trichosurus vulpecula,* Red-tailed Phascogale *Phascogale calura,* and Honey possum *Tarsipes rostratus)*. The relationship between fire and hollows, an important form of habitat to many mammals, is also examined.

The publication of past research, the elucidation of mechanisms and interactions between fire and ecological processes at the community level, and determining the relative

importance of scale, patchiness and fire interval are proposed as the principal priorities for future fire ecology research efforts in the southwest. The setting of clear conservation objectives and implementation of an adaptive experimental approach to fire management are seen as the most efficient and effective means of achieving ecological sustainability in relation to fire.

A3.2 Introduction

The impact of fire on fauna in Australian ecosystems has been a contentious and emotional issue for many years. Until the mid 1970s information was anecdotal, with no data on species richness and abundance before/after fire being available. The wildfire that burnt through the Nadgee Nature reserve in NSW in December 1972, however, heralded a new phase in fire ecology research and a rapid expansion in knowledge. The Nadgee fire affected an area where small and large mammal studies were already underway and thus presented a new and unique opportunity to gather before/after data on known populations of animals (see Newsome *et al*. 1975; Recher *et al*. 1975).

Since this opportunistic beginning a number of studies have been carried out and much has been learnt about the inter-relationships between fire, vegetation and fauna throughout many of Australia's ecosystems. Most studies have centered on forest and heath habitats in the south-east and south-west of the continent (eg. NSW (Nadgee and Myall Lakes), East Gippsland, Otways, and the south-west of WA; see reviews by Catling and Newsome 1981, Suckling and MacFarlane 1984, Christensen and Abbott 1989, Friend 1993, Wilson 1996, Wilson and Friend 1999). There have also been studies in mallee areas within Victoria and NSW (eg. Cheal *et al*. 1979), spinifex areas of central Australia during the 1980's (eg, Masters 1993), and most recently, large scale experimental studies on the tropical savannas of Northern Australia (Andersen *et al.* 1998). Most of these studies have examined the impact of fire on small mammals and birds, but very few studies have focused on reptiles and/or amphibians.

In this paper we focus specifically on mammals and their responses to fire (both prescribed fire and wildfire) in the forests, woodlands and shrublands of the mediterranean south-west of Western Australia. We seek to provide a brief overview of current knowledge of this topic, including any overarching frameworks that aid the understanding of response patterns and predictions. To highlight levels of understanding, we present information on a range of species representative of early, middle and late successional stages and examine the relationship between fire and hollows, an important form of habitat to many mammals (eg. for shelter and roosts). We also attempt to place the work undertaken in Western Australia in a broader context, so as to provide insight into where research and management effort should be directed in future.

A3.3 Current knowledge

A3.3.1 Mammals and fire in south-western Australia

Targeted research on the impacts of wildfire and/or prescribed fire on mammals in the south-west began in the early 1970's in the northern jarrah forest, primarily to investigate the effects of regular prescribed burning of these forests, which had commenced in the early 1960's. These earlier studies included preliminary work on small ground-dwelling mammals such as the Mardo *Antechinus flavipes* (Schmidt and Mason 1975) and more detailed research on the Tammar Wallaby *Macropus eugenii*, the Quokka *Setonix brachyurus* and the Woylie *Bettongia penicillata* by Christensen (1980). This mammal/fire ecology work (along with work on vegetation and birds) was documented by Christensen and Kimber (1975) in the first review of fire effects research in the south-west. They concluded that their "limited data on mammals demonstrate that no one prescribed burning regime will encourage maximum population levels of all the mammal species in an ecosystem."

A decade later a symposium on "Fire Ecology and Management in Western Australian Ecosystems" indicated that only limited progress on mammal/fire ecology research had been achieved in the south-west, but introduced a new era of more intensive experimental and space-for-time based research. This was the approach adopted by Bamford (1985, 1986) who carried out a number of spring and autumn experimental burns in Banksia woodlands and examined areas of differing fire ages. Bamford (1986) recorded high survival rates of most small mammal species, particularly where fire intensity was variable and undulating terrain contributed to an uneven burn. The relatively small size of these burns (<50 ha) enabled animals to survive by moving out of the affected areas into unburnt habitat (eg. *Sminthopsis griseoventer*). Conversely, individuals of the introduced House Mouse *Mus domesticus* (syn. *M. musculus*) moved into the burnt areas within days of the fire from surrounding unburnt areas and farmland, probably to take advantage of significant post-fire seed fall.

A further important and comprehensive review of fire impacts in the jarrah and karri forests was undertaken by Christensen and Abbott (1989) and provided some detail on response patterns of several species as well as commenting on the implications for management. They postulated that although there are variations on the theme, there is a general pattern describing the response to fire by living organisms in an ecosystem:

- There is a reduction in the numbers and sometimes species of organisms immediately after fire.
- There is a recovery in the numbers and species of organisms after fire. This recovery is often characterised by the appearance of species which were rare before the fire or were present in the ecosystem only as stored seed in the soil.

- Changes may occur in the species dominance and relative density after fire. These changes are often spectacular (e.g. fire weeds) but are almost always transient.
- Recovery from fire is achieved almost totally by propagation from within the burnt area, although recovery of vertebrates is often assisted (and sometimes is achieved entirely) from unburnt areas.
- The rate of post-fire recovery of animal species depends largely on vascular plant recovery patterns which in turn are influenced by the intensity and season of the fire and by the length of intervals between fires.
- Each species of organism has a well defined response to fire. This response is flexible, allowing organisms to react across a wide range of possible fire regimes. Nevertheless, there are limits to responses, associated with individual life history strategies.

With respect to mammals, the state of our knowledge at the time of Christensen and Abbott's (1989) review may be summarised as follows:

- Numbers of small and medium-sized terrestrial mammals are generally reduced by any fire which burns a substantial area of forest, either from the fire directly or by subsequent predation (Christensen and Abbott 1989).
- Responses to fire vary with the mammal species and with the characteristics and history of fire (and other disturbance) in the area. The recolonisation of species to a burnt area depends on the time taken for suitable habitat to regenerate and is generally largely achieved by surplus young animals from adjacent unburnt areas (Christensen and Abbott 1989).
- Large macropods (e.g. Western Grey Kangaroo *Macropus fuliginosus* and Western Brush Wallaby *Macropus irma*) are less adversely affected by fires, although large intense fires are detrimental, as they are for arboreal species such as possums.
- Quokkas (*Setonix brachyurus*) are thought to require dense thickets unburnt for 10 years or more (Christensen *et al*. 1986).
- Mainland Tammar Wallabies (*Macropus eugenii*) are fire dependent requiring periodic intense fires under dry conditions to regenerate the scrub thickets in which they live (Christensen 1980). Fire frequency of 25-30 years is thought necessary to maintain populations of Tammars in the presence of foxes *Vulpes vulpes* (Christensen and Maisey 1987).
- Woylie (*Bettongia penicillata*) populations may experience immediate severe, reductions by fire followed by a rapid increase, finally reaching stable pre-fire levels 4-5 years after fire. The population increase is due largely to emigration from adjacent unburnt areas, predominantly by males and as the vegetation in the burnt area recovers (Christensen 1980).

