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**The ecology and conservation of the
antilopine wallaroo (*Macropus antilopinus*)**

Thesis submitted by

Euan Gowar Ritchie

BSc (Hons) James Cook University

in March 2007

**for the degree of Doctor of Philosophy
in the School of Marine and Tropical Biology
James Cook University**



Top – Dry season, Mornington Sanctuary, Kimberley region, Western Australia. © E. Ritchie
Centre – Large male (left) and adult female (right) antilopine wallaroos (*Macropus antilopinus*). © D. Webb
Bottom – Wet season storm, Undara National Park, Einasleigh Uplands region, Queensland. © E. Ritchie

This thesis is dedicated to my late father Michael

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Statement on the contribution of others

Emily Bolitho (a collaborator) assisted with bioclimatic modelling and the production of distribution maps (Chapter 5). Dr. Mark Eldridge (a collaborator) assisted with the analysis of molecular data (Chapter 6). C.S.I.R.O (Davies laboratory) provided laboratory space and the use of equipment (Chapters 2 and 4).

Declaration on Ethics

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Human* (1999), the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997), the *James Cook University Policy on Experimentation Ethics. Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A814).

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Preface

Publications arising from this thesis:

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Abstract

Research into the factors which limit the distribution and abundance of species has a long tradition in ecology, and knowledge of such factors is vital for guiding the conservation of biodiversity. However, few studies have investigated the way in which intraspecific and interspecific differences in the niche requirements of species vary geographically, despite growing demand for such information in the face of large-scale environmental change, particularly the predicted effects of global warming.

The antilopine wallaroo (*Macropus antilopinus*) is a large macropod endemic to the extensive tropical savannas of northern Australia. This thesis investigates the ecology and conservation of the antilopine wallaroo across its distribution; in addition, I provide comparative information on other sympatric macropod species.

At 50 sites across northern Australia, I collected detailed information on the abundance and social behaviour of a number of macropod species as well as data on climate, fire history, habitat and resource availability. Using these data I constructed habitat models for species at varying spatial scales. Interpreting broad-scale patterns of species' distributions and abundance also requires an understanding of the individual requirements of species-specific characteristics, such as socio-ecology and behaviour. Therefore, I also conducted an intensive study of the behaviour of the antilopine wallaroo at one site in north Queensland.

The antilopine wallaroo occurred at 68% of the sites that I surveyed, and the abundance of this species varied substantially across its distribution. The factors influencing the distribution and abundance of the antilopine wallaroo varied according to the spatial scale of analysis. At the largest scale (complete distribution), availability of water, frequency of fire, geology (soil fertility) and land management were the most important factors, whereas within Queensland and at smaller bioregional scales, the abundance of a potential competitor (eastern grey kangaroo, *M. giganteus*) and aspects of habitat structure and composition were of greater importance. In contrast, the abundance of eastern grey kangaroos and common wallaroos (*M. robustus*) was strongly influenced by climate. The abundance of antilopine wallaroos increased after fire whereas the abundance of common wallaroos declined.

The antilopine wallaroo was the most gregarious macropod and group sizes increased significantly with population density. The eastern grey kangaroo and whiptail wallaby (*M. parryi*) were less gregarious than the antilopine wallaroo, and the common wallaroo and agile wallaby (*M. agilis*) were essentially solitary. Compared with other large tropical macropods, the antilopine wallaroo's pattern of reproduction was strongly seasonal, centred around the monsoon season. There was marked seasonal variation in the associations between sex and size classes of the antilopine wallaroo, which appear related to reproduction and sexual segregation in this species.

Climate change poses a significant risk to the continued survival of the antilopine wallaroo. The relatively restricted distribution, dependence on water and seasonal breeding pattern of the antilopine wallaroo makes this species the most vulnerable of the four large macropods in northern Australia. The capacity for climate change to alter habitat structure and influence fire regimes within this region is also likely to result in changes to both local and regional macropod communities.

Preliminary genetic data suggest that there has been recent restriction of gene flow between populations of antilopine wallaroos in Queensland and the rest of the species' distribution, which may be associated with an arid ecological barrier to dispersal at the base of the Gulf of Carpentaria. My results also indicate that hybridisation between the antilopine wallaroo and common wallaroo has occurred across the former species' range. Further work is therefore required to resolve the taxonomic status of the antilopine wallaroo and the phylogeny of large macropods.

The results of my study provide the most comprehensive information to date on the ecology and conservation of the antilopine wallaroo, and also filled a significant gap in our overall knowledge of macropodid marsupials by expanding our limited knowledge of the tropically-occurring members of this group. More broadly, my research has demonstrated spatial variation in the niche requirements of a large herbivore and has identified many of the key environmental and biological factors influencing the distribution and abundance of species that live in tropical savannas. In addition it has made a substantial contribution to a more comprehensive understanding of the global ecology and evolution of large herbivores.

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Chapter 1

General introduction

This thesis investigates the ecology and conservation of the antilopine wallaroo (*Macropus antilopinus*) across its geographic range.

Studying species' distribution and abundance: importance, current limitations and ways forward

Understanding the biological and environmental factors that limit the distribution and abundance of organisms is fundamental to ecology and central to our understanding of the niche concept (Andrewartha & Birch, 1954; Hutchinson, 1957, 1978). Importantly, this information is urgently required to inform conservation measures in the face of global challenges such as climate change to the survival of species (Hughes, 2003; Peterson *et al.*, 2001; Rondinini, Stuart & Boitani, 2005). In a recent review of studies of abundance patterns across species' ranges, Sagarin *et al.* (2006) highlighted the fact that, despite the many recent advances in ecology, we still lack the data necessary to tackle large-scale problems. Furthermore, few studies have explored in detail, or even considered the consequences, of the way, in which intraspecific species-habitat relationships vary according to spatial scale (Murphy & Lovett-Doust, *in press*; Peterson & Holt, 2003; Sagarin *et al.*, 2006). Collectively this dearth of information regarding the limits to species' distributions and the spatial variability of their habitat relationships is a serious obstacle to the effective management of species.

A major advance in ecology aimed at overcoming some of these problems is the development of the field of macroecology. Macroecological studies aim to understand the distribution and abundance of species at large spatial and temporal scales (Brown, 1995), and place emphasis on the statistical analysis of patterns rather than on experimental manipulations. A clear advantage of this approach is that it allows general conclusions to be drawn, in addition to promoting the broad synthesis of information. Local-scale studies are often not suitable for making inferences about the likely impacts on species of processes, such as fire regimes and climate change, which influence

species at regional and global scales (Sagarin *et al.*, 2006). Studying species at scales relevant to the size of their geographical ranges is therefore critically important for effective management.

Conservation status of Australia's mammals

Australia has the worst record for mammal conservation globally, being responsible for over half of the world's mammal extinctions in the past 200 years (Johnson, 2006; MacPhee & Flemming, 1999; Maxwell, Burbidge & Morris, 1996; Short & Smith, 1994). In fact of all the continental extinctions since 1500, Australia has been responsible for 73% (MacPhee & Flemming, 1997). Eighteen of Australia's native mammal species are presumed extinct and many species have experienced severe reductions in their geographical ranges, with rodents and macropods being most heavily affected (Strahan, 1995). Exotic predators (predominantly foxes, *Vulpes vulpes*, and cats, *Felis catus*) and habitat change are the two most commonly cited causes of these mammal declines and subsequent extinctions (Burbidge & Manly, 2002; Burbidge & McKenzie, 1989; Dickman, 1996; Lunney, 2001; Morton, 1990).

Tropical savannas comprise approximately one quarter of mainland Australia (~2,000,000 km²) and are home to many endemic vertebrate species. Unlike the situation in southern Australia, there has been very little land clearing in tropical savannas and many habitats remain relatively intact (Williams *et al.*, 2005). However, there are growing concerns that the spread of cane toads (*Bufo marinus*), inappropriate fire regimes and the intensification of cattle grazing are putting significant pressures on the ecological integrity of this region and its biota (Woinarski, Milne & Wanganeen, 2001). In particular, many mammal species are thought to be experiencing population declines; these include the common brushtail possum (*Trichosurus vulpecula*), northern quoll (*Dasyurus hallucatus*), golden-backed and black-footed tree rats (*Mesembriomys macrurus*, *M. gouldii*), brush-tailed rabbit rat (*Conilurus penicillatus*) and spectacled hare wallaby (*Lagorchestes conspicillatus*) (Braithwaite & Griffiths, 1994; Braithwaite & Muller, 1997; Ingleby, 1991; Pardon *et al.*, 2003; Price *et al.*, 2005; Woinarski, 2000; Woinarski *et al.*, 2001). The appropriate management of tropical savannas is therefore of critical importance to preserving Australia's biodiversity. This task is made difficult by the fact that there remains scant biological information on many of the vertebrate

species that occur in tropical savannas; field-based studies are typically expensive and logistically challenging due to the region's remote and rugged nature.

Antilopine wallaroos

The Superfamily Macropodoidea represents one of the most diverse marsupial assemblages, with 62 species occurring in Australia and Papua New Guinea (Dawson, 1995). Within this group there are six species referred to as the “kangaroos”: the eastern grey kangaroo (*Macropus giganteus*), western grey kangaroo (*M. fuliginosus*), red kangaroo (*M. rufus*), common wallaroo (*M. robustus*), black wallaroo (*M. bernardus*) and antilopine wallaroo (*M. antilopinus*). This group is distinguished from other macropodids by their large body size (20kg - ≤ 90kg) and mode of feeding, with all species feeding predominantly on grass and therefore being termed grazers (Dawson, 1995). There has been considerable ecological and evolutionary research into this group with the notable exceptions of black and antilopine wallaroos (Croft, 1982; Croft, 1987; Grigg, Hume & Jarman, 1989; Poole & Merchant, 1987; Press, 1989; Richardson & Sharman, 1976; Russell & Richardson, 1971). These are the only two large macropods to be restricted entirely to the tropics (Strahan, 1995), and are therefore interesting biologically and also important to preserve from a biodiversity perspective.

The ecological niche occupied by the antilopine wallaroo in the monsoonal tropical woodlands of northern Australia is most similar to those filled by the eastern and western grey kangaroos in the forests and woodlands of eastern and southern Australia, and by red kangaroos in the arid and semi-arid zones (Ritchie, in press). Antilopine wallaroos occur in a variety of vegetation types, ranging from scattered and open woodlands through to tall open forests, all with perennial grass-dominated understoreys. The typical habitat of antilopine wallaroos is gently undulating terrain and they are sympatric in parts of their range with common and black wallaroos and eastern grey and red kangaroos (Dunlop & Begg, 1981; Ritchie, in press). Their geographical range extends from the Cape York and Einasleigh Uplands bioregions of Queensland, across the top end of the Northern Territory and into the Kimberley region of Western Australia. There appears to be a gap in the range of the antilopine wallaroo between Queensland and the Northern Territory at the base of the Gulf of Carpentaria (Strahan, 1995), an area of semi-arid grasslands (Ford, 1987; Heatwole, 1987). This habitat may

be unsuitable for antilopine wallaroos and therefore represent a geographical barrier to dispersal between populations, as suggested for other species including Australian grass finches (Jennings & Edwards, 2005) and the large bentwing bat (*Miniopterus schreibersii*) (Cardinal & Christidis, 1999). Genetic studies are required to assess the importance of the Carpentarian barrier, specifically whether there may in fact be two genetically distinct populations of antilopine wallaroos in Australia, which would necessitate a review of the species' taxonomy and management (see Appendix 3).

Antilopine wallaroos are longer-limbed and more slender than black and common wallaroos, and superficially resemble grey and red kangaroos in their general appearance and behaviour. They show pronounced sexual body-size dimorphism, with the largest adult males being up to 3.6 times heavier than the smallest adult females (Johnson, 2003). Males are reddish-tan above and their underside is creamy white, with the tips of manus and pes being black. Females are typically pale grey around the head and forequarters, have distinctive white fringing of the ears but may be grey all over. Both sexes have characteristic large, 'swollen', black noses, particularly prominent in large males (Ritchie, in press).

Despite the antilopine wallaroo being a large conspicuous mammal (18-51kg Johnson, 2003), there has been little research on its behaviour and ecology. Only three field-based studies have been conducted, all at local scales in the Northern Territory (Croft, 1982; Croft, 1987; Russell *et al.*, 1971). Collectively these studies provide preliminary information on population structure and density, reproductive biology, diet and social behaviour. However to date there have been no long-term and systematic studies, and there is no information available for antilopine wallaroos for the Kimberley region of Western Australia or the Cape York and Einasleigh Upland bioregions of Queensland, an area comprising two-thirds of the species' geographical range.

There are numerous anecdotal reports of population decline in antilopine wallaroos in parts of the Northern Territory, Queensland and Western Australia (Peter Clark, Peter Johnson, Richard Noske, Tim Willing and John Woinarski, personal communications), and inappropriate fire regimes and the intensification of cattle grazing have been identified as possible threats. However the lack of basic biological and ecological information on the antilopine wallaroo across most of its range precludes appropriate management of the species. This void in our knowledge is of particular

concern given that six of 50 (12%) species of macropods have already become extinct since European settlement (Strahan, 1995), and that declines leading to extinction can occur rapidly, often within 1-2 decades (Woinarski *et al.*, 2001). The antilopine wallaroo is of value to indigenous people culturally and as bush tucker (Busby, 1988; Yibarbuk *et al.*, 2001), and is a species important for ecotourism.

Many species in northern Australia have large geographical ranges, but few studies have attempted to identify the ways in which resources, and variation in their availability, influence the large-scale distribution and abundance of species (Woinarski *et al.*, 2005). The antilopine wallaroo has an extensive geographical range (~ 650,000 km² estimated from Strahan, 1995) in comparison with the majority of Australia's terrestrial mammals. With this in mind, I investigated its ecology across its known range between 2002 and 2005. Interpreting broad-scale patterns of species' distributions and abundance also requires an understanding of the individual requirements of species, such as socio-ecology and behaviour. Therefore in addition to the broad-scale, I collected detailed social information on the species at two sites (Rocky Springs Station and Undara National Park) in 2004. During my study I also had the opportunity to collect information on other sympatric macropod species, and where available, this comparative data is presented. By studying the antilopine wallaroo across its range, I aimed to provide a detailed synopsis of the species' ecology and conservation status across Australia, thereby facilitating its management at both local and regional scales. This approach has two other major indirect benefits. Firstly it provides a useful case-study of the factors that limit the distribution and abundance of herbivores within tropical savannas. Secondly, by operating at a large spatial scale, it provides valuable information about processes affecting other sympatric species, and hence aids our understanding of the possible drivers of mammal decline in the tropical savannas of northern Australia.

The specific aims of my study were to:

- Record and model the patterns of distribution and abundance of the antilopine wallaroo across its geographical range, specifically identifying the key resource(s) that limit these patterns
- Describe the socioecology of the antilopine wallaroo and compare it with other sympatric macropod species
- Investigate patterns and processes behind sexual segregation behaviour in the antilopine wallaroo
- Model the likely impacts of climate change on the geographical range of the antilopine wallaroo and other sympatric large macropod species in the tropics.

Thesis organisation

Due to the broad scope of my PhD I have decided to present my thesis as a series of largely stand-alone data chapters. These chapters are not explicitly linked, but share a common theme; the ecology and conservation of the antilopine wallaroo. This decision is based on the fact that there are currently few data available for this species. Therefore a collection of chapters from broad subject areas will be particularly useful in making an immediate contribution to an understanding of the species' ecology and management, and a base from which further work can be planned. This thesis is organised as follows:

Chapter 2 documents patterns of distribution and abundance of the antilopine wallaroo across its geographical range. I provide similar information for the northern distributions of the sympatric common wallaroo and eastern grey kangaroo, and present models identifying the key biological and environmental factors that limit patterns of distribution and abundance for each species.

Chapter 3 describes the socioecology of the antilopine wallaroo across seasons and at multiple sites and presents comparative data for four other sympatric macropod species.

Chapter 4 presents the results of an intensive investigation into patterns of sexual segregation in the antilopine wallaroo at Rocky Springs Station in north Queensland,

with emphasis on the possible ecological and evolutionary drivers behind this behavioural phenomenon.

Chapter 5 models the likely impacts of current climate change scenarios for northern Australia (increased temperature and reduced or increased rainfall) on the geographical ranges of antilopine wallaroos and sympatric large macropods, assessing the likelihood of changes in macropod community assemblages and local and regional extinction probabilities.

Chapter 6 discusses the significance of my findings and outlines areas for future research.

Appendix 1 is a published manuscript which details an extension to the known range of the eastern grey kangaroo (*Macropus giganteus*) on Cape York Peninsula.

Appendix 2 is a manuscript (currently in review) that details the effect of an extensive, late, dry season fire on the abundance of three sympatric large macropod species in Undara volcanic national park, northern Australia.

Finally, in Appendix 3 I present preliminary information on the phylogeography (genetic differentiation across the landscape) of the antilopine wallaroo.

Chapter 2

Models of the distribution and abundance of the antilopine wallaroo, eastern grey kangaroo and common wallaroo in northern Australia

(In review *Ecological Monographs*; co-authored with Dr. Jennifer Martin, Dr. Andrew Krockenberger, Professor Stephen Garnett and Professor Christopher Johnson)

Abstract

Determining the biological and environmental factors that limit the distribution and abundance of organisms is central to our understanding of the niche concept and crucial for predicting how species may respond to large-scale environmental change, such as global warming. However, detailed ecological information for the majority of species has been collected only at a local scale, and insufficient consideration has been given to geographical variation in intraspecific niche requirements.

To evaluate the influence of environmental and biological factors on patterns of species distribution and abundance, we conducted a detailed, broad-scale study of the ecology of three large sympatric marsupial herbivores (family Macropodidae) across the tropical savannas of northern Australia: the antilopine wallaroo (*Macropus antilopinus*), common wallaroo (*M. robustus*) and eastern grey kangaroo (*M. giganteus*). Using information on species abundance, climate, fire history, habitat and resource availability, we constructed species' habitat models varying from the level of the complete distribution to smaller, regional areas. Multiple factors affected macropod abundance and the importance of these factors was dependent on the spatial scale of analyses. Fire regimes, water availability, geology and soil type (nutrient availability) and climate were most important at the large scale, whereas aspects of habitat structure and interspecific species abundance were important at smaller scales. The distribution and abundance of eastern grey kangaroos and common wallaroos was strongly

influenced by climate. Our results suggest that interspecific competition between antilopine wallaroos and eastern grey kangaroos occurs. The antilopine wallaroo and eastern grey kangaroo (grazers) preferred more nutrient-rich soils than the common wallaroo (grazer/browser), which we relate to differences in feeding modes. The abundance of antilopine wallaroos was higher in sites that were burnt whereas the abundance of common wallaroos was lower in burnt sites.

Future climate change predicted for Australia has the capacity to seriously affect the abundance and conservation of macropod species in tropical savannas. The results of our models suggest that in particular, the effects of changing climatic conditions on fire regimes, habitat structure and water availability may lead to species declines and marked changes in macropod communities.

Introduction

Understanding the biological and environmental factors that limit the distribution and abundance of organisms is fundamental to ecology (Andrewartha *et al.*, 1954), and is central to our understanding of the niche concept (Hutchinson, 1978). However, Sagarin and Gaines (2006) stress that despite the many advances in experimental ecology over recent decades, we are severely ‘observation-limited’ with regards to detailed information on abundance across species’ distributions, particularly at larger spatial scales. This information is urgently required to allow us to adequately address large-scale environmental changes, such as global climate change (Hughes, 2003; Peterson *et al.*, 2001; Rondinini *et al.*, 2005).

Consideration of how the distribution and abundance of species and their niche requirements vary geographically is important both ecologically and in an applied sense, but is not adequately addressed by the majority of studies (Murphy *et al.*, in press). Put simply, models constructed for one part of a species’ range may have limited predictive power for other areas; likewise generalised global models may fail to describe local conditions adequately (Murphy *et al.*, in press). Therefore, unless we collect detailed information on species-habitat relationships across their distributions, we risk failing to appreciate the ecological plasticity of species in response to the regional variation in environmental conditions. Information collected over smaller spatial distributions will almost certainly be inadequate to inform management plans. A recent advance in ecological research has been a shift away from null hypothesis testing, towards alternative approaches including the information theoretic approach (ITA) (Burnham & Anderson, 2002). When attempting to model the ecological complexity and variability of species-habitat relationships over large spatial scales, the ITA allows simultaneous comparison of the likelihood of competing models given the data and model set.

Among vertebrates, large herbivores provide an excellent group for macroecological study because they occur in a diverse array of habitats, exhibit considerable morphological variation, have extensive distributions, and shape ecosystem function through the effects of grazing (Cristoffer & Peres, 2003; Gordon,

Hester & Festa-Bianchet, 2004). Furthermore, large herbivores represent a significant part of human communities' food resources and economics, and have strong cultural significance in many parts of the world (Gordon *et al.*, 2004; Yibarbuk *et al.*, 2001). However, detailed information on the factors that limit the distribution and abundance of these species across their complete distributions is scarce (Gordon *et al.*, 2004; Sagarin *et al.*, 2006). More broadly, few studies have explored in detail how intraspecific species-habitat relationships vary according to spatial scale (Murphy *et al.*, in press; Peterson *et al.*, 2003). This is a serious concern for large herbivores because many of these species are threatened with local or global extinction (Ceballos *et al.*, 2005; Thuiller *et al.*, 2006), a situation likely to be exacerbated by the combined pressures of climate change (Root *et al.*, 2003) and the growing demand of human populations for food (Robinson & Bennett, 2004).

The tropical savannas of northern Australia cover approximately one-quarter of the continental mainland (~ 2,000,000 km²) and are home to the continent's highest diversity of large herbivorous mammals, the macropods (family Macropodidae; Strahan, 1995). This biome remains largely structurally intact as compared with the rangelands of southern Australia, where substantial habitat modification has occurred since European settlement (Williams *et al.*, 2005), and it therefore offers the opportunity to study the interaction between species and their environment within relatively unmodified landscapes. However, there is growing evidence that contemporary fire regimes and the intensification of cattle grazing, the two dominant processes of disturbance within the region, may be weakening the ecological integrity of the savanna (Woinarski & Ash, 2002; Woinarski *et al.*, 2001). A broad range of taxonomic groups and guilds, particularly small mammals (Woinarski *et al.*, 2001) and granivorous birds (Franklin, 1999), are experiencing population declines. The management of these species is hampered by a lack of detailed and systematic ecological data available for most species; and also by the fact that management (particularly fire) targeted towards some species may negatively affect others due to interspecific differences in niche requirements (Woinarski *et al.*, 2005). Prior knowledge of the ecology of savanna species will provide the potential to guide future management and prevent further species loss.

The biogeography of Australia's tropical savannas is influenced by the pronounced rainfall seasonality and the generally low and patchy spatial and temporal

availability of resources (Williams *et al.*, 2005). There is relatively minor longitudinal variation in the vegetation communities and topography across this extensive biome (Woinarski *et al.*, 2005); however, there is a strong coastal-continental gradient of decreasing rainfall from the northern coast inland. Most soils are old and leached of nutrients, with localised areas of younger, nutrient-rich soils which support more productive vegetation communities. The annual growth and nutrient availability of vegetation is strongly linked with seasonal rainfall (Ridpath, 1985). In comparison with temperate regions, temperature variation in tropical Australia is minor. Relative to other tropical savannas (e.g. those of Africa), this region has a low diversity and abundance of large, terrestrial predators, with the dingo (*Canis lupus dingo*; 12 – 24 kg) being the major and largest predator (Caughley *et al.*, 1980). These environmental and biological differences between the tropical savannas of Australia and comparable habitats globally mean that large macropods face a unique suite of ecological challenges relative to other large herbivores. Therefore, the study of Australia's tropical macropods promises to contribute substantially to an appreciation of the ecological variation that underlies the evolutionary diversity of large herbivorous mammals more broadly.

Here we report on a macroecological study of three large, sympatric macropods, the antilopine wallaroo (*Macropus antilopinus*), common wallaroo (*M. robustus*) and eastern grey kangaroo (*M. giganteus*). The antilopine wallaroo, endemic to Australia's tropical savannas, is particularly poorly studied (Croft, 1987) and may be in decline (Ritchie, unpublished), and has strong cultural significance for indigenous people of this region (Busby, 1988; Yibarbuk *et al.*, 2001). Our study area spanned the geographic range of the antilopine wallaroo (~ 650,000 km², estimated from Strahan 1995) and large proportions of the northern distributions of the other two species. We collected detailed information on climate, habitat and resource availability and the distribution and abundance of each macropod species. With reference to previous studies (Bowman, 1998; Caughley *et al.*, 1988; Caughley *et al.*, 1987; Dawson, 1995; Milewski & Diamond, 2000; Ogutu & Owen-Smith, 2003; Olf, Ritchie & Prins, 2002; van Langevelde *et al.*, 2003) we predict that, at the broad scale, large-scale factors (e.g. fire regimes, climate, geology, water availability and land management) will have the greatest influence on abundance, whereas at smaller scales, aspects of habitat structure and interspecific interactions will increase in their importance relative to other factors. We have reason to expect competition between the antilopine wallaroo and eastern grey

kangaroo, as they are very similar in body mass, feeding mode, dietary preference and social behaviour (Croft, 1987; Ritchie, in press; Strahan, 1995).

Our specific objectives were to: (1) collect large-scale data on the distribution and abundance of large macropods across tropical northern Australia; (2) using the ITA, construct species-habitat models for large macropods that explore intra- and interspecific niche variation across the landscape; (3) relate the factors identified in our models as limiting species distribution and abundance to the future conservation of these species under predicted climate change.

Methods

Study region

Three seasons are typically recognized for northern Australia: the wet season (mid December – March/April) when the majority of precipitation occurs associated with the onset of the monsoon (Woinarski *et al.*, 2005), the cool dry season (April to August) when there is little rainfall and temperatures are mild, and the hot dry season (September to mid December) with low rainfall but high temperature and humidity. The vegetation of the region consists largely of open forest and woodland dominated by *Eucalyptus* spp. and *Corymbia* spp., and a grassy understorey dominated by native perennial grasses such as black speargrass (*Heteropogon contortus*), wiregrass (*Aristida* spp.), firegrass (*Schizachyrium* spp.) and native sorghum (*Sorghum* spp.). Primary productivity is closely linked to the strong nexus between rainfall and fire. Monsoonal rains in the wet season result in a short but rapid period of vegetation production. The cessation of rain following the wet season and the extended dry season leads to a sharp decrease in the available nutrients in this vegetation, but also to an increase in its flammability due to drying (Williams *et al.*, 1999). Subsequently, many habitats burn due to direct human caused fires or lightning strikes in the late dry season associated with frequent storms (Williams *et al.*, 2004).

Survey design and technique

We surveyed 50 sites between 2003 and 2005 across northern Australia, spanning the geographic distribution of the antilopine wallaroo (Ritchie, in press), and the northern distributions of the common wallaroo and eastern grey kangaroo (Strahan, 1995) (Figure 2.1). We selected sites from 1:100,000 topographic maps, provided that they offered 4WD vehicle access. Sites were stratified to provide contrast in their underlying geology (basalt, granite and sandstone) and land management (conservation or grazing) and were representative of local habitat(s), based on an earlier reconnaissance survey of north Queensland in 2002. In Queensland we carried out our surveys in the late wet season/early dry season (April-May) and late dry season (October to November) along a single five kilometre transect at each site, to assess seasonal variation in macropod abundance. Transects were restricted to this length to

ensure they could be completed before animals became inactive due to increased temperatures after 8am (Ritchie, unpublished data). Based on a home range study by Croft (1987), this transect length ensured that each transect would intersect the home ranges of multiple individuals. Thus it was possible to acquire abundance estimates.

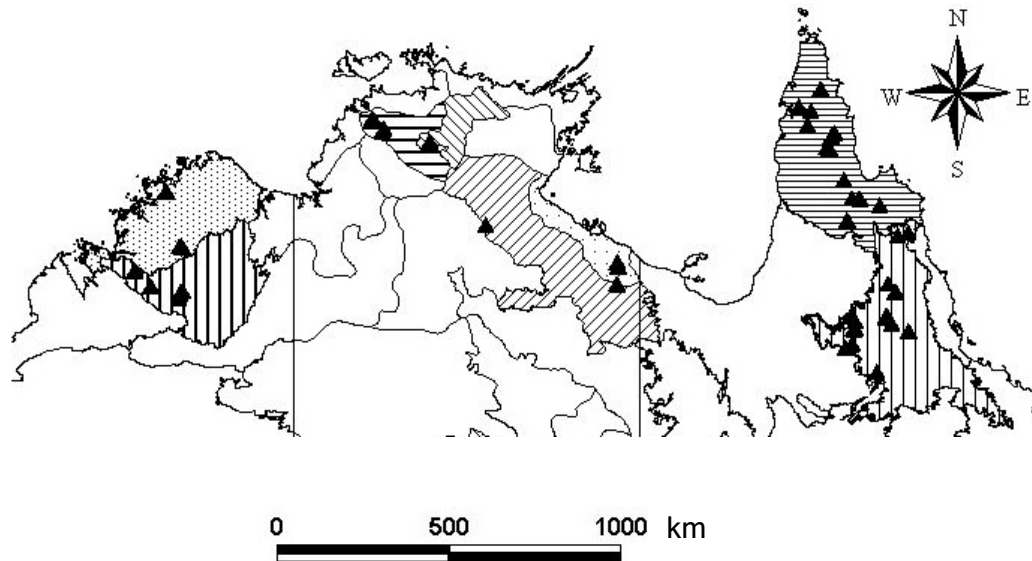


Figure 2.1 Map of the study region in northern Australia. Bioregion boundaries are represented by lines, shading indicates bioregions where surveys were conducted and survey sites by solid triangles. State boundaries are shown with thin straight black lines from left to right as follows, Western Australia, the Northern Territory and Queensland. Bioregions left to right: fine stipple, Northern Kimberley; solid vertical lines, Central Kimberley; solid horizontal lines, Pine Creek; declined thin line, Arnhem Plateau; inclined thin line, Gulf Fall and Uplands; sparse stipple, Gulf Coastal; fine horizontal lines, Cape York; thin vertical line, Einasleigh Uplands.

Preliminary analyses detected no significant difference in macropod abundance between seasons for any species. We surveyed sites in the Northern Territory and Western Australia in the early dry season (July-September). All sites (transects) were unsealed, minor dirt tracks with a very low frequency of use. Transects could not be surveyed at the peak of the wet season (January-February), because most were

inaccessible due to flooding. We surveyed transects over two consecutive days, consisting of two morning surveys (0530 - 0730 hours) and two afternoon surveys (1700 - 18.30 hours) (four replicates), which are periods when macropods are active. It was not possible to increase the time period between repeated surveys of transects due to the logistical constraints of travelling between sites (many sites were > 500 km apart). Detectability analyses (see Wintle *et al.*, 2004) showed that between four (Northern Territory and Western Australia) and eight (Queensland) surveys were sufficient to attain reliable presence/absence data and density estimates for each species.

We conducted surveys by driving a vehicle along each transect at 10-15 km/hr, while observers in the rear of the vehicle visually scanned the surrounding habitat. No observer bias was evident in the sighting data for any species. When a macropod was sighted we recorded the following: species, group size, habitat type and grass condition, location of the sighting (using a global positioning system), time, distance from the beginning of the transect (m), and the distance and angle of the individual(s) from the observer (m) (using a laser rangefinder). A group was defined as animals within visual contact of each other and no more than 50 metres apart (Johnson, 1983). We also kept a running tally of the number of cattle (*Bos indicus*), pigs (*Sus scrofa*), horses (*Equus caballus*) and dingos (*Canis lupus dingo*) seen on each transect (as well as dingo tracks) as an index of the abundance of other herbivore species (grazing pressure) and predator presence and abundance (dingoes). We calculated density estimates for each macropod species according to standard line transect methodology (Grigg *et al.*, 1989) and the guidelines in Buckland *et al.* (1993) using the program DISTANCE 4.1 (Thomas *et al.* 1998). Estimates of the density of clusters (groups) of macropods were calculated as:

$$\hat{D} = \frac{n}{2wL\hat{P}_a}$$

where n is the number of clusters sighted, L is transect length, w is the truncation distance and P_a is the detection probability within a strip of area $a = 2wL$. The relationship between number of sightings and perpendicular distance from transect lines were used to model the deterioration in detection probability with distance away from transect lines, thereby estimating P_a . Multiple detection functions were considered in the analysis (see Thomas *et al.* (1998) for a full list), and the most parsimonious model was selected using Akaike's Information Criterion (AIC). Density of each macropod species was calculated as the density of clusters multiplied by mean cluster size.

Average cluster size was adjusted (lowered) to account for the decline in probability of seeing smaller clusters with increasing distance from transect lines (for more detail see Buckland *et al.* (1993)).

