

Australia's Savanna Herbivores: Bioclimatic Distributions and an Assessment of the Potential Impact of Regional Climate Change

Euan G. Ritchie*

Elizabeth E. Bolitho

School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia

Accepted 2/22/2008; Electronically Published 10/20/2008

ABSTRACT

The future impacts of climate change are predicted to significantly affect the survival of many species. Recent studies indicate that even species that are relatively mobile and/or have large geographic ranges may be at risk of range contractions or extinction. An ecologically and evolutionary significant group of mammals that has been largely overlooked in this research is Australia's large marsupial herbivores, the macropodids (kangaroos). The aims of our investigation were to define and compare the climatic conditions that influence the current distributions of four sympatric large macropodids in northern Australia (*Macropus antilopinus*, *Macropus robustus*, *Macropus giganteus*, and *Macropus rufus*) and to predict the potential future impact of climate change on these species. Our results suggest that contemporary distributions of these large macropodids are associated with well-defined climatic gradients (tropical and temperate conditions) and that climatic seasonality is also important. Bioclimatic modeling predicted an average reduction in northern Australian macropodid distributions of $48\% \pm 16.4\%$ in response to increases of 2.0°C . At this temperature, the distribution of *M. antilopinus* was reduced by $89\% \pm 0.4\%$. We predict that increases of 6.0°C may cause severe range reductions for all four macropodids ($96\% \pm 2.1\%$) in northern Australia, and this range reduction may result in the extinction of *M. antilopinus*.

Introduction

The effects of increasing global temperature loom as possibly the largest single threat to the survival of species (Hughes 2003; Parmesan and Yohe 2003; Williams et al. 2003; Meyneke 2004; Thomas et al. 2004, 2006; Walther et al. 2005). 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 (Hughes et al. 1996; Hilbert et al. 2001; Root et al. 2003; Andrew and Hughes 2005) and by influencing the frequency and nature of key processes such as fire (Hughes 2003; Schumacher et al. 2006). It is crucial from a management perspective, therefore, that we have detailed information about the relationship between climate and the current distributions of species. This information may provide insight into how potential future variations in climate may affect the distribution and therefore survival of species.

Research into the impacts of global warming have focused considerable attention on species that are altitudinally restricted and/or have small geographic ranges (Williams et al. 2003; Shoo et al. 2005a), but there is growing recognition that species with wide geographic distributions may also be susceptible to the impacts of global warming (Forchhammer et al. 2001; Walther et al. 2002; Ogutu and Owen-Smith 2003). Large herbivores are one group predicted to be at significant risk from climate change. Through grazing, these mammals significantly influence the structure and function of many of the world's terrestrial ecosystems (Walther et al. 2005; Thuiller et al. 2006), and they are also highly valued both economically and culturally (Gordon et al. 2004). Therefore, the effective management of herbivore populations is of the utmost importance. One notable group of large herbivores that has been overlooked in climate-change research is Australia's large marsupials, the macropodids (family Macropodidae; Strahan 1995), recognized globally as the iconic kangaroos. Many of the large macropodids (which include both kangaroos and wallaroos) occur extensively within Australia's savannas, which themselves have recently been identified as being of global significance because of their large size, high endemism, and relative ecological integrity (Williams et al. 2005) as compared to the savannas of other continents (Woinarski et al. 2007). However, there is growing concern that this region and its unique biota, which occupies approximately one-quarter of mainland Australia ($\sim 2,000,000 \text{ km}^2$), are currently under threat from the intensification of the pastoralism industry and associated changes to fire regimes (Woinarski et al. 2001; Woinarski and Ash 2002). A broad range of taxonomic groups and guilds are experiencing population declines (Franklin 1999; Woinarski et al. 2001), including the endemic antilopine wallaroo *Macropus antilopinus* (Ritchie 2007).

Despite the significance of Australia's savannas in conserving global biodiversity, there remains little detailed ecological information for the majority of species that occur there, including information on their relationships with climate. This is a major concern because most of this region's land is dedicated to pas-

* Corresponding author; e-mail: euan.ritchie@jcu.edu.au.

toralism and livestock production, and rapid expansion of this industry is currently occurring (Williams et al. 2005). This is a trend that is likely to continue as a result of the prolonged drought occurring in southern Australia, possibly caused by long-term climate change. The drought has resulted in decreased agricultural production and calls for northern Australia to be further developed to compensate. Large macropodids are highly valuable economically, through both ecotourism and a commercial meat trade, and many species are an important traditional food source for indigenous people as well as holding strong cultural significance (Yibarbuk et al. 2001; Gordon et al. 2004). Therefore, it is critically important that we understand the ecology of Australia's native herbivores to ensure that any further economic development(s) will occur in an environmentally sustainable way.

Large macropodids comprise six species of herbivorous marsupials weighing between 20 and 90 kg (Dawson 1995). With the exception of the black wallaroo (*Macropus bernardus*), the large macropodids all have extensive geographic ranges (e.g., red kangaroo [*Macropus rufus*], >3,000,000 km²; Strahan 1995). The four largest macropodids can be roughly characterized as follows: the red kangaroo is an arid-zone species; the four subspecies of the common wallaroo (*Macropus robustus*) range from arid to mesic areas; the antilopine wallaroo is a tropical mesic species; and the eastern grey kangaroo (*Macropus giganteus*) is a largely mesic species, but it does extend into drier parts of southeastern Australia (Strahan 1995). The antilopine wallaroo is the largest macropodid confined solely to the tropical savannas of far northern Australia. This species may be more vulnerable to a changing climate than the other large macropodids because of its relatively restricted range (Busby 1988). This species also exhibits highly seasonal reproduction, strongly linked to rainfall in the monsoon season, which may further increase its vulnerability (Ritchie 2007). Caughley et al.'s (1987) classic study of kangaroos and climate contributed greatly to our understanding of large mammalian distributions, but it excluded information on the common and antilopine wallaroos. This precludes a synthesis of knowledge concerning the effects of climate on large macropodids and, more broadly, large mammalian herbivores in general.