- Brush-tail Possums (*Trichosurus vulpecula*) and Western Ring-tail Possums (*Pseudocheirus occidentalis*) are temporarily reduced as a result of intense fires in summer or autumn, but recovery is relatively fast (Inions 1985). Low intensity fires have minimal effect on possum populations.
- Numbats (*Myrmecobius fasciatus*) and the availability of termites (their food) are not significantly impacted by fire directly. However, the loss of habitat cover in the form of logs and thickets appears to increase mortality through predation (Friend 1994). Numbats seem to prefer areas burned relatively infrequently but can tolerate more frequent burning (Christensen and Abbott 1989). Autumn fires every 20 to 30 years at Dryandra would allow *Gastrolobium microcarpum* thickets maximum regeneration (Burrows *et al.* 1987) and shelter opportunities for Numbats.
- Southern Bush Rats (*Rattus fuscipes*) are slow to re-invade, building to maximum population levels 4-6 years after fire in karri forest, thereafter declining to lower numbers in long unburnt forest (Christensen and Kimber, 1975).
- Mardo (*Antechinus flavipes*) prefer forest with a deep litter layer (unburnt 10 years or more) (Christensen and Kimber, 1975; Sawle, 1979). Leaf litter insects (major parts of their diet) are also numerous in deep litter in unburnt areas.
- The House Mouse (*Mus domesticus*) invades burnt areas after fire, rapidly breeds, then disappears within a few years (Christensen and Abbott, 1989).
- The Red Fox *Vulpes vulpes* may have a significant effect on the recovery of native fauna following fire (Christensen 1980).

Although this was a substantial body of knowledge, Christensen and Abbott (1989) noted that “there is very little information on the long-term effects of repeated fires on the flora and fauna”. This is still true today (see later).

Since the 1985 symposium and Christensen and Abbott’s review, however, a considerable amount of intensive experimental and space-for-time based fire ecology work has been undertaken on small mammals (and other vertebrates) throughout a range of ecosystems in the south-west. These studies have embraced Banksia woodlands (Bamford 1986, see above), kwongan shrublands and *Allocasuarina* and *Eucalyptus* woodlands in the wheatbelt nature reserves (eg. Tutanning and Durokoppin Nature Reserves; Friend *et al.* 1997, G Smith *personal communication*, Friend *unpublished data*), mallee shrublands and heathlands near the south coast (eg. Stirling Range, Fitzgerald River and Scott River National Parks; R Wooller, *personal communication*, D Bradshaw *personal communication*, Friend *unpublished data*) and jarrah forest at Batalling (Friend *et al*. 1994, Friend *unpublished data*, Wayne *unpublished data*). Through their purposeful, experimentally-based study designs which included prescribed fires, wildfires and repeated fires, these studies have the potential to significantly advance our knowledge of the short and longer-term responses of small mammals to fire across a range of important ecosystems. Unfortunately, to date, much of this work remains unpublished. Burrows and Friend (1998), however, drew on their research on the responses of vegetation and small vertebrates to fire in the south-west to develop ecologically appropriate fire regimes for this region, while Friend (1995, 1999) summarised findings from his fire and small vertebrate research as follows:

1. The small vertebrate fauna inhabiting semi-arid woodlands and shrublands in Western Australia appears to be relatively resilient to single fire events of small scale and low to moderate intensity. The impact of repeated fires, however, is unknown.
2. Resilience may be greater in the seasonally dry shrublands and woodlands than in the more mesic but less seasonal habitats (eg. south-west forests). Adaptations for seasonal aridity may impart considerable resilience to fire. However, this does not mean that fauna will not change greatly under a high frequency fire regime; there are (fire) sensitive species and habitats within the Region (eg. *Phascogale calura),* that require special consideration.
3. Frequency and scale of burns are probably the two most important factors to consider in fire management. There is no evidence from these studies (eg. in Stirling Range National Park where both spring and autumn experimental burns have been conducted) that season of burn is of major significance.
4. Post-fire response patterns of most small vertebrate groups are closely tied to (and may be predicted from) their shelter, food and breeding requirements (life history parameters).

- mammal responses are reasonably predictable
- reptiles somewhat less
- amphibia show little relationship.

These patterns are derived from large scale wildfires throughout temperate Australia. Data from our smaller scale and lower intensity mallee-heath fires, however, have not shown such clear trends for small mammals (and reptiles).

1. Given the above, fauna can be grouped or categorised in terms of their life history attributes, particularly their shelter, breeding and dietary requirements. This greatly simplifies the prediction of fire impacts.
2. Results from space-for-time studies of potentially sensitive species in the Stirling Range National Park (eg. honey possum, *Tarsipes rostratus*) indicate clear trends with post-fire age of vegetation and set the frequency limits for a fire regime. These data suggest a minimum time required between burns in the Stirling Range National Park to achieve otherwise optimal population sizes of *Tarsipes* to be 15-20 years. Similar optimal fire intervals for vegetation in the Park have been found by L. McCaw

personal communication. In the lower rainfall areas of the Wheatbelt Region where vegetative growth is slower the minimum fire interval is likely to be 20-25 years.

3. With respect to animal abundance and composition, the effects of season, locality and year-to-year variability in climate, and stochastic events like droughts and locust plagues may outweigh any changes attributable to fire.

A3.3.2 Frameworks which aid understanding of response patterns

Habitat and fauna responses to fire will vary over space and time due to the complexity of interactions between the myriad of ecological factors and processes at play. A broad understanding of how a species or community may be expected to respond to a particular disturbance such as fire, may be achieved by quantifying four key characteristics of the disturbance type in question: timing, intensity, spatial attributes (scale, magnitude, patchiness) and disturbance history (including frequency). The interactions with and between other factors, (many of which remain unpredictable, such as elements of the climate, disease, and other stochastic events), will also have a substantial influence on how a community or species will ultimately respond to an event such as a fire. Naturally, the innate characteristics of the subject which is responding to disturbance also has a substantial bearing on the nature of the response.

A number of reviews and syntheses arising out of and alongside studies of fire and small mammals throughout south-eastern and south-western Australia have provided some insight into response mechanisms and enabled the development of unifying themes and frameworks which aid our understanding. These reviews (eg. Fox 1982, 1983, Friend 1993) have shown that there appears to be a reasonably consistent and predictable successional sequence of small mammals following fire in forest and mallee/heath ecosystems throughout Australia. A common theme is the rapid and early colonization by the exotic *Mus domesticus*, followed by *Pseudomys* spp., if extant. *Mus* appears to be a post-disturbance opportunist that exploits unfilled niches but does not necessarily substitute for *Pseudomys.*

A further reasonably consistent pattern is the increase in abundance of the dasyurids (primarily *Sminthopsis* spp.) in the mid-successional stage (eg. 3-5 years) following the decline in abundance of *Mus* and *Pseudomys*. Later, as the dasyurids decline in response to further habitat successional changes, the larger rodents (*Rattus* spp.) become dominant if extant in the region. This latter pattern is not a consistent trend, however, and may depend on habitat characteristics (eg. vegetation density) and the patchiness of the fire allowing refugial populations (eg. of *Rattus lutreolus*) to survive in moist areas with dense cover (see later).