Site descriptions and vegetation surveys

We surveyed five plots spaced 1.25 km apart along each transect, recorded each plot's location with a handheld Garmin GPS and took photo references. At each plot we recorded the following: altitude; water availability (either natural ephemeral sources, permanent natural streams, permanent artificial (dams and bores), permanent total (permanent natural and artificial combined) and total (ephemeral and permanent sources combined), within a 5km radius of each transect, which was determined by interviews with land owners, visual inspection and spatial data; boulders, rocks, pebbles, sand, dead trees, logs, grasses, vines and scalds all on individual scales from 0-5; height of the canopy (m) (measured with laser range finder); % projected foliage coverage and % crown separation of canopy; % projected foliage coverage and % crown separation of trees $\geq 5\text{m}$ to canopy; % projected foliage coverage and % crown separation of plants $\geq 2\text{m}$ and $\leq 5\text{m}$; % coverage of plants $\geq 1\text{m}$ and $\leq 2\text{m}$; % coverage of plants 0 to $\leq 1\text{m}$. To measure fine-scale pasture composition at each plot, we placed three pairs of 1m^2 quadrats along a 60m transect, spaced at 20 m intervals. In each quadrat we recorded the following information: grass species present; % bare ground; grass clump width (cm) and grass clump height (cm); greenness of grass (on a scale from 0 – 4); seeding index of grass (on a scale from 0 – 4); % grass coverage; % non-grass coverage; and the dry (oven-dried at 60°C for 24 hours) biomass of grass (g). Lastly, at each interval we recorded the circumference at breast height of the 10 closest trees $\geq 2\text{m}$ in height. Soil type (massive earth, sand, loam, duplex) was recorded from spatial data and ground-truthed by visual inspection.

Fire history

We compiled the fire history of all sites using Arcview 3.3 and Modis and NOAA derived digital satellite fire scar images provided by the Cape York Peninsula Development Association (<http://www.cypda.com.au>) and the Bushfire Council of the Northern Territory through the Department of Land Information, Western Australia

(<http://www.dli.wa.gov.au>). The intensity of fire varies according to its seasonal timing, with late season fires being more intense than early season fires, and this in turn influences the effect that fires may have on habitat structure and composition (Russell-Smith, 2002). We recorded: total number of fires, total number of early season fires (April - August), total number of late season fires (September - December), and the mean % of transect (0-25%, 26-50%, 51-75% and 76-100%) burnt by all fires from 2002 up to the time of survey of each transect.

Climate information

Climatic information was derived for each site using BIOCLIM (Houlder *et al.*, 2000). The following climatic data were compiled in view of their known influence on macropod distribution and abundance (Caughley *et al.*, 1987): annual mean temperature, maximum temperature of the warmest period, minimum temperature of the coldest period, annual temperature range, mean temperature of the wettest quarter, mean temperature of the driest quarter, annual precipitation, precipitation of the wettest period, precipitation seasonality (coefficient of variation), precipitation of the wettest quarter and precipitation of the driest quarter. Unlike Caughley *et al.* (1987), we did not include precipitation of the driest period since a zero value was recorded for all sites.

Statistical analyses

Species co-occurrence

To test for non-random patterns of co-occurrence of the three macropod species we calculated C-scores in EcoSim 7.72 (Gotelli & Entsminger, 2001). The C-score measures the mean number of checkerboard units between all possible pairs of species as outlined in Stone and Roberts (1990). A C-score significantly greater than that expected by chance is indicative of an assemblage structured by competition.

Modelling approach

Due to the high number of variables which might predict macropod abundance, we used a combination of correlation analyses and principal components analysis to either exclude variables that showed little relationship with abundance ($r \leq 0.3$), or

reduce multiple variables likely to be inter-correlated into principal component axes, before being used in the final set for the construction of models, as recommended by Quinn and Keough (2002). Principal components (rotated varimax) were constructed for climate (Table 2.1 and Table 2.2), vegetation structure (Table 2.3), grass layer (Table 2.4) and substratum (Table 2.5) variables. The distributions of all predictor variables were examined and transformed if required before analyses. We used the final set of variables to construct generalized linear models (using a Poisson distribution and log link function) of macropod species abundance at three scales (northern Australia, north Queensland and within the two major bioregions of north Queensland, Cape York and the Einasleigh Uplands). Only antilopine wallaroo abundance could be modelled across all levels, as the other two species have more restricted distributions within our study area.

We constructed *a priori* candidate models based on our knowledge and published information for each species. We explored the relative contribution of variables by sequentially removing them from candidate models and observing the effect this had on AIC differences. We selected the “best” model by comparing AIC differences and weights between models according to the protocol outlined in Burnham and Anderson (2002). We assessed our models for over-dispersion as recommended by Burnham and Anderson (2002) for studies using count data; however no models showed evidence of over-dispersion requiring adjustment of model statistics. We examined the relative importance of parameters across models by summing the weights of models in which they occurred (see Burnham *et al.*, 2002). We examined the relationship between abundance and species at the three different spatial scales mentioned: northern Australia - representing the complete distribution of the antilopine wallaroo and northern distribution of the common wallaroo; north Queensland - representing the Queensland distribution of the antilopine wallaroo and north eastern distributions of the common wallaroo and eastern grey kangaroo; and bioregional - Cape York, representing the far northern Queensland distribution of the antilopine wallaroo, and the Einasleigh Uplands, representing the southern north Queensland distribution of the antilopine wallaroo (Figure 2.1).

Table 2.1 Principal components (rotated varimax) of climate in northern Australia. Values in bold represent factor loadings contributing most to each axis. PC1 describes a gradient of lower minimum temperatures, increased temperature range and decreased rainfall. PC2 describes a gradient of increased temperature. PC3 describes a gradient of decreased rainfall seasonality.

Climate northern Australia			
	PC 1	PC 2	PC 3
variance	5.31	3.11	1.08
% variation	53.15	31.13	10.77
% cumulative variation	53.15	84.28	95.05
variable			
annual mean temperature	- 0.36	0.93	- 0.04
maximum temperature hottest period	0.45	0.85	- 0.13
minimum temperature coldest period	- 0.95	0.15	- 0.05
temperature range	0.90	0.33	- 0.03
temperature wettest quarter	0.13	0.96	- 0.19
temperature driest quarter	- 0.59	0.65	- 0.12
annual precipitation	- 0.97	0.03	0.22
precipitation wettest period	- 0.99	- 0.01	0.00
precipitation seasonality	0.09	0.20	- 0.97
precipitation wettest quarter	- 0.99	0.04	0.08

Table 2.2 Principal components (rotated varimax) of climate in north Queensland. Values in bold represent factor loadings contributing most to each axis. PC1 describes a gradient of increased temperatures, reduced temperature range and increased rainfall. PC2 describes a gradient of increased temperature and rainfall seasonality.

Climate north Queensland		
	PC 1	PC 2
variance	5.89	3.23
% variation	58.88	32.32
% cumulative variation	58.88	91.20
variable		
annual mean temperature	0.63	0.75
maximum temperature hottest period	- 0.24	0.94
minimum temperature coldest period	0.95	0.23
temperature range	- 0.95	0.22
temperature wettest quarter	0.20	0.95
temperature driest quarter	0.80	0.50
annual precipitation	1.00	0.04
precipitation wettest period	0.99	0.09
precipitation seasonality	0.11	0.70
precipitation wettest quarter	0.99	0.12

Table 2.3 Principal components (rotated varimax) of vegetation structure in northern Australia. Values in bold represent factor loadings contributing most to each axis. PC1 describes a gradient of decreased midstorey, understorey and shrub layer. PC2 describes a gradient of increased canopy cover and height. PC3 describes a gradient of smaller trees.

Vegetation structure			
	PC 1	PC 2	PC 3
variance	2.09	1.42	1.08
% variation	34.85	23.75	18.05
% cumulative variation	34.85	58.60	76.65
variable			
canopy height	-0.25	0.60	-0.28
% canopy cover	-0.21	0.95	0.04
tree circumference	0.13	0.00	-0.98
% 5m - canopy coverage	-0.60	0.30	0.09
% 2 - 5 m coverage	-0.86	0.13	0.11
% 1 - 2 m coverage	-0.93	0.24	0.11

Table 2.4 Principal components (rotated varimax) of the grass layer in northern Australia. Values in bold represent factor loadings contributing most to each axis. PC1 describes a gradient of increased grass coverage, height and biomass. PC2 describes a gradient of increased grass but reduced non-grass coverage. PC3 describes a gradient of increasing grass senescence.

Grass layer			
	PC 1	PC 2	PC 3
variance	2.15	2.12	1.06
% variation	30.71	30.33	15.17
% cumulative variation	30.71	61.04	76.21
variable			
% 0 - 1 m coverage	0.65	0.29	- 0.08
clump height	0.94	- 0.19	0.07
greenness	0.35	- 0.27	0.10
seeding	0.12	- 0.13	0.98
biomass	0.84	0.03	0.25
% grass	- 0.05	0.97	- 0.12
% non-grass	0.03	- 0.98	0.06

Table 2.5 Principal components (rotated varimax) of substratum in northern Australia. Values in bold represent factor loadings contributing most to each axis. PC1 describes a gradient of increased rockiness. PC2 describes a gradient of increased pebbles and sandiness.

Substratum	PC 1	PC 2
variance	1.87	1.22
% variation	46.63	30.44
% cumulative variation	46.63	77.06
variable		
boulders	0.47	0.41
rocks	0.67	-0.14
pebbles	0.29	0.68
sand	-0.50	0.59

Results

Distribution and abundance

Antilopine wallaroos were recorded at 34 sites (68%) and common wallaroos at 20 sites (40%) across northern Australia. There was large variation in the abundance of the three species (Figure 2.2). Within north Queensland (Figure 2.2a), eastern grey kangaroos were found at 11 sites (38%), antilopine wallaroos at 19 sites (65%) and common wallaroos at 14 sites (48%). Antilopine wallaroos occurred at an average density of 3.0 ± 0.5 (range 0.2 – 12.9) individuals/km² across northern Australia, 3.0 ± 0.6 (range 0.3 – 9.8) in north Queensland, 3.0 ± 1.1 (range 0.8 – 9.8) in the Cape York bioregion and 3.1 ± 0.9 (range 0.3 – 8.4) in the Einasleigh Uplands bioregion (see Figure 2.1 for bioregion locations). Common wallaroos occurred at an average density of 1.1 ± 0.2 (range 0.1 – 3.3) individuals/km² across northern Australia, and were significantly less abundant than antilopine wallaroos across this region (t-test, $t_{98} = 3.9$; $p < 0.000$; Figure 2.2). Within north Queensland (Figure 2.2a), common wallaroos occurred at an average density of 1.2 ± 0.3 (range 0.1 – 3.1) individuals/km² and eastern grey kangaroos at 1.0 ± 0.5 (range 0.1 – 5.8) individuals/km². Antilopine wallaroos were significantly more abundant than common wallaroos and eastern grey kangaroos in north Queensland (ANOVA, $F_{2,84} = 7.0$; $p = 0.002$; Figure 2.2a).

Species co-occurrence

Antilopine wallaroos and eastern grey kangaroos were found together significantly less often than expected (C score, $C = 112.0$, $p = 0.006$). Antilopine wallaroos and common wallaroos (C score, $C = 100.0$, $p = 0.8$) and eastern grey kangaroos and common wallaroos (C score, $C = 50$, $p = 0.5$) were neither positively nor negatively associated.

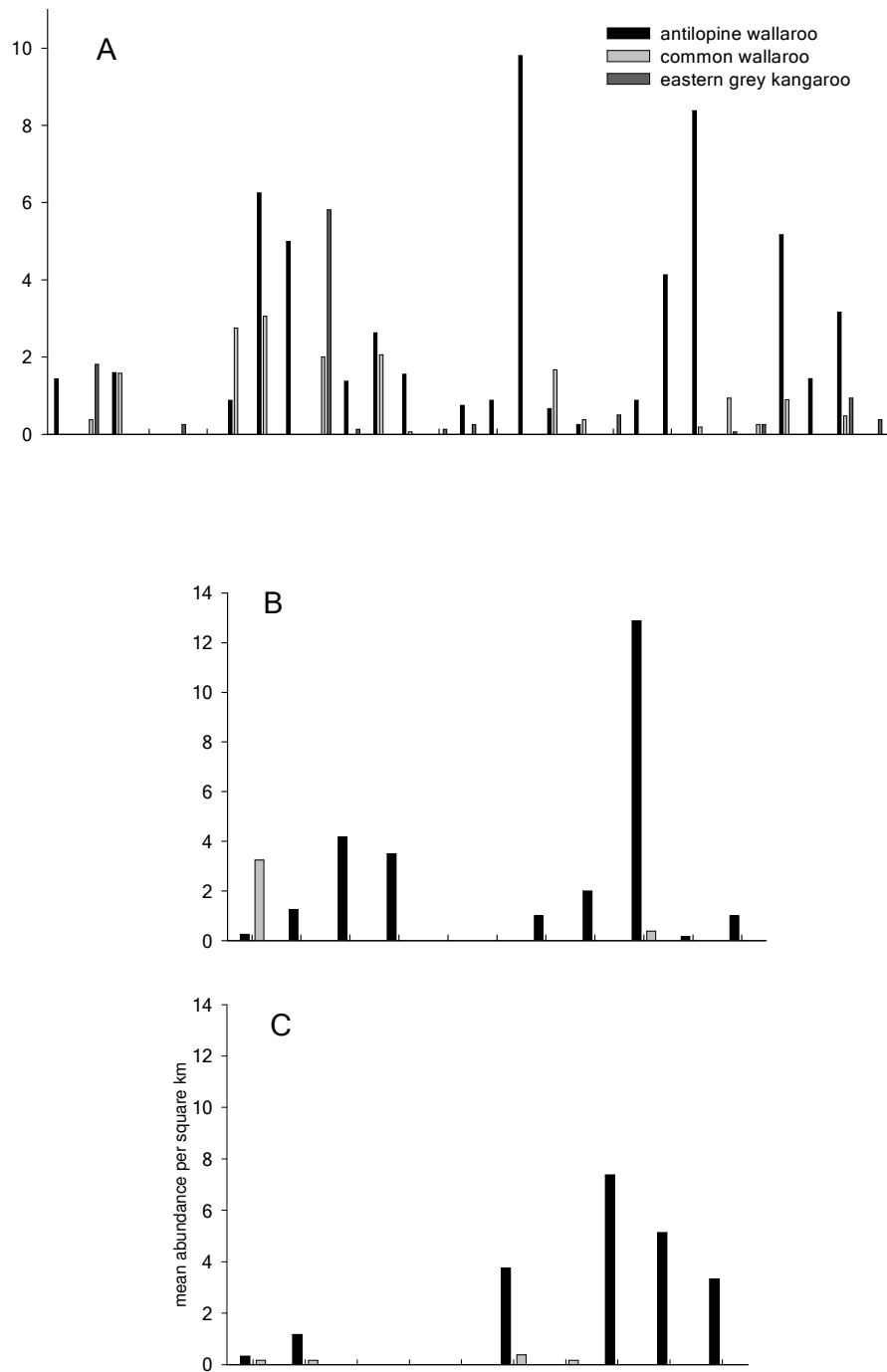


Figure 2.2 Mean abundance of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*) and eastern grey kangaroos (*M. giganteus*) across northern Australia. A – Queensland (Cape York and Einasleigh Uplands bioregions), B – Northern Territory, C – Kimberley region, Western Australia.

Fire frequency and regime

A total of 71 fires occurred in our study sites between 2002 and 2005, of which 22 (31%) were late season fires and 49 (69%) were early season fires. On average each site was burnt 1.5 ± 0.2 times (range 0 – 4); an average of $31\% \pm 4.4\%$ of its area was affected by each fire; eighteen sites (36%) were not burnt. Early season fires were more common than late season fires in the Northern Territory (early season, mean \pm s.e. = 2.1 ± 0.4 ; late season, mean \pm s.e. = 0.4 ± 0.2) and Western Australia (early season, mean \pm s.e. = 1.2 ± 0.2 ; late season, mean \pm s.e. = 0.6 ± 0.2), but nearly equal in frequency in Queensland (early season, mean \pm s.e. = 0.5 ± 0.2 ; late season, mean \pm s.e. = 0.4 ± 0.1). Across northern Australia, antilopine wallaroos were significantly more abundant at sites which were burnt more than once by late season fires between 2002 and 2005 (ANOVA, $F_{2, 47} = 12.2$; $p < 0.000$; Figure 2.3). Common wallaroos were significantly more abundant on unburnt sites across northern Australia (ANOVA, $F_{4, 45} = 5.6$; $p = 0.001$; Figure 2.4). Within north Queensland, there was no significant effect of fire frequency on eastern grey kangaroo abundance (Kruskal-Wallis, $\chi^2_3 = 3.5$, $p = 0.32$).

Models of abundance

Antilopine wallaroo

The availability of permanent water (+), frequency of late season fires (+), and abundance of eastern grey kangaroos (-) were the most consistent predictors of antilopine wallaroo abundance across all models (Table 2.6a-d). The form of the relationships between abundance and these parameters varied with spatial scale. At the largest scale (complete range - northern Australia), water availability, fire frequency, geology and land management were key influences on abundance (Table 2.6a), whereas at a regional scale (north Queensland), in addition to water availability and fire frequency, the abundance of eastern grey kangaroos and soil type were also important (Table 2.6b). At the smallest scale (bioregional – Cape York and Einasleigh Uplands), vegetation structure and grass layer composition were important predictors of antilopine wallaroo abundance (Table 2.6c and d).

An interaction between geology and land management affected antilopine wallaroo abundance across the species' range (Table 2.6a). Antilopine wallaroos were most abundant on cattle grazing sites with basaltic geology (Figure 2.5) and showed a highly significant positive trend with increased availability of permanent water (Figure 2.6). The abundance of common wallaroos showed a weaker positive correlation with water availability, and eastern grey kangaroos showed a weak negative correlation with water availability. The availability and sources of water varied between regions, with approximately twice as many permanent natural sources in Western Australia and the Northern Territory as in Queensland, whereas there were ten times more permanent artificial sources in Queensland than in the other regions. Dams and bores in the Einasleigh Uplands bioregion accounted for most of the artificial sources of water in Queensland. In north Queensland, antilopine wallaroos were most abundant on massive earths and sandy soils (Figure 2.7). Eastern grey kangaroos were also more abundant on massive earths, and common wallaroos on loams and sandy soils (Figure 2.7).

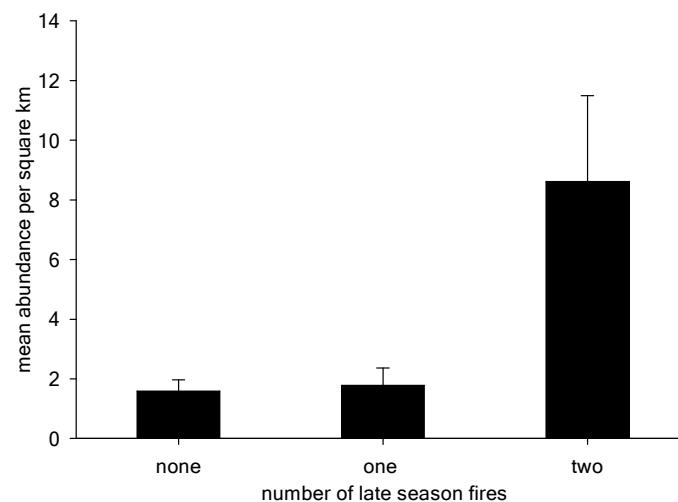


Figure 2.3 Relationship between the mean abundance (\pm standard error) of antilopine wallaroos and the number of times sites were burnt by late season fires for northern Australia between 2002 and 2005.

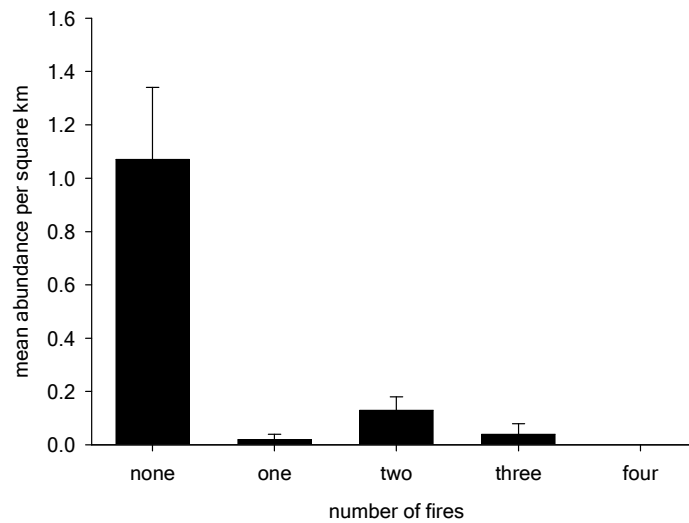


Figure 2.4 Relationship between the mean abundance (\pm standard error) of common wallaroos for northern Australia and the number of times sites were burnt between 2002 and 2005.

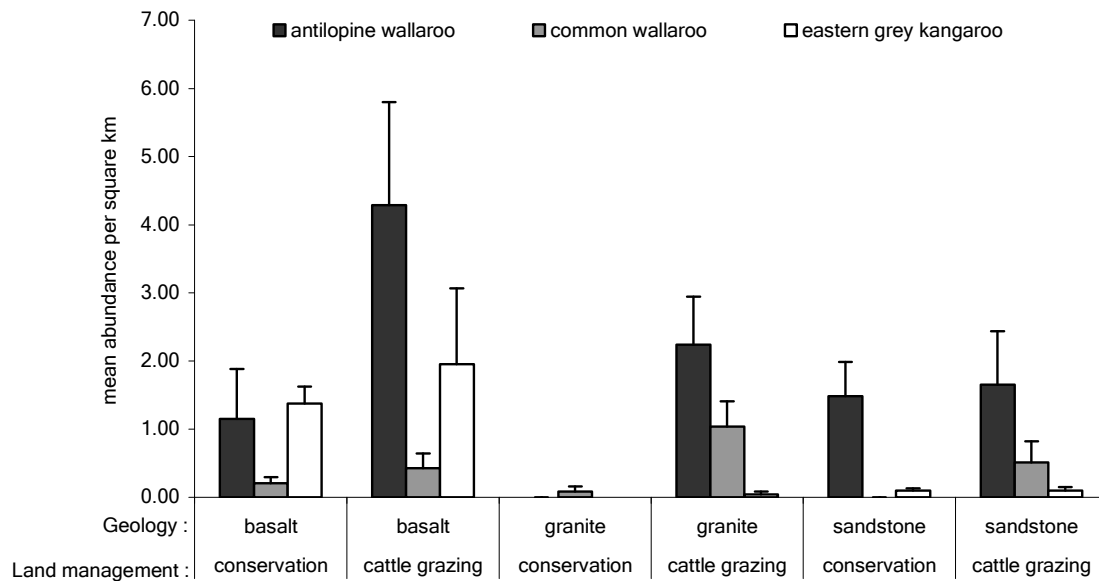


Figure 2.5 The mean abundance (\pm standard error) of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*) and eastern grey kangaroos (*M. giganteus*) in relation to geology and land management, across northern Australia.

The relatively low incidence of co-occurrence of antilopine wallaroos and eastern grey kangaroos across north Queensland was consistent with the negative relationship between the abundance of the two species (Table 2.6 b-d). There were key differences in the factors affecting antilopine wallaroo abundance between bioregions within north Queensland (Table 2.6c and d). In Cape York, antilopine wallaroos were most abundant in habitat with increased water availability, high fire frequency, and increased canopy height and cover. Contrastingly, in the Einasleigh Uplands, antilopine wallaroo abundance was most affected by the composition of the grass layer and the amount of mid- and under-storey vegetation, with water availability being less important. The effect of the presence of eastern grey kangaroos on antilopine wallaroo abundance was relatively similar between bioregions.

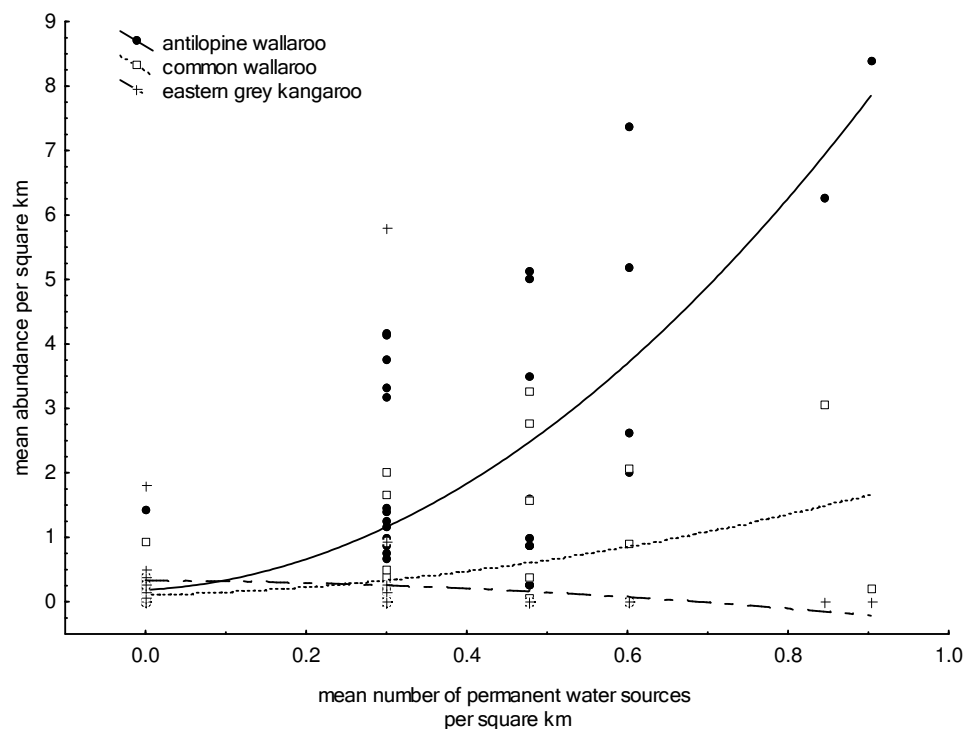


Figure 2.6 Relationship between the abundance of large macropods and the availability of permanent water in northern Australia. Antilopine wallaroo, *Macropus antilopinus* ($r = 0.68$, $p < 0.0000$); common wallaroo, *M. robustus* ($r = 0.36$, $p = 0.01$); eastern grey kangaroo, *M. giganteus* ($r = -0.12$, $p = 0.41$).

Common wallaroo

Across northern Australia, the frequency of fire (-), climate (+) and geology (+) were the best predictors of common wallaroo abundance (Table 2.7 a-b). Common wallaroo abundance was lower at sites that were burnt and in conservation areas (Figure 2.4 and Figure 2.5), and higher on cattle grazing sites of granitic geology (Figure 2.5). Common wallaroos were also more abundant in areas of increased temperature variation and decreased rainfall and more rocky habitats (see Table 2.1 and Table 2.5). Within north Queensland, common wallaroos were less abundant in areas of higher temperature and increased rainfall and more abundant in open habitats (Table 2.2 and Table 2.7b).

Eastern grey kangaroo

The abundance of eastern grey kangaroos in north Queensland was correlated with the abundance of antilopine wallaroos (-), geology (+ and -), and climate (-) (Table 2.2 and Table 2.8). Eastern grey kangaroos were most abundant on sites of basaltic geology, and unlike common wallaroos, less abundant at sites with granitic geology (Figure 2.5).

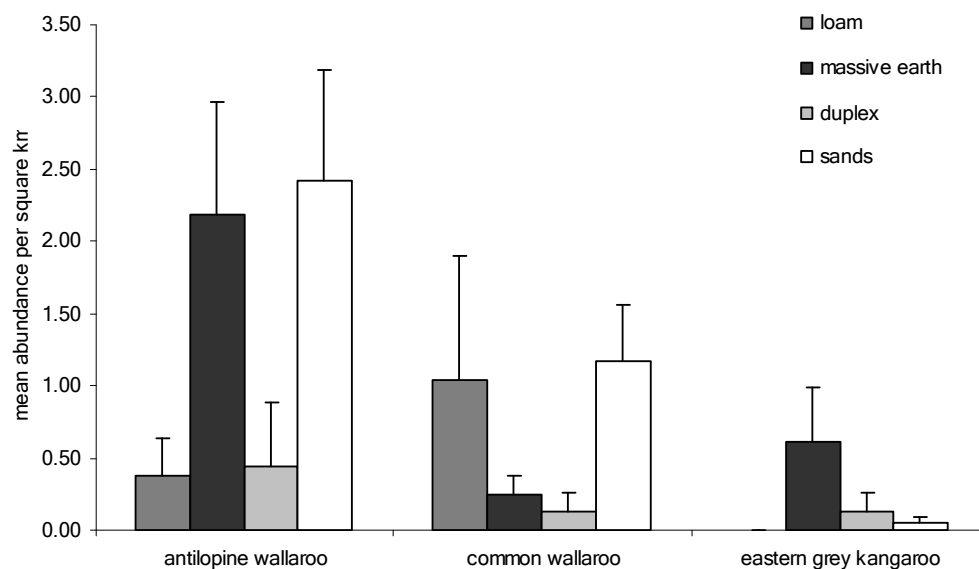


Figure 2.7 The mean abundance (\pm standard error) of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*) and eastern grey kangaroos (*M. giganteus*) in relation to soil type, across north Queensland.

Table 2.6a – d Summary habitat models of antilopine wallaroo (*Macropus antilopinus*) abundance across (a) Northern Australia, (b) North Queensland and (c) Cape York and (d) Einasleigh Uplands bioregions. * indicates an interaction term. PC = principle component axis (refer to supplementary tables). AIC_c = model score; models with smaller scores are better than models with larger scores. Δ_i = model score differences, 0 is the “best” model; values between 0 and 2 have substantial support; values greater than 2 have considerably less support. w_i = Akaike model weights, which is the weight of evidence in favour of model *i* being the best model given that one of the models in the set must be the best model. Estimate relative importance was calculated by summing w_i across all models in which parameters occurred (increasing values signify increasing importance up to a maximum of 1) according to Burnham (2002). Models in bold have substantial support ($\Delta_i < 2$).

(a) northern Australia		antilopine wallaroo			AIC_c	Δ_i	w_i
permanent water (total)	number of late season fires	geology	land management	geology*land management	163.02	0.00	0.52
permanent water (total)	number of late season fires	geology			165.15	2.13	0.18
permanent water (total)	number of late season fires	land management	geology*land management		166.02	3.00	0.12
permanent water (total)	number of late season fires	geology	land management		166.28	3.26	0.10
permanent water (total)	number of late season fires	geology*land management			166.91	3.89	0.08
	level of effect	estimate	relative importance				
intercept		-3.65					
permanent water (total)		3.20	1.00				
number of late season fires		0.35	1.00				
geology	basalt	2.72	0.80				
geology	granite	-5.01	0.80				
land management	conservation	-2.64	0.80				
geology*land management	basalt*cattle grazing	2.30	0.78				

(b) north Queensland		antilopine wallaroo				
eastern grey kangaroo abundance	permanent water (total)	number of late season fires	soil type	AIC_c	Δ_i	w_i
eastern grey kangaroo abundance	permanent water (total)	number of late season fires		73.22	0.00	0.61
permanent water (total)	number of late season fires	soil type		75.30	2.08	0.22
permanent water (total)	number of late season fires			77.10	3.88	0.09
				77.11	3.89	0.09
	level of effect	estimate	relative importance			
intercept		-1.70				
permanent water (total)		3.42	1.00			
number of late season fires		0.77	1.00			
eastern grey kangaroo abundance		-1.39	0.83			
soil type	loam	-0.74	0.70			
soil type	massive earth	0.82	0.70			
soil type	duplex	-0.87	0.70			

(c) Cape York		antilopine wallaroo		AIC_c	Δ_i	w_i
permanent water (total)	number of late season fires	PC 2 (vegetation structure)		43.88	0.00	0.37
eastern grey kangaroo abundance	permanent water (total)	number of late season fires	PC 2 (vegetation structure)	44.66	0.78	0.25
permanent water (total)	PC 2 (vegetation structure)			46.86	2.98	0.08
eastern grey kangaroo abundance	permanent water (total)	PC 2 (vegetation structure)		47.02	3.14	0.08
eastern grey kangaroo abundance	permanent water (total)	number of late season fires		47.11	3.24	0.07
eastern grey kangaroo abundance	number of late season fires	PC 2 (vegetation structure)		47.15	3.27	0.07
eastern grey kangaroo abundance	permanent water (total)			47.41	3.53	0.06
	estimate	relative				
intercept	-2.17	importance				
permanent water (total)	4.58	0.93				
PC 2 (vegetation structure)	0.48	0.86				
number of late season fires	0.48	0.77				
eastern grey kangaroo abundance	-1.88	0.54				

(d) Einasleigh Uplands		antilopine wallaroo				
				AIC_c	Δ_i	w_i
eastern grey kangaroo abundance	PC 1 (vegetation structure)	PC 2 (grass layer)		32.41	0.00	0.31
PC 1 (vegetation structure)	PC 2 (grass layer)			33.21	0.81	0.21
permanent water (total)	PC 1 (vegetation structure)	PC 2 (grass layer)		33.30	0.89	0.20
eastern grey kangaroo abundance	permanent water (total)	PC 1 (vegetation structure)	PC 2 (grass layer)	34.37	1.96	0.12
permanent water (total)	PC 2 (grass layer)			34.76	2.35	0.10
permanent water (total)				35.38	2.98	0.07
	estimate	relative				
intercept	1.58	importance				
PC 2 (grass layer)	-2.60	0.93				
PC 1 (vegetation structure)	1.35	0.83				
permanent water (total)	0.33	0.48				
eastern grey kangaroo abundance	-0.73	0.43				

Table 2.7 a and b. Summary habitat models of common wallaroo (*Macropus robustus*) abundance for (a) northern Australia and (b) North Queensland. * indicates an interaction term. PC = principle component axis (refer to supplementary tables). AICc = model score, models with smaller scores are better than models with larger scores. Δ_i = model score differences, 0 is the “best” model; values between 0 and 2 have substantial support; values greater than 2 have considerably less support. w_i = Akaike model weights, which is the weight of evidence in favour of model *i* being the best model given that one of the models in the set must be the best model. Estimate relative importance was calculated by summing w_i across all models in which parameters occurred (increasing values signify increasing importance up to a maximum of 1) according to Burnham (2002). Models in bold have substantial support ($\Delta_i < 2$).