There is marked variation in the behavioral, morphological, and physiological adaptations among macropodid species (Dawson 1995; Dawson et al. 2000a). The red kangaroo, being arid adapted, has the ability to produce concentrated urine, reducing its reliance on free water (Dawson et al. 1975; Blaney et al. 2000), and it has been found to drink with less regularity than other macropodids (Dawson 1995). This species has a short reflective coat that helps to reduce heating of the body due to solar radiation. The red kangaroo also has a lower field metabolic rate and a more labile daytime body temperature than the more mesic eastern grey kangaroo (McCarron et al. 2001). The common wallaroo, which occurs in both mesic and arid areas, differs from the other large macropodids in how it regulates its body temperature and controls water loss in hot conditions. In contrast to other species, particularly the eastern

grey kangaroo and antilopine wallaroo, which rely heavily on evaporative cooling through licking, the common wallaroo seeks cool shelter sites (microclimates), such as rocky ledges and caves, in the hottest part of the day (Dawson and Denny 1969; Dawson 1995). Evaporative cooling increases water loss and therefore entails a higher dependence on water availability, which has been found in both the eastern grey kangaroo and antilopine wallaroo (Blaney et al. 2000; Ritchie et al. 2008). When available, eastern grey kangaroos will seek dense shade on hot days to assist their temperature regulation and reduce water loss (McCarron 1990). The physiology of the antilopine wallaroo is least known of the larger species. However, this species does have one unique morphological adaptation, a large nasal cavity that appears externally as a swollen rostrum, which likely enhances evaporative cooling (through panting) in humid conditions in the tropics (Dawson 1995; Ritchie et al. 2008).

With these differences in adaptations between macropodid species, we predict that the four species in our study may differ with respect to the components of climate that shape their distribution patterns and, likewise, their respective susceptibility to the patterns of climate change predicted for Australia (Hughes 2003). Here, we present a detailed examination of the bioclimatic distributions of these four species in northern Australia. Our aims were to determine and compare the climatic envelopes of each macropodid species and the climatic variables that may be responsible for maintaining species' distributions and range borders, and to predict the likely impact of climate change (warming) on these species' future distributions in northern Australia. We predict that the antilopine wallaroo will be most susceptible to future climate change because of its smaller geographic range, adaptation to tropical (warm and wet) rather than arid (hot and dry) or mesic (cool and wet) conditions, and its dependence on seasonal rainfall for reproduction. In contrast, we predict that the other three species will be less vulnerable to climate change. The red kangaroo and common wallaroo are better adapted to sustain hotter climates on average than the antilopine wallaroo, and the eastern grey kangaroo may be somewhat buffered by the effects of increasing temperature because of its predominant occurrence in the cooler eastern seaboard of Australia. However, finally, with large increases in temperature, we predict that all species will show reductions in their distributions in northern Australia.

Material and Methods

Study Region and Locality Data

The climate of northern Australia is characterized by pronounced rainfall seasonality (Williams et al. 2005) but, in comparison with temperate regions, little temperature variation between seasons. There is minor longitudinal change in the vegetation communities and topography across this vast biome (Woinarski et al. 2005); however, there is a pronounced coastal-continental gradient of decreasing rainfall from the northern coast inland.

We restricted our modeling of macropodid distributions to

between 11°S and 30°S latitude (“northern Australia”; Fig. 1), encompassing the complete geographic range of the antilopine wallaroo and approximately 50% of that of the eastern grey kangaroo, 66% of that of the red kangaroo, and 80% of that of the common wallaroo (based on Strahan 1995). This restriction was made because there is a significant change in climate regime below 30°S, from seasonal summer rainfall to less seasonal winter-dominated rainfall (<http://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 we did not capture the maximum 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 in Australia, 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 since conditions experienced by this species south of our defined study region are cooler and wetter. In contrast, the semiarid 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. Additional records were obtained from other sources (see “Acknowledgments”). 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 ex-

cluded from the final data set. We further removed any multiple records less than 2.5 km apart to reduce spatial autocorrelation. A total of 3,514 records were included in the analysis, as follows: antilopine wallaroo, 1,102 records; common wallaroo, 913 records; eastern grey kangaroo, 1,233 records; and red kangaroo, 266 records.

Bioclimatic Parameter Selection and Modeling

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 et al. 2005). We investigated the influence that the addition and subtraction of variables had on each macropodid species’ modeled distribution before selecting the final set of variables. To avoid problems of overfitting of our models, we chose to include 11 variables in BIOCLIM (Hutchinson et al. 1984; Busby 1991): 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 judged to be significant in influencing the distributions of large macropodids and have also been used in a previous study of kangaroos and climate (Caughley et al. 1987). Precipitation of the driest period was

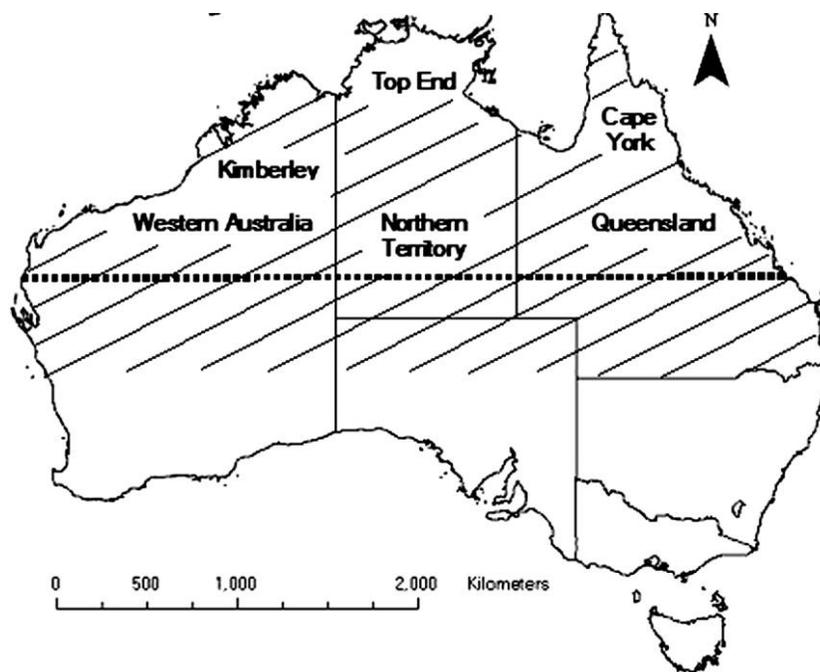


Figure 1. Study region showing political boundaries (Western Australia, Northern Territory, and Queensland), regions, and the Tropic of Capricorn (*dashed line*).