In some situations and habitats seral responses may be truncated (eg. banksia/heath patterns in south-western Australia (Bamford 1986) compared with those in the south-east);

there is a rapid succession in the south-west, perhaps indicating a fauna well adapted to relatively frequent fires (Friend 1993).

By calculating a "fire response index" (logarithm of the ratio of post-fire to pre-fire abundance of each species) Fox (1983) was able to classify the species in his Myall Lakes study area as occupying an "early regeneration niche" (eg. *M.domesticus, P. gracilicaudatus, P novaehollandiae* and *I. obesulus*) or a "late regeneration niche" (eg. *A.stuartii, R.fuscipes* and *R. lutreolus*). Fox (1982) summarized these seral responses by proposing a "habitat accommodation model" whereby species enter the succession when their specific habitat requirements are met, and are replaced or decline in abundance as conditions become suboptimal and their competitive ability is reduced.

Such a linkage between fauna and vegetation succession has been confirmed in long-term studies in forest habitats (Fox 1996, Monamy and Fox 2000) where early successional species (eg. *Pseudomys novaehollandiae*) began to increase in abundance in long-unburnt sites (20-30 years old) and late successional species like *Rattus fuscipes* began to decline. This correlated with a senescing and opening up of the understorey vegetation, in effect “regressing” to its earlier post-fire physiognomy. *Mus domesticus* does not appear able to reinvade when the forest understorey opens up after two decades, but its abundance is probably closely linked to its abundance in the region as a whole, rather than determined by site-specific factors. This work also explained why the late successional species *Rattus lutreolus* may colonise earlier in some situations (eg. Nadgee after the 1980 wildfire; Catling 1986) and at Myall Lakes after the 1994 wildfire; Monamy and Fox 2000); it reflects the importance of the presence of refugial areas of dense low vegetation or the rapid regrowth of dense vegetation in some (exceptional) circumstances which are required by *R. lutreolus*. This pattern also arises because of the superior competitive ability of *R. lutreolus* over early successional *Pseudomys* (eg. *P. gracilicaudatus*, Higgs and Fox 1993).

The long-term work by Barry Fox and his colleagues (Fox 1996) has shown that, given sufficient time, post-fire succession of eastern Australian mammals in coastal heathlands does become a sequential replacement of species rather than a replacement of dominance or shifts in relative abundance, as earlier believed. The successional trajectory may be regarded as a property of the community rather than of the individual species. Most importantly, this work has shown that the mammal community is not in fact responding to any temporal (time-since-fire) axis; rather the mammals are responding to the vegetation succession as measured through vegetation density and structure (Monamy and Fox 2000). It is important to realise that this outcome could only be identified through long-term monitoring at permanently established study sites.

Relationships between ‘habitat complexity scores’ and mammal distribution and abundances have also been demonstrated recently by Catling *et al*. (2001), indicating that time-since-fire *per se* is not necessarily a strong indicator of mammal presence or abundance. Utilising the ability of airborne videography to accurately predict habitat complexity (Coops and Catling 1997), Catling and Coops (1999) have used this technology to predict mammal distribution and abundances at a landscape scale and thus model and predict response patterns up to 25 years after wildfire (Catling *et al*. 2001). This offers a potentially powerful tool for testing and using in other areas and habitats.

Friend (1993) reviewed the impact of fire on small vertebrates and examined life history parameters (shelter and food requirements, and activity and breeding patterns) for small mammals occupying early (eg. *Mus domesticus, Pseudomys* spp.), middle (eg. *Sminthopsis* spp.) and late (eg. *Antechinus* and *Rattus* spp.) successional stages after fire. Such a synthesis was seen as a necessary first step to developing a predictive model of fire impact for small vertebrates.

This review indicated that small mammal species which survive fire and/or favour early post-fire successional stages generally shelter in burrows in relatively open areas with low ground vegetation and little leaf litter cover. They have non-specialized omnivorous diets, and can vary their reproductive patterns in response to climatic or habitat cues. Mid-successional species require denser vegetation and shelter in more flammable refuges (eg. hollow logs and grass trees), are less general in their diets, and have a more rigid seasonal, though polyoestrous, breeding strategy. Finally, late-successional species show considerable specificity in diet, shelter in flammable refuges in relatively dense vegetation, and may have a seasonal and highly synchronized breeding season.

There is thus a trend of increased specificity and reduced flexibility in small mammal species' life history parameters concomitant with increased impact of fire, and later post-fire recolonization. These relationships support Fox's and Catling's and their colleagues findings (above) that mammal species respond to habitat successional cues (eg. cover, structure and floristics), which may or may not be closely related to a temporal axis, but which greatly influence the shelter and food resources available for mammals.

A3.4 Species case studies from south-western Australian ecosystems

In order to better illustrate and further explore many of the post-fire reponse patterns and longer-term successional changes documented for small mammals in the south-west, we present information below on a range of species generally representive of early, middle and late successional stages. This information is drawn mainly from the unpublished studies carried out by the authors, but is also placed in the context of other relevant studies and data from other areas of Australia.

A3.4.1 House mouse *Mus domesticus*

The introduced house mouse (*Mus domesticus* Rodentia: Muridae) is a small (8-25g) rodent which is almost ubiquitous throughout Australian environments, largely owing to its very generalised and highly adaptable life history traits. It shelters in shallow burrows or beneath almost any cover, is omnivorous, feeding on a wide range of seeds, fungi, insects and human food, and breeds opportunistically in response to environmental cues (Singleton 1995). Most fire effects studies in Australia have reported an immediate and dramatic increase in this species following fire (see recent reviews by Friend 1993, Whelan 1995, Wilson 1996 and Wilson and Friend 1999) and most results from fire studies in the south-west forests have also clearly demonstrated the opportunistic behaviour of *Mus domesticus* after such disturbance (Christensen and Abbott 1989, Wayne *et al*. 2001).

In the drier remnant mallee heathlands and shrublands of the south-west, however, although *Mus* usually increased in abundance immediately following fire (Bamford 1986, R Wooller *personal communication*) its occurrence was neither unique (ie. it had been recorded prior to the fire cf. most forest studies; Newsome *et al*. 1975, Christensen and Kimber 1975) nor statistically significant in many cases (eg. Tutanning NR and Stirling Ranges NP, Friend *unpublished data*). The reasons for such differences are not clear, but may relate to the fragmented nature of these habitats which have allowed house mice to establish permanent populations. Such patterns may also indicate relatively high levels of competition between species in the post-fire habitat niche and truncation of the seral response, perhaps signifying a fauna well adapted to relatively frequent fires (Catling & Newsome 1981).