(a) northern Australia		common wallaroo				AIC_c	Δ_i	w_i
PC 1 (substratum)	number of fires	PC 1 (climate)	land management			35.19	0.00	0.28
PC 1 (substratum)	number of fires	PC 1 (climate)	geology	land management		35.80	0.61	0.21
PC 1 (substratum)	number of fires	PC 1 (climate)	land management	geology*land management		36.07	0.88	0.18
PC 1 (substratum)	number of fires	PC 1 (climate)	geology	land management	geology*land management	36.34	1.15	0.16
PC 1 (substratum)	number of fires	PC 1 (climate)	geology	geology*land management		37.85	2.66	0.07
number of fires	PC 1 (climate)	geology	land management			38.79	3.60	0.05
number of fires	PC 1 (climate)	land management	geology*land management			38.98	3.79	0.04
	level of effect	estimate	relative importance					
intercept		-2.55						
number of fires		-0.73	1.00					
PC 1 (climate)		0.98	1.00					
land management	conservation	-1.57	0.93					
PC 1 (substratum)		0.25	0.91					
geology	basalt	0.39	0.49					
geology	granite	2.10	0.49					
geology*land management	granite*cattle grazing	0.67	0.46					

(b) north Queensland		common wallaroo		AIC_c	Δ_i	w_i
openness	PC1 (climate)	geology		39.61	0.00	0.28
openness	number of fires	PC1 (climate)		40.19	0.58	0.21
openness	number of fires	PC1 (climate)	geology	40.89	1.28	0.15
openness	PC1 (climate)			41.09	1.48	0.13
openness	number of fires			42.14	2.54	0.08
number of fires	PC1 (climate)			42.43	2.82	0.07
PC1 (climate)				43.30	3.70	0.04
openness	number of fires	geology		43.41	3.80	0.04
	level of effect	estimate	relative importance			
intercept		-5.65				
openness		1.26	0.89			
PC1 (climate)		-1.56	0.88			
number of fires		-0.35	0.54			
geology	basalt	-0.87	0.47			
geology	granite	0.03	0.47			

Table 2.8 Summary habitat model of eastern grey kangaroo (*Macropus giganteus*) abundance for North Queensland. PC = principle component axis (refer to supplementary tables). AIC_c = model score, models with smaller scores are better than models with larger scores. Δ_i = model score differences, 0 is the “best” model; values between 0 and 2 have substantial support; values greater than 2 have considerably less support. w_i = Akaike model weights, which is the weight of evidence in favour of model i being the best model given that one of the models in the set must be the best model. Estimate relative importance was calculated by summing w_i across all models in which parameters occurred (increasing values signify increasing importance up to a maximum of 1) according to Burnham (2002). Models in bold have substantial support ($\Delta_i < 2$).

north Queensland		eastern grey kangaroo			
antilopine wallaroo abundance	PC 2 (climate)	geology	AIC_c	Δ_i	w_i
antilopine wallaroo abundance	geology		29.66	0.00	0.81
			32.61	2.94	0.19
	level of effect	estimate	relative importance		
Intercept		-2.04			
antilopine wallaroo abundance		-1.15	1.00		
geology	basalt	1.30	1.00		
geology	granite	-0.24	1.00		
PC 2 (climate)		-1.46	0.81		

Discussion

Few studies have examined in detail the environmental and biological factors limiting the distribution and abundance of organisms at both the level of their complete distributions, and at smaller spatial scales (Murphy *et al.*, in press; Peterson *et al.*, 2003). There is an increasing demand for this detailed ecological information, in view of its importance in guiding conservation measures in the face of global climate change (see Hughes, 2003; Peterson *et al.*, 2001; Rondinini *et al.*, 2005; Sagarin *et al.*, 2006). Our results indicate clear interspecific differences in the factors affecting the abundance of three sympatric large herbivores across the tropical savannas of northern Australia. In particular, by modelling the abundance of one species, the antilopine wallaroo, across its geographic distribution and at finer scales, we provide evidence of the way in which our understanding of the niche requirements of a species strongly depends on the scale at which it is studied. At larger scales, broad-scale factors (fire regimes, climate, soil type and geology, water availability and land management) were the best predictors of macropod abundance, whereas at finer scales, aspects of habitat structure and species interactions increased in relative importance.

Factors influencing niche variation in large herbivorous marsupials

The abundance of macropods was influenced by a suite of abiotic and biotic factors, and these relationships varied spatially both within and between species. The most important factors were geology and soil type, fire regime, land management, climate, water availability, species abundance of the other species and aspects of habitat structure. Geology affected the abundance of all species, and was closely linked with land use. A partial explanation for this relationship may be the tendency in Australia for grazing properties to be located in more productive areas than conservation reserves (Pressey, 1995). Short *et al.* (1983) similarly found that red kangaroos were most abundant on sheep grazing properties, and less abundant on vacant crown land in Western Australia. In Queensland, high abundances of antilopine wallaroos occurred in the Einasleigh Uplands bioregion, which supports relatively intense cattle grazing, and provides a large number of artificial watering points. Our models suggest that permanent water is a key factor influencing the abundance of antilopine wallaroos; therefore the creation of watering points in otherwise dry habitat may have facilitated

the occupation of such habitats by this species. The creation of watering points is also believed to have aided the recent expansion of eastern grey kangaroos into arid habitats (Dawson, McTavish & Ellis, 2004). Lastly, and also related to geology, common wallaroos across northern Australia were more abundant in rockier areas, as is found in other parts of the species' distribution (Croft, 1987). Habitats with underlying granite geology typically have boulders and rock outcrops, and these are an important shelter resource facilitating thermoregulation by this species and reducing its dependence on free water in areas of high temperature (Dawson, 1995; Dawson & Denny, 1969). In contrast, antilopine wallaroos do not use rock shelters (Ritchie, in press) and this may be one reason why they are more reliant on water sources.

Soil fertility

Our results suggest different responses among the three macropod species to variation in soil fertility. Soil fertility strongly influences the production of biomass and nutritional quality of grasslands (Bell, 1982), and is therefore expected to affect the abundance of large herbivores (McNaughton *et al.*, 1989; Olff *et al.*, 2002). In contrast to other parts of the world, Australia's savannas are characterised by very low soil fertility and therefore low nutrient availability in pasture species (Williams *et al.*, 2005). In addition, the distribution of nutrients across this region is marked by its spatial heterogeneity (Woinarski *et al.*, 2005). Geology and soil type provide good proxies for soil fertility at the coarse scale (Mutanga *et al.*, 2004). Volcanic soils (basalt) are more fertile than other soils in northern Australia (Kanowski *et al.*, 2001), and supported higher abundances of antilopine wallaroos and eastern grey kangaroos. The low but heterogeneous nature of soil fertility across northern Australia may explain in part why the abundance of the antilopine wallaroo was likewise highly variable across its distribution. This hypothesis has an underlying assumption that factors influencing the abundance of species decrease from the core to the edges of species' distributions, but clearly, as highlighted by our study, this is an over-simplified view of natural ecosystems. In contrast, common wallaroos were more abundant in areas of lower nutrient availability, specifically granite- and sandstone-derived soils. This difference may be explained by the dichotomy in feeding strategies between common wallaroos and the other two species. The antilopine wallaroo and eastern grey kangaroo are both grazers, and favour nutrient-rich grasses in their diets (Dawson, 1995; Fossan, 2005).

On the other hand, the common wallaroo is a mixed feeder, including large amounts of non-grass (e.g. forbs) in its diet (Dawson, 1995) and it also has the capacity to feed on foods with low nitrogen content (Freudenberger & Hume, 1992). Therefore, variation in feeding modes and differences in digestive capabilities may be an important factor contributing to niche separation between these species, as Freudenberger and Hume (1992) demonstrated in two subspecies of wallaroo (common wallaroo – *M. r. robustus* and euro *M. r. erubescens*) associated with different habitats.

Fire regimes

We found that fire frequency and intensity have significantly different effects on the abundance of the common wallaroo and antilopine wallaroo in northern Australia. Fire is a pervasive disturbance process globally and significantly shapes ecosystem structure and function (Bond & Keeley, 2005; Bowman, 1998; van Langevelde *et al.*, 2003). Antilopine wallaroos were most abundant at sites where there had been two late dry season fires in the previous 3 years, whereas common wallaroos were significantly more abundant on unburnt sites. We suggest that this difference is due to the effect that fire, and its seasonal timing, have on habitat structure and composition. Late season fires are typically intense and result in the overall opening up of habitat, removal of woody species and the rejuvenation of grasses (Bowman, 1998; Yibarbuk *et al.*, 2001). Grazing species such as antilopine wallaroos may be favoured under such a regime, and many studies detail the traditional use of fire by aboriginal people in northern Australia to concentrate and hunt these macropods, which move into recently burnt habitat to feed on fresh, nutrient-rich grass (Bowman, 1998; Bowman, Garde & Saulwick, 2001b; Yibarbuk *et al.*, 2001). Our results also suggest that such an effect may be cumulative, as no difference in antilopine wallaroo abundance was found between unburnt sites and sites burnt only once, whereas abundance greatly increased in areas burnt twice. An alternative interpretation is that grasses may respond to fire with stronger and more rapid growth on fertile soils than on infertile soils, and that the difference could therefore be due to the soil preferences of the two wallaroo species.

It is at first perplexing that common wallaroos should be disadvantaged by the fire regime detailed above, particularly as grass forms a substantial proportion of their diet (Dawson, 1995), and they favour more open habitats (Table 2.6b). One possible

explanation is that although these fires may increase openness and grass condition, they also remove woody plants and forbs (browse). As mentioned earlier, common wallaroos browse on a variety of plants, and woody and forb species represent a significant part of the diet where grasses are in limited supply, particularly during the extended dry season (Telfer & Bowman, 2006). Continued removal of browse by fire and increases in grass biomass within habitats may confer an advantage to more specialised grazing species such as antilopine wallaroos and eastern grey kangaroos, and disadvantage more generalist feeders such as common wallaroos. The rockier habitats typical of the common wallaroo, may in addition to aiding thermoregulation, also act as a buffer against fire, therefore providing more browse. A landscape-scale manipulation of habitats through fire would greatly increase our understanding of how this dynamic disturbance process may contribute towards the structuring of macropod assemblages.

Climate

Our results build on earlier work by Caughley et al. (1987) and Caughley et al. (1988) who examined the distribution and abundance of temperate kangaroos in relation to climate. Our work elucidates the ways in which the distribution of large macropods in northern Australia is influenced by the climatic extremes characteristic of the tropics. Climate has a significant influence on the distribution and abundance of large herbivores globally, either directly through physiological effects and/or indirectly via effects on habitats and resources (Ehleringer, Cerling & Dearing, 2002; Ogutu *et al.*, 2003). The abundances of common wallaroos and eastern grey kangaroos, which are at their far northern limits of distribution within our study region, were influenced strongly by climate. The eastern grey kangaroo showed a negative response to increased temperature and rainfall seasonality, representative of tropical conditions, whereas the common wallaroo favoured areas of lower rainfall and greater temperature variation, representative of increasing aridity. No work to date has compared the eco-physiology of sympatric antilopine wallaroos, common wallaroos and eastern grey kangaroos, and its effects on their respective abilities to occupy tropical habitats. Antilopine wallaroos do however have two morphological adaptations which may be related to coping with the climatic conditions experienced in this region: a highly vascularised area close to the inside surface of the hind-legs which are licked to aid evaporative cooling; and their most obvious morphological adaptation, a large nasal cavity that appears externally as a

swollen rostrum, which likely enhances evaporative cooling (through panting) in humid air (Dawson, 1995; Ritchie, in press). Evaporative cooling entails water loss and this may further help to explain the reliance of antilopine wallaroos on water, whereas common wallaroos may use rock shelters to reduce their dependence on water. More broadly, therefore, differences in behavioural and morphological adaptations are likely to explain much of the variation in the distribution and abundance of macropod species within tropical savannas. In turn, these may be related to regional variation in water availability.

Competition

We predicted the occurrence of competition among the species in our study, and although the nature of our evidence is correlative rather than experimental, the strength of the negative association between the abundances of antilopine wallaroos and eastern grey kangaroos in sympatry is consistent with competition. Interspecific competition has previously been proposed as an explanation for observed patterns of species co-occurrence among large mammalian herbivores (Wegge, Shrestha & Moe, 2006; Young, Palmer & Gadd, 2005). However there is little experimental support for this suggestion due to the difficulties associated with working with these large animals. Although the potential for it to occur has been noted (Dawson, 1995), interspecific competition between large marsupial herbivores has not been recorded. If populations of one or the other of these species are limited by competition, this would conflict with the conclusions of Caughley et al. (1987) that the distribution of large macropods in Australia is most likely to be determined by the response of each species to climate, rather than the outcome of interspecific interactions. In north Queensland, where antilopine wallaroos and eastern grey kangaroos are sympatric over large areas of their range (Strahan, 1995), we found climate to be an important factor influencing eastern grey kangaroos but not antilopine wallaroos. At the same level of modelling, there was no clear evidence suggestive of separation according to habitat structure. The one site where they occurred together in moderate densities was located on basalt soil, which suggests that more productive habitats may support both species, but nutrient-poor areas (the majority of northern Australia) may not. This result further highlights the possible impacts of low availability and spatial heterogeneity of resources in northern Australia on the structure of macropod communities.

Habitat structure

We have shown how broad-scale factors may have important influences on macropod abundance at a landscape scale, but our models suggest that, at smaller scales, aspects of fine habitat structure are also important. It is clear from our results that the antilopine wallaroos' niche in north Queensland differs between bioregions. In the Einasleigh Uplands bioregion, abundance is highest in habitats with less cover (open woodland), and areas with an understorey containing both grass and non-grass species. In the Cape York bioregion, abundance is higher in habitats of increased canopy height and cover (tall woodland – forest). This highlights the intraspecific variation and flexibility of the niche requirements of this species and the way in which consideration of spatial scale greatly influences our perception of species' overall ecology based on parameters we measure. By studying this species across its geographic distribution and at smaller scales we have shown that, in relation to habitat structure, the antilopine wallaroo has a broad ecological niche.

Conservation of herbivores in tropical Australia: implications of climate change

The results of our study have identified many of the key factors influencing the abundance of large macropods across the tropical savannas of northern Australia. This information allows a deeper understanding of how the conservation of these species may be affected under changed conditions. We predict that climate change may have important ecological consequences for these species. Availability of water, structure and composition of habitats, and fire regimes may all be altered. Climate change scenarios for northern Australia not only predict increased temperature and possibly slightly increased annual rainfall but also increased uncertainty of rainfall events and the possibility of longer, harsher dry seasons (Hughes, 2003; Walsh *et al.*, 2001). Even if overall rainfall increases, the availability of water in many areas may decrease as higher temperatures increase rates of evaporation causing (Walsh *et al.*, 2001) water loss in this region (negative water balance). Of the three species we studied, the antilopine wallaroo is most dependent on access to water. Reduced water availability may be exacerbated if rainfall becomes less predictable. As the breeding season of antilopine wallaroos is tightly centred around monsoonal rains (Ritchie, in press), any disturbance

to or reduction of these rainfall events could negatively impact the breeding phenology of this species, leading to possible localised population declines.

Increased temperatures and rainfall in northern Australia will also influence the structure and composition of habitats and the frequency of fire. As we have shown, there are differences between the three macropods in their habitat preference and there is therefore potential for species to be affected in different ways under changing climate and habitat. There are a number of effects on the structure and composition of savanna that changes in climate may have. First, increased temperature and rainfall may result in habitat thickening due to increased numbers/growth of woody plants (Hughes, 2003), and these plants may be favoured by elevated levels of CO₂ (which is thought to favour C3 over C4 plants, and also simply provide more carbon for plants to engineer structural tissue), a number of studies provide evidence that this may be already occurring (Archer, Schimel & Holland, 1995; Bowman, Walsh & Milne, 2001a). Second, under these conditions, rainforest may invade woodlands (Bowman *et al.*, 2001a), leading to a reduction of habitat for large macropods. Third, due to possible increased fuel loads associated with longer, hotter dry seasons, the risk and frequency of fire are expected to increase (Howden *et al.*, 1999). Clearly therefore, under some conditions (such as increasing cover) common wallaroos may be disadvantaged, though this could be counterbalanced by a potential increase in food (woody plants). Likewise, we predict that antilopine wallaroos would be favoured by an increase in fire frequency and severity. What is most evident is that the nature of these changes is likely to be complex and will involve multiple interactive effects between fire regimes, rainfall and habitat structure. Managers will therefore need to be aware of and address this complexity in future conservation plans for species in tropical savannas.

Conclusion

Identifying the factors that limit the distribution and abundance of organisms has a long tradition in ecology. However few studies have explored in detail how intra- and interspecific niche requirements vary geographically and across spatial-scales. Our study demonstrates that the seasonally challenging environment of tropical savannas influences the distribution and abundance of large, sympatric macropods, a biologically, economically and culturally significant group of mammalian herbivores. Our work

identifies key biological and environmental factors affecting the abundance of these species, and suggests ways in which these factors may affect the survival of these species when climate changes. Our study therefore contributes both to an increased general understanding of the global ecology and evolution of large herbivores, and to their management.

Chapter 3

Socio-ecology of the antilopine wallaroo with observations on other sympatric macropods

(In review *Austral Ecology*)

Abstract

The social behaviour of a species influences key ecological traits including diet selection and habitat preference, hence an understanding of social behaviour informs management decisions. Large herbivores show considerable variation in their morphology and socio-ecology; however our ability to make generalisations about this group is limited by our lack of knowledge of the social behaviour of tropical marsupials. Importantly, there is increasing concern that many northern Australian mammal species, including the endemic antilopine wallaroo (*Macropus antilopinus*), are experiencing range declines.

I studied the socio-ecology of five sympatric species of macropod across 50 sites in the tropical savannas of northern Australia between 2002 and 2005. This included three large-bodied species: the antilopine wallaroo, common wallaroo (*M. robustus*), and eastern grey kangaroo (*M. giganteus*); and two medium-sized species, the agile wallaby (*M. agilis*) and whiptail wallaby (*M. parryi*). Here I report on their reproductive patterns, group size and composition and social dynamics, with particular emphasis on the antilopine wallaroo. The antilopine wallaroo was the most gregarious species, and group sizes increased significantly with population density. The eastern grey kangaroo and whiptail wallaby were less gregarious, and the common wallaroo and agile wallaby were essentially solitary. Group size did not differ significantly between seasons for any species. Reproductive patterns differed between the three large-bodied species, with the antilopine wallaroo being the most strongly seasonal in its breeding. There was marked seasonal variation in the associations between sex and size classes of the antilopine wallaroo, which appear to be related to reproduction. Investigation of the links between body size, breeding seasonality and socio-ecology in tropical macropods offers great

potential to develop a more general understanding of the diversity and evolution of the behavioural patterns of large herbivores.

Introduction

The social behaviour of species influences key ecological traits including diet selection and habitat preference (Caughley, 1964; Jarman & Jarman, 1973; Johnson & Bayliss, 1981; Moore, Coulson & Way, 2002): these traits may in turn have important management implications. The macropods (Macropodidae: Marsupialia) are a diverse group of herbivores ranging in body mass from 500 g to over 85 kg (Strahan, 1995). Accompanying this diversity in morphology is pronounced variability in social behaviour (Coulson, 1997; Croft, 1989; Jarman & Coulson, 1989; Johnson, 1983), but few studies have simultaneously explored intraspecific and interspecific variation in behaviour by comparing the socio-ecology of species within communities of sympatric macropods (Croft, 1987; Kaufmann, 1974). Our understanding of macropod social behaviour, and the generalisations that can be made for this group and for large herbivores more broadly, are further limited by the paucity of information available for tropical species, in particular the antilopine wallaroo (*Macropus antilopinus*) and black wallaroo (*M. bernardus*) (Croft, 1987; Press, 1989; Russell *et al.*, 1971). The antilopine wallaroo is the largest macropod endemic to the tropics (Ritchie, in press), is of significant cultural importance to indigenous people (Busby, 1988; Yibarbuk *et al.*, 2001), and is highly valued by the local ecotourism industry. However, there is growing concern that populations of this species have recently declined (Ritchie, in press), which may be representative of a more general decline of mammals in northern Australia (Pardon *et al.*, 2003; Woinarski *et al.*, 2001).

Tropical savannas comprise roughly one quarter of mainland Australia, and differ from temperate regions in having a climate that is characterised by pronounced rainfall seasonality rather than variation in temperature (Ridpath, 1985; Williams *et al.*, 2005). We might predict, therefore, that patterns of reproduction and social behaviour of tropical macropods will be driven by rainfall-related variations in resource availability rather than the temperature-dependent patterns of temperate species. To investigate this hypothesis, between 2002 and 2005 I recorded reproductive seasonality, group size and composition and social dynamics across seasons for five macropod species that occur in areas of sympatry in northern Australia. This included three large-bodied species (25 – 85 kg: the antilopine wallaroo, common wallaroo, *M. robustus* and eastern grey kangaroo, *M. giganteus* (Strahan, 1995); and two medium-sized species (4.8 – 19 kg):

the agile wallaby, *M. agilis* and whiptail wallaby, *M. parryi* (Strahan, 1995). During this period I also studied the macroecology and conservation status of the antilopine wallaroo, and as a result was able to collect more detailed information for the antilopine wallaroo than for the other species.

Having identified some of the gaps in our knowledge regarding the socio-ecology of macropods and that of large herbivores more broadly, I had two major aims: 1. to provide a detailed account of the pattern of reproduction, group size and composition and social dynamics of the antilopine wallaroo across its distribution and between seasons; and 2. to compare the socio-ecology of the five sympatric macropod species.

Methods

Study region and species

I surveyed 50 sites across northern Australia between May 2002 and November 2005, comprising ten in the Kimberley region of Western Australia, eleven in the Northern Territory and 29 in Queensland (Figure 3.1). Three distinct seasons are recognised for this region: the wet season (late December to March/April) when the majority of rain falls, the cool-dry season (late April to September) when there is little rainfall and temperatures are mild, and the hot-dry season (October to late December) when there is little rainfall and temperatures and humidity are highest (see Ridpath, 1985). Vegetation structure and floristics varied locally, but as is typical for this region (Woinarski *et al.*, 2005), consisted predominantly of open woodland/forest dominated by mixed *Eucalyptus* and *Corymbia* spp. and an understorey of native perennial grasses such as black speargrass (*Heteropogon contortus*), fire grasses (*Schizachyrium* spp.), native sorghum (*Sorghum* sp.), and wiregrasses (*Aristida* spp.).

My study area encompassed the entire geographical distribution of the antilopine wallaroo and parts of the northern distributions of the other four species (Strahan, 1995). Another large endemic species, the black wallaroo (*M. bernardus*), could be not included in this study due to its restricted range and the logistical difficulty associated with surveying its habitat (remote sandstone escarpments Strahan, 1995).

Survey design

Across the 50 sites I conducted a total of 424 surveys, each along five km of minor unsealed tracks (2120 km total effort), twice both at dawn (survey period 0530 - 0830) and pre-dusk (survey period 1645 - 1830). Sites in Queensland were surveyed in both the late wet season and late dry season between 2002 and 2005. Sites in Western Australia and the Northern Territory were surveyed in the cool dry season of 2005. Therefore although there were differences in the seasons in which I surveyed regions of the antilopine wallaroo's range, I considered all sites together to give an overall perspective on the antilopine wallaroo's socioecology due to the relatively minor variation in latitude and climate between sites. I acknowledge that small differences (~ few weeks) in the timing of reproduction and social behaviours may exist between sites,

associated with variation in the arrival of the monsoon season between regions. However, I had no a priori reason to expect that the overall patterns would be substantially different.

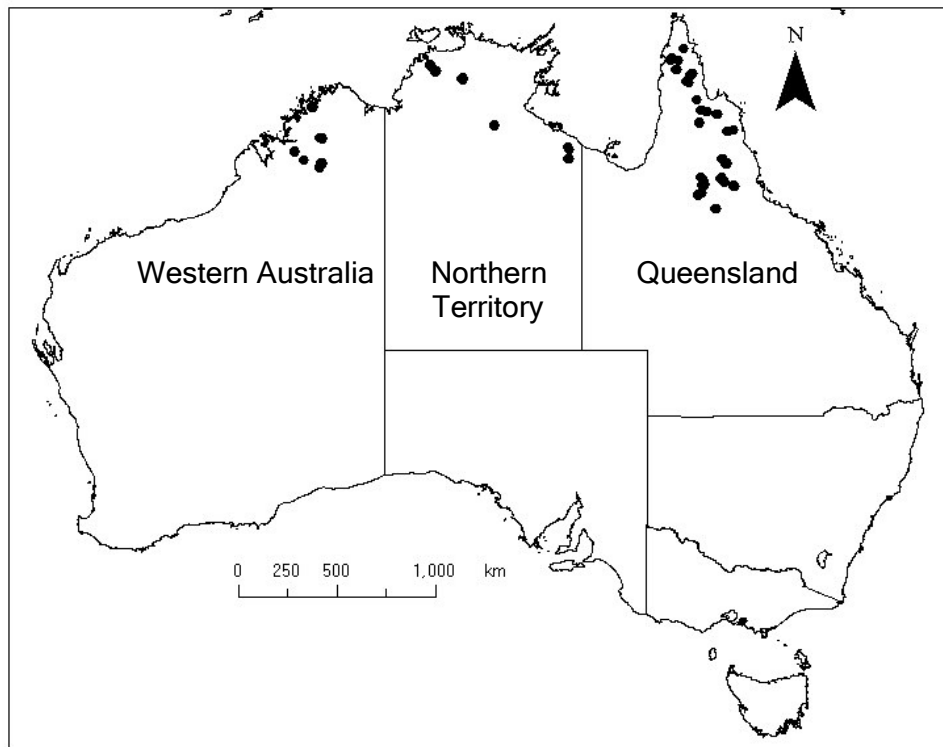


Figure 3.1 Map of study region with study sites marked by solid dots.

For each group encountered, I recorded the perpendicular distance (using a laser range-finder) from the observer to the closest animal(s), group size and sex of all individuals. Groups were classed into three categories, all-female, all-male and mixed. A group was defined as ≥ 1 individuals occurring no more than 50 m apart and within visual contact of each other (Jarman & Southwell, 1986). I counted females with pouch-young or dependent young-at-foot as a single unit (group size of one). Using binoculars or a telescope, I classed individuals into the following categories: subadult (antilopine wallaroo subadults were further divided into male or female, due to pronounced sexual dichromatism), adult female (with or without pouch-young or dependent young-at-foot), and adult male. I divided adult male antilopine wallaroos further into three body-size classes; small males (comparable in height to adult females), medium males (taller than adult females and small males and with moderate muscular development of the chest

and arms), and large males (more pronounced muscular development of the chest and arms than medium males). Classifying individuals according to this method has been used in many previous studies of macropods (e.g. Johnson, 1983; Johnson *et al.*, 1981).

Analysis

I calculated the density of species at sites by strip transects because traditional distance sampling techniques were not possible for some combinations of sites and species due to a lack of sufficient observations (Thomas *et al.*, 1998-2003). To ensure there were no significant differences in sightability between species, I first examined the distances of observations for the total data sets for each species. Using this information, 200 m was found to be the distance beyond which observations became increasingly right-truncated. Therefore, transect widths were set at 400 m wide (200 m to either side of the observer). I estimated species density per square kilometre by dividing the total number of individuals observed by the strip area, averaged over the number of transects surveyed.

For analysis of reproductive patterns, I pooled sites for each species. I calculated the proportion of females with pouch-young by dividing the total number of females observed with pouch-young by the total number of females that I was able to visually assess for the presence of pouch-young (excluding, for example, females that were partly obscured by vegetation). Because it was not possible to visually assess every female, this measure does not include all females in the population. I calculated the proportion of females with young-at-foot by dividing the number of adult females with young by the total number of adult females (young-at-foot were readily visible at all sites).

I calculated both mean and typical group size (the size of groups in which each individual occurred divided by the total population, see Jarman, 1974) for all species to allow comparison with other studies and calculated adult sex ratios of samples of populations by dividing the total number of adult males by the sum total of all adults of both sexes. I calculated the proportion of subadults in relation to adults in each sample by dividing the number of subadults by the sum total of all subadults and adults. For analysis of the seasonal proportions of group types, I pooled data across sites. I counted the frequency with which each sex and size class was found alone, in a group with its

own sex only, in a mixed-sex group or in the company of its own sex. Expected frequencies were calculated by the method of Croft (1987) and tested against observations using contingency table analysis. When significant results were found I used standardised residuals to determine which groupings were responsible for the differences (Everitt, 1977).

Data were pooled in all cases for which I had multiple samples within a season and/or between years at a site. I also pooled data for the cool-dry and hot-dry seasons for the analyses of seasonal differences in mean and typical group size and population structure. Variables were transformed where required according to standard protocols (Zar, 1996). For all species, surveys in which < 10 groups were recorded were excluded from the analyses; hence not all species are covered throughout the Results section. All statistical analyses were performed in JMP 4.0.

Results

Reproductive patterns

Antilopine wallaroos showed a highly seasonal breeding pattern, with significantly more females having pouch-young in the hot-dry season than in the cool-dry and wet seasons (Figure 3.2a; $\chi^2 = 663$, d.f. = 2, $p < 0.001$). Conversely, there were more females with young-at-foot in the wet season than in the dry season (Figure 3.2b; $\chi^2 = 436$, d.f. = 2, $p < 0.001$). In common wallaroos, there were also significantly more females with young-at-foot in the wet season than in the hot-dry season (Figure 3.2b, $\chi^2 = 9.9$, d.f. = 2, $p < 0.05$), but there was no significant difference in the number of females with pouch-young between seasons (Figure 3.2a; $\chi^2 = 5.9$, d.f. = 2, $p > 0.1$). Eastern grey kangaroos differed from the two wallaroo species in showing no significant differences in the seasonal presence of either pouch-young (Figure 3.2a; $\chi^2 = 0.5$, d.f. = 1, $p > 0.25$) or young-at-foot (Figure 3.2b; $\chi^2 = 0.2$, d.f. = 1, $p > 0.5$).

Group sizes

Differences in group sizes between the five macropods were evident, but for all species except whiptail wallabies, groups of one were the most commonly observed (Figure 3.3). Agile wallabies and common wallaroos were the most solitary species whereas whiptail wallabies occurred most commonly in pairs. Eastern grey kangaroos were often observed alone, but were also frequently found in groups of two to four. Antilopine wallaroos were the most gregarious species, occurring in groups of three to five more frequently than the other species; 8% of groups contained seven or more individuals. These differences were reflected in the mean and typical group sizes of each species (Figure 3.4). On average, antilopine wallaroo groups were significantly larger than agile wallaby and common wallaroo groups (Figure 3.4a; $F_{4, 54} = 15.9$, $p < 0.0001$), and antilopine wallaroo individuals occurred in significantly larger groups than agile wallabies, common wallaroos or eastern grey kangaroos (Figure 3.4b; $F_{4, 54} = 17.0$, $p < 0.0001$).