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

We modeled and mapped distributions for each species under current and future climatic conditions using the BIOCLIM script for ArcView 3.1 (A. Moussalli; available as a free download from <http://www.esri.com>). We generated maps using a 12-s 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%). Since the accuracy of BIOCLIM for distribution modeling has recently been questioned (Araujo and 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 that are overestimates of the current distributions. 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 modeling, see a study by Nix (1986).

Climate-Change Scenarios

Australia's size and associated high diversity of bioregions makes it difficult to obtain consensus about the likely nature and extent of climate change expected in the next 100 yr (Hughes 2003). However, for the majority of mainland Aus-

tralia, it is generally accepted that temperatures will increase by 0.4°–2°C by 2030 and by 1°–6°C by 2070 (Hughes 2003). Rainfall predictions are much more variable and dependent on the models used to generate them, with predictions for northern Australia ranging from –5% to +5% mean annual rainfall by 2030 and from –10% to +10% mean annual rainfall by 2070 (Hughes 2003). To account for this variability, we generated models of species distributions for all four macropodid species under the following climate-change scenario combinations: +0.4°C mean annual temperature with each of –5%, +5%, –10%, and +10% mean annual rainfall; +2°C mean annual temperature with each of –5%, +5%, –10%, and +10% mean annual rainfall; and +6°C mean annual temperature with each of –5%, +5%, –10%, and +10% mean annual rainfall. To assess the impact of climate change on each species' future range, we compared the amount of northern Australian core area after the application of each climatic 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 ANOVA. 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 were described as percentages of current distributions. All statistical analyses were performed in JMP 4.0 and Statistica 6.0.

Table 1: Summary of climate envelopes for large macropodids in northern Australia

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 (°C)	24.96	20.2	27.7	20.21	12.3	26.1	23.31	13.8	28.7	23.03	18.7	26.6
Maximum temperature of warmest period (°C)	34.97	29.4	39.5	30.71	21.9	36.7	34.90	26.0	40.9	37.01	32.8	40.9
Minimum temperature of coldest period (°C)	13.03	6.9	20.8	7.70	5.00	16.9	9.78	5.00	18.9	7.28	2.4	13.5
Temperature annual range (°C)	21.93	11.9	30.0	23.01	14.2	32.4	25.13	13.7	33.7	29.74	21.7	33.7
Mean temperature of wettest quarter (°C)	27.18	23.7	30.5	24.44	16.8	28.2	26.52	12.3	31.8	27.29	12.5	31.7
Mean temperature of driest quarter (°C)	21.77	15.6	25.2	16.25	7.9	23.9	20.00	9.3	26.9	19.09	12.7	26.2
Annual precipitation (mm)	1,079.17	517.00	1,859.00	1,017.37	187.00	2,405.00	732.57	198.00	2,547.00	378.47	178.00	806.00
Precipitation of wettest period (mm)	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; mm)	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 (mm)	755.38	375.00	1,260.00	503.00	76.00	1,271.00	474.88	70.00	1,445.00	216.12	75.00	612.00
Precipitation of driest quarter (mm)	.66	.00	79.00	93.02	.00	291.00	18.62	.00	194.00	14.47	.00	91.00

Table 2: Summary of principal components (PC) analysis (rotated varimax) of climate variables influencing the distributions of large macropodids in northern Australia

	PC1	PC2
Variation explained (%)	40.26	31.83
Variance	4.43	3.50
Annual mean temperature	-.25	.66
Maximum temperature of warmest period	.35	.62
Minimum temperature of coldest period	-.69	.50
Temperature annual range	.88	.00
Mean temperature of wettest quarter	.03	.32
Mean temperature of driest quarter	-.32	.67
Annual precipitation	-.96	-.24
Precipitation of wettest period	-.96	.26
Precipitation seasonality (coefficient of variation)	-.31	.89
Precipitation of wettest quarter	-.97	.22
Precipitation of driest quarter	-.08	-.95

Note. Numbers in boldface represent factor loadings used to describe each axis.

Results

Current Distributions of Large Macropodids in Northern Australia

The climatic envelopes of each species are summarized in Table 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 twice the annual rainfall. The eastern grey kangaroo occurs in areas typically lower in temperature but with less seasonal rainfall than the other species; it also occurs in wetter areas than red kangaroos and common wallaroos but drier areas than antilopine wallaroos. The antilopine wallaroo occurs in areas of higher mean temperature but lower temperature variation and areas of higher, more seasonal rainfall than the other species.

PCA summarized the climate experienced by all four species into two environmental gradients (principal component axes; Table 2). Principal component 1 (PC1) describes a gradient of lower rainfall and cooler temperatures but higher temperature variation (subtropical conditions). Principal component 2 (PC2) describes a gradient of increasing temperature and higher rainfall seasonality (tropical conditions). There was significant separation between all species along these axes using Tukey's post hoc tests (PC1: $F_{3,3514} = 513.14$, $P < 0.0001$; antilopine wallaroo: -0.61 ± 0.03 ; common wallaroo: 0.40 ± 0.03 ; eastern grey kangaroo: -0.05 ± 0.02 ; red kangaroo: 1.39 ± 0.03 ; PC2: $F_{3,3514} = 1043.48$, $P < 0.0001$; antilopine wallaroo: 0.69 ± 0.01 ; common wallaroo: 0.36 ± 0.02 ; eastern grey kangaroo: -0.91 ± 0.03 ; red kangaroo: 0.11 ± 0.04). The antilopine wallaroo showed the strongest positive association with tropical conditions and the narrowest climate space (Fig. 2). Common wallaroos showed a stronger association with tropical condi-

tions than subtropical conditions and, eastern grey kangaroos showed the opposite trend; these two species occupied the largest climatic space. The climate space of the common wallaroo encompasses that of both the red kangaroo and the antilopine wallaroo as well as a large proportion of the climate space 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 quarter (Fig. 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 occurrence of antilopine wallaroos to that of red kangaroos.