A3.4.2 Ash-grey mouse *Pseudomys albocinereus*

The native ash-grey mouse *(Pseudomys albocinereus* Rodentia: Muridae) has many ecological similarities to the house mouse. It also shelters in burrows in sandy soil, is generalist in its diet and breeds opportunistically, with a considerable reproductive capacity (Morris 1995). Like *M. domesticus*, the ash-grey mouse is a disturbance opportunist, with population density highest in the first few years after fire. Pit-trap grid data gathered from an 8 year-old buffer strip and an adjacent fifty-year-old area in the Stirling Range NP (Friend, *unpublished data*) showed a dramatic difference in abundance, there being 6-10 times more animals captured in the younger vegetation. Most of the other *Pseudomys* species throughout Australia are also known to respond to plant species richness and cover attributes characterising the early post-fire phase in mallee/heath communities (Sutherland and Dickman 1999). However the western form of the heath mouse *P. shortridgei* appears to occupy the opposite end of the post-fire sere, occurring in mallee-heath habitats that have not been burnt for forty years (Baynes *et al.* 1987), while the rare western mouse *Pseudomys occidentalis* also appears to favour long-unburnt vegetation (Whisson and Kitchener 1995).

A3.4.3 Little long-tailed dunnart *Sminthopsis dolichura*

The response of the little long-tailed dunnart *(Sminthopsis dolichura* Marsupialia; Dasyuridae) to fire was studied in Tutanning and Durokoppin Nature Reserves (Friend *et al*. 1997, G Smith *personal communication*). This animal is a small (20-30g) insectivorous ground-dwelling marsupial which shelters in low shrubs, under bark or in hollows in logs. It has a high reproductive rate with females capable of raising more than one litter per year. Males do not die after breeding (Friend and Pearson 1995).

Following relatively small scale (100-300ha) experimental autumn fires in these two Reserves, the little long-tailed dunnart populations remained steady for 2 months, but then fell significantly, as did the population in the control (long unburned) plots at Tutanning. For the first 18 months or so after the Tutanning fire, the populations in both burned and long unburned plots followed similar trends, although the population in the burned plots remained consistently lower than those in the long-unburned plots. However, by about 24 months after fire there was no significant difference between the two sites. This slightly delayed increase of the *S. dolichura* population following fire was due to both dispersal and *in situ* breeding by animals which survived the fire. Their non-arboreal habits, high reproductive capacity and fairly generalized food and dietary requirements enable these animals to persist and respond to the conditions prevailing in the early postfire stages. Similar findings have been reported for other *Sminthopsis* species (Fox 1982, 1990, Fox and Whitford 1982, Friend 1993).

A3.4.4 Common brushtail possum *Trichosurus vulpecula hypoleucus*

The common brushtail possum (or koomal) is the largest (1000-2500g) of the possums and arboreal mammals of the southwest and occurs within many habitats, but especially forests and woodlands. It has a fairly generalized vegetarian diet of eucalypt and shrub leaves, flowers, buds and fruits and occasionally meat and some fungi when available. In comparison with the western ringtail possum or ngwayir *Pseudocheirus occidentalis* (the only other medium-sized possum present within the southwest), the common brushtail possum is unable to build its own dreys and is a more extensive user of hollows within standing trees and logs (Wayne *et al.* 2000, Wayne *unpublished data*). On the basis of their reliance on hollows, the relative frequency of occurrence of suitable hollows and the size of their home range, the common brushtail possum is considered by Abbott and Whitford (*in press*) to be one of the most sensitive species to changes in hollow abundance within the southwest forests. The authors subsequently concluded that this species remains one of the best ‘indicator’ species candidates for monitoring any critical reduction in the long-term supply of large hollows at small spatial scales.

According to Christensen and Abbott (1989), low intensity fires have a minimal effect on common brushtail and western ringtail possum populations. This has been further supported by the results of long term monitoring within Perup jarrah forest (Burrows and Christensen, *submitted*) in which there was no discernable impact on the capture rates of common brushtail possums (or woylies *B. penicillata*, Southern brown bandicoots *Isoodon obesulus* and Western quolls *Dasyurus geoffroii*) after three successive spring burns over a 26 year period. Inions (1985), by contrast, found that there were population declines immediately after a high intensity fire (up to 1500 kW m^{-1}) also in Perup. Population recovery was apparently rapid with an indirect index of population size (den tree densities) suggesting a 300% increase on the pre-fire abundance of possums 32 months after the fire. Inions *et al.* (1989) suggested that this may have resulted from an influx of possums that were attracted by the epicormic growth on the eucalypt trees in response to the fire.

Similar trends were observed as part of the Batalling experimental research on the impacts of prescribed autumn and spring management burns on the fauna of the eastern jarrah forest. Population abundance estimates derived from trapping data for the common brushtail possum suggest that, compared with adjacent unburnt (control) forest, there was no significant ($p = 0.77$) impact on the abundance of common brushtail possums as a result of a single low intensity prescribed spring burn. On the other hand, the moderate to high intensity prescribed autumn burn experienced at Batalling did result in a significantly ($p = 0.014$) lower possum abundance than was observed in adjacent unburnt control areas (Wayne, *unpublished*). The time taken for population recovery in the autumn burnt areas remains unknown at this stage.

The actual mechanisms behind these different fire effects on brushtail possum populations remain to be elucidated. It seems most likely that fire intensity, rather than the season of the disturbance *per se*, is the major determinant of the difference between responses to the spring and autumn fires. The demographic dynamics behind the increased impact from higher intensity autumn fires also remain to be determined. The extent to which declines are a result of direct or subsequent deaths, emigration of previously established adults or dispersing subadults from burnt to unburnt areas, and/or a lack of successful breeding and recruitment in fire affected areas are key issues which need to be addressed.

Successional changes after fire amongst species of medium and large mammals within the southwest are generally less evident than they appear for small vertebrates, and are perhaps limited to shifts in relative abundance between species. With respect to possums, changes in relative dominance have been observed over medium to long terms in several areas (B. Jones *personal communication* and G. Liddelow *personal communication*). In at least some of these cases, fire has been implicated as a causal factor for these changes but this remains to be adequately tested. In terms of their life history traits, the response patterns for the common brushtail possum after a moderate to intense fire would predict that abundances would peak in the early to mid successional stages relative to the western ringtail possum, which would be expected to achieve optimal numbers somewhat later. The interactive relationship between these possum species and fire, amongst other factors, is the subject of a study currently underway (A. Wayne).

A3.4.5 Red-tailed phascogale *Phascogale calura*

The small (40-60 grams) carnivorous red-tailed phascogale *(Phascogale calura* Marsupialia: Dasyuridae) occurs in remnant wandoo *(Eucalyptus wandoo, E. accedens)* and rock sheoak *(Allocasuarina huegeliana)* communities in the Western Australian wheatbelt. The species is arboreal, utilizing tree hollows for refuge and for nesting sites. It has a highly synchronous breeding season during late winter, after which all males die (Bradley 1995).