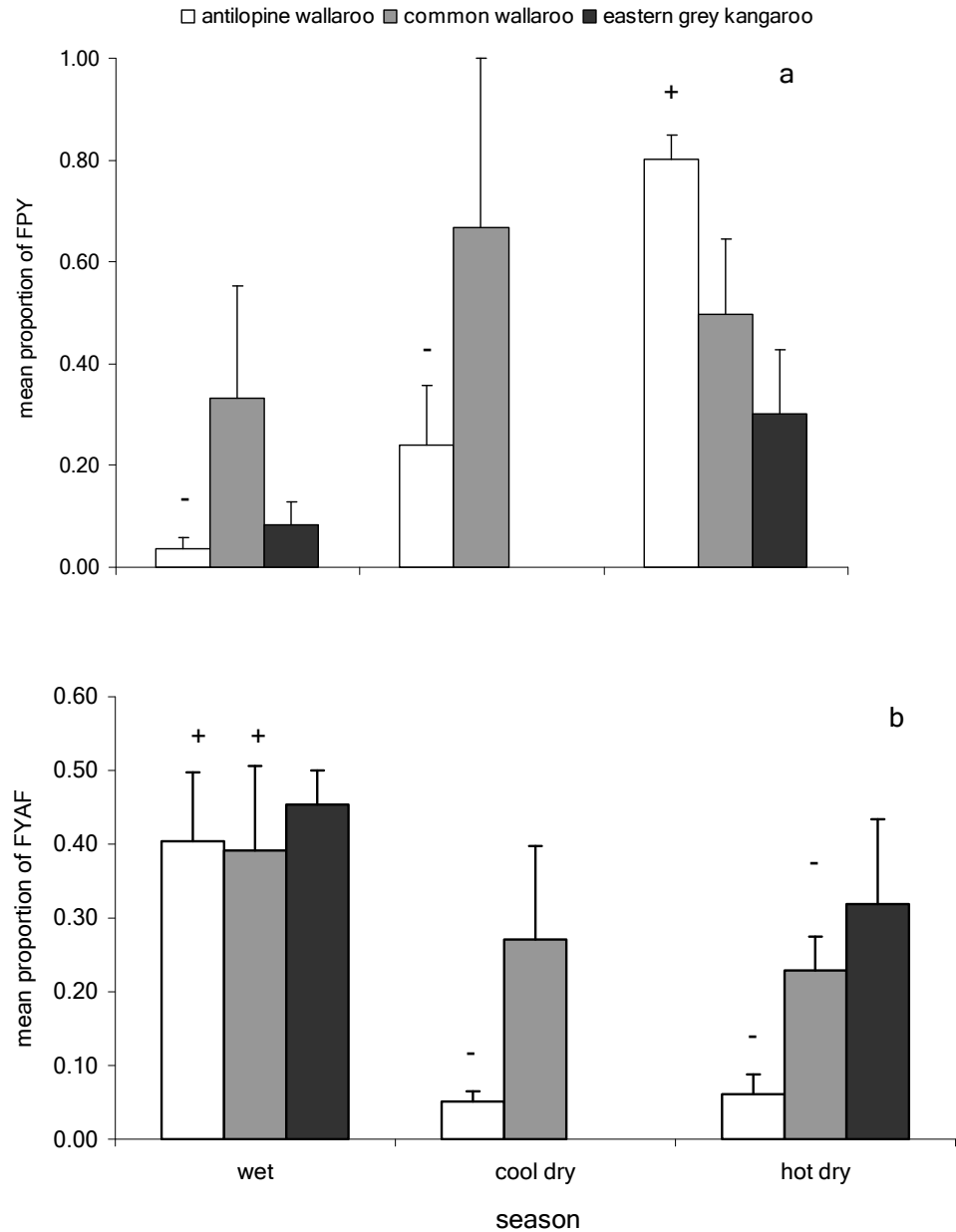


Figure 3.2 Seasonal proportions of adult females with pouch-young (FPY) (a) and young-at-foot (FYAF) (b) for antilopine wallaroos, *Macropus antilopinus*, (N = 19 sites), common wallaroos, *M. robustus*, (N = 10 sites) and eastern grey kangaroos, *M. giganteus*, (N = 3 sites) in northern Australia. Bars with standardised residuals greater or less than 1.96 are marked with + and – respectively.

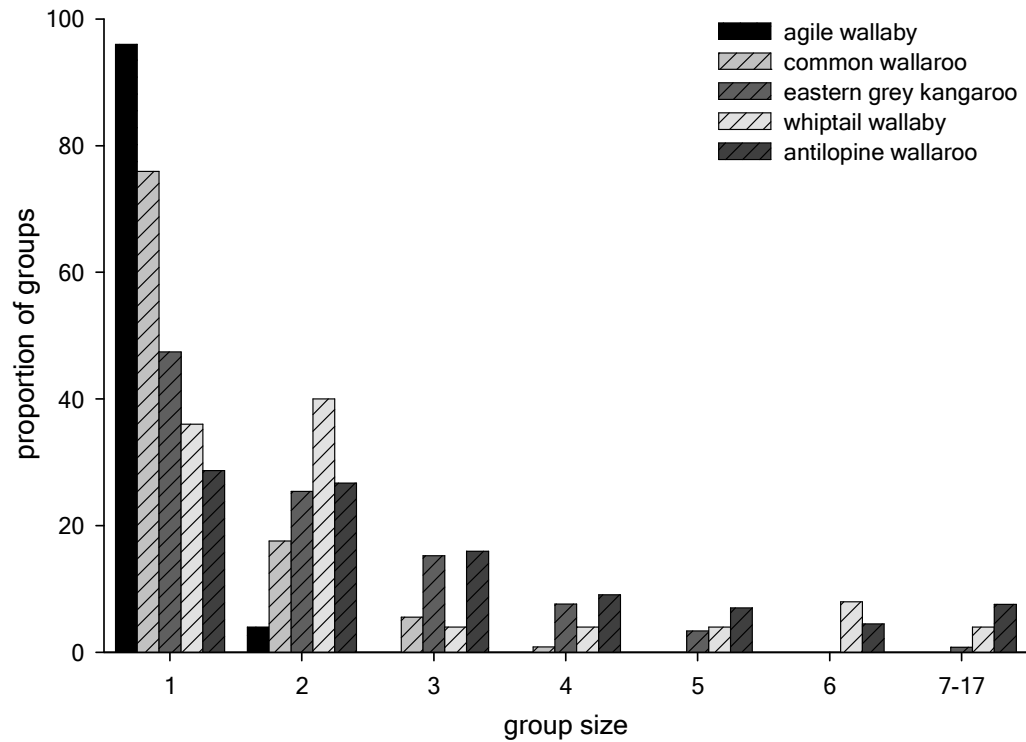


Figure 3.3 Group sizes for sympatric macropods in northern Australia: antilopine wallaroo, *Macropus antilopinus*, (N groups = 1084), common wallaroo, *M. robustus*, (N groups = 341), whiptail wallaby, *M. parryi*, (N groups = 25), agile wallaby, *M. agilis*, (N groups = 23), eastern grey kangaroo, *M. giganteus*, (N groups = 188).

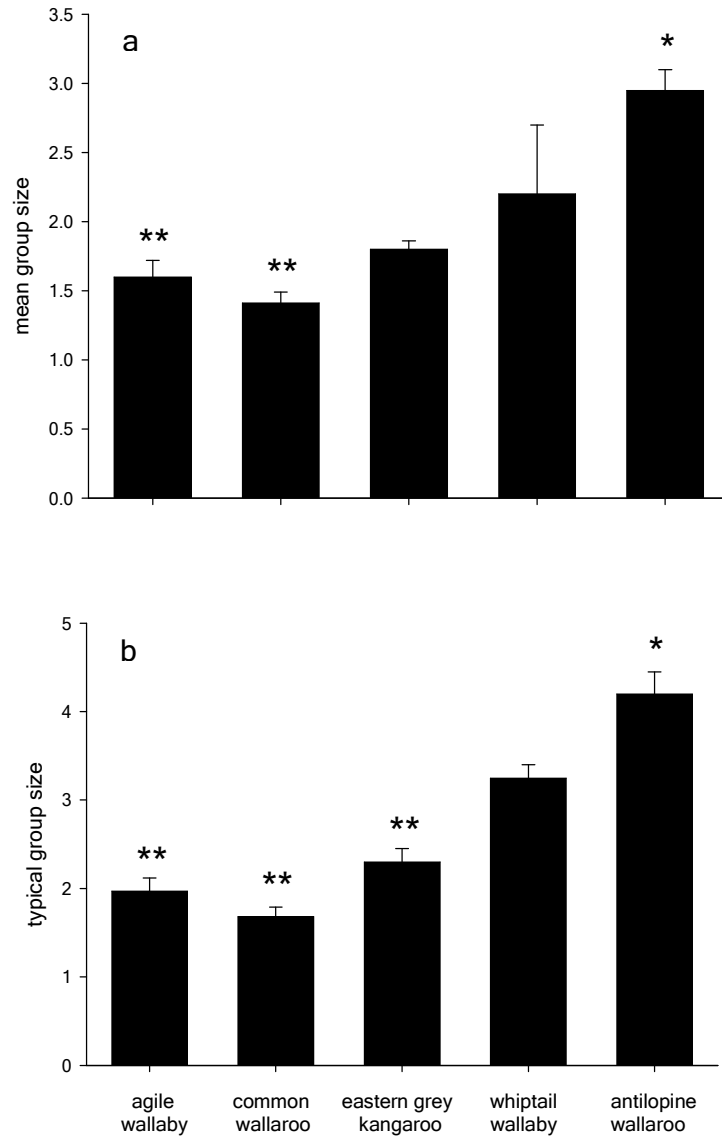


Figure 3.4 Mean \pm S.E. of (a) mean and (b) typical group size for sympatric macropods in northern Australia. Antilopine wallaroo, *Macropus antilopinus*, (N sites = 32), common wallaroo, *M. robustus*, (N sites = 16), whiptail wallaby, *M. parryi*, (N sites = 2), agile wallaby, *M. agilis*, (N sites = 6), eastern grey kangaroo, *M. giganteus*, (N sites = 4). Bars marked with asterisks indicate significant differences between species using Tukey's post-hoc tests.

Antilopine wallaroo group sizes varied little between seasons, with groups of one and two being most common year-round, except that there was a large number of groups of two in the cool-dry season (Figure 3.5). Groups of three to nine also occurred regularly, and I recorded groups of up to 17 individuals. There was geographical variation in seasonal group sizes of antilopine wallaroos (Figure 3.6). At Rocky Springs station (Figure 3.6a-c), which supports relatively high densities of antilopine wallaroos, group size patterns were similar to those observed for antilopine wallaroos overall (Figure 3.5). However, at Undara National Park (Figure 3.6d-f), which supports moderate densities of antilopine wallaroos, group sizes of three and nine occurred frequently in the cool-dry season, and overall I observed fewer large groups (Figure 3.5).

There was a significant correlation between both mean (Figure 3.7a; $F_{1,22} = 15.1$, $p = 0.0008$, $r^2 = 0.41$) and typical group sizes (Figure 3.7b; $F_{1,22} = 15.4$, $p = 0.0007$, $r^2 = 0.41$) and the population density of antilopine wallaroos. There was no significant relationship between mean ($F_{1,11} = 0.2$, $p = 0.7$) and typical ($F_{1,11} = 0.06$, $p = 0.8$) group sizes and the density of common wallaroos. There was no significant seasonal variation in either the mean or typical group sizes of antilopine wallaroos, common wallaroos or agile wallabies between seasons (Table 3.1).

Demography

There was a significant positive correlation between population density and the proportion of adult males in antilopine wallaroo populations (Table 3.2; $r = 0.58$, $p = 0.003$), but not for common wallaroos (Table 3.3; $r = 0.23$, $p = 0.4$) or eastern grey kangaroos (Table 3.4; $r = -0.46$, $p = 0.4$). The proportion of males in the adult population was significantly lower in the dry season than in the wet season for both antilopine wallaroos (Table 3.2; $t = 2.4$, d.f. = 22, $p = 0.02$) and common wallaroos (Table 3.3; $t = 2.2$, d.f. = 12, $p = 0.04$). This trend was reversed for eastern grey kangaroos, but was not significant (Table 3.4; $t = -2.8$, d.f. = 3, $p = 0.06$). There was a significantly higher proportion of subadults relative to adults in the dry season than in the wet season for antilopine wallaroos (Table 3.2; $t = -4.6$, d.f. = 22, $p = 0.0001$) and common wallaroos (Table 3.3; $t = -2.4$, d.f. = 12, $p = 0.03$), but not eastern grey kangaroos (Table 3.4; $t = -3.0$, d.f. = 3, $p = 0.056$). On average, small males were the

least common of the male antilopine wallaroo size classes; large males the most common (Table 3.2).

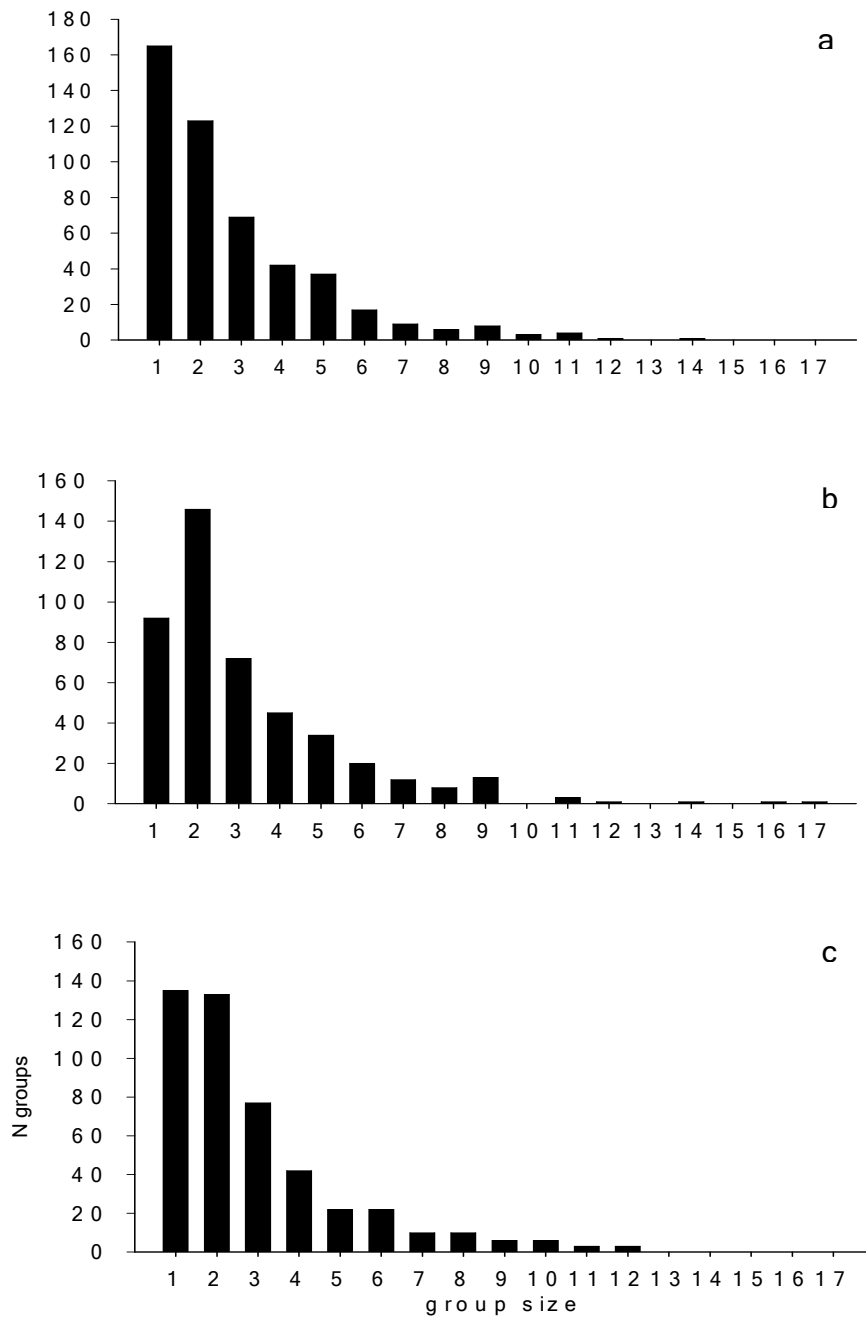


Figure 3.5 Seasonal distribution of antilopine wallaroo (*Macropus antilopinus*) group sizes. a = wet season (January - May), b = cool-dry season (June - September) and c = hot-dry season (November - December).

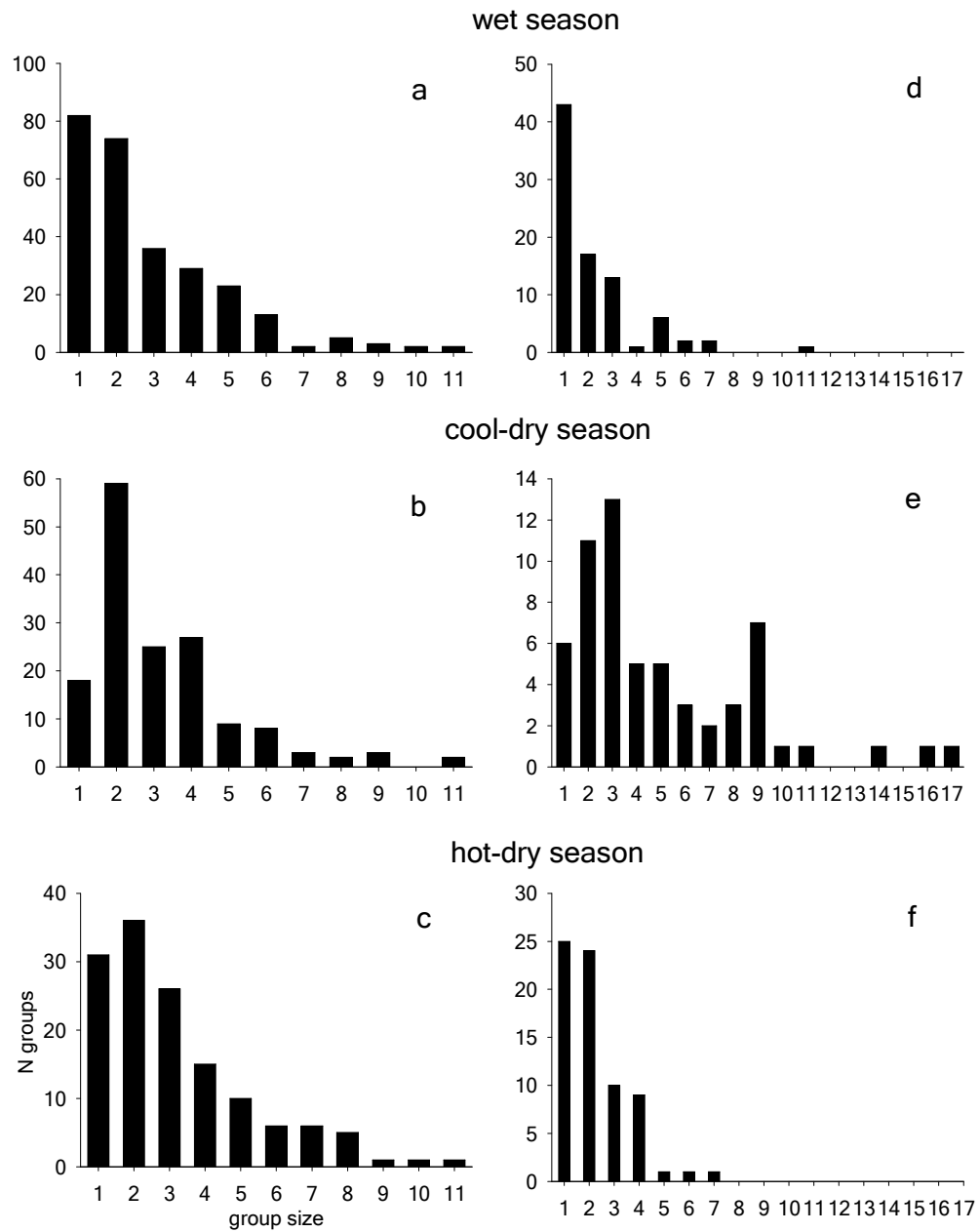


Figure 3.6 Seasonal distribution of antilpine wallaroo (*Macropus antilopinus*) group sizes at Rocky Springs station (a-c) and Undara National Park (d-f), in north Queensland, Australia.

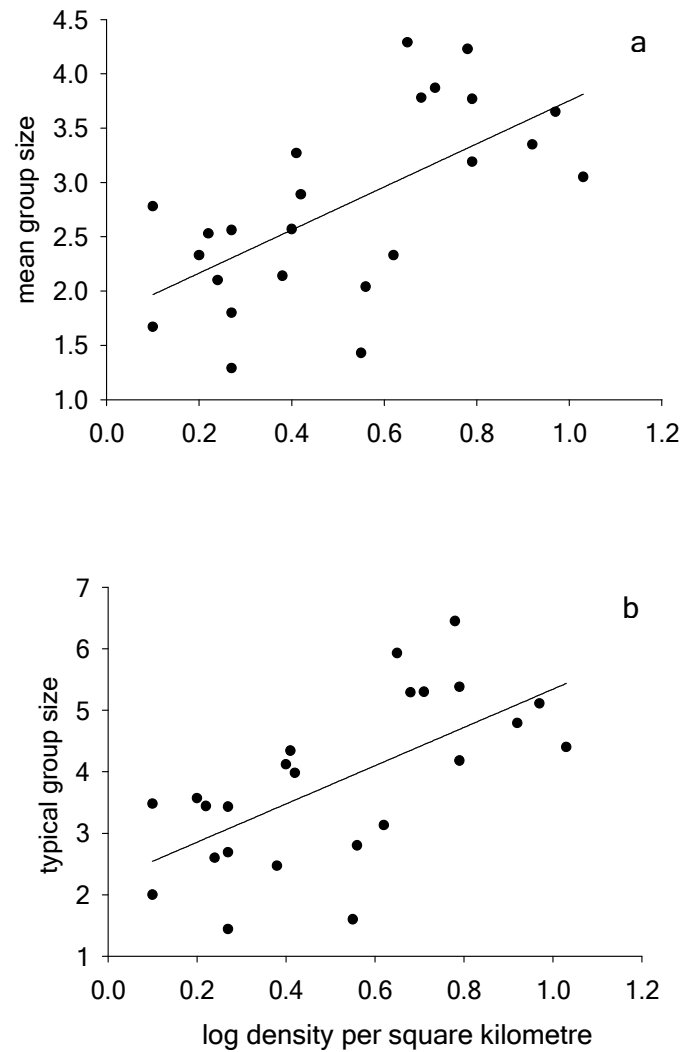


Figure 3.7 Relationship between log density (km²) and mean (a) and typical group size (b) in the antilopine wallaroo (*Macropus antilopinus*) across Australia (N = 24 sites).

Table 3.1 Summary statistics of seasonal mean and typical group sizes of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*) and agile wallabies (*M. agilis*) in northern Australia.

species	group	wet season	dry season	<i>t</i>-test	<i>d.f.</i>	<i>p</i>
antilopine wallaroo	mean	2.92 (0.4)	2.96 (0.3)	-0.1	17	0.9
	typical	4.19 (0.5)	4.04 (0.4)	0.2	17	0.8
common wallaroo	mean	1.48 (0.1)	1.33 (0.1)	1.2	20	0.3
	typical	1.71 (0.2)	1.58 (0.1)	0.7	20	0.5
agile wallaby	mean	1.30 (0.0)	1.72 (0.1)	-2.2	6	0.07
	typical	1.53 (0.1)	2.26 (0.3)	-1.93	6	0.09

Table 3.2 Summary of seasonal population structure for the antilopine wallaroo in northern Australia. Queensland (Qld), Northern Territory (N.T.), Western Australia (W.A.). National Park is abbreviated to N.P, conservation reserves are indicated by (C). AM:AF = proportion of adult males in the population, SA:A proportion of subadults relative to adults, SM = small male, MM = medium-sized male, LM = large male.

season	site	density	AM:AF	SA:A	SM	MM	LM	N
wet	Ironhurst (Qld)	6.25	0.43	0.00	0.07	0.53	0.40	37
	Lornevale 1 (Qld)	2.63	0.48	0.00	0.07	0.64	0.29	40
	Lornevale 2 (Qld)	1.56	0.42	0.00	0.15	0.31	0.54	36
	Merluna (Qld)	9.81	0.49	0.00	0.17	0.30	0.52	143
	Rocky Springs (Qld)	8.38	0.51	0.05	0.31	0.29	0.40	1016
	Undara N.P. (C) (Qld)	3.17	0.46	0.02	0.07	0.50	0.43	227
	mean (\pm s.e.)	5.30 (1.37)	0.47 (0.01)	0.01 (0.01)	0.14 (0.04)	0.43 (0.06)	0.43 (0.04)	
cool-dry	Chillagoe (Qld)	1.60	0.23	0.08				98
	Mt.Elizabeth 1 (W.A.)	7.38	0.25	0.28	0.43	0.36	0.21	91
	Mt.Elizabeth 2 (W.A.)	5.13	0.43	0.18	0.28	0.33	0.39	52
	Mt.Ringwood (N.T.)	1.5	0.33	0.22	0.29	0.29	0.43	60
	Nutwood (N.T.)	12.88	0.58	0.18	0.20	0.28	0.52	183
	Peppan (C) (Qld)	4.13	0.50	0.08	0.00	0.45	0.55	50
	Rocky Springs (Qld)	8.38	0.42	0.25	0.42	0.21	0.37	505
	Undara N.P. (C) (Qld)	3.17	0.42	0.13	0.19	0.42	0.39	335
	mean (\pm s.e.)	5.52 (1.37)	0.40 (0.04)	0.18 (0.03)	0.26 (0.06)	0.33 (0.03)	0.41 (0.04)	
hot-dry	How Long (Qld)	0.88	0.22	0.31				59
	Ironhurst (Qld)	6.25	0.40	0.09	0.26	0.37	0.37	70
	Lornevale 1 (Qld)	2.63	0.31	0.10				29
	Lornevale 2 (Qld)	1.56	0.27	0.13	0.67	0.06	0.28	93
	Mungkan Kandju N.P. (C) (Qld)	0.75	0.26	0.00				38
	Merluna (Qld)	9.81	0.86	0.08	0.00	0.16	0.84	26
	Mistletoe (Qld)	0.67	0.36	0.04	0.45	0.05	0.50	85
	Rocky Springs (Qld)	8.38	0.46	0.12	0.26	0.33	0.42	507
	Springvalley (Qld)	5.17	0.29	0.19	0.38	0.15	0.46	63
	Sudley (Qld)	1.44	0.42	0.03	0.00	0.69	0.31	42
	Undara N.P. (C) (Qld)	3.17	0.36	0.07	0.48	0.00	0.52	147
	mean (\pm s.e.)	3.70 (0.98)	0.38 (0.05)	0.11 (0.03)	0.31 (0.08)	0.22 (0.08)	0.46 (0.06)	

Table 3.3 Summary of seasonal population structure for the common wallaroo (*Macropus robustus*). Queensland (Qld), Northern Territory (N.T.). National Park is abbreviated to N.P, conservation reserves are indicated by (C). AM:AF = proportion of adult males in the population, SA:A proportion of subadults relative to adults.

season	site	density	AM:AF	SA:A	N
wet	How Long (Qld)	2.75	0.45	0.00	11
	Ironhurst (Qld)	3.06	0.50	0.00	22
	Kinrara (Qld)	2.00	0.50	0.09	11
	Lornevale 1 (Qld)	2.06	0.42	0.00	12
	Undara N.P. (C) (Qld)	0.48	0.48	0.00	30
	mean (\pm s.e.)	2.07 (0.45)	0.47 (0.02)	0.02 (0.02)	
cool-dry	Calvert Hills (N.T.)	3.25	0.23	0.03	29
	Chillagoe (Qld)	1.58	0.24	0.07	41
	Undara N.P. (C) (Qld)	0.48	0.57	0.00	17
	mean (\pm s.e.)	1.77 (0.81)	0.35 (0.11)	0.03 (0.02)	
hot-dry	Chillagoe (Qld)	1.58	0.47	0.00	15
	How Long (Qld)	2.75	0.40	0.06	17
	Ironhurst (Qld)	3.06	0.57	0.04	85
	Kinrara (Qld)	2.00	0.32	0.14	22
	Mistletoe (Qld)	1.67	0.38	0.02	55
	Rocky Springs (Qld)	0.19	0.31	0.13	16
	Undara N.P. (C) (Qld)	0.48	0.30	0.06	33
	mean (\pm s.e.)	1.68 (0.40)	0.39 (0.04)	0.06 (0.02)	

Table 3.4 Summary of seasonal population structure for the eastern grey kangaroo (*Macropus giganteus*) in north Queensland. National Park is abbreviated to N.P, conservation reserves are indicated by (C). AM:AF = proportion of adult males in the population, SA:A proportion of subadults relative to adults.

season	site	density	AM:AF	SA:A	N
wet	Kinrara	5.81	0.16	0.03	33
	Undara N.P. (C)	0.94	0.18	0.01	62
	mean (± s.e.)	3.38 (2.44)	0.17 (0.01)	0.02 (0.01)	
hot-dry	Blackbraes N.P. (C)	1.81	0.42	0.08	48
	Kinrara	5.81	0.24	0.10	62
	Undara N.P. (C)	0.94	0.38	0.05	41
	mean (± s.e.)	2.85 (1.50)	0.35 (0.05)	0.08 (0.01)	

Group dynamics

The composition of antilopine wallaroo groups changed seasonally (Figure 3.8). In the wet season there were significantly more mixed-sex groups than expected and correspondingly fewer all-male and all-female groups. In the cool-dry season there were significantly fewer mixed-sex groups and more all-female groups. In the hot-dry season, significantly fewer mixed-sex groups and more all-female and all-male groups occurred.

There was considerable variation in the seasonal grouping patterns of antilopine wallaroo sex and size classes (Table 3.5). During the wet season (February), large and medium-sized males occurred in fewer single-sex groups, large males were found alone and medium-sized males in more mixed-sex groups than expected. Females occurred in more single-sex groups and less often in mixed-sex groups than expected over the same period. Females with young-at-foot were never found alone. Small and medium-sized males and females without young-at-foot occurred in the company of their own sex more than expected, whereas large males and females showed the reverse trend.

Towards the end of the wet season (March), females with young-at-foot occurred less frequently in mixed-sex groups and more often alone, and females without young-at-foot occurred in single-sex groups more often and were found alone less than expected. Small-males occurred more often in mixed-sex groups. Overall the pattern of grouping was similar to that present in February except that large males were found more often with their own sex.

In the cool-dry season (July – September; Table 3.5) large males occurred alone more often, and both large and medium-sized males occurred less often, in mixed-sex groups than expected. Females occurred more often in mixed-sex groups, and females with young-at-foot were also often found alone. Small males occurred more often in mixed-sex groups. In July subadult males occurred more often in mixed-sex groups whereas subadult females were more often in single-sex groups. In September subadult males occurred less in mixed-sex groups and more often in single-sex-groups. Grouping patterns did not differ from those expected in the hot-dry season (Table 3.5).

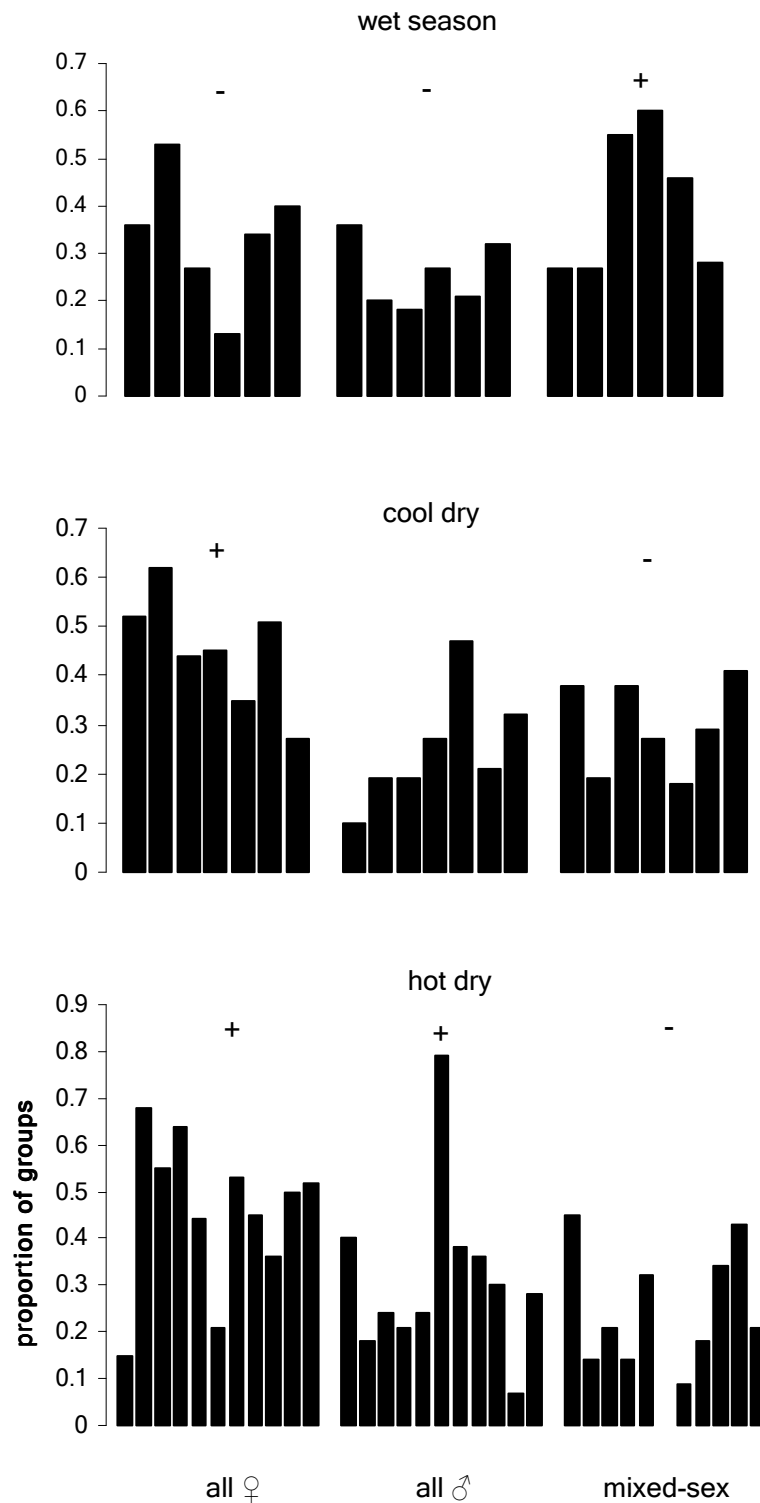


Figure 3.8 Seasonal variation in antilopine wallaroo (*Macropus antilopinus*) group composition across Australia (N = 16 sites). Each bar represents a specific location, noting that not all sites are represented in all seasons. Groupings of bars with standardised residuals greater or less than 1.96 are marked with + and – respectively.