The largely sympatric common wallaroo and red kangaroo have greater core and marginal bioclimatic distributions in northern Australia than the antilopine wallaroo and eastern grey kangaroo (Fig. 4). Both the common wallaroo and the 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 (left to right in Fig. 1, the Kimberley region of Western Australia, the top end of the Northern Territory, and the Cape York region of Queensland). 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. In northern Australia, the core distribution of the eastern grey kangaroo is largely confined to eastern Queensland but extends into northern Queensland, where the eastern grey kangaroo is sympatric with the antilopine wallaroo and common wallaroo.

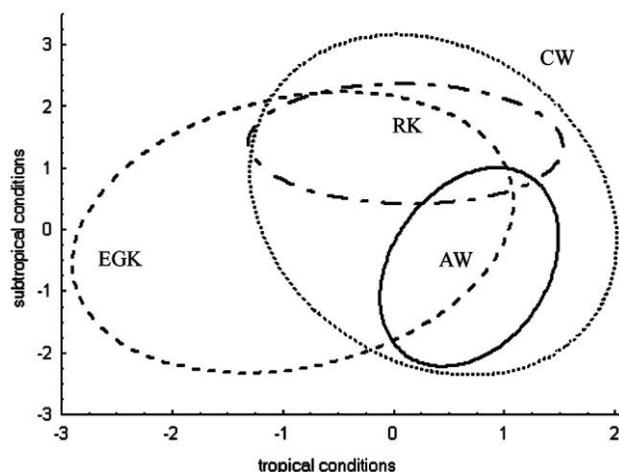


Figure 2. Climate spaces (95% confidence interval ellipses) for large macropodids in northern Australia. Solid line = antilopine wallaroo, dotted line = common wallaroo, dashed line = eastern grey kangaroo, dot-dashed line = red kangaroo.

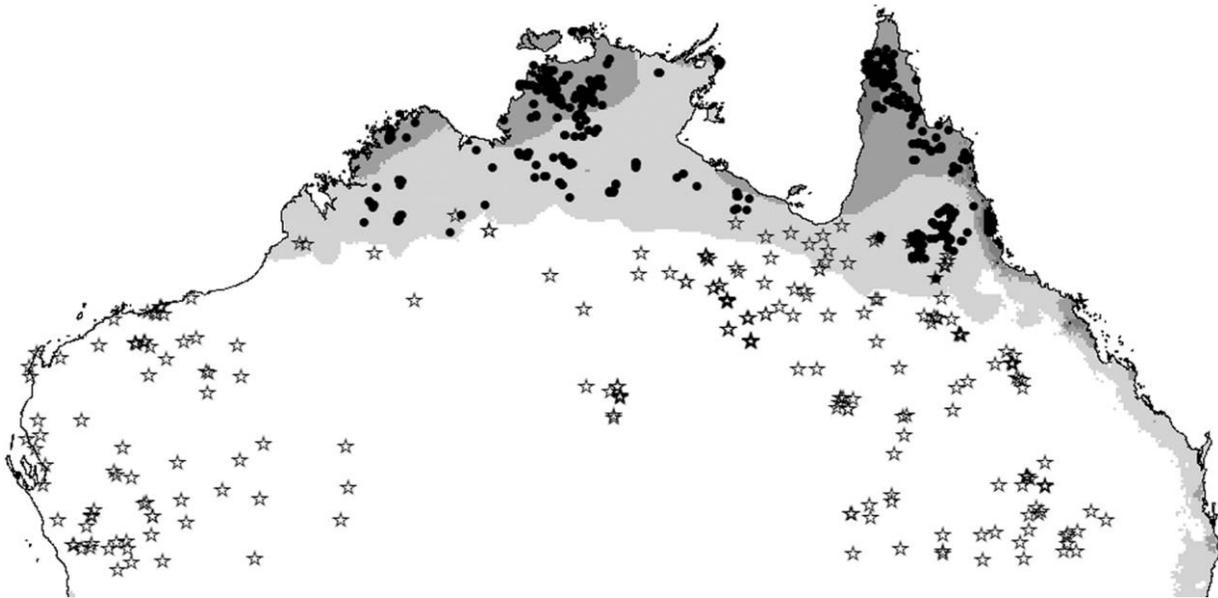


Figure 3. Map of precipitation of the wettest period and the distribution of antilopine wallaroos (*filled circles*) and red kangaroos (*stars*). Darker shading indicates areas of increasing precipitation; lighter shading indicates less precipitation.

Changes to Species' Distributions under Climate-Change Scenarios

The core distributions of all species in northern Australia decreased on average by 9% ($\pm 4.5\%$) in response to a 0.4°C increase in temperature combined with either increasing or decreasing rainfall. There were three exceptions to this trend (+0.4°C with -10%, +5%, and +0% rainfall) that resulted in minor increases ($0.4\% \pm 0.2\%$) in the core distribution of eastern grey kangaroos (Fig. 5). The core distribution of antilopine wallaroos was most reduced ($22\% \pm 1\%$) in response to 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, and +6.0°C with +5% rainfall (Fig. 6). With an increase of 2.0°C and variation in rainfall, the northern Australian core distributions of all species were greatly reduced, averaging $48\% \pm 16.4\%$ across all species. Again, the core range of antilopine wallaroos was the most reduced of the four species ($89\% \pm 0.4\%$), and suitable climatic conditions for this species disappear entirely in the Northern Territory and Western Australia, as do those for common wallaroos. Under the same scenarios, red kangaroos contract south, whereas eastern grey kangaroos again show less change relative to the other species. When temperatures increase by 6.0°C, there are drastic reductions in the northern Australian 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.