This species was also investigated during the experimental autumn fire carried out at Tutanning Nature Reserve (G Friend and J A Friend *unpublished data*). The fire directly killed three out of ten radio-collared phascogales while they were taking refuge in hollows in sheoak trees. However the rate of recolonization of the burned areas by animals from surrounding unburned areas was rapid and within several months the numbers of animals known to be alive in burned and unburned trapping grid sites was not significantly different. This can largely be attributed to the relatively small size of the experimental burn and the mobility of the animals. Thus, fire scale, and particularly the size of the fire in relation to the size and mobility of the animal, is an important determinant of the likely response pattern of the species to fire.

Another important response to fire displayed by the red-tailed phascogales was the rapidity with which they changed their nest site selection from rock sheoak trees and grass trees (which were consumed or killed by the fire) to wandoo trees. The latter were better able to withstand the fire and suffered less direct physical impact because of lower fire intensity in these areas. Although this demonstrated the phascogale’s flexibility and adaptability to disturbances such as fire, this change in nesting habits also placed animals at additional risk. To reach feeding grounds from their new nests in wandoo trees, individuals had to travel across the ground, predisposing themselves to predation. These observations, gained only through intensive radio-tracking (J A Friend *unpublished data*), show the potential importance of the interactions between fire and other processes like predation in determining the longer-term outcome for a species or populations.

These interactive effects were further emphasised in the two years following the fire. Initially, the rock sheoak thicket regenerated profusely after the fire from seed stored in the canopy. However, nine months after the fire, the region experienced a serious locust plague which virtually destroyed the sheoak regeneration, permanently changing this site from a rock sheoak thicket capable of eventually supporting red-tailed phascogales to a shrubland/grassland affording little habitat for the species. This is an excellent example of how the scale and timing of disturbance (fire) may interact with episodic events such as locust plagues and drought to produce a net impact on a species which is markedly different from that originally predicted or expected.

A3.4.6 Honey possum *Tarsipes rostratus*

The honey possum *(Tarsipes rostratus* Marsupialia: Tarsipedidae) is a unique marsupial with a highly specialized diet of pollen and nectar which it gleans from the flowers of the floristically rich heathlands that characterize much of south coastal areas of Western Australia. It occurs in similar vegetation as the ash-grey mouse, but has vastly different life history and habitat requirements and displays a very different fire response pattern. This small (10-20 grams) animal breeds continuously and its high metabolic rate requires it to take in food on a daily basis (Renfree *et al*. 1984), often necessitating considerable movement amongst individuals; these movement patterns may differ considerably between sexes (Bradshaw and Bradshaw *in press*).

Honey possums may be severely affected by large scale high-intensity fires which result in complete or near complete landscape burn-out (Richardson and Wooller 1991, Bradshaw *personal communication,* Friend *unpublished data*). The animals, which usually reside in the elevated vegetation (but do not build nests), are either killed by the intense fire, or if they manage to survive the flames, they are likely to be predated or starve within a couple of days if they cannot access suitable flowers. However, if fires are of low intensity and relatively small or patchy, these animals can survive in the landscape and fairly rapid recolonization is facilitated. They will begin to reinvade the burned areas from unburned pockets as soon as a sufficient proportion of the regenerating plants produce pollen and nectar, which may be within 12-18 months of fire (Friend *unpublished data*).

In the Stirling Range NP, honey possum population density was strongly related to time since fire, or age of vegetation, with density increasing quickly in the first five years after fire and reaching a maximum at about 15-20 years after fire (Friend *unpublished data*). The relationship between honey possum density and time since fire is nonlinear, with about 80% of the potential maximum density of animals being reached within the first five years of fire. The time taken to reach maximum density (10-15 years) correlates well with the time it takes for most plants in south coast mallee-heath vegetation types to reach peak flowering age (L McCaw, *personal communication*). The relationship between honey possum density and time since fire is similar to the relationship between the number of plants which have flowered and time since fire (L McCaw and R Wooller, *personal communications*) suggesting that temporal and spatial availability of nectar and pollen is an important factor controlling site carrying capacity.

A3.5 Fire and hollows

Hollows within standing trees and logs are an important habitat resource that are used by 42 vertebrate species (including 16 mammals) within south-west forests (Abbott and Whitford, *in press*). Impacts of fire on this important and potentaill limiting resource may have direct ramifications on the abundances and sustainability of populations of species dependent on them. It is therefore worth specifically considering this habitat resource when examining the effects of fire on mammals.

Inions (1985 and 1989) examined the effects of a high intensity fire on the availability of hollows used by the common brushtail possum and western ringtail possum within the jarrah forest at Perup Nature Reserve. Less than 1% of all trees within the forest stands studied were recorded as being used as den trees by possums. He found that 38% of the hollow bearing den trees used by these possums were destroyed by a single high intensity fire (1000-1500 kW m^{-1}). The dead trees that were previously inhabited by possums were disproportionately most affected, whilst most (87%) of the healthy den trees and their hollows remained intact. Of those that remained after the fire, only 64% were in use 32 months later. Nonetheless, there was a substantial post-fire increase in the total number of hollows being used by possums, many of which were new hollows created by the fire. As a consequence of the disproportionate destruction of older and dead trees and the formation of new hollows, or the deepening of existing ones in younger trees, the average age and size of trees containing suitable hollows decreased substantially.

Tree size is one of the principal factors associated with the increased likelihood of a tree bearing hollows suitable for various fauna, particularly larger species such as possums (e.g. Inions *et al*. 1989, Wayne *et al.* 2000, Whitford and Williams 2001). Aside from land clearing and timber harvesting by humans, the principal natural cause for the destruction of larger marri and jarrah trees is through the process of ‘hollow butt’ formation (Whitford and Williams, 2001), whereby the tree butt is progressively hollowed out and weakened. Although complex, fire is considered the major factor for the initiation and development of ‘hollow butts’.

An examination of the factors affecting the abundance of log hollows in the jarrah forest by Williams and Faunt (1997) found that log size and the degree of fire damage were the most important factors associated with the number of hollows within logs. The study’s findings with respect to fire were as one would intuitively expect; *viz*. those logs that had been subjected to minor or moderate degrees of damage resulted in more hollows, whilst there were fewer hollows in logs that had undergone extensive fire damage. In a similar vein, J. A. Friend (*personal communication*) researched the effects of fire on numbats within the wandoo woodland at Dryandra and found that although a hot autumn fire destroyed about 50% of the hollow logs suitable for numbats, the fire created almost as many. In contrast, a more moderate spring burn destroyed about 25% of the hollow logs, but only replaced them with about 3% of the original number. Five years after the spring burn, further recruitment had been neglible and as a consequence, there remained a substantial deficit in the number of hollows available to numbats. On the other hand, in the area where the hot autumn burn had occurred, the number of numbat hollows approximated the pre-fire levels only 2 years later.