Table 3.5 Seasonal grouping patterns of antilopine wallaroo (*Macropus antilopinus*) population classes at Rocky Springs station in north Queensland, Australia. SM = small male, MM = medium-sized male, LM = large male, AF+PY = adult females with or without pouch-young, FYAF = adult females with dependent young-at-foot, SAM = subadult male, SAF = subadult females. Cells in bold (+ or -) indicate combinations with standardised residuals greater or less than 1.96.

season	group type	SM	MM	LM	AF+PY	FYAF	SAM	SAF	N groups	N	X ²	p
wet February 2004	alone	6.7	12.5	+ 19.0	5.9	- 0.0	33.3		106	271	50.7	<0.001
	single-sex	20.0	- 0.0	- 9.5	+ 27.5	+ 32.9	0.0					
	mixed-sex	73.3	+ 87.5	71.4	- 66.7	- 67.1	66.7					
	with own sex	+ 86.7	+ 72.9	- 58.7	+ 78.4	- 47.4	33.3					
March 2004	alone	- 0.0	4.2	11.8	- 4.9	+ 36.5			71	184	52.3	<0.001
	single-sex	24.2	25.0	26.5	+ 31.7	- 7.7						
	mixed-sex	+ 75.8	70.8	61.8	63.4	- 55.8						
	with own sex	+ 78.8	+ 79.2	+ 70.6	+ 78.0	- 25.0						
cool-dry July 2004	alone	2.7	9.5	+ 8.8	- 0.0	+ 42.9	0.0	0.0	90	290	94.9	<0.001
	single-sex	21.6	38.1	35.3	29.6	- 0.0	- 0.0	+ 51.3				
	mixed-sex	75.7	- 52.4	- 55.9	70.4	57.1	+ 100	- 48.7				
	with own sex	- 67.6	76.2	+ 82.4	+ 81.7	- 42.9	- 29.7	+ 100				
September 2004	alone	0.0	8.3	+ 18.2	3.5	11.1	0.0		62	194	36.1	<0.005
	single-sex	- 23.1	50.0	54.5	41.2	- 11.1	+ 65.0					
	mixed-sex	+ 76.9	41.7	- 27.3	+ 55.3	+ 77.8	- 35.0					
	with own sex	+ 88.5	75.0	- 72.7	+ 90.6	- 55.6	- 62.5					
hot-dry November 2004	alone	0.0	6.7	22.2	5.7	27.8	0.0	25.0	40	114	16.0	NS
	single-sex	42.9	33.3	48.1	37.1	33.3	0.0	50.0				
	mixed-sex	57.1	60.0	29.6	57.1	38.9	100	25.0				
	with own sex	78.6	86.7	74.1	88.6	66.7	100	75.0				
wet January 2005	alone	0.0	5.1	11.1	- 1.5	+ 16.0	0.0	5.6	88	332	60.7	<0.001
	single-sex	- 2.7	15.4	11.1	20.9	14.8	+ 52.8	11.1				
	mixed-sex	+ 97.3	79.5	77.8	77.6	- 69.1	- 47.2	83.3				
	with own sex	+ 91.9	82.1	- 74.1	+ 89.6	- 72.8	+ 94.4	83.3				
N total		177	159	234	394	243	117	61	457	1385		

In the early wet season of 2005 (January, Table 3.5) large males occurred less with their own sex than expected. Females with young-at-foot occurred less with their own sex and in mixed-sex groups and were more often found alone, whereas females without young-at-foot occurred more often with their own sex and were less often alone. Subadult males occurred more often with their own sex and in single-sex groups and less in mixed-sex groups. Small males occurred more often in mixed-sex groups and with their own sex.

Discussion

My study provides the first broad-scale comparison of the socio-ecology of five macropod species that occur in areas of sympatry in northern Australia, a group that has been little studied in this region (Braithwaite *et al.*, 1985). This enables comparisons to be made between the social behaviour of macropods in the tropics and that of macropods in temperate Australia (e.g. Jarman and Coulson 1989; Croft (1989) and, more broadly, with other large-bodied mammalian herbivores, such as ungulates (Jarman, 1974). I found a significant positive correlation between mean and typical group size (a measure of gregariousness) and density in antilopine wallaroos, but not in common wallaroos, a similar-sized species. I detected no differences in the mean or typical group size between seasons for any species.

Overall, the antilopine wallaroo was the most gregarious of the larger species; this finding concurs with the limited previous studies of this species (Croft, 1982; Croft, 1987; Russell *et al.*, 1971). The common wallaroo and agile wallaroo were essentially solitary, as was also found by Croft (1987) and Johnson (1980). The whiptail wallaby and eastern grey kangaroo were both more gregarious than the common wallaroo and agile wallaby, findings consistent with those of another comparative study by Kaufmann (1974), but less gregarious than the antilopine wallaroo.

Reproductive patterns

I detected seasonal variation in reproductive patterns between species; the antilopine wallaroo was the most seasonal in its breeding while the eastern grey kangaroo and common wallaroo were less seasonal. In the antilopine wallaroo, females carried pouch-young over the dry season and young vacated the pouch in the wet season. Based on a captive study of antilopine wallaroo female reproductive cycles (gestation 34 days, pouch life 270 days, Poole *et al.*, 1987), and without having directly aged pouch-young, I infer that most young are born in the mid to late wet season (February to March). This agrees with the conclusion of Russell and Richardson (1971) but not that of Croft (1987). I detected a significant seasonal trend of more subadult antilopine wallaroos and common wallaroos being present in the population during the dry than the wet season. This may represent the recruitment of young from the previous

year into this population class for both species. In support of my hypothesis regarding the antilopine wallaroo mating period, I frequently observed social behaviour associated with mating in February and March, including copulations, displays of male aggression and fighting, and male mate-guarding of females (Ritchie, unpublished). The adaptive significance of this reproductive strategy is probably that females carry young over the extended dry season, when food resources are depleted, and young then exit the pouch in the following wet season (period of peak lactation), when resources are replenished (Ridpath, 1985). This may be optimal for offspring survival, and may buffer females against the high energetic demands of peak lactation (Merchant, 1989).

A key factor likely to have shaped the evolution of macropod reproductive strategies, and hence potentially influencing social dynamics, is embryonic diapause. Embryonic diapause occurs in many macropods, and allows females to resume the development of fertilised embryos without the delay of mating and early gestation following the exit of the pouch by an older sibling or through the loss of a young during periods of un-favourable environmental conditions, typically drought (Tyndale-Biscoe & Renfree, 1987). The death or loss of one young removes the inhibition of diapause, and the previously fertilised embryo is born and enters the pouch. In cases where poor environmental conditions continue, this young may also be lost and females may enter anoestrus until favourable environmental conditions return. This reproductive pattern is commonly observed in two species closely related to the antilopine wallaroo, (red kangaroo and common wallaroo), and is thought to be an adaptation to the more seasonally unpredictable habitats they occupy. It remains unclear whether antilopine wallaroos display this trait, but anecdotal evidence (the timing of the reproductive cycle) suggests that they do not (Poole *et al.*, 1987). Their lack of embryonic diapause, if confirmed, may explain at least in part why their breeding is so much more seasonal than that of many other macropods. In the highly seasonal tropical savannas, selection may favour reproduction that is closely tied to the arrival of the monsoon, therefore ensuring an adequate supply of resources for both mothers and young. Interestingly, this explanation for reproductive seasonality of the tropical antilopine wallaroo could apply equally to the observed pattern of seasonal reproduction in the temperate western grey kangaroo (*M. fuliginosus*), a species known to lack embryonic diapause (Tyndale-Biscoe, 2005). My results suggest some seasonality of breeding in the common wallaroo, but this species may breed less seasonally than antilopine wallaroos because it

does show embryonic diapause (Tyndale-Biscoe *et al.*, 1987). This may allow common wallaroos to take advantage of opportunities to breed following aseasonal rain (dry-season storms) resulting in increased local food resources. Likewise, agile wallabies, which are also sympatric with antilopine wallaroos have embryonic diapause and show a less seasonal pattern of reproduction (Bolton *et al.*, 1982). The relationship between diapause and breeding seasonality clearly warrants further investigation and establishing whether or not antilopine wallaroos have embryonic diapause would aid our understanding of the evolution of reproductive strategies in macropods, and in turn the social and mating systems of large mammals.

Why are some species social?

In his study of three tropically-occurring macropods, Croft (1987) wondered why all three species were not gregarious. The results of my study also raise the question as to why three species (antilopine wallaroos, eastern grey kangaroos and whiptail wallabies) occurred in groups, and two others (common wallaroos and agile wallabies) were essentially solitary. Croft attempted to explain the patterns he observed in relation to the risk of predation from the dingo, a known predator of macropods (Jarman & Wright, 1993; Robertshaw & Harden, 1986). He argued that the common wallaroo, which occurs in steeper and rockier habitats, may be somewhat protected from dingoes because it may be more difficult for them to launch an attack in this habitat; that antilopine wallaroos may rely on fast, co-ordinated scattering in more flat, open habitats; and that agile wallabies, being smaller in size, may use available shrubby cover for protection. In my study region, where dingoes were frequently observed (Ritchie, unpublished), common wallaroos and antilopine wallaroos frequently occurred in open savannah woodland, with relatively little topographic relief or rockiness. Thus common wallaroos did not have the advantage of steep, rocky habitats in these areas as suggested by Croft. Clearly the proximate and ultimate reasons underlying grouping in macropods and its relationship with predator avoidance require further investigation.

Demography

Across populations of antilopine wallaroos, I detected a significant positive correlation between the proportion of adult males and density of populations; I did not find this relationship for either common wallaroos or eastern grey kangaroos. This finding at first appears counter-intuitive, as one would assume that the number of adult females, rather than of adult males, would be the best predictor of a population's potential for increase. This result also suggests that in low-density populations, males may be disadvantaged in comparison with females, possibly related to an environmental factor(s). Importantly, biases in adult sex ratios may result in sex-ratio biases of offspring in favour of the rarer sex within populations through compensatory mechanisms (Hardy, 2002), and this requires further study.

Group dynamics

The seasonal grouping pattern of antilopine wallaroos was relatively consistent between sites. In the wet season there were significantly more mixed-sex groups than single-sex groups, probably explained by the aggregation of sexes associated with the mating period. Within the wet season, grouping patterns varied according to sex and size-class. All the male size-classes were found in high frequency in mixed-sex groups, with small and medium-sized males occurring in single-sex groups significantly less than expected. Large males were also found alone more often than expected, which is consistent with Croft (1982) but not Croft (1987). In the latter study, he found that medium males were most often found alone, illustrating the variability of antilopine wallaroo social behaviour. In my study, it is possible that large males were often found alone because they were moving between groups in order to increase their encounters with females in oestrus, as has been suggested in other large macropods (Johnson, 1983; Southwell, 1984; Taylor, 1983). This raises the possibility that reproductive tactics of males differed according to body size and/or social rank. Small- and medium-sized males may be more likely than large males to attempt to acquire mating opportunities by staying longer within groups containing females, rather than roaming between groups and thereby potentially increasing the likelihood of conflict with large males. It is often suggested that male reproductive success in kangaroos increases with body size (e.g. Croft, 1981a, b; Grant, 1973) but to date this has not been confirmed using genetic

techniques. Females were typically not found alone in the wet season, a result also found by Croft (1987), but in January females with young-at-foot were found alone more than expected, as in western grey kangaroos (Johnson, 1983). Johnson (1987) suggested that this may be a tactic to reduce the potential for small young to become separated from their mothers, and hence vulnerable to predation, in large groups.

In both the cool-dry and hot-dry seasons there were fewer mixed-sex groups of antilopine wallaroos than expected. Correspondingly there were significantly more all-female groups in the cool-dry season, and significantly more of both all-female and all-male-groups in the hot-dry season. Large males and medium-sized males occurred less often in mixed-sex groups, and large males were found more often alone or in the company of their own sex. Presumably as mating opportunities ceased, males left females to forage alone, or sought interaction with other males, such as the establishment of a male dominance hierarchy, a commonly observed seasonal behavioural pattern in many mammals (Croft, 1985; Pelletier & Festa-Bianchet, 2006).

In the dry season antilopine wallaroo females with pouch-young were found more often in mixed-sex groups with small males. This observation suggests possible behavioural compatibility/tolerance between these two sex and size classes (e.g. foraging activity related to equality in body size (see Illius & Gordon, 1987; Ruckstuhl & Kokko, 2002a), and/or that small males may join females because they are too small to join all-male groups, where they may be physically threatened by larger males. Females with young-at-foot often occurred alone in July, perhaps for reasons discussed previously, but were found in mixed-sex groups more often in September, possibly as the risk of losing young in large groups decreased with the age and experience of young. A particularly interesting result is that subadult males occurred in mixed-sex groups more often in July, probably with their mothers, but in September subadult males were more often found in single-sex groups, which may be indicative of dispersal from their mothers and natal range. Continued behavioural and genetic investigation will help to elucidate significance of the patterns observed.

My study compares the socio-ecology of macropods in the highly seasonal environment of northern Australia's tropical savannas, and highlights both inter- and intraspecific seasonal behavioural plasticity. Further work is required to elucidate the factors that have influenced the evolution of differences in the patterns of reproduction

and social behaviour observed. In particular, the examination of the importance of body-size and breeding seasonality, and their behavioural consequences in the family Macropodidae, may offer insight into other mammalian groups and behavioural phenomena including sexual segregation.

Chapter 4

Sexual segregation in the antilopine wallaroo

(In review *Oecologia*; co-authored with Dr. Jennifer Martin, Peter Fossan & Professor Christopher Johnson)

Abstract

Sexual segregation occurs widely among sexually size-dimorphic, seasonally breeding and gregarious species. In mammals, sexual segregation has been studied extensively in temperate ungulates, but we know comparatively little about its prevalence or pattern in other groups, in particular marsupials. The family Macropodidae is a diverse group that is ecologically analogous to the ungulates in many respects. Macropods are most diverse in the tropics, where rainfall is highly seasonal and strongly influences resource availability. In this region therefore, we would predict that some macropod species breed seasonally. In contrast, seasonal temperature variation is considered a primary driver of resource availability and of female reproductive cycles in many temperate mammals.

We present a quantitative, multi-season study of a large tropical marsupial, the antilopine wallaroo (*Macropus antilopinus*). We recorded reproductive biology, group composition and group dynamics, and measured the degree of sexual segregation in a population of antilopine wallaroos in north Queensland, Australia. Antilopine wallaroo mating was highly synchronous (February to March). Groups aggregated and were predominantly mixed during the wet season (mating period), and progressively shifted to single-sex groups during the dry season. Sexual segregation peaked in the hot dry season due to a high proportion of all-male groups, which may be consistent with the establishment of a male dominance hierarchy. The degree of sexual segregation in antilopine wallaroos was strongly related to female reproductive condition. Our study establishes that in this tropical marsupial sexual segregation is linked to pronounced seasonality of rainfall and female reproductive biology. Male social behaviour (e.g.

learning skills and establishing a dominance hierarchy, as in ungulates) may also be important in determining segregation patterns. Our results emphasize that the evolution of sexual segregation in tropical marsupials and temperate ungulates appears to be influenced by reproductive phenologies that are associated with differing environmental conditions.

Introduction

Sexual segregation occurs when males and females of a species separate into single-sex groups, typically outside the breeding season (Conradt, 1998; Ruckstuhl & Neuhaus, 2002b). This behaviour is common in gregarious, seasonally breeding and sexually-size dimorphic vertebrates, and has been studied in a broad range of taxonomic groups including sharks, teleosts, birds, reptiles and mammals (Ruckstuhl & Neuhaus, 2005). The study of sexual segregation is important because of its potential ecological consequences which include effects on species movement patterns, spacing and habitat preferences, population regulation, distribution and gene flow. These are key considerations for the management of economically valuable and/or rare species (Clemmons & Buchholz, 1997). Two main types of sexual segregation are widely recognised: social segregation – where the sexes occur in different groups within the same habitat (Bonenfant *et al.*, 2004; Conradt, 1999; Michelena *et al.*, 2004; Weckerly *et al.*, 2004); and habitat segregation – where the sexes occupy different habitats (Caister, Shields & Gosser, 2003; Conradt, Clutton-Brock & Thomson, 1999; Miller & Litvaitis, 1992). Social segregation can arise independently from habitat segregation (Bon & Campan, 1996).

Three hypotheses to account for sexual segregation have attracted considerable research attention. The predation-risk hypothesis suggests that males may select more risky but higher-quality foraging areas, whereas females may select lower-quality foraging areas but with less perceived predation risk to their offspring (Corti & Shackleton, 2002; Main, Weckerly & Bleich, 1996; Mooring *et al.*, 2003; Ruckstuhl *et al.*, 2002b). The forage-selection hypothesis proposes that due to the allometric relationship between metabolic requirements and body size (gut capacity), females with young, juveniles or smaller individuals may feed in areas of higher quality but less overall biomass, whereas males and/or larger individuals may feed in areas of lower quality but higher overall biomass (Illius *et al.*, 1987; Main *et al.*, 1996; Ruckstuhl & Neuhaus, 2000; Ruckstuhl *et al.*, 2002b). Finally, the activity-budget hypothesis suggests that as a consequence of increased sexual body-size dimorphism, males and females may differ in their activity budgets, resulting in the instability and fracturing of group cohesion due to the energetic costs of maintaining cohesion in a mixed sex group

(Ruckstuhl, 1998; Ruckstuhl *et al.*, 2000; Ruckstuhl *et al.*, 2002b; Yearsley & Perez-Barberia, 2005). Bowyer and Kie (2004), Yearsley and Perez-Barberia (2005) and Michelena *et al.* (2006) have recently questioned the power of the activity-budget and forage-selection hypotheses to explain sexual segregation, and Perez-Barberia *et al.* (2005) have examined the potential influence of social factors on sexual segregation.

Despite extensive research into sexual segregation (Ruckstuhl *et al.*, 2005), there are two important gaps in our current knowledge. Firstly, there are few quantitative studies of the occurrence, pattern and possible driving mechanisms of sexual segregation in marsupials (MacFarlane & Coulson, 2005a), a diverse mammal assemblage. The family Macropodidae includes species which are strongly sexually size-dimorphic and gregarious, and which breed seasonally (Johnson, 2003). They therefore provide an excellent opportunity to study sexual segregation. Secondly, very few studies have investigated seasonal patterns of sexual segregation (Bonenfant *et al.*, 2004). Studying patterns of sexual segregation across multiple seasons is critical to understanding the environmental drivers causing it. Pronounced rainfall seasonality, which is characteristic of much of the tropics, has a dramatic effect on the distribution and availability of resources, which in turn is likely to strongly influence the reproductive biology and behaviour of social grazing species. In temperate regions temperature variation has the greatest influence on resource availability, and hence in shaping the evolution of reproductive strategies. We expect that patterns of sexual segregation commonly observed in temperate mammals also occur in tropical mammals, including marsupials. However, we predict that the evolution of reproductive strategies and sexual segregation in the tropics is in response to the challenge of pronounced rainfall seasonality, and not temperature as in temperate species.

Here we present a quantitative, multi-season study of sexual segregation in a large-bodied, tropical marsupial, the antilopine wallaroo (*Macropus antilopinus*). Large macropods such as antilopine wallaroos are considered ecologically analogous to ungulates of similar body mass (Jarman, 1983). The antilopine wallaroo is an ideal species for studying sexual segregation because it displays strong sexual size dimorphism, with the largest males being up to a maximum of 3.6 times heavier than females (adult males: mean 34.2, range 18.6 - 51.0 kg; adult females: mean 19.9, range 14 - 25 kg; Johnson 2003), and highly seasonal breeding (Chapter 3). We predict that social segregation in antilopine wallaroos should be lowest during the mating period,

when males and females are expected to aggregate, and will increase through the dry season, as females enter anoestrus. Further, we predict that males will leave mixed-sex groups as the proportion of “attractive” females decreases in the population. In antilopine wallaroos, female attractiveness to males is highest when young first exit the pouch and become dependent young at foot, during which time adult females enter oestrus (Poole *et al.*, 1987). Males may enter all-male groups for social interaction (e.g. learning fighting skills and establishing a dominance hierarchy) prior to the next mating season. In large macropods and ungulates, development of skills in fighting and assessing opponents is thought to be important to the establishment of male hierarchies, and ultimately to male mating success (Coulson, 1989; Coulson, 1997; Croft, 1989; Croft & Snaith, 1991; Pelletier *et al.*, 2006).

Methods

Study area

We conducted our study in a 400-ha section of Rocky Springs cattle station (-18.1S, 144.4E), in north Queensland, Australia (Figure 4.1). The soil was basaltic, derived from the nearby extinct Undara volcanic crater, and the topography was largely flat with occasional small hills of boulders. Vegetation at the site was relatively uniform open savannah woodland dominated by mixed *Eucalyptus* spp. and the native perennial grasses, black speargrass (*Heteropogon contortus*) and branched wiregrass (*Aristida calycina*) (Figure 4.2). The dingo (*Canis lupus dingo*), the main predator of antilopine wallaroos, occurs in the study area (D. Buchanan pers. obs.) but is evidently rare, and was not recorded during surveys.

The climate of the area is characteristic of the Australian dry tropics, with highly seasonal rainfall (wet season - late December to March, mean 640 mm; dry season - April to November, mean 148 mm), whereas temperature variation is modest (mean daily maximum ranges from 26.4 °C in July to 35.1 °C in November) (www.bom.gov.au). Three seasons are recognised for this region: the wet season (mid-December to March/April) when the majority of rain falls, the cool dry season (late April to September) when there is little rainfall and temperatures are mild, and the hot dry season (September to mid-December) when there is little rainfall and temperatures and humidity are highest. Monthly rainfall (mm) was measured at Rocky Springs Station during the study.

Study population

We monitored a population of antilopine wallaroos at Rocky Springs Station between November 2003 and January 2005. This period encompassed the three distinct seasons (wet, cool dry and hot dry). Two species of large macropod were present within the study area: antilopine wallaroos, and the less abundant common wallaroo (*M. robustus*), which was rarely sighted. Male and female antilopine wallaroos can be easily sexed due to the combination of pronounced differences in muscular development and prominent sexual dichromatism (males are predominantly red; females are red with grey forequarters (Johnson, 2003; Ritchie, in press). Knowledge of the female reproductive

cycle is derived from only a few captive individuals in a previous study, indicating an oestrous cycle of approximately 41 days, gestation 34 days, pouch life 270 days and pouch-young exit to oestrus 49 days (Poole *et al.*, 1987).

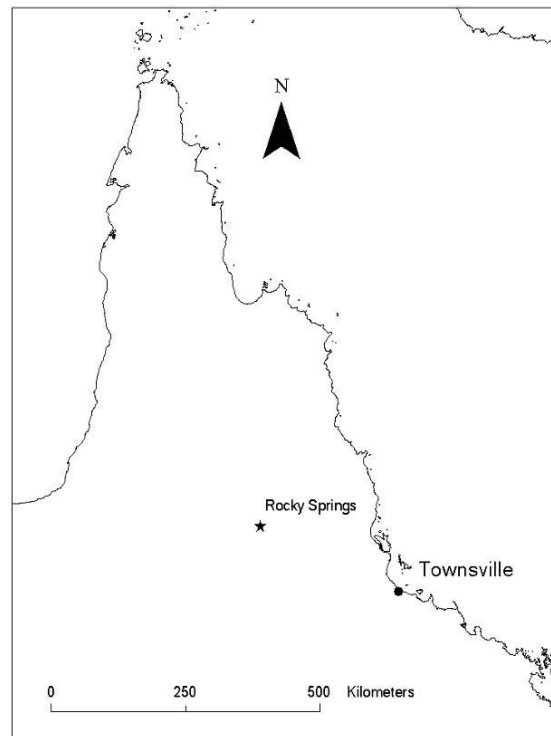


Figure 4.1 Location of study site.



Figure 4.2 Typical habitat at study site. © E. Ritchie

Survey data

Over the study period, we conducted 70 visual surveys from a vehicle driven along a 5-km unsealed track, either at dawn (survey period 0530-0830 hours) or pre-dusk (survey period 1645-1830 hours). Preliminary analysis of our data found no indication of significant detectability differences between different group types across seasons. For each group encountered, we recorded group size and the sex and body-size class of all individuals within the group. Using binoculars and telescopes, we classed individuals into the following categories: sub-adult (either male or female), adult female (with or without pouch-young/dependent young at foot), small males (equal in height to adult females), medium males (taller than adult females and small males and with moderate muscular development of the chest and arms) and large males (more pronounced muscular development of the chest and arms than medium males) (Figure 4.3). Classifying individuals according to this method is one accepted technique which has been used in previous studies of large macropods (Johnson, 1983; Johnson *et al.*, 1981). Females with a pouch-young or dependent young at foot were counted as a single unit (group size of one) and sub-adults were omitted from the group size and group composition data-set, as they are not considered behaviourally independent from their mothers (Croft, 2004).

Statistical analyses

Social segregation

We calculated social segregation coefficients (SC_{social}) for antilopine wallaroos in all months surveyed by the method of Conradt (1998). The values of SC_{social} are interpreted as follows: 0 indicates no segregation or random mixing of the sexes within groups; any value greater than 0 indicates segregation, with 1 signifying that animals are found only in single-sex groups; negative values signify aggregation, where sexes occur together in groups more often than expected from random mixing. We calculated SC_{social} for $k \geq 2$ for all groups in which we could assign individuals to a sex and body-size class. Mixed-sex groups were divided into two categories and SC_{social} was calculated for each: those including females with dependent young at foot (+FYAF), and those for females without dependent young at foot (-FYAF). This is because intraspecific interactions of female antilopine wallaroos with both adult males and other adult

females vary with their own reproductive status (Ritchie, unpublished). Conratt (1998) recommended this approach for calculating social segregation coefficients in these situations. Females with pouch-young were included for both categories. We followed Conratt (1998) in calculating SC_{social} for months in which we had observed ≥ 30 groups, and in using non-parametric tests in our analysis.



Figure 4.3 Small male (A), large male (B), subadult male (C) and adult female (D) antilopine wallaroos (*Macropus antilopinus*).

Images A, C & D © D. Webb; Image B © E. Ritchie.

Seasonal group composition and size

We calculated the proportion of single-sex (all-male or all-female) and mixed-sex groups during each season. Using contingency table analyses we tested whether group composition for group sizes from two to four was significantly different from random for both the wet and dry seasons (cool and hot dry combined). Expected frequencies were calculated on the basis of the sex ratio of the population and all possible combinations within each group size. Group types that occurred significantly more often than expected were identified using standardised residuals as outlined by Everitt (1977). We included groups containing females with dependent young. In this analysis we could not use larger group sizes and divide females into the two categories, because this would have resulted in too few samples for the wet season. All analyses were performed in JMP 4 and Statistica 6.0.

Results

Reproductive biology

There was a significant positive relationship between the proportion of females with dependent young at foot (+FYAF) and monthly rainfall (Spearman $Rho = 1.0$, $p < 0.0001$). In the hot dry season, all females that we were able to visually assess had pouch-young. The majority of females subsequently had young at foot in the wet season (Figure 4.4). The proportion of females with pouch-young increased from the cool dry to the hot dry seasons (probably due to larger pouch-young becoming more visible). The proportion of sub-adults in the population increased in the cool dry season as young at foot became sub-adults.

In February and March, adult males and females with small young at foot (+FYAF) were found together in mixed groups, however females without dependent young at foot (-FYAF) were more often alone (Figure 4.5).

Social segregation

There was a significant negative relationship between the proportion of females with dependent young at foot (+FYAF) and social segregation (SC_{social}), (Spearman $Rho = -0.99$, $p = 0.0003$). Social segregation (SC_{social}) was lowest in the wet season (January - March) and increased steadily during the dry season (April - November), peaking in November (Figure 4.5). There was a significant difference in the degree of segregation for groups with females and young at foot and those with females without young at foot, between the wet and dry seasons (+FYAF, $Z = -2.5$, $p = 0.01$, mean SC_{social} wet season = 0.008 ± 0.04 dry season = 0.38 ± 0.07 ; -FYAF, $Z = -2.2$, $p = 0.03$, mean SC_{social} wet season = 0.25 ± 0.07 dry season = 0.39 ± 0.07). There was no significant difference in the degree of segregation between the two group types ($Z = 1.4$, $p = 0.2$, mean SC_{social} +FYAF = 0.21 ± 0.09 -FYAF = 0.32 ± 0.05).

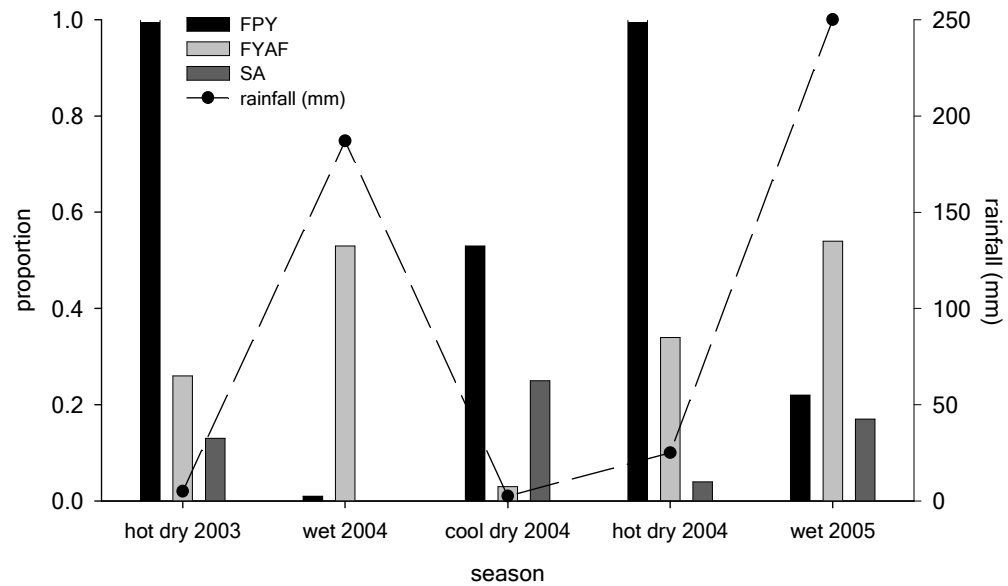


Figure 4.4. Reproductive biology of the antilopine wallaroo and rainfall (mm) at Rocky Springs Station, north Queensland, November 2003 – January 2005. FPY = proportion of adult females with visible pouch-young as a proportion of the adult females in the population. FYAF = proportion of adult females with dependent young at foot as a proportion of the adult females in the population. SA = proportion of sub-adults in the population. Note: FPY was calculated only for adult females for which the pouch was visible, and therefore did not represent all females in the population.

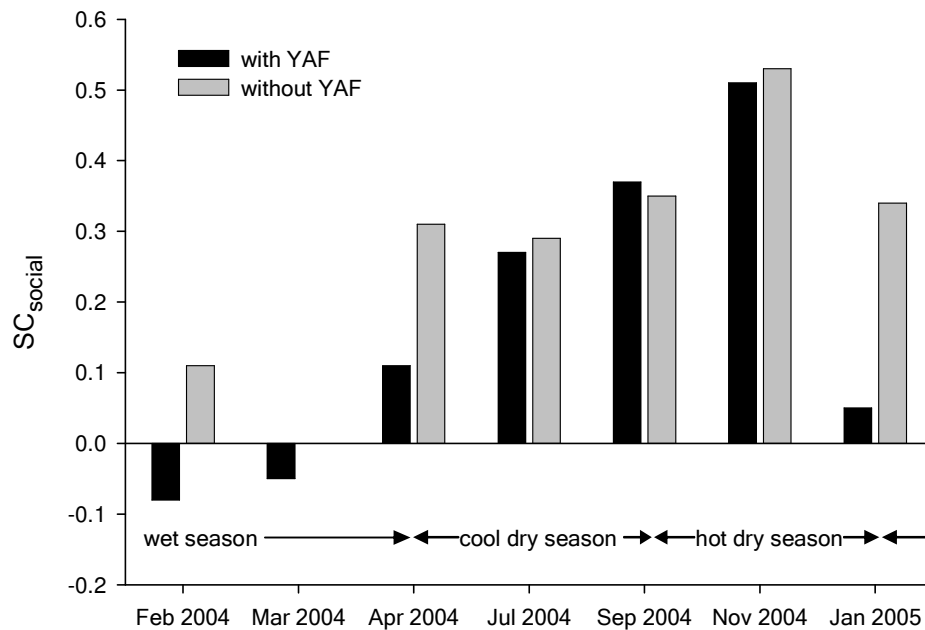


Figure 4.5. Social segregation in the antilopine wallaroo at Rocky Springs Station, north Queensland, February 2004 to January 2005, as estimated by the segregation coefficient SC_{social} . A negative SC_{social} value indicates aggregation, a value of 1 indicates total segregation, and a value of 0 indicates random association (Conradt, 1998). SC_{social} is presented for groups which include females and dependent young at foot (+FYAF) and groups that lack females with dependent young at foot (-FYAF).