Discussion

Our results indicate that the distribution of large macropodids in northern Australia is strongly associated with two principal, well-defined climatic gradients (tropical and subtropical). It also appears that climatic seasonality (rainfall variation) may be an important factor controlling distributional limits, particularly that between the antilopine wallaroo and the red kangaroo. Our findings provide a good example of the ways in which climate influences the local and regional assemblages of large herbivores. In addition, we have highlighted the strong differences in sensitivity to changes in climate among a closely related group of taxa, all of which have large, overlapping current distributions. Future variations in climatic gradients that govern the distributions of macropodids have the potential to result in significant distributional changes for our study species. The distributions of macropodids in northern Australia appear to be particularly sensitive to predicted climatic change, with an increase of as little as 0.4°C resulting in range contractions. With increases of 2.0°C or more, the core distributions of all four species in northern Australia 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 or above the range of 2°–6°C, which is widely considered to be a *fait accompli* by 2070. Indeed, it is also of conservation significance that under these same conditions, the distribution of the Barrow Island wallaroo (*Macropus robustus isabellinus*), a unique subspecies of the common wallaroo, would also disappear. Our results demonstrate that large macropodids, despite being highly mobile and having

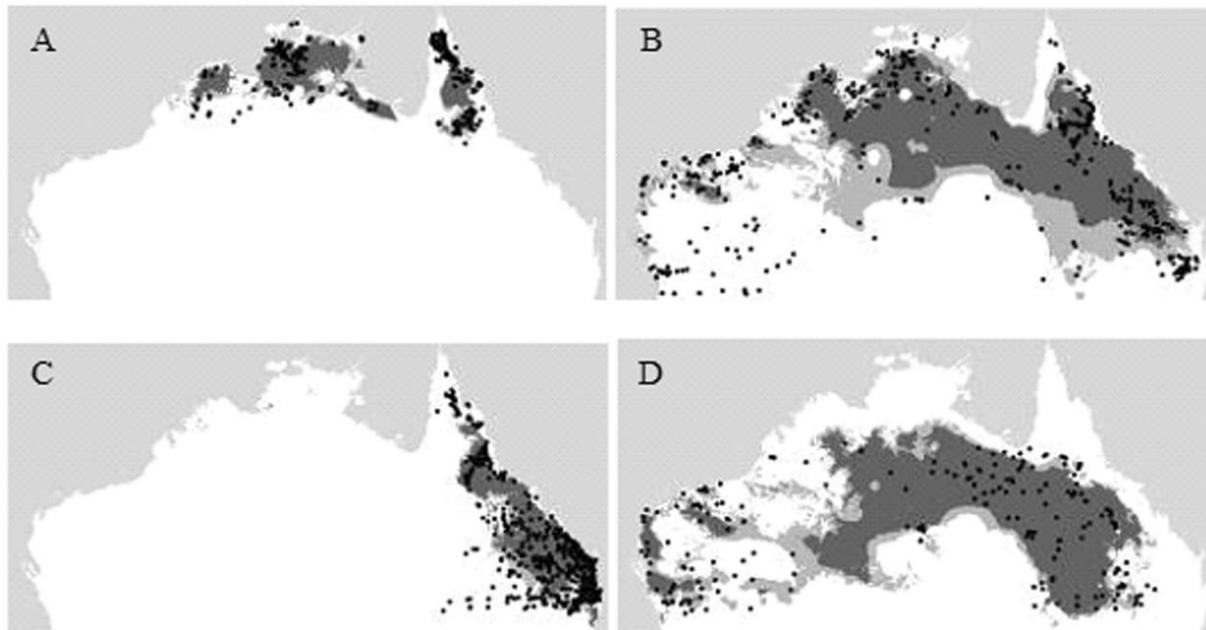


Figure 4. Current bioclimatic distributions of large macropodids in northern Australia. Core ranges (5%–95%) are represented in dark gray and marginal ranges (2.5%–97.5%) in light gray. Filled circles represent actual locations for each species. A, Antilopine wallaroo; B, common wallaroo; C, eastern grey kangaroo; D, red kangaroo.

relatively large distributions, are at significant potential 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 (Ogutu and Owen-Smith 2003; Weladji and Holand 2003; Callaghan et al. 2004; Derocher et al. 2004).

Rainfall Seasonality and Reproduction

Macropodids have evolved a diverse array of adaptations that allow them to occupy a vast range of climates and habitats in Australia (Dawson and Denny 1969; Dawson 1995; Dawson et al. 2000a, 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. The influence of climate on reproduction, and therefore population growth, is a critical consideration. At present, a tight distributional boundary exists between the red kangaroo and the antilopine wallaroo, the former being largely aseasonal in its reproduction (Frith and Sharman 1964), the latter highly seasonal (Ritchie 2007). It is often suggested that one reason why the red kangaroo is well suited to occupying arid habitats is the reproductive adaptation known as embryonic diapause (Tyndale-Biscoe and Renfree 1987; Dawson 1995). This adaptation allows females to regulate the timing of the development of young in response to temporal variability in resource availability (caused by infrequent rain), which is characteristic of the Australian arid zone (Norbury et al. 1994; Dickman et al. 2001). It remains unclear whether antilopine wallaroos possess this adaptation, but limited evidence suggests they do not

(Poole and Merchant 1987). The lack of embryonic diapause could explain why antilopine wallaroo breeding is highly seasonal, centered around monsoonal rains (E. G. Ritchie, unpublished data), and why their current range does not extend further south into more arid habitats, where red kangaroos possibly have a competitive advantage in reproduction.

Water Availability under Increased Temperature

There are currently no detailed and reliable predictions for the effects of climate change on the monsoon for northern Australia, so it is not possible to model the response of species' distributions to changes in rainfall seasonality per se. However, more generalized predictions for northern Australia are for increased variability and severity of the dry season in the future (Houghton et al. 2001), which may have at least one important ecological consequence. Permanent water holes are an important resource for many species during the extended dry season (James et al. 1999; Redfern et al. 2003), when most rivers and streams typically dry up. An extensive comparative ecological study of three macropodid species in northern Australia by Ritchie et al. (2008) found that the antilopine wallaroo's distribution and abundance was highly dependent on the availability of standing water. In addition, reproduction in both the antilopine wallaroo and the Barrow Island wallaroo is thought to be dependent on seasonal rainfall (Russell and Richardson 1971; Ritchie 2007). In contrast, the sympatric common wallaroo and red kangaroo are both well adapted to cope with reduced water availability because of behavioral and physio-