Whether these patterns are also true for other wandoo and jarrah forests remains to be determined.

It is evident from this and other evidence (e.g. Lindenmayer *et al.* 1993, Gibbons *et al.* 2000) that fire is an important factor in the creation, development and destruction of hollows. It seems likely that either no fire at all or mild burns alone may not be sufficient to maintain a consistent supply of hollows over the long term. Although high intensity fires appear to be an important factor determining hollow abundance, the number of hollows in an area of forest is obviously finite and dependant on there being a sufficient source of trees with the potential to form hollows. Clearly, the maintenance of the number of suitable hollows available for fauna cannot be sustainable over the long term if the destruction of existing hollows and potential hosts exceeds the recruitment of potential replacements. Therefore, logging, an excessive frequency in the number of moderate to high intensity prescribed burns, and/or the incidence of destructive summer wildfires, may pose as much or greater a threat to the sustainability of hollow abundance as the complete absence of fire. As a consequence, there is clearly a need to balance the management of these habitats in an integrated manner that not only takes into account the constructive and destructive factors for hollow abundance but also other ecological, conservation and management implications.

A3.6 Knowledge gaps and future directions

The above brief overview of our current knowledge of the relationships between fire and mammals in south-western Australia indicates that we now have reasonable insight into the response patterns of a range of small and (to a lesser extent) medium-sized mammals, as well as some degree of confidence in predicting both the short and the longer-term effects of fire on species and the seral patterns of communities. This confidence, however, is tempered by recognition of the vast array of influences and events which may combine to determine post-fire outcomes. For example, fire and predation alone may not have a major effect on some species, but the interaction between them may have substantial and long lasting impacts that may threaten population viabilities. Interactions between potential threats, episodic disturbances and pressures upon species and communities mean that the exact nature of the responses to fire by different habitats and communities can be as diverse as the communities themselves. This uncertainty represents a significant barrier to confidently using fire to achieve desired conservation outcomes. Unfortunately, until we gain detailed knowledge of impacts and can model the interaction effects of various threats and disturbances, a high level of sophistication in knowledge and predictability will remain unattainable.

To come to terms with dealing with these knowledge gaps, it is useful to break the problem down into its components and begin working on those issues that are practical to address in a realistic timeframe and with a realistic budget. Many of these issues have been summarised in recent reviews by Whelan (1995) and Sutherland and Dickman (1999). These authors correctly point out that there is already a considerable wealth of information on patterns of population response to single fires (and multiple fires in some cases) across a range of species and ecosystems. This is true of ecosystems in the south-west, as indicated above. What is both apparent and unfortunate, however, is that much of this information is not readily available because it has not been fully analysed and published, and beyond that, interpreted and extended to the implementation phase of fire management. This should be seen as the highest immediate priority for fire ecology research in south-west Western Australia.

Beyond this species level knowledge, however, the key issues that require attention in future fire ecology research, in Western Australia and elsewhere, are about (a) mechanisms and interactive effects at the community level, and (b) the importance of scale, patchiness and fire interval in determining mortality, emigration and survival within a site.

The first set of issues can best be teased out and understood through experimental manipulations of resources (eg. habitat, shelter, food), competitive interactions and predation rates (Sutherland and Dickman 1999). Newsome and Catling (1983) took such an approach in developing demographic models of changes in food, shelter and predators to explain abundance trends during plagues of *Mus domesticus*. They then extended these models to examine post-fire population trends for small and large mammals after the Nadgee fire. Although the results were not clear, they did help elucidate some of the mechanisms at play in determining the post-fire structure and succession of mammal communities. Sutherland (1998) carried this line of investigation further through experimental manipulations of food and nest site availability to help explain recovery patterns of small mammals after fire in Ku-ring-gai Chase National Park (NSW). She concluded that, aside from food and shelter resources, site related interspecific competition is an important but largely overlooked factor. Interspecific competition between *Rattus lutreolus* and *Pseudomys gracilicaudatus* was also found to be a critical factor determining the post-fire small mammal assemblage in wet heaths at Myall Lakes NP (Higgs and Fox 1993). Apart from these few studies, this whole area of important research has received scant attention.

The issues relating to scale, patchiness and fire interval and how they influence individual mortality, emigration and survival are, from a fire management standpoint, both the most important and the most easily manipulated. Examining these issues through prescribed burns will also throw critical new light on how various types of wildfire are likely to impact on mammal populations and communities. The answers to this set of issues will only be gleaned by treating prescribed management fires as a series of large scale experiments and, through monitoring and ‘learning by doing’ (M Gill, *personal communication*), refining prescriptions and management actions as one learns. Such an adaptive experimental management approach (Walters 1986) is increasingly recognised as the most fruitful path for research and management to progress.

A3.7 Conclusions

Fire is an integral part of the ecology of the terrestrial habitats of south-western Australia. The mammal species of these ecosystems, like the other constituents of their communities, display a variety of physical and behavioural adaptations that have enabled them to persist in this fire-prone environment. Since the biodiversity and health of these systems are dependant in part on fire, it is not a question of whether contemporary society uses fire as a management tool for conservation, but rather *how* fire is best used.

The quintessential role of applied science and ecology is to provide managers of these ecosystems with the information required to best determine how fire should be used to optimise ecological sustainability and biodiversity. It is therefore clear that one of the highest priorities for fire ecology is that the large volume of past research be sufficiently published, synthesised and reviewed in order to maximise our current understanding. Having done so, future research should be directed to better understanding the complexity of the mechanisms and interactions between ecological processes that determine species and community responses. In so doing, this information can be used to improve modelling and predictions which are currently over-simplified and incomplete. Ecological responses to the scale (size and patchiness) and frequency of fire also remain important and require particular further attention. In many cases, much of this knowledge is best derived from long term experimental studies which to date have been few.

In terms of conservation management, clear objectives are required to both inform how fire should be used and help highlight what ecological knowledge is lacking. In turn, applied researchers need to be responsive of the need to fill these knowledge gaps. In a similar manner, it is important that managers appreciate both the complexity of fire ecology and that their activities need to be sufficiently responsive to reflect this level of sophistication. Due to the complexity of the interactions between the myriad of ecological factors and processes at play, the responses to fire by species and communities will be highly variable. Responses are also dependant on the characteristics of the fire itself (ie. intensity, scale, timing and frequency), and variation over space (eg. climate, hydrology, aspect, topography, nutrients, proximity to same and different communities, variation in species composition, dominance and interactions) and time (eg. different disturbance histories, significant rainfall and seasonal events, etc). Consequently, no one burning regime will optimise circumstances for different communities or the different component species within any one community. Similarly, no one burning regime will be appropriate for any one community because of the inherent spatial and temporal variation.