Group dynamics

The proportion of mixed-sex groups was highest during the mating period (February-March); single-sex groups predominated in the dry season (Figure 4.6). All-female groups were most common in the cool dry season and all-male groups most common in the hot dry season (November). All-female and all-male groups were significantly larger in the hot dry season than in the cool dry and wet seasons ($F_{2, 65} = 4.8$, $p = 0.01$, $F_{2, 50} = 4.0$, $p = 0.02$ respectively, Figure 4.7). There was no significant difference in the size of mixed-sex groups between seasons ($F_{2, 178} = 0.8$, $P = 0.4$, Figure 4.7). The proportion of large males in mixed-sex groups decreased from the wet season

to the hot dry season, and the proportion of large males in all-male groups increased over this period (Figure 4.8). A similar pattern was observed for medium males, but there was no change from the cool to hot dry seasons (Figure 4.8). Group composition did not differ from random during the wet season ($\chi^2 = 15.55$, d.f. = 11, $p > 0.05$; Table 4.1), but was significantly different from random in the dry season ($\chi^2 = 62.76$, d.f. = 11, $p < 0.001$; Table 4.1). All-male groups of three and four and all-female groups of two and three occurred significantly more than expected, whereas combinations of mixed groups occurred significantly less than expected (Table 4.1).

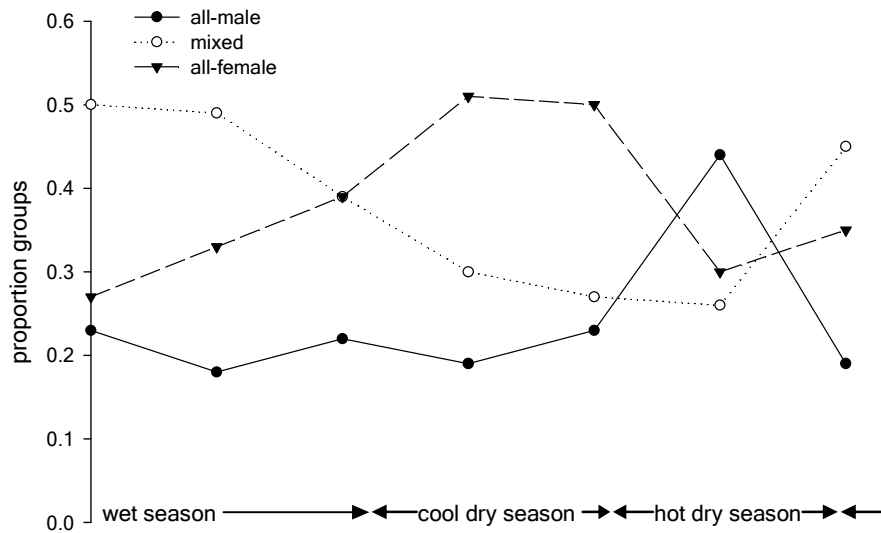


Figure 4.6. Proportion of all-male, mixed and all-female antilopine wallaroo groups from February 2004 to January 2005, at Rocky Springs Station, north Queensland.

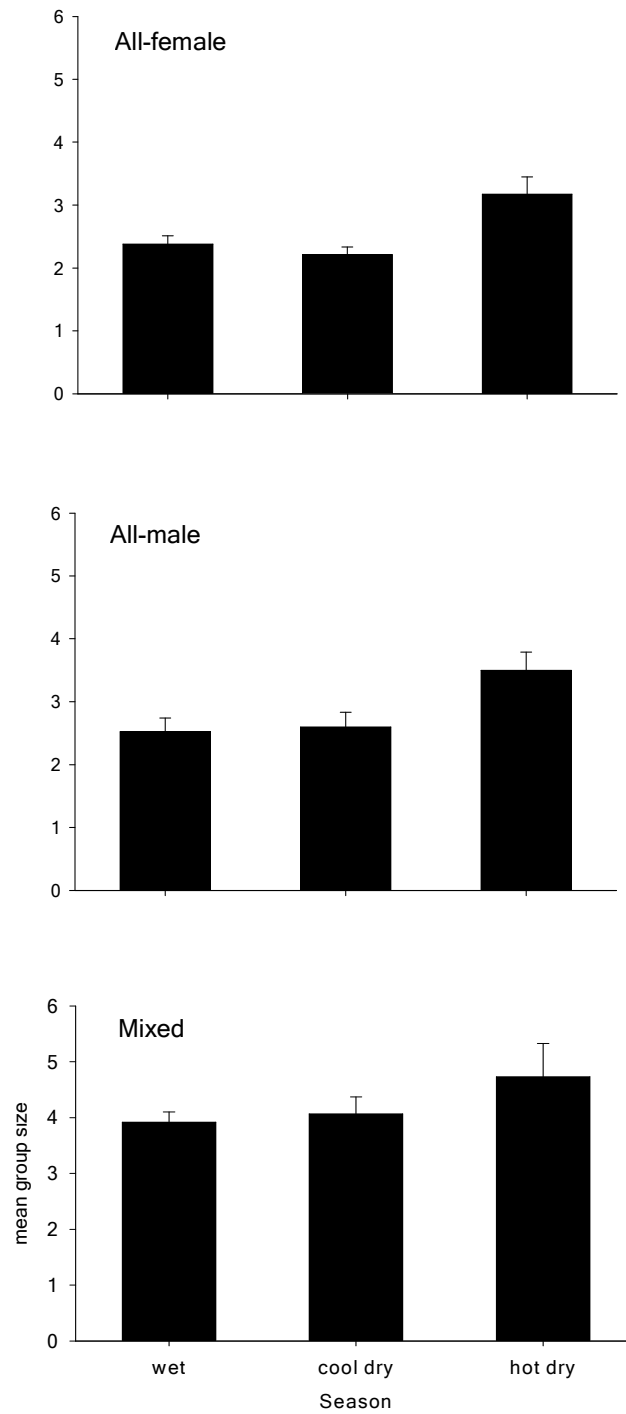


Figure 4.7. Seasonal mean (\pm s.e.) group sizes for all-female groups ($N = 68$), all-male groups ($N = 53$) and mixed-sex groups ($N = 181$) in antilopine wallaroos, at Rocky Springs Station, north Queensland.

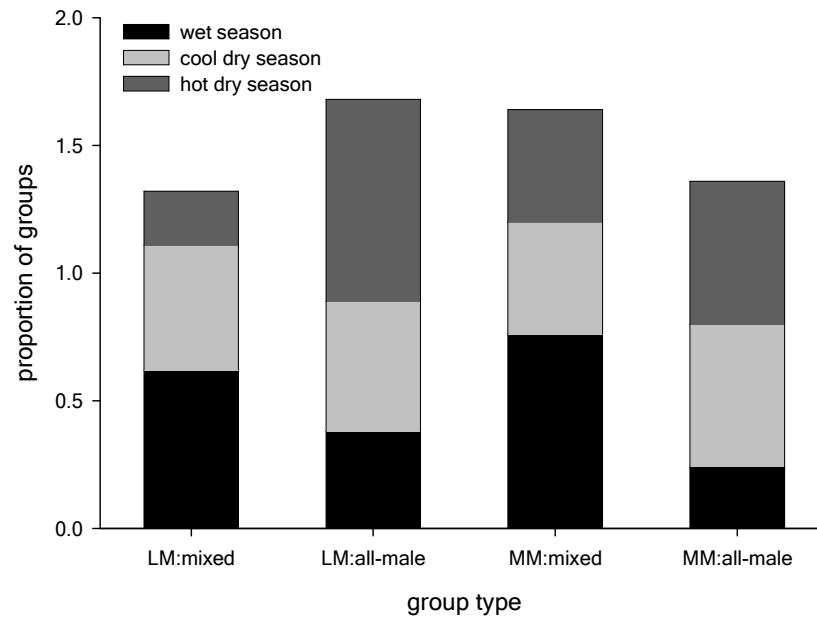


Figure 4.8. Proportion of large (LM) and medium (MM) male antilopine wallaroos in all-male and mixed-sex groups with each season, at Rocky Springs Station, north Queensland.

Table 4.1. Seasonal group composition for the antilopine wallaroo at Rocky Springs Station, north Queensland, for group sizes of two, three and four. M = male, F = female. Standardised residuals greater (+) or less (-) than 1.96 are marked.

Group type	MM	MF	FF	MMM	MMF	MFF	FFF	MMMM	MMMf	MMFF	MFFF	FFFF
Wet season	11	38	22	5	11	14	3	3	10	4	2	1
Dry Season	16	-12	+29	+7	-5	8	+7	+5	3	-1	2	2

Discussion

Our study demonstrates a clear link between rainfall seasonality, reproductive phenology and social segregation in a tropical marsupial. Few studies have identified and quantified the biological and environmental mechanisms underlying sexual segregation (see MacFarlane & Coulson, 2005b; Ruckstuhl *et al.*, 2006). The seasonal pattern of segregation we recorded may be associated with male social behaviour. We recorded levels of social segregation equivalent to those reported in many temperate ungulate populations, including red deer (*Cervus elaphus*) (Conradt 1998) and alpine ibex (*Capra ibex ibex*) (Bon *et al.*, 2001), and similar to those recorded in two other temperate macropod species, western grey kangaroo (*M. fuliginosus*) and red kangaroos (*M. rufus*) (MacFarlane *et al.*, 2005b).

The annual pattern of reproduction in antilopine wallaroos appears strongly linked to seasonal rainfall, as evidenced by the significant relationship between rainfall and proportion of females with dependent young at foot. Based on published data regarding the female reproductive cycle in antilopine wallaroos (Poole *et al.*, 1987), we infer that, in our population, the majority of mating occurred in February and March. This appears to be a reproductive strategy that allows mothers to carry young in the pouch over the extended dry season, when resources are most scarce, and for young to exit the pouch at the beginning of the wet season when resources are most abundant, ensuring a nutrient-rich source of grass for young, growing animals. This may also increase the probability of females meeting the additional energetic costs associated with advanced lactation (Merchant, 1989). This phenology of reproduction appears to be a key factor underlying the regulation of social segregation in antilopine wallaroos, as demonstrated by the significant relationship between female attractiveness to males (presence of a dependent young) and the degree of social segregation. A similar pattern was suggested by MacFarlane and Coulson (2005b) in their study of two temperate macropod species. Our study and that of Bonenfant *et al.* (2004) highlight the importance of considering both reproductive and social behaviour in detail when interpreting seasonal patterns of social segregation.

The composition of antilopine wallaroo groups changed considerably between seasons. The majority of groups were mixed during the wet season (the mating period), whereas single-sex groups predominated in the dry season. Our observations suggest a

pattern similar to that shown by sexually dimorphic ungulates, such as red deer, (Clutton-Brock, Iason & Guinness, 1987), white-tailed deer (*Odocoileus virginianus*) (Kie & Bowyer, 1999) and alpine ibex (Bon *et al.*, 2001) in which single-sex groups are common and come together briefly during the rut. Our results indicate that the seasonal social behaviour of the sexes differs.

All-male groups were most common and significantly larger in the hot dry season than during the other two seasons, with group sizes of three and four occurring significantly more than expected. We suggest that this result may be accounted for by males seeking social interaction with other males, with the formation of a male dominance hierarchy as a possible outcome, as is common in many polygynous mammals (Croft, 1985; Hynes *et al.*, 2005; Johnson, 1989; Pelletier *et al.*, 2006). Male dominance is a strong correlate of mammalian male mating success (Johnson, 1989; Pelletier *et al.*, 2006; Watson, Croft & Crozier, 1992) but this remains to be confirmed in antilopine wallaroos and other large macropods. We predicted that males would leave mixed-sex groups containing females and join all-male groups when mating opportunities were reduced. This prediction is supported by the concurrent trends of numbers of both large and medium males (the size-classes most likely to be mating with females) increasing in all-male groups with the advance of the dry season, and of females with dependent young at foot decreasing in number.

All-female groups were common throughout the study, but were proportionally higher in number in the cool dry season (July-September). All-female groups were also significantly larger and occurred significantly more often than expected in the dry season. Females may disassociate from mixed groups which contain adult males for at least four reasons. Firstly, this may simply be an artefact of adult males leaving mixed groups. However the numbers of all-male groups did not increase markedly during the cool dry season, so this appears unlikely. Secondly, females may assemble in all-female groups as a tactic to avoid male harassment. Mortality arising from male harassment has been recorded in sheep (*Ovis aries*) (Reale, Bousses & Chapuis, 1996). Thirdly, females may leave large mixed groups to reduce the risk of young being confused and losing their mothers in situations in which a group scatters at high speed, such as when a predator (e.g. dingo) attempts to attack a group (Ritchie, pers. obs.; see Johnson, 1987). Lastly, females may separate from males due to differences in foraging behaviour, related to body size (Illius *et al.*, 1987; Jarman, 1974). However a detailed intraspecific

study of diet, which examined both the composition and amounts of plant species eaten in antilopine wallaroos conducted at the same site (Peter Fossan, unpublished), did not find differences in diet between the sexes that were consistent with predictions of the forage-selection hypothesis.

The tropical savannas of northern Australia represent a seasonally-challenging environment to macropods, with significant temporal variation in the abundance and quality of pastures associated with pronounced differences in rainfall between seasons. Our study demonstrates how this environmental factor (rainfall seasonality) is linked with the evolution of synchronous breeding in a tropical marsupial and associated patterns of sexual segregation. The similarity of patterns of sexual segregation we observed in tropical antilopine wallaroos with those reported for temperate ungulates (e.g. red deer and alpine ibex), may suggest the parallel evolution of this behaviour in marsupials and ungulates under differing environmental pressures (rainfall and temperature seasonality).

Chapter 5

Climate change and the distribution of large, tropical macropods

(In review *Austral Ecology*; co-authored with Elizabeth E. Bolitho)

Abstract

The impacts of future climate change are predicted to significantly affect the survival of species. Recent studies indicate that even species which are relatively mobile and/or have wide distributions may be at risk of range contractions. However, one group that has been largely overlooked is Australia's large herbivorous marsupials, the macropods. We defined the climatic conditions which influence the current distributions of four sympatric large macropods in northern Australia (antelope wallaroo *Macropus antilopinus*, common wallaroo *M. robustus*, eastern grey kangaroo *M. giganteus* and red kangaroo *M. rufus*), and predicted the impact of future climate change on these species.

Our results suggest that the contemporary distribution of these large macropods is associated with well-defined climatic gradients. An increase in mean annual temperature of 0.4 °C causes a reduction of 9% in the core distributions of all macropods. With an increase of 2.0 °C, all species show large reductions in distribution (48% ± 16.4%) and the core distribution of the antelope wallaroo is reduced by 89 ± 0.4%. Our results predict that an increase of 6.0 °C will cause severe range reductions for all four macropods (96 ± 2.1%) and the likely extinction of the antelope wallaroo. These results demonstrate that large macropods, like other large mammals, are at significant risk of decline in response to climate change, and we highlight the urgent need for studies of the environmental limits of species' distributions and the development of mechanistic models to inform conservation measures.

Introduction

The effects of increasing global temperature loom as the largest threat to the survival of species (Hughes, 2003; Meyneke, 2004; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Thomas, Franco & Hill, 2006; Walther *et al.*, 2005; Williams, Bolitho & Fox, 2003). Such climate change also has the potential to undermine conservation efforts (e.g. habitat reserves Thuiller *et al.*, 2006) by causing considerable structural change to existing habitats (Andrew & Hughes, 2005; Hilbert, Ostendorf & Hopkins, 2001; Hughes, Cawsey & Westoby, 1996; Root *et al.*, 2003) and by influencing the frequency and nature of key processes such as fire regimes (Hughes, 2003; Schumacher *et al.*, 2006). It is crucial to the development of management strategies to accumulate detailed information about current distributions of species and potential future variations under different climate change scenarios.

Research into the impacts of global warming has focused considerable attention on species which are either altitudinally restricted and/or have small geographic ranges (Shoo, Williams & Hero, 2005a; Williams *et al.*, 2003), but recently there has been growing recognition that species with wide geographic distributions may also be vulnerable (Forchhammer *et al.*, 2001; Ogotu *et al.*, 2003; Walther *et al.*, 2002). The family Macropodidae (recognised globally as the iconic kangaroos) includes six species of large herbivorous marsupials (20 – ≤90 kg) (Dawson, 1995), which have been largely overlooked with respect to climate change. With the exception of the black wallaroo (*Macropus bernardus*), the large macropods all have extensive geographic ranges (e.g. red kangaroo (*M. rufus*) > 3,000,000 km² Strahan, 1995). The antilopine wallaroo (*M. antilopinus*) is the largest macropod confined solely to the tropical savannas of northern Australia. This species may be more vulnerable to a changing climate than other large macropods given its smaller range (Busby, 1988). This species also exhibits highly seasonal reproduction, strongly linked to rainfall in the monsoon season, which may further increase its vulnerability (Chapter 3). The antilopine wallaroo is of significant cultural and economic importance to Indigenous people of the region (Busby, 1988; Yibarbuk *et al.*, 2001) and to ecotourism, but the distribution, ecology and general biology of this species remain poorly understood (Croft, 1982; Croft, 1987; Russell *et al.*, 1971).

Caughley et al.'s (1987) classic study of kangaroo distribution and climate concluded that the extent of sympatry and allopatry between species was likely to be determined by the response of each species to climatic variation, rather than by interspecific interactions. This study contributed greatly to our understanding of large mammal distribution patterns, but without information on common wallaroos (*M. robustus*) and antilopine wallaroos, generalisations for large macropods as a whole cannot yet be made. In northern Australia, the four largest macropods can be roughly characterised as follows: the red kangaroo is an arid-zone species, the four sub-species of the common wallaroo range from arid to mesic areas, the antilopine wallaroo is a tropical mesic species, and the eastern grey kangaroo (*M. giganteus*) is largely a subtropical mesic species (Strahan, 1995). There is marked variation in the ecological and physiological adaptations among these species (Dawson, 1995; Dawson *et al.*, 2000a; Dawson *et al.*, 1969). Intuitively, we predict that these four species may differ in respect to the components of climate that shape their distribution patterns, and therefore in their respective susceptibility to the patterns of climate change predicted for this region (Hughes, 2003). Here, we present a detailed examination of the bioclimatic distributions of these four species. Our aims are to determine the climate space of each macropod species and the climatic variables that may be responsible for maintaining species' ranges and borders; and to predict the likely impact of climate change on these species' future distributions, including areas of sympatry. We predict that the antilopine wallaroo will be more susceptible than the other sympatric species to the effects of future climate change due to its smaller geographic range and its dependence on seasonal rainfall (Chapter 3).

Methods

We restricted our modelling of macropod distributions to between - 11 and - 30 degrees of latitude (“northern Australia”, Figure 5.1); encompassing the complete geographic range of the antilopine wallaroo, and approximately 50% of the ranges of the eastern grey kangaroo, 66% of the red kangaroo and 80% of the common wallaroo (based on Strahan, 1995). This restriction was made because there is a significant change in climate regime south of - 30 degrees of latitude, from seasonal summer rainfall to less seasonal winter dominated rainfall (www.bom.gov.au). Confining our study area to northern Australia reduced the complication of trying to incorporate differences in predictions for climate change across multiple regions of Australia in our models (see Hughes 2003). Although this meant excluding some information on climatic conditions experienced by common wallaroos, red kangaroos and eastern grey kangaroos, we are most interested in the effects of warming, and therefore the southern limits of these species are less important than the northern limits. Further, this methodological restraint is likely to apply only to the eastern grey kangaroo, given that conditions experienced by this species south of our defined study region are cooler and wetter. In contrast, the semi-arid to arid conditions experienced by the common wallaroo and red kangaroo vary considerably less outside our study area.

We collected locality data for all species during extensive field-based surveys between 2002 and 2005 (Chapter 2). Additional records were obtained from other sources (see acknowledgements). We then assessed the reliability of all records with reference to current known distributions and according to our own and expert knowledge of each species; dubious records were excluded from the final data set. We removed any multiple records less than 2.5 km apart to reduce spatial autocorrelation. A total of 3514 records was included in the analysis as follows: antilopine wallaroo (1102 records), common wallaroo (913 records), eastern grey kangaroo (1233 records) and red kangaroo (266 records).

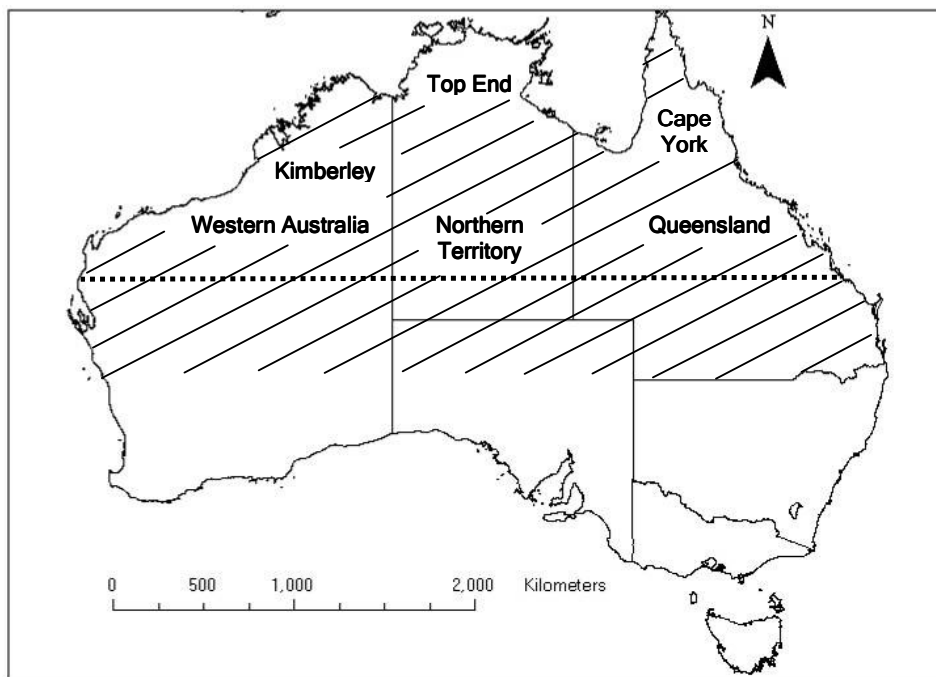


Figure 5.1 Study area (shaded) showing political boundaries, major regions and the Tropic of Capricorn (dashed line).

Bioclimatic parameter selection and modelling

The choice of bioclimatic variables for models and maps produced in BIOCLIM (Houlder *et al.*, 2000) can have significant effects on the final output of predicted distributions, particularly for single species (Beaumont, Hughes & Poulsen, 2005). We investigated the influence that the addition and subtraction of variables had on each macropod species' modelled distribution prior to selecting the final set of variables. To avoid problems of over-parameterisation of our models, we limited models to 11 variables in BIOCLIM (Busby, 1991; Hutchinson *et al.*, 1984): annual mean temperature, maximum temperature of warmest period, minimum temperature of coldest period, annual temperature range, mean temperature of wettest quarter, mean temperature of driest quarter, annual precipitation, precipitation of wettest period, precipitation seasonality (coefficient of variation), precipitation of wettest quarter and precipitation of driest quarter. We chose these variables because they are generally regarded as significant in influencing the distributions of large macropods, and because they have also been used in a previous study of kangaroos and climate (Caughley *et al.*,

1987). Precipitation of the driest period was not included as a variable because, for all species, and for the majority of sites, a zero value was recorded.

We modelled and mapped distributions for each species under current and future climatic conditions using the BIOCLIM script for ArcView 3.1 (Adnan Moussalli), available as a free download from www.esri.com. We generated maps using a twelve second digital elevation model, with output restricted to core distribution (5 - 95% of the spread of values for all 11 climatic variables) and marginal distribution (2.5-97.5%). Given that the accuracy of BIOCLIM for distribution modelling has recently been questioned (Araujo & Rahbek, 2006; Elith *et al.*, 2006), we examined the maps of current distribution for the four species carefully and compared these with their known distributions, which included extensive ground-truthing across northern Australia (~150,000 km of survey). In all cases, the generated maps corresponded closely with the known distributions of the four species. It is worth noting that BIOCLIM, by its nature, produces models which are over-estimates of the current distribution. The models do not factor in other important variables such as soil type, vegetation and topography which further constrain species' distributions. Our models of changes to distributions under climate change are therefore likely to be conservative. For more detailed information on bioclimatic modelling see Lindenmayer *et al.* (1991) and Nix (1986).

Climate change scenarios

Australia's size and associated high diversity of bioregions make it difficult to obtain consensus about the likely nature and extent of climate change expected during the next 100 years (Hughes, 2003). However, for the majority of mainland Australia, it is generally accepted that mean temperatures will increase by 0.4 °C to 2 °C by 2030 and by 1 °C to 6 °C by 2070 (Hughes, 2003). Rainfall predictions are much more variable and dependent upon the models used to generate them, with predictions for northern Australia ranging from -5 to +5% mean annual rainfall by 2030 and -10 to +10% mean annual rainfall by 2070 (Hughes, 2003). To account for this variability, we generated models of species distributions for all four macropod species under the following climate change scenario combinations: + 0.4 °C mean annual temperature with each of - 5, + 5, - 10, + 10% mean annual rainfall; + 2 °C mean annual temperature with each of - 5, + 5, - 10, + 10% mean annual rainfall; and + 6 °C mean

annual temperature with each of - 5, + 5, - 10, + 10% mean annual rainfall. To assess the impact of climate change on each species' future range, we compared the amount of core distribution area following the application of each climatic scenario. To investigate how climate change may affect large macropod assemblages, we constructed distribution maps showing areas of sympatry between the species for each climate change scenario.

Analysis

Using all chosen climate variables, we generated summary bioclimatic envelopes for each species. We reduced these variables into two climatic gradients (component axes) using principal components analysis (PCA) and tested for differences in these gradients between species using analysis of variance. We rotated the axes (varimax) to assist in interpretation, and used factor loadings greater than 0.6 to describe each axis as recommended by Quinn and Keough (2002). Changes in distributions with the climate change scenarios were described as percentages of current distributions. All statistical analyses were performed in JMP 4.0 and Statistica 6.0.

Results

Current distributions of large macropods in northern Australia

The current climatic envelopes of each species are summarised in Table 5.1. The red kangaroo occurs in areas with higher maximum temperatures, higher temperature ranges and lower annual precipitation than the other species. The common wallaroo has the broadest climatic envelope of all the species, differing from the red kangaroo in that it occurs in areas with less temperature variation and an average of double the annual rainfall. The eastern grey kangaroo occurs in areas typically lower in temperature but with less rainfall seasonality than the other species, and in areas wetter than those occupied by red kangaroos and common wallaroos but drier than those occupied by antilopine wallaroos. The antilopine wallaroo occurs in areas of higher mean temperature but lower temperature variation, and of higher, more seasonal rainfall than the other species.

PCA summarised the climate experienced by all four species into two environmental gradients (principal component axes; Table 5.2). Principal component one (PC1) describes a gradient of increasing temperature and higher rainfall seasonality (tropical conditions). Principal component two (PC2) describes a gradient of lower rainfall and cooler but higher temperature variation (subtropical conditions). There was significant separation between all species along these axes using Tukey's post hoc tests (PC1, $F_{3, 3514} = 1043.48$, $p < 0.0001$, antilopine wallaroo = 0.69 ± 0.01 , common wallaroo = 0.36 ± 0.02 , eastern grey kangaroo = -0.91 ± 0.03 and red kangaroo = 0.11 ± 0.04 ; PC2, $F_{3, 3514} = 513.14$, $p < 0.0001$, antilopine wallaroo = -0.61 ± 0.03 , common wallaroo = 0.40 ± 0.03 , eastern grey kangaroo = -0.05 ± 0.02 and red kangaroo = 1.39 ± 0.03). The antilopine wallaroo showed the strongest positive association with tropical conditions and the narrowest climate space (Figure 5.2). Common wallaroos showed a stronger association with tropical conditions than subtropical conditions and eastern grey kangaroos showed the converse trend; these two species occupied the largest climatic space. The climate space of the common wallaroo encompasses that of both the red kangaroo and antilopine wallaroo, and a large proportion of that of the eastern grey kangaroo. The red kangaroo showed a positive association with both tropical and subtropical conditions, and had the second-smallest climate space, which overlapped only marginally with that of the antilopine wallaroo. The geographic boundary between

red kangaroos and antilopine wallaroos is strongly associated with rainfall of the wettest period (Figure 5.3), with a small zone of sympatry between the two species. At this border (where there is a transition from higher to lower rainfall in the wettest period), there is a sharp change in the decline in the occurrence of antilopine wallaroos and increase in the occurrence of red kangaroos.

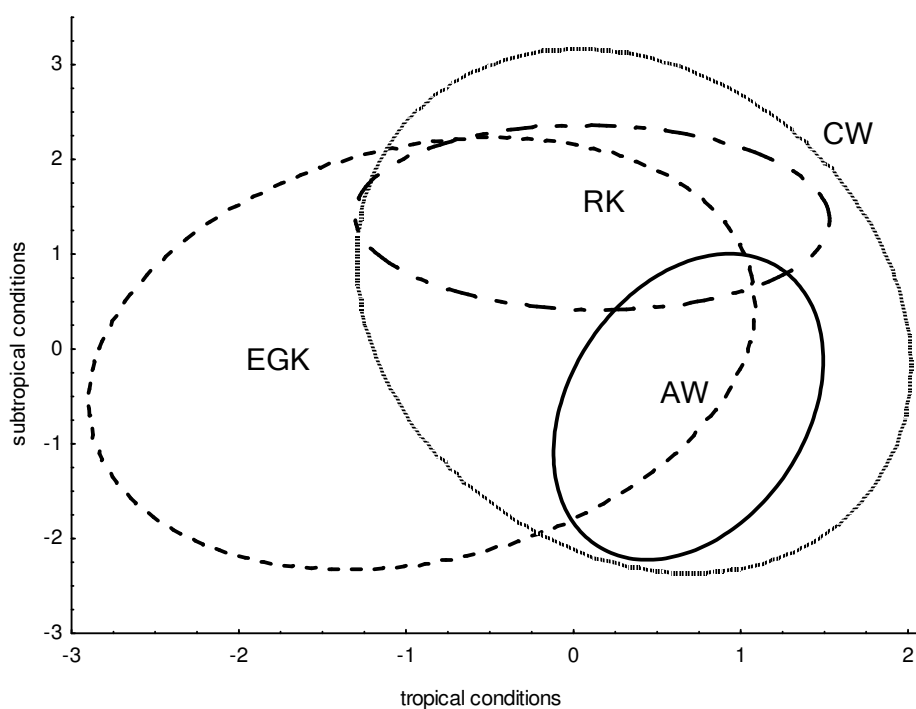


Figure 5.2 Climate spaces (95% confidence interval ellipses) for large macropods in northern Australia. Antilopine wallaroo = AW, common wallaroo = CW, eastern grey kangaroo = EGK and red kangaroo = RK.

Table 5.1 Summary of current climate envelopes for large macropods in northern Australia. Temperature is in degrees Celsius and rainfall in millimetres.

Climate parameter	Antilopine wallaroo			Eastern grey kangaroo			Common wallaroo			Red kangaroo		
	MEAN	MIN	MAX	MEAN	MIN	MAX	MEAN	MIN	MAX	MEAN	MIN	MAX
Annual mean temperature	24.96	202.00	277.00	20.21	123.00	261.00	23.31	138.00	287.00	23.03	187.00	266.00
Maximum temperature of warmest period	34.97	294.00	395.00	30.71	219.00	367.00	34.90	260.00	409.00	37.01	328.00	409.00
Minimum temperature of coldest period	13.03	69.00	208.00	7.70	5.00	169.00	9.78	5.00	189.00	7.28	24.00	135.00
Temperature annual range	21.93	119.00	300.00	23.01	142.00	324.00	25.13	137.00	337.00	29.74	217.00	337.00
Mean temperature of wettest quarter	27.18	237.00	305.00	24.44	168.00	282.00	26.52	123.00	318.00	27.29	125.00	317.00
Mean temperature of driest quarter	21.77	156.00	252.00	16.25	79.00	239.00	20.00	93.00	269.00	19.09	127.00	262.00
Annual precipitation	1079.17	517.00	1859.00	1017.37	187.00	2405.00	732.57	198.00	2547.00	378.47	178.00	806.00
Precipitation of wettest period	69.67	38.00	111.00	46.84	7.00	129.00	45.41	6.00	125.00	21.07	7.00	60.00
Precipitation seasonality (coefficient of variation)	117.27	98.00	129.00	65.66	30.00	129.00	100.63	31.00	132.00	81.17	34.00	135.00
Precipitation of wettest quarter	755.38	375.00	1260.00	503.00	76.00	1271.00	474.88	70.00	1445.00	216.12	75.00	612.00
Precipitation of driest quarter	0.66	0.00	79.00	93.02	0.00	291.00	18.62	0.00	194.00	14.47	0.00	91.00

Table 5.2 Summary of principal components analysis (rotated varimax) of climate variables influencing the distributions of large macropods in northern Australia. Numbers in bold represent factor loadings used to describe each axis.