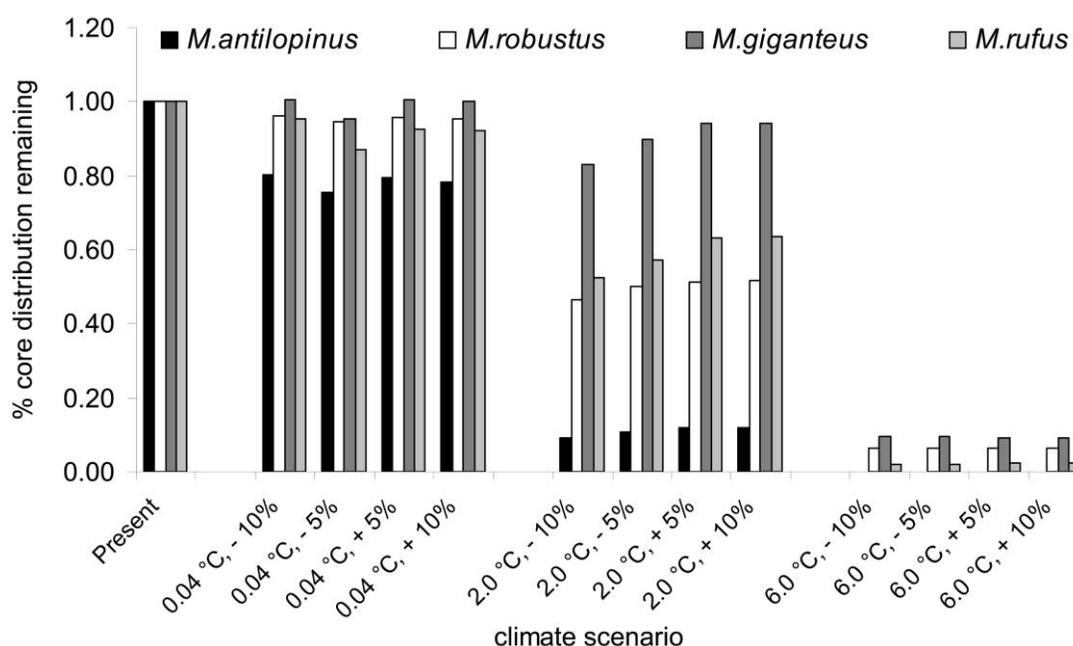


Figure 5. Percentage of core bioclimatic distribution remaining for large macropodids in northern Australia under modeled climate-change scenarios. All temperatures represent increases from current conditions, and minus or plus signs after temperatures indicate increased or decreased annual rainfall.

logical adaptations mentioned above (see “Introduction”). If dry seasons are to become hotter and rainfall events more unpredictable, habitats may become depleted of available pasture for grazing, and water holes may dry up through increased rates of evapotranspiration. This may result in starvation and failed reproduction, and animals may have to move larger distances to find water or, for those species that are less mobile, may die from dehydration. 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*).

Distributional Limits and Climate: Ecological Considerations

We acknowledge that our study is correlative rather than mechanistic in its nature and that the distributional shifts predicted by our models may be mitigated or amplified in ways opposite to those predicted by other factors besides climate (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 macropodids in northern Australia. There are a number of factors to consider when assessing the impact that climate change is likely to have on a species. Indeed, the question of to what degree current habitat use underrepresents the potential full distribution of a species (realized vs. fundamental niche) is an important one. In this regard, we believe

there are at least two key factors to consider: the availability of suitable habitat and population size and connectivity.

It is already evident that species that are not restricted by altitude are reacting to climate change by shifting away from the equator (Parmesan et al. 1999; Parmesan and Yohe 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 because 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 rely on them. In the case of our study, it remains uncertain whether antilopine wallaroos could shift from their preferred habitat of savanna woodland (Ritchie et al. 2008) to habitat currently occupied by the more arid-adapted common wallaroo and red kangaroo (arid grasslands). Thus, even if the suitable climatic environment of the antilopine wallaroo were to become available further south of its current distribution, this species’ preferred habitat (savanna woodland) might not occur in the same area.

Population size and connectivity may influence the susceptibility of a species to stochastic events. Our modeling shows that macropodid distributions may contract in size, but equally importantly, they may become increasingly fragmented and isolated with increasing temperature. This is an important finding because in addition to the possible direct physiological stresses to individuals caused by a changing climate, there is the potential for smaller populations to suffer deleterious effects such as inbreeding and reduced dispersal. Recovery of small populations from such events as disease would therefore be re-

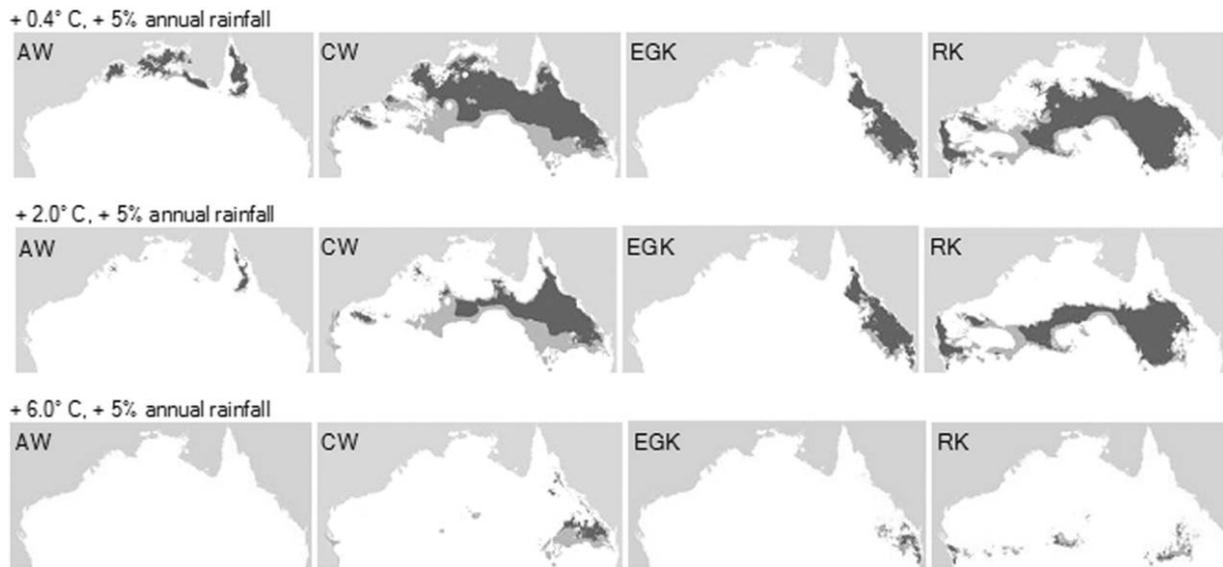


Figure 6. Future bioclimatic distributions of large macropodids in northern Australia under different climate-change scenarios. Core ranges (5%–95%) are represented in dark gray and marginal ranges (2.5%–97.5%) in light gray. AW = antilopine wallaroo, CW = common wallaroo, EGK = eastern grey kangaroo, RK = red kangaroo. *Top*, +0.4°C and +5% annual rainfall; *middle*, +2.0°C and +5% annual rainfall; *bottom*, +6.0°C and +5% annual rainfall.

duced. 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. Further, human activities have already restricted the distribution of many species to the least productive or more climatically challenging parts of their distribution and therefore may further limit their ability to respond to climate change.