Much of our understanding of these processes remains inadequate. In the meantime, we know enough to understand that fire response patterns, especially at the community level, can be complex and diverse. As a result, it seems dangerous to over-simplify burning regimes to the point of having only one prescription that serves to satisfy either all communities or even all examples of the same community. This clearly places pressure on managers that remain compelled to act with incomplete knowledge.

The use of existing models and predictive approaches such as those based on an understanding of the various species' life histories, help in the interim to fill some of the knowledge gaps and serve as extremely valuable tools for decision making by conservation managers. It is important, however, to remain mindful that the models and knowledge upon which they are developed are not perfect and are by default, simplifications of patterns observed in at least some circumstances. Similarly there is a need for both researchers and managers to be wary of the degree of extrapolation and its concomitant dangers.

It is our belief that the most effective means of improving our understanding of fire ecology and conservation is through a high level of interaction between researchers and managers and by the use of the adaptive management approach. In conjunction with the setting of clear conservation objectives and through monitoring, such an approach will aid in the iterative improvement of both research and management activities and enable a relative measure of success to be determined, thereby improving the opportunities of achieving and maintaining ecological sustainability.

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A3.9 References

Abbott, I. and Whitford, K. (in press). Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: Strategic risk assessment in relation to ecology, policy, planning, and operations management. *Pacific Conservation Biology.*

Andersen, A.N., Braithwaite, R.W., Cook, G.D., Corbett, L.K., Williams, R.J., Douglas, M.M., Gill, A.M., Setterfield, S.A. and Muller, W.J. (1998). Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. *Australian Journal of Ecology* **23**, 95-110.

Bamford, M.J. (1985). The fire-related dynamics of small vertebrates in Banksia woodland: a summary of research in progress. In: '*Fire Ecology and Management in Western*

Australian Ecosystems'. (ed. J Ford), pp. 107-110. WAIT Environmental Studies Group Report No. 14.

Bamford, M.J. (1986). *The dynamics of small vertebrates in relation to fire in* Banksia *woodland near Perth, Western Australia*. Ph.D. Thesis, Murdoch University, Perth.

Baynes, A., Chapman, A. and Lynam, A.J. (1987). The rediscovery, after 56 years, of the Heath Rat *Pseudomys shortridgei* (Thomas, 1907) (Rodentia: Muridae) in Western Australia. *Records of the Western Australian Museum* **13**, 319-22.

Bradley, A.J. (1995). Red-tailed phascogale *Phascogale calura*. In: *Mammals of Australia*. (ed. R. Strahan) pp. 102-103. Reed Books, Sydney.

Bradshaw, S.D. and Bradshaw F.J (in press). Short-term movements and habitat use by the marsupial honey possum *Tarsipes rostratus*. *Journal of Zoology*.

Burrows, N.D. and Friend, G.R. (1998) Biological indicators of appropriate fire regimes in southwest Australian ecosystems. In*: "Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription"* (eds. T.L. Pruden and L.A. Brennan) pp. 413-421. Tall Timbers Fire Ecology Conference Proceedings No. 20, Tall Timbers Research Station, Tallahassee, FL.

Burrows, N.D. and Christensen, P.E.S., (*submitted*). Long-term trends in native mammal capture rates in a jarrah forest in south-west Australia.

Burrows N. D., McCaw, W.L. and Maisey, K.G., (1987). Planning for fire management in Dryandra Forest. In: *Nature Conservation: the Role of Remnants of Native Vegetation.* (eds. D.A. Saunders, G.W. Arnold, A.A. Burbidge and A. Hopkins), pp. 306-312. Surrey Beatty and Sons, Sydney.

Catling, P.C. (1986). *Rattus lutreolus*, colonizer of heathland after fire in the absence of *Pseudomys* species? *Australian Wildlife Research* **13**, 127-139.

Catling, P.C. and Newsome, A.E. (1981). Responses of the Australian vertebrate fauna to fire: an evolutionary approach. In *Fire and the Australian Biota*, (eds. A.M.Gill, R.H.Groves and I.R.Noble), pp.273-310. Australian Academy of Science, Canberra.

Catling, P.C. and Coops, N.C. (1999). Prediction of the distribution and abundance of small mammals in the eucalypt forests of south-eastern Australia from airborne videography. *Wildlife Research* **26**, 641-650.

Catling, P.C., Coops, N.C. and Burt, R.J. (2001). The distribution and abundance of ground-dwelling mammals in relation to time since wildfire and vegetation structure in south-eastern Australia. *Wildlife Research* **28**, 555-564.

Cheal, P.D., Day, J.C. and Meredith, C.W. (1979). *Fire in the National Parks of North-Western Victoria*. National Parks Service, Victoria. 219pp.

Christensen, P.E.S. (1980). The biology of *Bettongia pencillata* Gray 1837, and *Macropus eugenii* (Desmarest, 1871) in relation to fire. Bulletin 91, Forests Department of Western Australia.

Christensen, P. E. S., and Abbott, I. (1989). Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. *Australian Forestry* **52(2)**, 103-121.

Christensen P.E.S., and Kimber, P. (1975). Effect of prescribed burning on the flora and fauna of the south-west Australian forests. *Proceedings of the Ecological Society of Australia* **9**, 85-106.

Christensen P.E.S., Wardell-Johnson, G. and Kimber, P. (1986). Birds and fire in southwestern forests. In: *Birds of the Eucalypt forests and Woodlands: Ecology, Conservation, Management.* (eds A. Keast, H.F. Recher, H. Ford and D. Saunders), pp. 291-299. Surrey Beatty and Sons, Sydney.

Christensen, P. E. S. and Maisey, K. (1987). The use of fire as a management tool in fauna conservation reserves. In: *Vegetation Remnants: their role in Nature Conservation.* (eds D.A. Saunders, G.W. Arnold, A.A. Burbidge and A. Hopkins), pp. 323-329. Surrey Beatty and Sons, Sydney.

Coops, N.C., and Catling, P.C. (1997). Using airborne multispectral videography to predict habitat complexity in eucalypt forests for wildlife management. *Wildlife Research* **24**, 691-703.

Fox, B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology,* **63,** 1332-41.

Fox, B.J. (1983). Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. In: *Mediterranean-Type Ecosystems: The Role of Nutrients,* ed. E.J.Kruger, D.T.Mitchell & J.U.M.Jarvis. Springer-Verlag, Berlin. pp.473-89.

Fox, B.J. (1990). Changes in the structure of mammal communities over successional time scales. *Oikos*, **59**, 321-29.

Fox, B.J. (1996) Long term studies of small mammal communities from disturbed habitats in eastern Australia. In *Long Term Studies of Vertebrate Communities*. (eds. M.L. Cody and J.A. Smallwood), pp.467-501. Academic Press, San Diego.

Fox, B.J. & Whitford, D. (1982). Polyoestry in a predictable coastal environment: reproduction, growth and development in *Sminthopsis murina* (Dasyuridae: Marsupialia). In: *Carnivorous Marsupials,* (ed. M.Archer), pp. 39-48. Royal Zoological Society of New South Wales, Sydney.