Axis	PC1	PC2
Variation explained %	31.83	40.26
Variance	3.50	4.43
Climate parameter		
Annual mean temperature	0.66	-0.25
Maximum temperature of warmest period	0.62	0.35
Minimum temperature of coldest period	0.50	-0.69
Temperature annual range	0.00	0.88
Mean temperature of wettest quarter	0.32	0.03
Mean temperature of driest quarter	0.67	-0.32
Annual precipitation	-0.24	-0.96
Precipitation of wettest period	0.26	-0.96
Precipitation seasonality (coefficient of variation)	0.89	-0.31
Precipitation of wettest quarter	0.22	-0.97
Precipitation of driest quarter	-0.95	-0.08

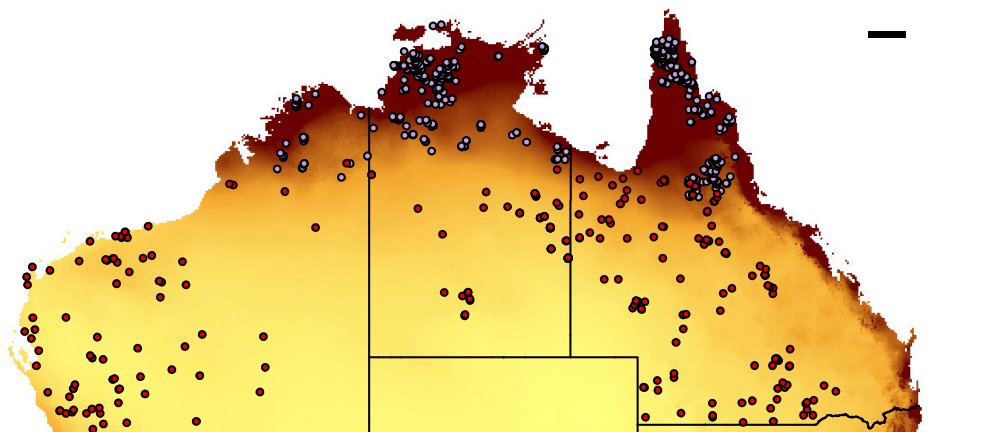


Figure 5.3 Map of precipitation of the wettest period and the distribution of antilopine wallaroos (light blue dots) and red kangaroos (red dots). Areas of higher precipitation are shaded darker and lower precipitation lighter.

The largely sympatric common wallaroo and red kangaroo have greater core and marginal bioclimatic distributions than the antilopine wallaroo and eastern grey kangaroo (Figure 5.4). Both the common wallaroo and red kangaroo are distributed predominantly in the drier interior of Australia, except that the core range of the common wallaroo extends further north than does that of the red kangaroo. The common wallaroo is sympatric in large parts of its range with the antilopine wallaroo. The core distribution of the antilopine wallaroo is confined to the far northern regions of Australia; a gap in its range occurs between Queensland and the Northern Territory. The core distribution of the eastern grey kangaroo is largely confined to eastern Queensland but extends into northern Queensland where it is sympatric with the antilopine wallaroo and common wallaroo.

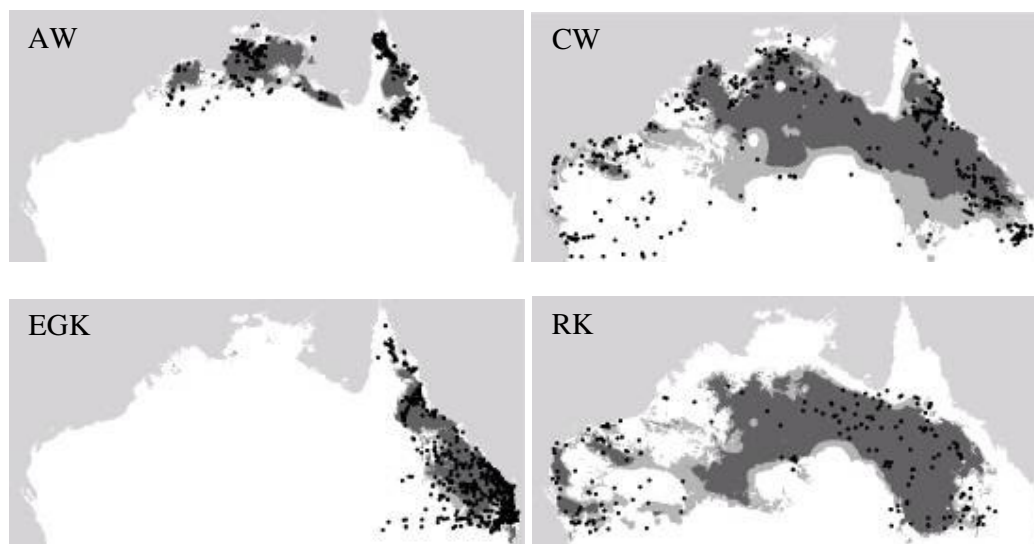


Figure 5.4 Current bioclimatic distributions of large macropods in northern Australia. Core ranges (5 – 95 %) are represented in dark grey and marginal ranges (2.5 - 97.5 %) in light grey. Solid dots represent actual locations for each species. AW = antilopine wallaroo, CW = common wallaroo, EGK = eastern grey kangaroo, RK = red kangaroo. Points occurring outside of shaded areas were included in the initial construction of models but occurred outside of the 97.5% confidence limits of the final model outputs.

Changes to species' distributions under climate change scenarios

The core distributions of all species decreased on average by 9% ($\pm 4.5\%$) with a 0.4 °C increase in temperature combined with either increasing or decreasing rainfall. There were three exceptions to this trend (+ 0.4 °C and - 10 %, + 5 % and + 10 % rainfall) which resulted in minor increases ($0.4\% \pm 0.2 \%$) in the core distribution of eastern grey kangaroos (Figure 5.5). The core distribution of antilopine wallaroos was most reduced ($22 \pm 1 \%$) with an increase of 0.4 °C, whereas the core distribution of eastern grey kangaroos was reduced by only $1 \pm 1.3 \%$ under the same conditions.

Changes to species' distributions are graphically represented for + 0.4 °C, + 2.0 °C, + 6.0 °C and + 5 % rainfall in Figure 5.6. With an increase of 2.0 °C and variation in rainfall, the core distributions of all species were greatly reduced, averaging $48 \pm 16.4\%$ across all species. Again, the core range of antilopine wallaroos was most reduced ($89 \pm 0.4\%$), and suitable climatic conditions for this species and common wallaroos disappear entirely in the Northern Territory and Western Australia. Under the same scenarios, red kangaroos contract south whereas eastern grey kangaroos again show less change than the other species. When temperatures increase by 6.0 °C, there are drastic reductions in the core distributions of all species, averaging $96 \pm 2.1 \%$, and no suitable climatic conditions remain for the antilopine wallaroo. The distributions of the remaining three species contract to the south and become increasingly patchy.

Patterns of sympatry under current and future climates

Overall, the degree of sympatry between species decreases under predicted future climate scenarios (Figure 5.7). Sympatry between antilopine wallaroos and red kangaroos is at present very limited in both Queensland and the Northern Territory, and disappears completely with temperature increases. The antilopine wallaroo remains sympatric with both eastern grey kangaroos and common wallaroos up to an increase of 2 °C, beyond which a suitable climatic environment for the antilopine wallaroo disappears (Figure 5.7). Relatively large areas of sympatry between common wallaroos and red kangaroos remain up to an increase of 6 °C. The eastern grey kangaroo occurs in moderate-sized areas of sympatry with both common wallaroos and red kangaroos up to an increase of 2 °C, beyond which eastern grey kangaroos are no longer sympatric with red kangaroos and show only minimal overlap with common wallaroos.

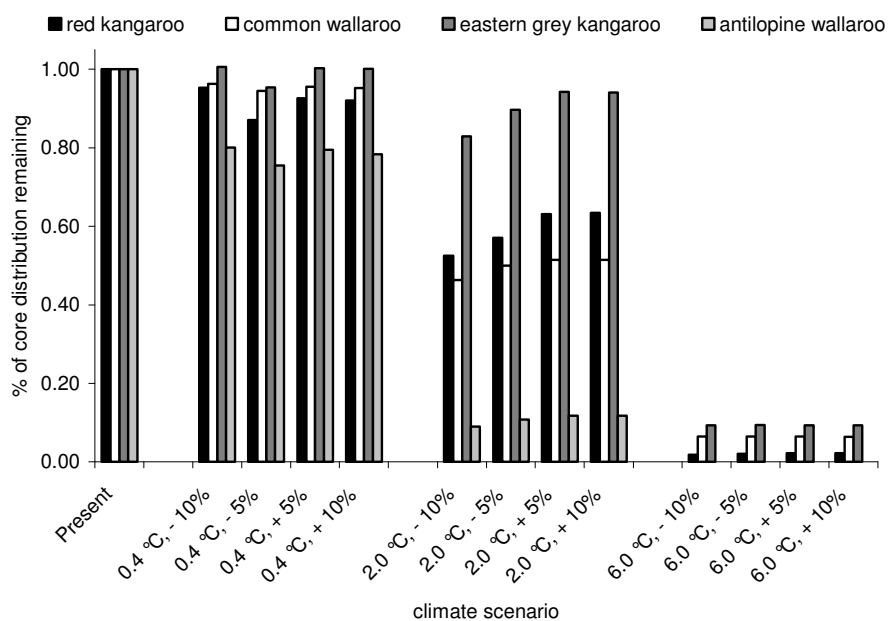
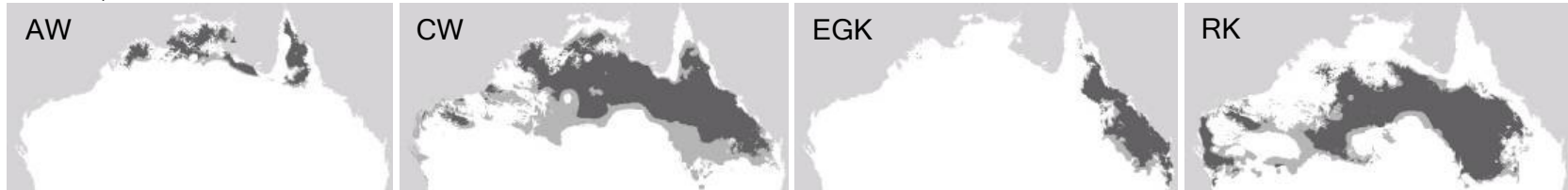
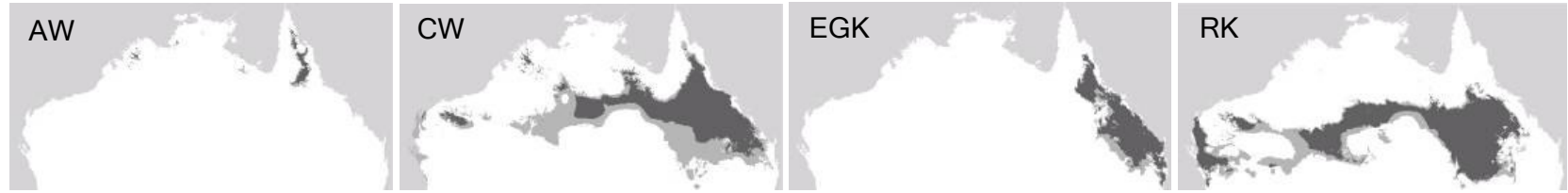


Figure 5.5 Percentage of core bioclimatic distribution remaining for large macropods in northern Australia, under modelled climate change scenarios. All temperatures represent increases from present and – or + signs after temperatures indicate increased or decreased annual rainfall.

+ 0.4° C, + 5% annual rainfall



+ 2.0° C, + 5% annual rainfall



+ 6.0° C, + 5% annual rainfall

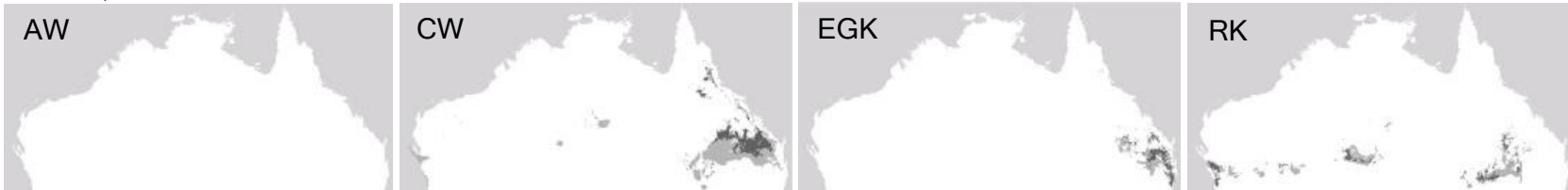
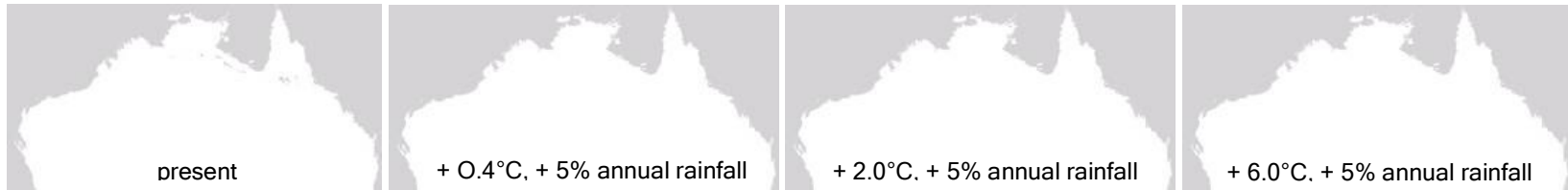
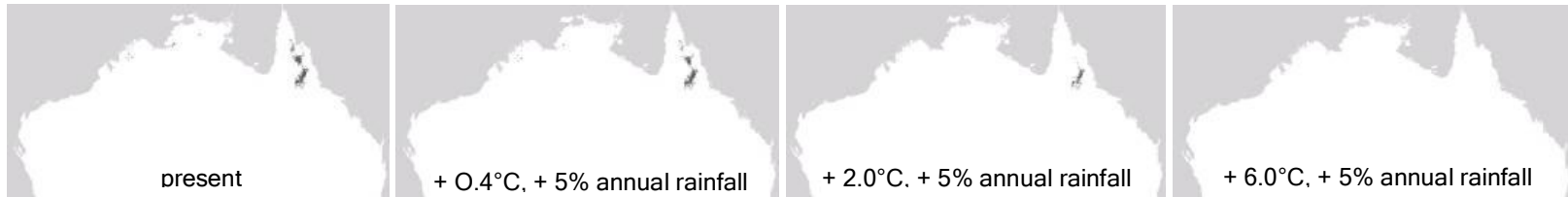


Figure 5.6 Future bioclimatic distributions of large macropods in northern Australia under climate change scenarios. Core ranges (5 – 95 %) are represented in dark grey and marginal ranges (2.5 - 97.5 %) in light grey. AW = antilopine wallaroo, CW = common wallaroo, EGK = eastern grey kangaroo, RK = red kangaroo.

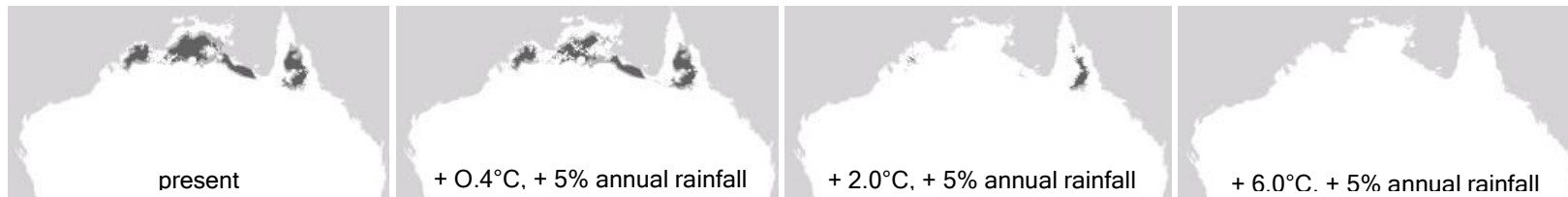
antilopine wallaroo and red kangaroo



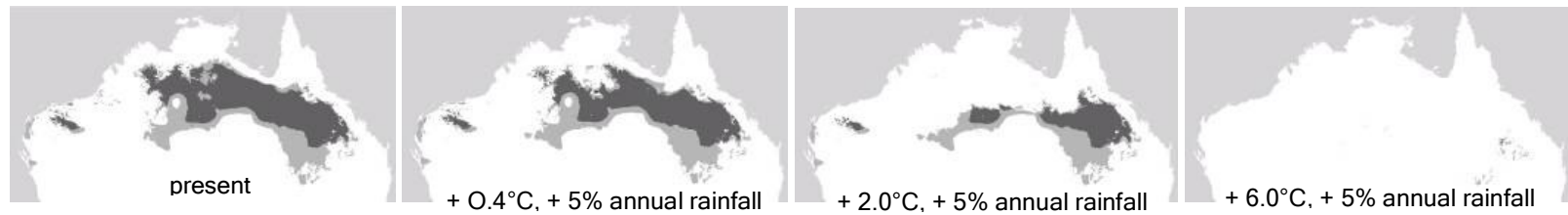
antilopine wallaroo and eastern grey kangaroo



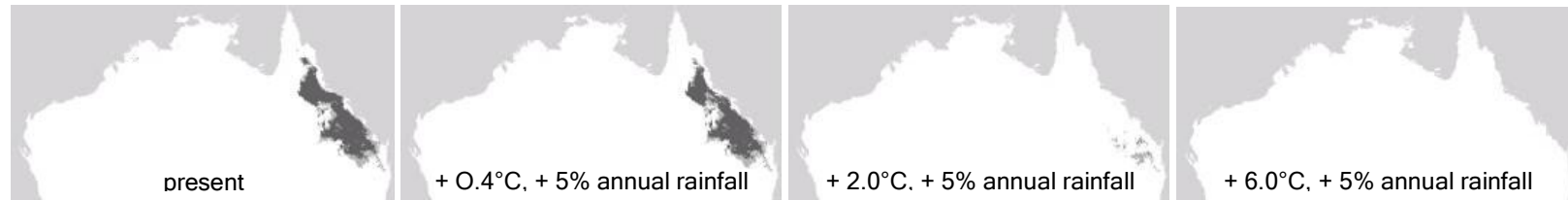
antilopine wallaroo and common wallaroo



common wallaroo and red kangaroo



common wallaroo and eastern grey kangaroo



red kangaroo and eastern grey kangaroo

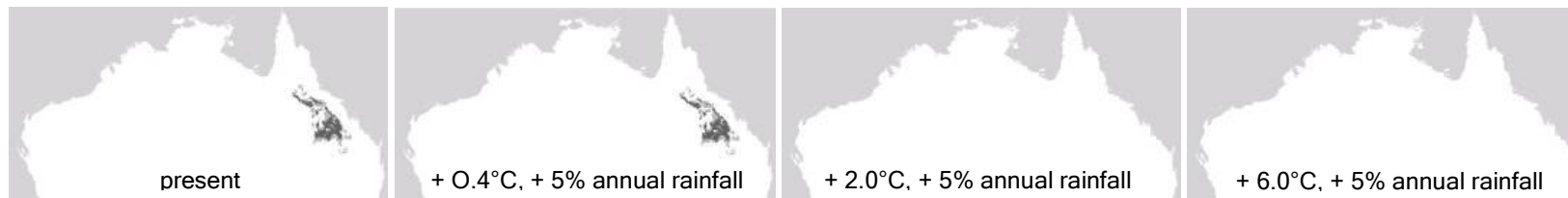


Figure 5.7 Areas of sympatry between large macropods in northern Australia under climate change scenarios. Dark grey indicates areas where species overlap in their core distribution (5 – 95 %) and light grey their marginal distribution (2.5 - 97.5 %).

Discussion

Our results indicate that the distribution of large macropods in northern Australia is strongly associated with two principal climatic gradients (tropical and subtropical). These findings demonstrate the way in which large-scale processes may influence the composition of macropod communities, but, perhaps more importantly, highlight the sensitivity of different species to changes in climate. Our modelling suggests that future variation in climatic gradients governing the distributions of macropods has the potential to result in significant distributional changes for our study species. The distributions of macropods appear to be particularly sensitive to predicted climatic change with an increase of as little as 0.4°C resulting in substantial contraction of projected ranges. For increases beyond 2.0°C, the core distributions of all four species were severely reduced. As we predicted, the antilopine wallaroo appears to be the most vulnerable of the four species. We highlight the finding that all currently suitable climatic habitat of this species disappears with temperature increases in the range of $\geq 2 - 6^{\circ}\text{C}$, widely considered to be inevitable by 2070. Our results demonstrate that large macropods, despite being highly mobile and having relatively large distributions, are at significant risk of severe range contraction and/or possible extinction, as a result of future climate change. This finding is echoed in studies of other large mammals (Callaghan *et al.*, 2004; Derocher, Lunn & Stirling, 2004; Ogutu *et al.*, 2003; Weladji & Holand, 2003).

Distributions of large macropods in northern Australia

Macropods have evolved a diverse array of adaptations which allow them to occupy a vast range of climates and habitats in Australia (Dawson, 1995; Dawson *et al.*, 2000a; Dawson *et al.*, 1969; Dawson *et al.*, 2000b). It is these adaptations, and their variation among species, that will presumably be crucial in determining the responses of individual species to climate change. Consider, for example, reproduction in the red kangaroo and antilopine wallaroo, the former being largely aseasonal (Frith & Sharman, 1964), the latter highly seasonal (Chapter 3). It is often suggested that one reason why the red kangaroo is able to occupy arid habitats is the reproductive adaptation known as embryonic diapause (Dawson, 1995; Tyndale-Biscoe *et al.*, 1987). This adaptation allows females to regulate the timing of the development of young in response to

temporal variability in resource availability, which is characteristic of the Australian arid zone (Dickman *et al.*, 2001; Norbury, Norbury & Oliver, 1994). It remains unclear whether antilopine wallaroos possess this adaptation but anecdotal evidence suggests that they do not (Poole *et al.*, 1987). The lack of embryonic diapause could explain why antilopine wallaroo breeding is highly seasonal, centred around monsoonal rains (Chapters 2 and 3), and why their range does not extend into arid habitats, presumably where red kangaroos may have a competitive advantage in reproduction.

A second hypothesis is that red kangaroos have a competitive physiological advantage over antilopine wallaroos in their ability to reduce water loss and cope with low water availability (Dawson, 1995). There are currently no reliable predictions for the effects of climate change on the monsoon in Australia so we did not model the response of species' distributions to changes in rainfall seasonality. There is very limited overlap in the current ranges of red kangaroos and antilopine wallaroos (see Figure 5.3). Flannery (2004) has speculated that red kangaroos may have speciated from populations of antilopine wallaroos on the edge of the arid zone. Resolving this issue requires a well-resolved molecular phylogeny and broad phylogeographic assessment for the Macropodidae.

Our modelling suggests that temperature may have more influence on macropod distributions than rainfall. A limitation of our approach, however, common to many climate change studies, is that we did not consider the importance of rainfall seasonality, as discussed above. There are currently no detailed predictions for the effects of climate change on the seasonality of rainfall in Australia, and of particular interest for this study, the effect on the monsoon. However, more generalised predictions for northern Australia are for increased variability and severity of the dry season in the future (Houghton *et al.*, 2001), which may have important ecological consequences. Ephemeral water holes are an important resource for species in the dry season (James, Landsberg & Morton, 1999; Redfern *et al.*, 2003), when rivers and streams typically stop flowing. If dry seasons are to become more severe and unpredictable, waterholes may dry up. This may result in animals having to move larger distances to find water, or lower survival for those species that are less mobile. A recent model simulation by Saltz *et al.* (2006) demonstrated that scenarios of increased variation of rainfall predict marked changes in population size and in some cases increased extinction probability for the Asiatic wild ass (*Equus hemionus*).

Impacts of climate change on species' distributions: the importance of ecological considerations

We acknowledge that our study is correlative rather than mechanistic in its nature (for discussion of this distinction see Kearney, in press), and that other factors besides climate may be as important in limiting species' distributions (e.g. habitat preferences and interspecific interactions). However, if we accept the strong nexus between distribution and environment (Lawton, 1995), our results do provide evidence that climate change has the capacity to cause significant changes to the distributions of large macropods.

There are at least five important, non-mutually-exclusive factors that must be considered when assessing the impact that climate change is likely to have on large macropods: nutrient availability and habitat preferences (Chapter 2); speed of climate change; population size and connectivity; direct and synergistic effects; and interspecific and community effects (Chapter 2). The first two of these, nutrient availability and habitat preferences, and the speed of climatic changes, are intimately related. It is already evident that species which are not restricted by altitude are reacting to climate change by shifting away from the equator (Parmesan *et al.*, 1999; Parmesan *et al.*, 2003; Root *et al.*, 2003). Latitudinal movement may ensure the survival of some species, but for species from other regions this may not be possible, as soil types and topography (which strongly influence the composition and nutrient availability of vegetation) are unlikely to shift at the same pace as the animals that are reliant upon them. Again we use antilopine wallaroos and red kangaroos to illustrate this point. It is easy to suggest that as temperatures increase, antilopine wallaroos may be able to migrate south. However, it is important to note that the edge of the range of the antilopine wallaroo and the beginning of that of the red kangaroo is marked by a transition from sandy and alluvial soils to cracking clays and nutrient-poor desert sands. The diet of the antilopine wallaroo consists of > 80% tropical grasses (Fossan, unpublished data) whereas red kangaroos feed on both grasses and forbs which grow in arid areas (Belovsky *et al.*, 1991; Dawson & Ellis, 1994). It remains uncertain whether antilopine wallaroos would graze arid zone plants. So even if the suitable climatic environment of the antilopine wallaroo were hypothetically to shift south with

increasing temperature, with the speed at which climate is predicted to change (see Hughes, 2003), it seems unlikely that desert habitats would become tropical savanna in less than 70 years. Therefore, the preferred habitat and food source of antilopine wallaroos would disappear.

The third consideration, population size and connectivity, relates to the fracturing of species' distributions and their subsequent increased susceptibility to stochastic events. Our modelling shows that not only will macropod ranges decline in size, but also in connectivity. This has important consequences because, as they become smaller and more isolated, populations are likely to become more vulnerable to chance events (e.g. disease). Recovery of populations from such events will be affected by reduced immigration. Indeed, Shoo *et al.* (2005b) point out that consideration of population size is just as important as distribution size when considering the potential impacts of climate change.

The fourth consideration is the direct response of the species themselves, and synergistic effects. Ecological adaptations and their variation among species will presumably be crucial in the responses of individual species to climate change. The antilopine wallaroo, as a seasonal breeder (Chapters 3 and 4), may well decline at a faster rate than our models suggest. If monsoons begin to fail or shift, antilopine wallaroo breeding may be reduced or fail. Cases of climate-induced changes to breeding cycles and population density have been shown in many species (Anders & Post, 2006; Chambers, Hughes & Weston, 2005; Parmesan *et al.*, 2003). Coupling a decline in reproduction with a declining food source and a reduction in immigration predicts a dire future scenario for the antilopine wallaroo.

Lastly, to understand the likely impacts of climate change on species' distributions, it is vital that we incorporate interspecific and community interactions as considerations into study designs (Humphries, Umbanhowar & McCann, 2004; Peterson *et al.*, 2002; Romme & Turner, 1991). For example, species turnover may increase with global climate change as demonstrated by Thuiller *et al.*'s (2006) study of African mammals. Species turnover may pose significant challenges to reserve design, particularly where individual species are being targeted for conservation. Our results indicate that there are likely to be significant changes to the distributions of macropod assemblages in northern Australia, with an overall reduction in areas of sympatry.

South-east Queensland is most likely to support the highest diversity of large macropods in the future according to predicted distributions.

Our study provides evidence that climate change has the capacity to cause large-scale range contractions and the possible extinction of large macropods in northern Australia. The extinction of the antilopine wallaroo would constitute a significant cultural and economic loss to Indigenous people of northern Australia (Busby, 1988), a situation similar to that being experienced by residents of the Arctic and caribou (Weladji *et al.*, 2003). Our predictions regarding climate change are testable at the margins of the range of the antilopine wallaroo, where it is likely to be most sensitive. Monitoring in these areas will provide guidance for management. To understand how climate change is likely to affect macropods, and other species, in finer detail, there is an urgent need for studies that determine the factors limiting species' distributions (Hughes, 2003; Peterson *et al.*, 2001). Such information will then allow a shift from correlative approaches to mechanistic models of species distributions (see Kearney, *in press*; Kearney & Porter, 2004), and therefore better inform conservation managers on actions that can be taken to mitigate the impacts of climate change on species' survival.

Chapter 6

General discussion

My study identifies and models the factors influencing the distribution and abundance of the antilopine wallaroo (*Macropus antilopinus*) across its geographical distribution and at smaller spatial scales; reports on the socio-ecology and patterns of behaviour of multiple populations of several species of large, tropical, sympatric macropods; and provides an initial assessment of the susceptibility of large macropods to future climate change in northern Australia.

Specifically, I have shown that:

Across its distribution, abundance of the antilopine wallaroo was largely controlled by the frequency of fire (+), the availability of permanent water (+) and an interaction between soil fertility (geology/soil type) and land management. Antilopine wallaroos were most abundant on cattle grazing properties with basalt soils. Within Queensland, the influence of interspecific interactions (abundance of eastern grey kangaroos, *M. giganteus*) and aspects of habitat structure and composition were also important. Different factors affected the distribution and abundance of two sympatric species, the eastern grey kangaroo and common wallaroo (*M. robustus*). In particular, climate was a key influence on the abundance of both species and fire had a negative effect on the abundance of the common wallaroo. I have identified some minor and one major discontinuity in the antilopine wallaroo's range that appear to be imposed by contemporary habitat and climate features. A complete understanding of this species' macroecology requires that we understand the history of these breaks (barriers), and their effects on the species' evolution and genetic structure. I have begun investigating this through a phylogeography study, which I summarise in Appendix 3.

The antilopine wallaroo was the most gregarious macropod in northern Australia and had a highly seasonal pattern of reproduction. Social dynamics appeared to be closely associated with breeding phenology, and the nature of associations between sexes and size-classes changed seasonally from predominantly mixed during the mating

period (wet season) to single-sex in the non-mating period (dry season). The social behaviour of other sympatric macropod species varied from essentially solitary (common wallaroos and agile wallabies, *M. agilis*) to gregarious (eastern grey kangaroos and whiptail wallabies, *M. parryi*). The strongly seasonal pattern of breeding of the antilopine wallaroo was not shared by sympatric populations of eastern grey kangaroos and common wallaroos.

The antilopine wallaroo exhibited moderate levels of sexual segregation (social) that appeared to be strongly linked to this species' seasonal breeding, which in turn was associated with highly seasonal rainfall, characteristic of tropical savannas. There may be different explanations for segregation of the two sexes outside the breeding season; for males the group composition data were consistent with the possibility that males form all-male groups in which interactions leading to the establishment of a dominance hierarchy occur.

Models of potential climate change for northern Australia demonstrated a significant potential threat to the survival of large macropods, particularly the antilopine wallaroo, which appears most sensitive and which may suffer severe range contractions with temperature increases in the range of 2 - 6° C above present conditions.

Niche requirements of large macropods within Australia's tropical savannas

My study has identified and modelled many of the key environmental and biological factors limiting the distribution and abundance of the antilopine wallaroo across its geographical distribution, and also those factors limiting the northern distributions and abundance of the sympatric eastern grey kangaroo and common wallaroo. Few studies have collected detailed information at this scale, despite its theoretical (Murphy *et al.*, in press; Peterson *et al.*, 2001; Sagarin *et al.*, 2006) and applied importance (Gordon *et al.*, 2004; Hughes, 2003; Rondinini *et al.*, 2005). I show that different factors may be important to explaining species abundance patterns at different scales, which demonstrates that general predictions from small-scale studies are likely to be over simplified. My study indicates that the distribution and abundance of the antilopine wallaroo appears to reflect the spatio-temporal variability of resource distribution that is characteristic of Australia's tropical savannas. In addition, I have provided the only comprehensive study of the socio-ecology and behaviour of the

antelope wallaroo and sympatric macropods in tropical Australia. The combination of these broad-scale ecological data with more detailed, fine-scale social information on tropical macropods, contribute substantially to a greater understanding and synthesis of the ecological and evolutionary relationships within the family Macropodidae, which, prior to my study, were based predominantly on studies in temperate Australia (Grigg *et al.*, 1989).

In an applied context, my research identifies the individual requirements of the antelope wallaroo and, to a lesser degree, the common wallaroo and eastern grey kangaroo, potentially greatly assisting in their conservation and management. More broadly, the scale of my study will facilitate insights into some of the processes and drivers (e.g. fire regimes, land management and climatic gradients) that may be important in shaping the distribution patterns of other species inhabiting tropical savannas, and in turn contribute towards their conservation. I have shown that the antelope wallaroo's specific niche requirements make it the most susceptible of the large macropods to suffer range contraction in response to predicted future climate change in northern Australia.

Future directions

Having established a series of sampling sites which have revealed the limits to distribution and abundance of the antelope wallaroo, it will be crucial to systematically re-survey the sites in the future to monitor the populations and assess their responses to climatic changes. I also acknowledge that despite the scale of my study, there still remain large areas of Northern Australia that were not surveyed due to logistical constraints. Included are those habitats that were not easily accessible by vehicle tracks (in particular the Arnhem Land plateau).

A logical next step would be to experimentally manipulate the critical factors identified in models to investigate their relative importance to the abundance of macropod species. Fire appears to have a particularly important effect on the abundance of antelope wallaroos (+) and common wallaroos (-), and this could be tested with a landscape experiment employing a variety of regimes. The strength of the negative association between eastern grey kangaroos and antelope wallaroos is strongly suggestive of interspecific competition, which has not yet been demonstrated in large

macropods (Dawson, 1995). Detailed analysis of the diets and habitat use of these two species in sympatry and allopatry in north Queensland may provide further clues to the nature of this relationship and the possible presence of niche partitioning between the species. Coupling this information with the results from my study, and also collecting physiological information for the antilopine wallaroo, may allow the distinction between the fundamental and realised niche of this species to be characterised; such characterisation has rarely been achieved (see Kearney *et al.*, 2004). This would permit the development of a more mechanistic understanding of the limits to distribution and abundance of the antilopine wallaroo, and the ways in which the species may be specifically affected by climate change.