Our study provides evidence that climate change has the capacity to cause large-scale range contractions and the possible extinction of one macropodid species from 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 of the caribou and residents of the Arctic (Weladji and Holand 2003). Our predictions regarding climate change are testable at the margins of the range of 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 macropodids and, more broadly, other species in finer detail, there is an urgent need for studies that determine the factors limiting species' distributions (Peterson et al. 2001; Hughes 2003; Ritchie et al. 2008). Such information could then be incorporated into mechanistic models of species distributions (see Kearney and Porter 2004) and therefore better inform conservation managers on what action can be taken to mitigate the impacts of climate change on species' survival.

Acknowledgments

We would like to thank Sam Fox, Peter Johnson, Steve Murphy, Michelle Watson, John Winter, John Woinarski, Department of

Conservation and Land Management, Kakadu National Park, Northern Territory Museum, Northern Territory Parks and Wildlife Service, Queensland Parks and Wildlife Service, Queensland Museum, and the Environmental Protection Agency (Wildnet) for locality data; we also thank traditional owners, national parks rangers, and station owners for access to sites, logistical support, and their hospitality. Funding for this project to E.G.R. was partly provided by the Australia and Pacific Science Foundation, Australian Geographic, Cooperative Research Centre Tropical Savannas, an Ecological Society of Australia Student Research Award, an Ethel Mary Read Research Award (Royal Zoological Society New South Wales), Joyce Vickery Research Awards (Linnean Society of New South Wales), and a Supplementary Internal Research Award (James Cook University). Sam Fox, Brett Goodman, Chris Johnson, Mike Kearney, Angus Martin, and Jenny Martin provided useful comments on earlier drafts.

Literature Cited

- Andrew N.R. and L. Hughes. 2005. Diversity and assemblage structure of phytophagous Hemiptera along a latitudinal gradient: predicting the potential impacts of climate change. *Glob Ecol Biogeogr* 14:249–262.
- Araujo M.B. and C. Rahbek. 2006. How does climate change affect biodiversity? *Science* 313:1396–1397.
- Beaumont L.J., L. Hughes, and M. Poulsen. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol Model* 186:250–269.
- Blaney C.E., T.J. Dawson, H.C.K. McCarron, R. Buffenstein,

- and A.K. Krockenberger. 2000. Water metabolism and renal function and structure in eastern grey kangaroos (*Macropus giganteus*): responses to water deprivation. *Aust J Zool* 48: 335–345.
- Busby G.W. 1988. Possible impacts of climate change on Australia's flora and fauna. Pp. 375–386 in G.I. Pearman, ed. *Greenhouse: Planning for Climate Change*. CSIRO Division of Atmospheric Research, Melbourne.
- Busby J.R. 1991. BIOCLIM: a bioclimatic analysis and predictive system. Pp. 64–68 in C.R. Margules and M.P. Austin, eds. *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. CSIRO, Canberra.
- Callaghan T.V., L.O. Bjorn, Y. Chernov, T. Chapin, T.R. Christensen, B. Huntley, R.A. Ims, et al. 2004. Responses to projected changes in climate and UV-B at the species level. *Ambio* 33:418–435.
- Caughley G., J. Short, G.C. Grigg, and H. Nix. 1987. Kangaroos and climate: an analysis of distribution. *J Anim Ecol* 56:751–761.
- Dawson T.J. 1995. Kangaroos. University of New South Wales Press, Sydney.
- Dawson T.J., C.E. Blaney, A.J. Munn, A.K. Krockenberger, and S.K. Maloney. 2000a. Thermoregulation by kangaroos from mesic and arid habitats: influence of temperature on routes of heat loss in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*). *Physiol Biochem Zool* 73:374–381.
- Dawson T.J. and M.J.S. Denny. 1969. A bio-climatological comparison of the summer day micro-environments of two species of arid zone kangaroo. *Ecology* 50:329–332.
- Dawson T.J., M.J.S. Denny, E.M. Russell, and B.A. Ellis. 1975. Water use and diet preferences of free ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. *J Zool (Lond)* 177:1–23.
- Dawson T.J., A.J. Munn, C.E. Blaney, A.K. Krockenberger, and S.K. Maloney. 2000b. Ventilatory accommodation of oxygen demand and respiratory water loss in kangaroos from mesic and arid environments, the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Macropus rufus*). *Physiol Biochem Zool* 73:382–388.
- Derocher A.E., N.J. Lunn, and I. Stirling. 2004. Polar bears in a warming climate. *Integr Comp Biol* 44:163–176.
- Dickman C.R., A.S. Haythornthwaite, G.H. McNaught, P.S. Mahon, B. Tamayo, and M. Letnic. 2001. Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildl Res* 28:493–506.
- Elith J., C.H. Graham, R.P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R.J. Hijmans, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Forchhammer M.C., T.H. Clutton-Brock, J. Lindstrom, and S.D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *J Anim Ecol* 70:721–729.
- Franklin D.C. 1999. Evidence of disarray amongst granivorous bird assemblages in the savannas of northern Australia, a region of sparse human settlement. *Biol Conserv* 90:53–68.
- Frith H.J. and G.B. Sharman. 1964. Breeding in wild populations of the red kangaroo, *Megaleia rufa*. *CSIRO Wildl Res* 9:86–114.
- Gordon I.J., A.J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *J Appl Ecol* 41:1021–1031.
- Hilbert D.W., B. Ostendorf, and M.S. Hopkins. 2001. Sensitivity of tropical forests to climate change in the humid tropics of north Queensland. *Austral Ecol* 26:590–603.
- Houghton J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, et al. 2001. IPCC Third Assessment Report: Climate Change 2001. Cambridge University Press, Cambridge.
- Houlder D.J., M.F. Hutchinson, H.A. Nix, and J.P. McMahon. 2000. ANUCLIM. Version 5.1. Centre for Resource and Environmental Studies, Australian National University, Canberra.
- Hughes L. 2003. Climate change and Australia: trends, projections and impacts. *Austral Ecol* 28:423–443.
- Hughes L., E.M. Cawsey, and M. Westoby. 1996. Climatic range sizes of *Eucalyptus* species in relation to future climate change. *Glob Ecol Biogeogr Lett* 5:23–29.
- Hutchinson M.F., T.H. Booth, J.P. McMahon, and H.A. Nix. 1984. Estimating monthly mean-values of daily total solar-radiation for Australia. *Sol Energy* 32:277–290.
- James C.D., J. Landsberg, and S.R. Morton. 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *J Arid Environ* 41:87–121.
- Kearney M. and W.P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Lawton J.H. 1995. Population dynamic principles. Pp. 147–163 in J.H. Lawton and R.M. May, eds. *Extinction Rates*. Oxford University Press, Oxford.
- McCarron H.C.K. 1990. Environmental Physiology of the Eastern Grey Kangaroo (*Macropus giganteus* Shaw). PhD diss. University of New South Wales, Sydney.
- McCarron H.C.K., R. Buffenstein, F.D. Fanning, and T.J. Dawson. 2001. Free-ranging heart rate, body temperature and energy metabolism in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*) in the arid regions of South East Australia. *J Comp Physiol B* 171:401–411.
- Meyneke J.O. 2004. Effects of global climate change on geographic distributions of vertebrates in North Queensland. *Ecol Model* 174:347–357.
- Nix H.A. 1986. A biogeographic analysis of the Australian elapid snakes. Pp. 4–15 in R. Longmore, ed. *Atlas of Elapid Snakes*. Australian Government Publishing Service, Canberra.
- Norbury G.L., D.C. Norbury, and A.J. Oliver. 1994. Facultative behavior in unpredictable environments: mobility of red kangaroos in arid Western Australia. *J Anim Ecol* 63:410–418.