Friend, G.R. (1993) Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia - a review. *Biological Conservation* **65**, 99-114.

Friend, G.R. (1995) Impact of fire on fauna in remnant vegetation - research findings and their implications for management. In: *“Remnant vegetation ten years on - a decade of research and management.”* Proceedings of the Dryandra Workshop, September 1993. (ed. K.J. Wallace) pp. 11-13. Department of Conservation and Land Management.

Friend, G.R. (1999) Fire and faunal response patterns – a summary of research findings. In: “*Management of Fire for the Conservation of Biodiversity – Workshop Proceedings*” (eds. G.R. Friend, M. Leonard, A. Maclean and I. Sieler) pp. 39-45. Department of Natural Resources and Environment, Melbourne.

Friend, G.R. and Pearson, D.J. (1995) Little Long-tailed Dunnart *Sminthopsis dolichura*. In: *Mammals of Australia*. (ed. R. Strahan) pp. 132-133. Reed Books, Sydney.

Friend, G.R., Morris, K.D. and Thomson, C. (1994) “Bountiful Batalling” *Landscope* **9(4)**; 16-22.

Friend, G.R., Johnson, B.W., Mitchell, D.S. and Smith, G.T. (1997) Breeding, population dynamics and habitat relationships of *Sminthopsis dolichura* (Marsupialia: Dasyuridae) in semi-arid shrublands of Western Australia. *Wildlife Research* **24**; 245-262.

Friend, J.A., (1994). *Recovery Plan for the Numbat 1995-2004*. Western Australian Wildlife Management Program No. 18.

Gibbons, P., Lindenmayer, B., Barry, C. and Tanton, M. T. (2000). Hollow formation in eucalypts from temperate forests in southeastern Australia. *Pacific Conservation Biology*. **6**; 218-228.

Higgs, P. and Fox, B.J. (1993). Interspecific competition: a mechanism for rodent succession after fire in wet heathland. *Australian Journal of Ecology* **18**, 193-201.

Inions, G. (1985). *The interactions between possums, habitat trees and fire*. Hons thesis. Australian National University, Canberra ACT. 220pp.

Inions, G.B., Tanton, M.T., and Davey, S. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* Kerr, 1792, and the ringtail possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**; 449-458.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Tanton, M.T., Nix, H.A. (1993). The abundance and development of cavities in Ieucalyotusl trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management.* **60**; 77-104.

Monamy, V. and Fox, B.J. (2000). Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. *Austral Ecology* **25**, 580-587.

Masters, P. (1993). The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**, 803-13.

Morris, K.D. (1995). Ash-grey Mouse *Pseudomys albocinereus.* In: *The Mammals of Australia.* (Ed. R. Strahan) pp. 583-584. Reed Books, Sydney.

Newsome, A.E. and Catling, P.C. (1983). Animal demography in relation to fire and shortage of food: some indicative models. In: *Mediterranean-Type Ecosystems: The Role of Nutrients,* (eds. E.J.Kruger, D.T.Mitchell and J.U.M.Jarvis). pp. 490-505. Springer-Verlag, Berlin.

Newsome, A.E., McIlroy, J.C. and Catling, P.C. (1975). The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. *Proceedings of the Ecological Society of Australia* **9**, 107-23.

Recher, H.F., Lunney, D. and Posamentier, H.G. (1975). Effects of wildfire on small mammals at Nadgee Nature Reserve, New South Wales. In: *Third Fire Ecology Symposium*. pp.30-36. Forestry Commission of Victoria, Melbourne.

Renfree, M.B., Russell, E.M. and Wooller, R.D. (1984). Reproduction and life history of the honey possum, *Tarsipes rostratus*. In: *Possums and Gliders*. (eds. A.P. Smith and I.D. Hume). pp.427-37. Surrey Beatty and Sons, Sydney.

Richardson, K.C., and R.D. Wooller. (1991). *The effect of fire on honey possum populations*. Report on Project P114. World Wide Fund for Nature, Australia.

Sawle, M, (1979). *Habitat components of* Antechinus flavipes *(Waterhouse 1983) in the karri forest, south-west of Western Australia*. Honours thesis, Murdoch University.

Schmidt, R. and Mason, M. (1975). Fire and fauna in the northern jarrah forest of Western Australia. *Western Australian Naturalist* **12**, 162-164.

Singleton, G.R. (1995). House Mouse *Mus domesticus*. In: *The Mammals of Australia.* (Ed. R. Strahan) pp. 646-647. Reed Books, Sydney.

Suckling, G and MacFarlane M. (1984). The effects of fire on forest fauna – a review. In: *Fighting Fire With Fire.* (ed E H M Ealey). pp. 107-128. Graduate School of Environmental Science, Monash University, Melbourne.

Sutherland, E.F. (1998). *Fire, resource limitation and small mammal populations in coastal eucalypt forest.* Ph.D. thesis. University of Sydney.

Sutherland, E.F. and Dickman C.R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405-419.

Walters, C. (1986). *Adaptive Management of Renewable Resources*. MacMillan Publishing, New York.

Wayne, A., Ward, C., Rooney, J., and Wheeler, I. (2000). The immediate impacts of timber harvesting and associated activities on the Ngwayir (*Pseudocheirus occidentalis*) in the Jarrah forest of Kingston State Forest Block. Progress Report. Department of Conservation and Land Management.

Wayne, A., Wheeler, I., Ward, C. and Rooney, J. (2001). The impacts of timber harvesting associated activities on the small terrestrial vertebrates of the Jarrah forest. Progress Report. Department of Conservation and Land Management.

Whelan, R.J. (1995). *The Ecology of Fire*. Cambridge University Press. United Kingdom. 346pp.

Whisson, L. and Kitchener, D.J. (1995). Western Mouse *Pseudomys occidentalis*. In: *The Mammals of Australia.* (Ed. R. Strahan) pp. 613-614. Reed Books, Sydney.

Whitford, K.R. and Williams, M.R. (2001). Survival of jarrah (*Eucalyptus marginata* Sm.) and marri (*Corymbia calophylla* Lindl.) habitat trees retained after logging. *Forest Ecology and Management* **146**; 181-197.

Williams, M.R. and Faunt, K. (1997). Factors affecting the abundance of hollow logs in jarrah forest of south-western Australia. *Forest Ecology and Management* **26**; 405-419.

Wilson, B.A. (1996) Fire effects on vertebrate fauna and implications for fire management and conservation. In: *"Fire and Biodiversity - The Effects and Effectivenes of Fire Management"* Proceedings of the Biodiversity and Fire Conference, October 1994, Melbourne. pp. 131-147. Biodiversity Series Paper No. 8, Department of Environment, Sport and Territories.

Wilson, B.A. and Friend, G.R. (1999) Responses of Australian mammals to disturbance: a review. *Australian Mammalogy* **21**; 87-105.