I have demonstrated that the pattern of reproduction of the antilopine wallaroo is highly seasonal in comparison with most large macropods (Chapters 3 and 4), with the exception of the temperate western grey kangaroo, *M. fuliginosus* (MacFarlane *et al.*, 2005b), a species lacking embryonic diapause. It remains unknown whether the antilopine wallaroo possesses this trait, but limited indirect evidence suggests that it does not (Poole *et al.*, 1987). Confirming its presence or absence in the antilopine wallaroo may provide useful insights into the evolution of this species' reproductive pattern in relation to the seasonal climate of northern Australia. Further, the seasonal reproductive patterns of these two species are strongly linked with sexual segregation behaviour (Chapter 4 and MacFarlane *et al.*, 2005b). If indeed antilopine wallaroos lack embryonic diapause, consideration of both species may help to explain why similar patterns of social behaviour have evolved in parallel in response to seasonal variation in climate within both tropical and temperate Australia. Lastly, the mating system of the antilopine wallaroo should be examined via a genetic study. It is generally assumed that male body size is a primary determinant of male mating success in large macropods (Grigg *et al.*, 1989), but this has not been tested in any species to date. This information will provide further understanding of sexual segregation behaviour and the social and mating systems of macropods.

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Appendix 1

An extension to the known range of the eastern grey kangaroo (*Macropus giganteus*) on Cape York Peninsula

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The eastern grey kangaroo (*Macropus giganteus*) is one of Australia's widest-ranging large macropodids, occurring in open forests, woodlands, subalpine woodland, farmland, and semi-arid regions throughout most of eastern Australia (Menkhorst and Knight 2001). However current general accounts (e.g. Poole 1995, Menkhorst and Knight 2001) regard *M. giganteus* as being absent from the northern Cape York Peninsula.

As part of a study of the macroecology and conservation of the antilopine wallaroo (*M. antilopinus*) on Cape York Peninsula, I collected locality data for all macropodids encountered during surveys. Here I report on a significant northern extension of the known range of *M. giganteus* to Bramwell Station (Latitude -12.15, Longitude 142.72), approximately 330 km beyond its reported range. I sighted one adult male and two adult female *M. giganteus* on 22 May 2004 from a vehicle in mixed, open Eucalyptus woodland. I distinguished *M. giganteus* from *M. robustus* and *M. antilopinus* (the other two large sympatric macropodids) by its distinctive hairy muzzle, uniform grey coat and distinct black tail tip, whereas both *M. robustus* and *M. antilopinus* have relatively bare muzzles, lack a distinct black tail tip, are shorter and of more muscular build and their colouration is different, particularly *M. antilopinus*, which is red and white (see Poole 1995 and Menkhorst and Knight 2001). The figure 1 shows the new locality data for *M. giganteus* and all Queensland records. I have made numerous sightings outside *M. giganteus*' reported range, with Bramwell Station representing the most northerly sighting. The two western-most Cape York sightings are from Strathgordon Station (Latitude -14.76, Longitude 142.12) and Mungkan Kandju National Park (Latitude -13.58, Longitude 142.68).

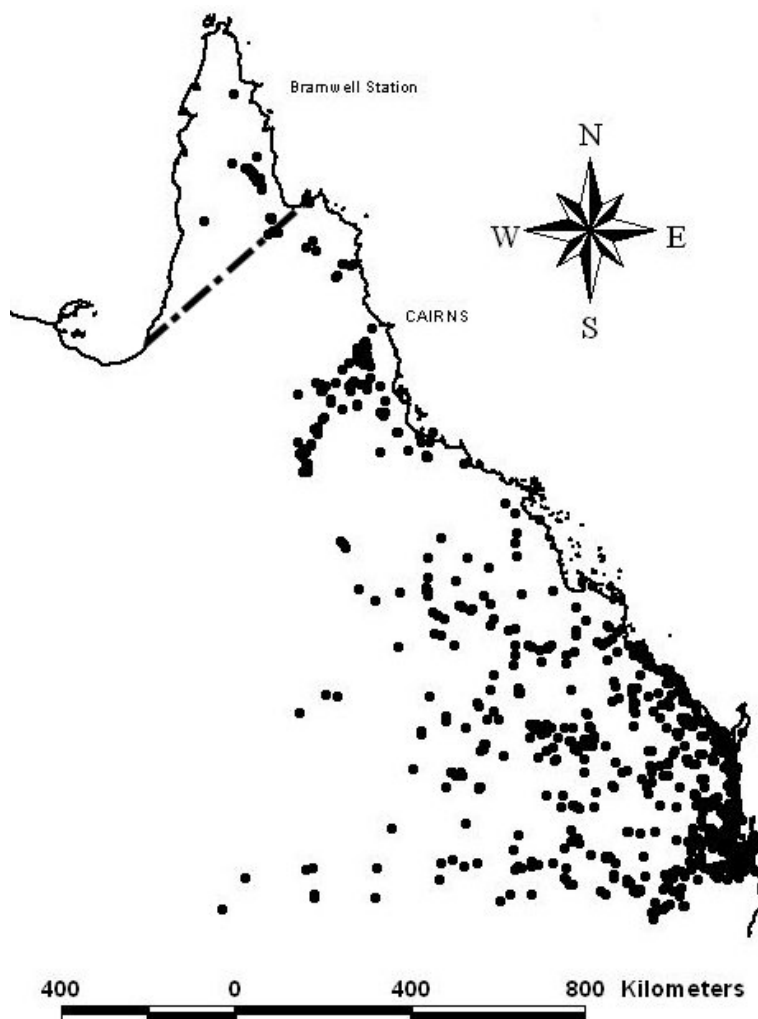


Figure 1 Distribution of the eastern grey kangaroo (*Macropus giganteus*) in Queensland. The broken black line represents the approximate previously assumed limit to *M. giganteus*' range (Poole 1995). Dots in Cape York above the black line occur outside *M. giganteus*' current known range. The most northerly dot indicates the record from Bramwell Station.

Whether this is a genuine range shift remains unclear: it is possible that *M. giganteus* has always occupied this area but has not been recorded because of observer error or low survey effort due to the relative inaccessibility of the area. It is also important to note that the edges of range maps are known for their inaccuracy. If there has been an expansion of range it is presumably a consequence of habitat change, possibly associated with the effects of cattle grazing, the dominant land use on Cape

York Peninsula (e.g. altered fire regimes, the establishment of permanent water, removal of dingos; see Calaby and Grigg 1989 and Flannery 1994). Alternatively the shift may be the result of subtle habitat alteration associated with climate change or other unidentified factors.

Establishing the cause of this range extension is important. There is much conjecture over the way in which European settlement has shaped the current distribution and abundance patterns of Australia's macropodids (Calaby and Grigg 1989, Auty 2004). However, perhaps the most interesting element of these changes to macropodid distributions is the effect they are having on interspecific interactions and macropodid community ecology in general.

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Appendix 2

The effect of an extensive, late, dry season fire on the abundance of three sympatric large macropod species in Undara volcanic national park, northern Australia.

In review: Australian Mammalogy

Abstract

Fire is a prominent feature of the tropical savannas of Northern Australia but there remains little information as to its effect on the species which inhabit this region. In November 2003 a large, late, dry season wildfire burnt the majority of Undara Volcanic National Park over two days. I recorded the abundance of three macropod species (Macropodidae) in Undara Volcanic National Park before and after this fire and thereby had the opportunity to examine their short-term responses to fire. There were no significant changes in the abundance of antilopine wallaroos (*Macropus antilopinus*), eastern grey kangaroos (*Macropus giganteus*) and common wallaroos (*Macropus robustus*) from pre- to post-fire. I suggest that in this case the severity of the fire was ameliorated by the onset of the wet season and the subsequent rapid regeneration of grass. The speed and scale of this fire would have likely posed a greater threat to smaller, less mobile or specialist species.

Introduction

Fire is a dominant feature of Australia's landscape, and there has been a considerable amount of research into its relationship with the Australian biota (see Gill *et al.*, 1981). However, our knowledge of fire ecology until very recently has been biased towards southern Australia (Caughley *et al.* 1985, Johnson 1995, Meers and Adams 2003, Williams *et al.* 2003) and we therefore require more studies to allow appropriate management of fire and its effects in the savannas of northern Australia. Tropical savannas comprise approximately one quarter (1.9 million km²) of mainland

Australia, with fire and rainfall seasonality being the two most dominant abiotic influences. The typical contemporary burning regime in much of this area is one of large, late, dry season fires, with a small fire return interval (Edwards et al. 2001). Because of this, many areas have seen a reduction in the local diversity of plant species and habitat complexity. The traditional regime employed by indigenous people was one of frequent, but small-scale fires, with longer fire return intervals (Yibarbuk et al. 2001). This apparent shift in the fire regime has been postulated as one possible cause of the large-scale vertebrate decline, that is currently occurring in Northern Australia (Woinarski et al. 2001, Woinarski and Fisher 2003, Woinarski et al. 2004).

The tropical savannas of northern Australia are characterised by a small and geographically sparse human population. In addition, much of this area is remote, which generates a significant obstacle to field-based research. Recent advances in satellite imagery and the development of geographical information system (G.I.S.) technologies provide a solution to this obstacle. There is now relatively accurate and broad-scale information on the occurrence of fire across northern Australia (see www.firenorth.org.au).

I studied a macropod (Macropodidae) community at Undara Volcanic National Park (North Queensland) between 2002 and 2005, as part of a larger project investigating the macroecology and conservation of the antilopine wallaroo (*Macropus antilopinus*) in Queensland. Between November 23 and 25 2003, a large wildfire burnt greater than 80% of this park over two days; I was surveying this area on the day of the fire. This provided a rare opportunity to investigate the way in which macropod species respond in the short-term to a fire of this magnitude. This information is particularly valuable as there is little documentation of the effects of fire in northern Australia on large, highly mobile marsupials, such as members of the *Macropus* genus. Here I report on the abundance of three macropod species before and after the 2003 Undara fire.

Methods

Study site

The investigation was conducted at Undara Volcanic National Park (-18° 17' S 144° 37' E), 275 km southwest of Cairns (Figure 1a). The study area consisted of a five km long transect (between -18° 14' 13.4", 144° 33' 35.2" and -18° 16' 20.9", 144° 32'

31.4"), which was on an unsurfaced and restricted access track otherwise used only by park staff. Undara Volcanic National Park consists of tropical savanna woodland, interspersed with vine thickets and dry rainforest which grow in and around the lava tubes. The soils are predominantly basaltic, derived from the Undara shield volcano which erupted approximately 190,000 years ago. Undara Volcanic National Park arguably supports the richest local macropod fauna of anywhere in Australia, with twelve species recorded (Johnson, 2003). Less than 5mm of rain fell in the area in the month prior to the fire but more than 100mm fell in the month immediately after the fire (Australian Bureau of Meteorology). The three macropod species encountered within my study area were the antilopine wallaroo, common wallaroo (*Macropus robustus*), and the eastern grey kangaroo (*Macropus giganteus*).

Survey technique

I surveyed the study area six times between November 2002 and November 2005 (comprising four dry seasons and two wet seasons). During each of these survey periods, the transect was surveyed twice in the afternoon and twice in the morning. I decided to use repeat surveys to increase the precision of my abundance estimates, considering the high mobility and large home ranges of each of the three macropod species (Strahan, 1995). Surveys were conducted each morning beginning at first light (5.30-7.30am) and each afternoon (5-6.30pm), approximately one and a half hours before dark. Surveys were conducted from a vehicle driving at 10 km/hr, with observers in the rear of the vehicle visually scanning the habitat for any macropods. When a macropod was spotted, the vehicle would stop and I recorded the species observed and the group size. The abundance of each macropod species per kilometre was calculated by dividing the number seen by the length of the transect, averaged over the four transects for each of the six survey periods. Due to the low number of replicates I could not use conventional line transect methodology to estimate abundance reliably. However I was confident that there were no significant sightability issues, as the habitat of the transect was relatively uniform along its entirety, and my studies in Queensland have indicated no significant sightability differences between the three macropod species in this study (Ritchie, unpublished).

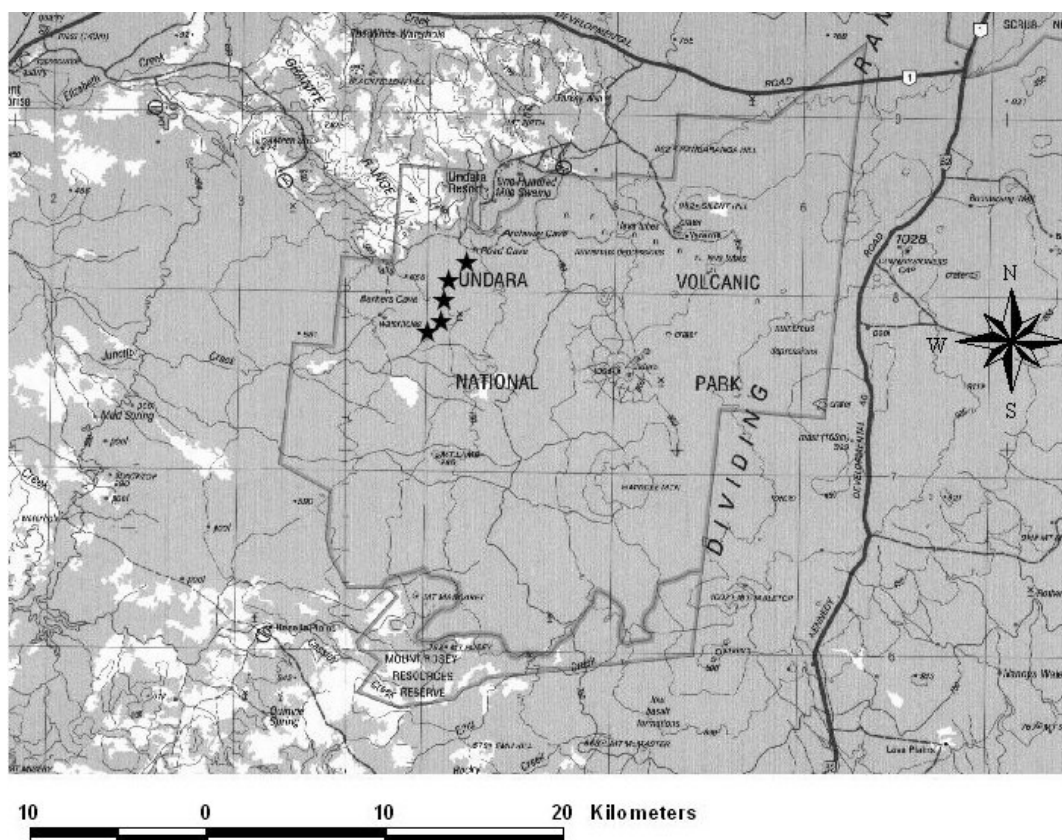


Figure 1a The study site at Undara Volcanic National Park. Each star represents a vegetation survey site and together the total length of the transect.

Vegetation survey

The dry season survey was conducted from November 23 to 24 2003, prior to the fire, and the wet season survey was conducted from February 16-19 2004, after the fire. For each period, I completed vegetation surveys at 5 sites, spaced 1 km apart along the 5 km transect. At each site, I visually measured the greenness of the grass on an increasing scale from 0-4, and the percent coverage of the canopy at four intervals (canopy - 5 m, 5 m – 2 m, 2 m – 1m and <1 m). I measured the biomass of grass by clipping and weighing all grass within a 1 m quadrat. I did this six times (each pair of quadrats spaced 20 m apart) at each of the five sites, making a total of 30 replicates.

Fire mapping

The Cape York Peninsula Development Association provided Modis satellite monthly fire scar summary data for 2002-2005. I used this data in Arcview 3.3 to examine the timing, location and extent of fires in Undara Volcanic National Park during this period. Modis satellite imagery provides a resolution of 250 m.

Macropod abundance

To examine the effect of fire on each macropod species I compared their relative abundance pre- (dry seasons of November 2002 and 2003) and post-fire (dry seasons of November 2004 and 2005). The wet season abundances of the three macropods were not recorded pre-fire. I therefore decided to exclude wet season abundances post-fire from the analysis, as wet season abundances are typically higher than dry season abundances (Ritchie, unpublished), and may have confounded results.

Results

Fire information

An extensive fire occurred in Undara Volcanic National Park between 23 and 25 November 2003 (Figure 1b). The fire burnt the transect area on the evening of November 24. The fire was intense and caused extensive crown firing; the ground layer was almost completely burnt with few patches remaining unburnt. Unburnt patches were largely confined to the collapsed lava tubes, which due to their rockiness are partly protected from fire. Fires occur regularly in Undara Volcanic National Park (Ritchie, unpublished), however this was the only fire to occur in the transect area from 2002-2005.

Vegetation summary

There were no major differences in the structural complexity of the habitat pre and post fire (Table 1). The percent coverage, greenness and biomass of grass were higher 12 weeks post fire than immediately pre fire.

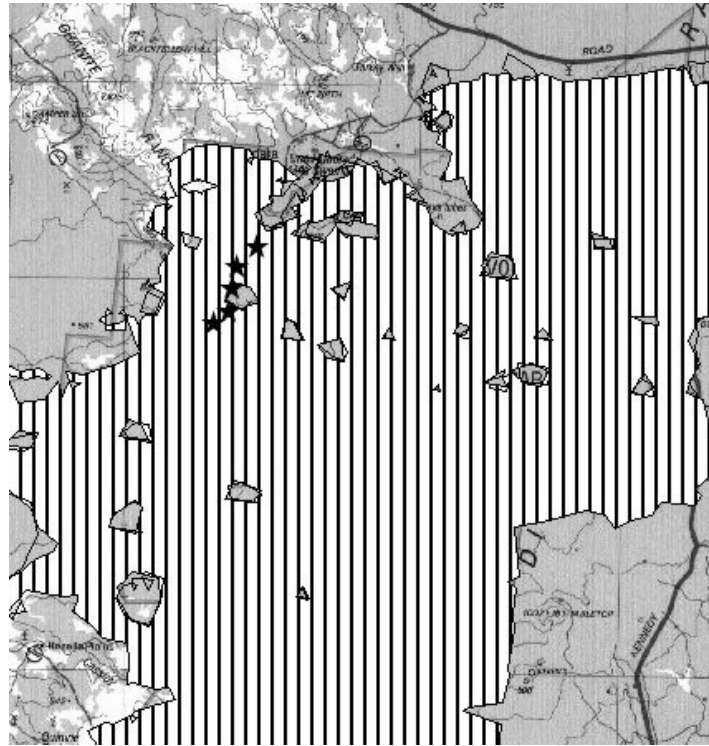


Figure 1b The study site showing the extent of the fire, represented by the horizontal bars.

Macropod abundance pre and post fire

The three species behaved differently with respect to abundance pre and post fire (Figure 2 and Table 2). Antilopine wallaroos were the most abundant of the three species throughout the study, and increased in abundance in the wet season of 2004 (post fire). Eastern grey kangaroos increased during this same time period whereas common wallaroos decreased in abundance. However, there were no significant changes in abundance for any species between the dry seasons pre- and post-fire.

Table 1. Vegetation summary pre- and post-fire for Undara Volcanic National Park. Values show mean (standard error).

	dry season (November 2003)	wet season (February 2004)
% Coverage		
Canopy	10 (5)	10 (1.9)
Canopy-5m	5 (0.3)	5 (1.5)
5m-2m	5 (1.2)	5 (1.5)
2m-1m	5 (0.3)	5 (0.7)
<1m	50 (20.8)	75 (6.7)
Greenness	0.9 (0.05)	2.5 (0.1)
Biomass g/m	98 (23.4)	272 (46.8)

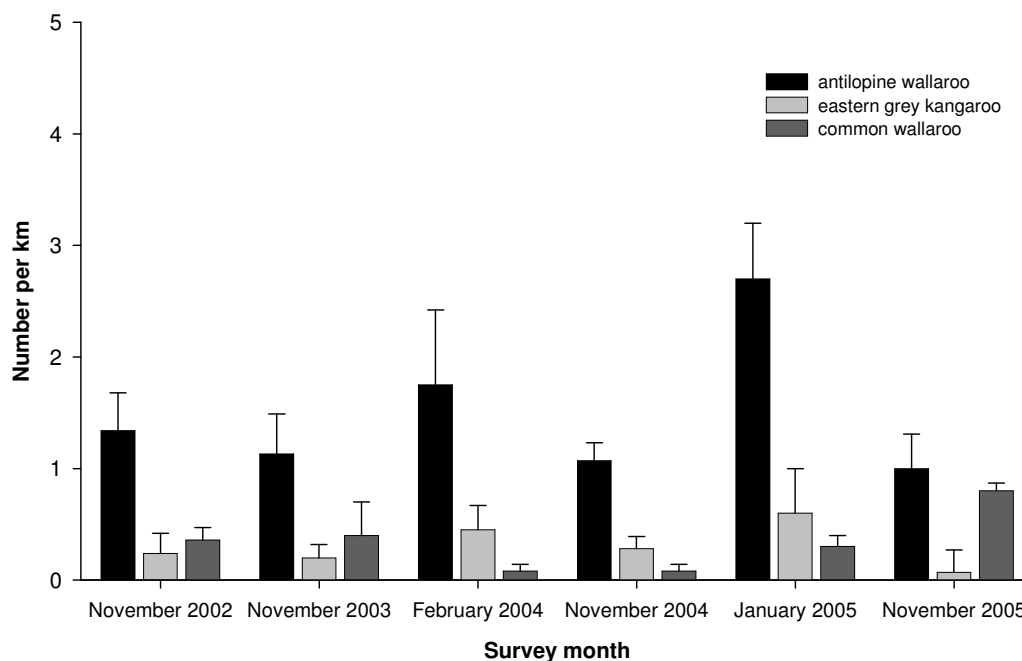


Figure 2. Abundance of antilopine wallaroo (*Macropus antilopinus*), eastern grey kangaroo (*M. giganteus*) and common wallaroo (*M. robustus*) at Undara Volcanic National Park pre and post fire.

Table 2. Test results comparing abundance of antilopine wallaroo (*Macropus antilopinus*), eastern grey kangaroo (*M. giganteus*) and common wallaroo (*M. robustus*) at Undara Volcanic National Park pre- and post-fire.

species	t-test	d.f.	<i>p</i>
<i>M. antilopinus</i>	1.8	2	0.2
<i>M. giganteus</i>	0.4	2	0.7
<i>M. robustus</i>	-0.2	2	0.9

Discussion

My study shows that the extensive late dry season fire in Undara Volcanic National Park in November 2003, had no lasting effects on the relative abundance of three large macropod species (antilopine wallaroos, eastern grey kangaroos and common wallaroos). I suggest that the severity of the fire was ameliorated by the rapid onset of the wet season and the subsequent rapid regeneration of grass. In addition, small patches of unburnt grass confined to collapsed lava tubes may have supported macropods in the interim. There were some differences in the pre- and post-fire abundance trends of each macropod species, as was found by (Southwell and Jarman 1987), but in my study these differences were not significant. It appears likely that the initial wet season post-fire increase in abundance of antilopine wallaroos and eastern grey kangaroos in 2004 were most likely attributable to the change in the habitat associated with the onset of the wet season (increased grass biomass), as a similar trend from dry to wet seasons was also observed in 2005. However without increased replication of fires and wet season surveys of abundance, this remains to be determined.

Although this study is small in its geographical and temporal scale, it raises two important issues of broad-scale importance. Firstly, the timing of fires is crucial. Consider a fire of this geographical magnitude occurring earlier in the dry season (August – October). This potentially would result in a prolonged period of minimal forage due to the complete absence of rain, which assists grass regeneration following fire. In my study population eastern grey kangaroos and antilopine wallaroos would be disadvantaged most, as they both consume a high proportion of grass in their diets, whereas common wallaroos are more generalist browsers, readily switching between

grasses, forbs and shrubs (Ritchie, unpublished). Therefore, some species may be forced to move large distances in order to find areas with sufficient food. This scenario highlights a second issue: the scale of fires relative to animal size and mobility. Some animals that also occur in this park would have likely perished as a result of this fire, for two reasons. Firstly, the size and speed of this fire would have killed animals that were not highly mobile or able to seek refuge. Secondly, those animals that survived the fire would have been faced with a habitat that was substantially different in terms of its structure and successional stage. In the case of specialist species, critical resources (food and shelter) may have been completely removed by the fire (see Woinarski et al. 2005).

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Appendix 3

Phylogeography of the antilopine wallaroo

The distribution of the antilopine wallaroo is marked by a break in the species' range between Queensland and the Northern Territory at the base of the Gulf of Carpentaria (Figure 1). This gap, the Carpentarian barrier (Cb) (Heatwole, 1987), is linked with a transition from savanna woodland (preferred habitat of the antilopine wallaroo; Chapter 2) to semi-arid grasslands associated with cracking clay soils (preferred habitat of the red kangaroo, *M. rufus*, Strahan, 1995). Historically, gene flow between populations of antilopine wallaroos in the Northern Territory and Queensland may have occurred widely across the Carpentarian plain, prior to the most recent marine inundation of this area (~ 20,000 ka, Chivas *et al.*, 2001). Following this event, the only possible connection between populations in Queensland and the rest of the species' range was across the Cb. However this area is semi-arid and has previously been implicated as a factor in the speciation of grass finches (Jennings *et al.*, 2005) and the bentwing bat, *Miniopterus schreibersii* (Cardinal *et al.*, 1999). Given that the Cb is unsuitable habitat for the antilopine wallaroo (Chapter 2), it may also have prevented dispersal and gene flow in this species, which would have important taxonomic and management implications.

While conducting extensive regional surveys during my study I had the opportunity to collect DNA samples across the range of the antilopine wallaroo, and began an investigation into the phylogeography of the antilopine wallaroo in collaboration with Professor Chris Johnson and Dr. Mark Eldridge. Initial analyses revealed that the phylogeography of this species is substantially more complex than we had predicted. It is clear that additional samples and further analyses will be required to fully elucidate the broad-scale genetic structuring of this species; hence only preliminary results are presented here.

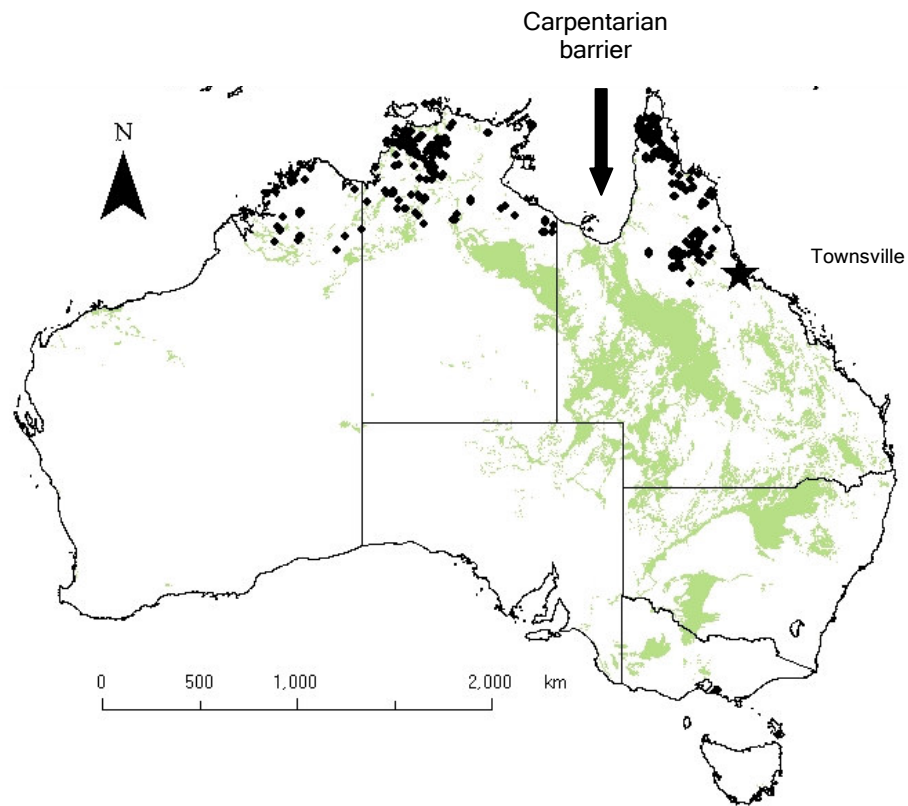


Figure 1. Map of known localities of the antilopine wallaroo, *Macropus antilopinus*, (small dots), and the distribution of cracking clay soils (green shading). The position of the Carpentarian barrier (Cb) is indicated.

Our specific aims were to answer two questions:

- (1) Has the Carpentarian barrier restricted gene flow between populations of the antilopine wallaroo in Queensland and the rest of the species' distribution?
- (2) Are there sufficient genetic differences between populations of antilopine wallaroos across the species' range to warrant taxonomic reassessment?

Results to date show that low levels of genetic divergence are present between the Northern Territory and Queensland populations of the antilopine wallaroo (~ 2.4%), with no major phylogeographic break between the two populations. However, no haplotypes are shared across the Cb which is suggestive of a recent and significant restriction to gene flow across this barrier. There is a regional pattern of grouping in lineages that is currently unresolved, with Queensland haplotypes at one end of the

phylogenetic tree and the Northern Territory and Western Australia haplotypes at the other (Figure 2).

An unexpected result is that one lineage of mitochondrial DNA (confined largely to the Kimberley region of Western Australia) appears to be more closely related to that of the common wallaroo than to other antilopine wallaroo lineages (Figure 2), which suggests that common wallaroos and antilopines may have interbred. Further work is clearly required to resolve both the phylogenetic relationships of lineages of the antilopine wallaroo and the taxonomic relationship between the common wallaroo and antilopine wallaroo, particularly within the Kimberley region of Western Australia.

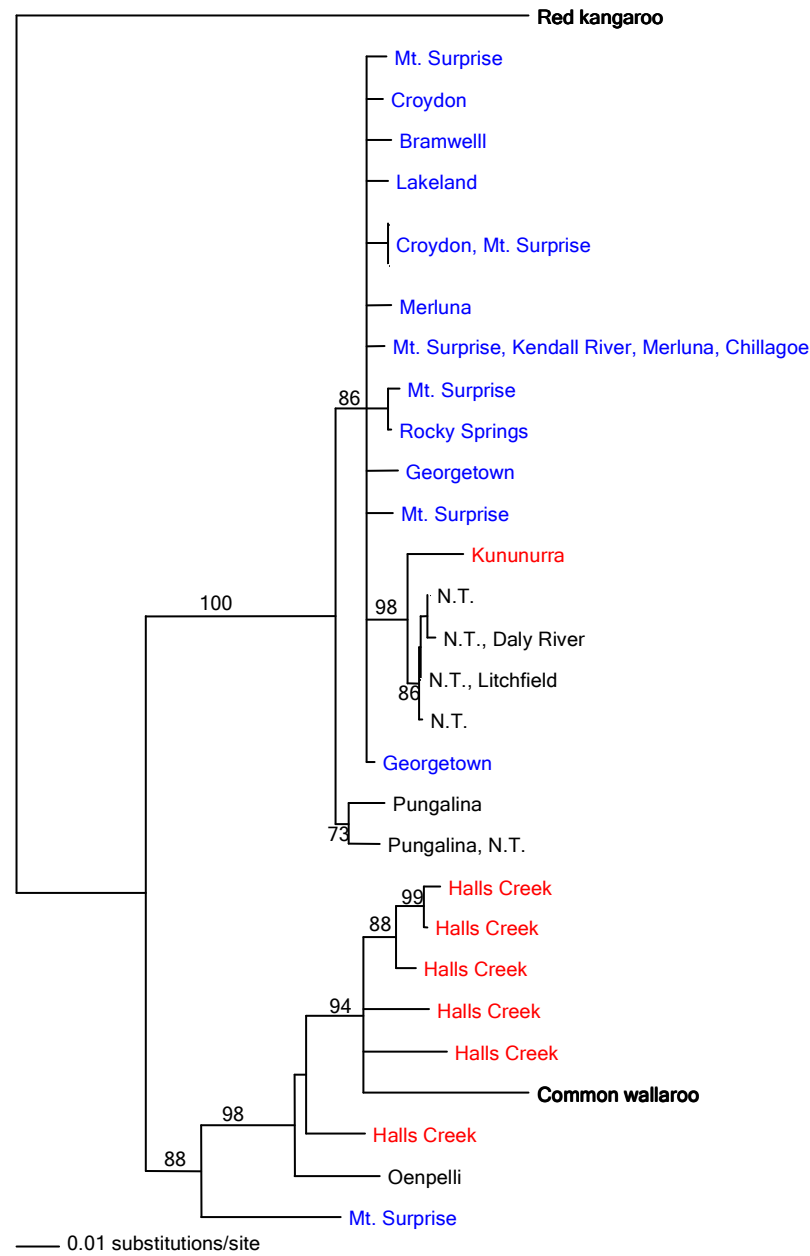


Figure 2. Phylogenetic tree of the antilopine wallaroo (*Macropus antilopinus*). Numbers indicate bootstrap support using 1000 bootstrap replicates of neighbour-joining (Kimura two-parameter distances) and maximum parsimony techniques in PAUP* version 4.0 (Swofford, 2000). Red kangaroo (*M. rufus*) and common wallaroo (*M. robustus*) sequences were used as outgroups. Clades associated with geographic areas are colour coded, Queensland (blue), Western Australia (red) and Northern Territory (black).

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