- Ogutu J.O. and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol Lett* 6:412–419.
- Parmesan C., N. Ryrholm, C. Stefanescu, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Parmesan C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Peterson A.T., V. Sanchez-Cordero, J. Soberon, J. Bartley, R.W. Buddemeier, and A.G. Navarro-Siguenza. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecol Model* 144:21–30.
- Poole W.E. and J.C. Merchant. 1987. Reproduction in captive wallaroos: the eastern wallaroo *Macropus robustus robustus*, the euro *Macropus robustus erubescens*, and the antilopine wallaroo *Macropus antilopinus*. *Aust Wildl Res* 14:225–242.
- Quinn G.P. and M.J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Redfern J.V., R. Grant, H. Biggs, and W.M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107.
- Ritchie E.G. 2007. *The Ecology and Conservation of the Antilopine Wallaroo (Macropus antilopinus)*. PhD diss. James Cook University, Townsville.
- Ritchie E.G., J.K. Martin, A.K. Krockenberger, S. Garnett, and C.N. Johnson. 2008. Large-herbivore distribution and abundance: intra- and interspecific niche variation in the tropics. *Ecol Monogr* 78:105–122.
- Root T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Russell E.M. and B.J. Richardson. 1971. Some observations on the breeding age structure dispersion and habitat of populations of *Macropus robustus* and *Macropus antilopinus* (Marsupialia). *J Zool (Lond)* 65:131–142.
- Saltz D., D.I. Rubenstein, and G.C. White. 2006. The impact of increased environmental stochasticity due to climate change on the dynamics of Asiatic wild ass. *Conserv Biol* 20:1402–1409.
- Schumacher S., B. Reineking, J. Sibold, and H. Bugmann. 2006. Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. *Landsc Ecol* 21:539–554.
- Shoo L.P., S.E. Williams, and J.M. Hero. 2005a. Climate warming and the rainforest birds of the Australian wet tropics: using abundance data as a sensitive predictor of change in total population size. *Biol Conserv* 125:335–343.
- . 2005b. Potential decoupling of trends in distribution area and population size of species with climate change. *Glob Change Biol* 11:1469–1476.
- Strahan R. 1995. *The Mammals of Australia*. Reed New Holland, Sydney.
- Thomas C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, et al. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Thomas C.D., A.M.A. Franco, and J.K. Hill. 2006. Range retractions and extinction in the face of climate warming. *Trends Ecol Evol* 21:415–416.
- Thuiller W., O. Broennimann, G. Hughes, J.R.M. Alkemade, G.F. Midgley, and F. Corsi. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob Change Biol* 12:424–440.
- Tyndale-Biscoe H. and M.B. Renfree. 1987. *Reproductive Physiology of Marsupials*. Cambridge University Press, Cambridge.
- Walther G.-R., L. Hughes, P. Vitousek, and N.C. Stenseth. 2005. Consensus on climate change. *Trends Ecol Evol* 20:648–649.
- Walther G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.M. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Weladji R.B. and O. Holand. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia* 136:317–323.
- Williams R.J., J. Carter, G.A. Duff, J.C.Z. Woinarski, G.D. Cook, and S.L. Farrer. 2005. Carbon accounting, land management, science and policy uncertainty in Australian savanna landscapes: introduction and overview. *Aust J Bot* 53:583–588.
- Williams S.E., E.E. Bolitho, and S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc R Soc B* 270:1887–1892.
- Woinarski J.C.Z. and A.J. Ash. 2002. Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecol* 27:311–323.
- Woinarski J.C.Z., B. Mackey, H. Nix, and B. Traill. 2007. *The Nature of Northern Australia*. Australian National University E Press, Canberra.
- Woinarski J.C.Z., D.J. Milne, and G. Wanganeen. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecol* 26:360–370.
- Woinarski J.C.Z., R.J. Williams, O. Price, and B. Rankmore. 2005. Landscapes without boundaries: wildlife and their environments in northern Australia. *Wildl Res* 32:377–388.
- Yibarbuk D., P.J. Whitehead, J. Russell-Smith, D. Jackson, C. Godjuwa, A. Fisher, P. Cooke, et al. 2001. Fire ecology and aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *J Biogeogr* 28:325–343.