

LARGE-HERBIVORE DISTRIBUTION AND ABUNDANCE: INTRA- AND INTERSPECIFIC NICHE VARIATION IN THE TROPICS

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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, broadscale study across the tropical savannas of northern Australia on the ecology of three large, sympatric marsupial herbivores (family Macropodidae): 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 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 were strongly influenced by climate. Our results suggest that interspecific competition between antilopine wallaroos and eastern grey kangaroos may occur. 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 on sites that were burned, whereas the abundance of common wallaroos was higher on unburned 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.

Key words: Australia; climate change; conservation; fire; kangaroo; macroecology; Macropus; marsupial; species habitat model; sympatric niches; tropical savanna; wallaroo.

INTRODUCTION

Understanding the biological and environmental factors that limit the distribution and abundance of organisms is fundamental to ecology (Andrewartha and Birch 1954), and is central to our understanding of the niche concept (Hutchinson 1978). Although considerable effort has been devoted to identifying factors that influence species abundance, Sagarin et al. (2006) stress that, despite the many advances in experimental ecology over recent decades, we are severely "observation-limited" with regard 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 (Peterson et al. 2001, Hughes 2003, 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 and Lovett-Doust 2007). Put simply, models constructed for one part of a species' range may have limited predictive power for other areas; likewise generalized global models may fail to describe local conditions adequately (Murphy and Lovett-Doust 2007). 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

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in environmental conditions. Information collected over smaller spatial distributions will almost certainly be inadequate to inform conservation and management plans. A recent advance in ecological research has been a shift away from null hypothesis testing toward alternative approaches, including the information theoretic approach (ITA) (Burnham and 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 and Peres 2003, Gordon et al. 2004). Furthermore, large herbivores represent a significant part of the food resources and economies of human communities, and have strong cultural significance in many parts of the world (Yibarbuk et al. 2001, Gordon et al. 2004). 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 (Peterson and Holt 2003, Murphy and Lovett-Doust 2007). 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 and 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 et al. 2001, Woinarski and Ash 2002). 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 toward 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 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 localized areas of younger, nutrient-rich soils that 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*) (we used Strahan [1995] as the source of all these names and refer the reader to this publication for appropriate authorities). The antilopine wallaroo, endemic to Australia's extensive tropical savannas, is particularly poorly studied (Croft 1987) and may be in decline (E. G. Ritchie, *unpublished data*), and has strong cultural significance for indigenous people of this region (Busby 1988, Yibarbuk et al. 2001). This lack of detailed information regarding the antilopine wallaroo means that we are currently without an overall synthesis of the ecology and conservation status of native large herbivores at a continental scale in Australia. This is a major concern, because the majority of this continent's land is dedicated to pastoralism and livestock production, and rapid expansion of this industry is occurring within the tropical savannas (Williams et al. 2005). This trend is likely to continue with the added pressures of a persistent drought in temperate Australia, possibly due to long-term climate change, which has resulted in

decreased agricultural production and calls for the north to be further developed. Therefore, it is of vital importance that we have an understanding of the ecology of Australia's native large, tropical herbivores, which have evolved in this region, to ensure that any further economic development(s) will occur in an environmentally sustainable way.

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 (Figs. 1 and 2). We collected detailed information on climate, habitat, and resource availability and the distribution and abundance of each macropod species. With reference to previous studies (Caughley et al. 1987, 1988, Dawson 1995, Bowman 1998, Milewski and Diamond 2000, Olf et al. 2002, Ogutu and Owen-Smith 2003, 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 behavior (Croft 1987, Strahan 1995, Ritchie 2008).

Our specific objectives were: (1) to collect large-scale data on the distribution and abundance of large macropods across tropical northern Australia; (2) using this information and the ITA, to construct species-habitat models for large macropods that explore intra- and interspecific niche variation across the landscape; and (3) to relate the factors identified in our models as limiting species distribution and abundance to the future conservation and management of these species in northern Australia 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 understory dominated by native perennial grasses such as black speargrass (*Heteropogon contortus*), wiregrass (*Aristida* spp.), firegrass (*Schizachyrium* spp.), and native sorghum (*Sorghum* spp.). We used *Flora of Australia* (Orchard 1999) as the source of all these names and refer readers to this publication for appropriate authorities. Primary productivity is closely



FIG. 1. Map of the distributions (in black) of (a) the antilopine wallaroo (*Macropus antilopinus*), (b) eastern grey kangaroo (*M. giganteus*), and (c) common wallaroo (*M. robustus*) in Australia. Note that the eastern grey kangaroo also occurs in the island state of Tasmania.

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).

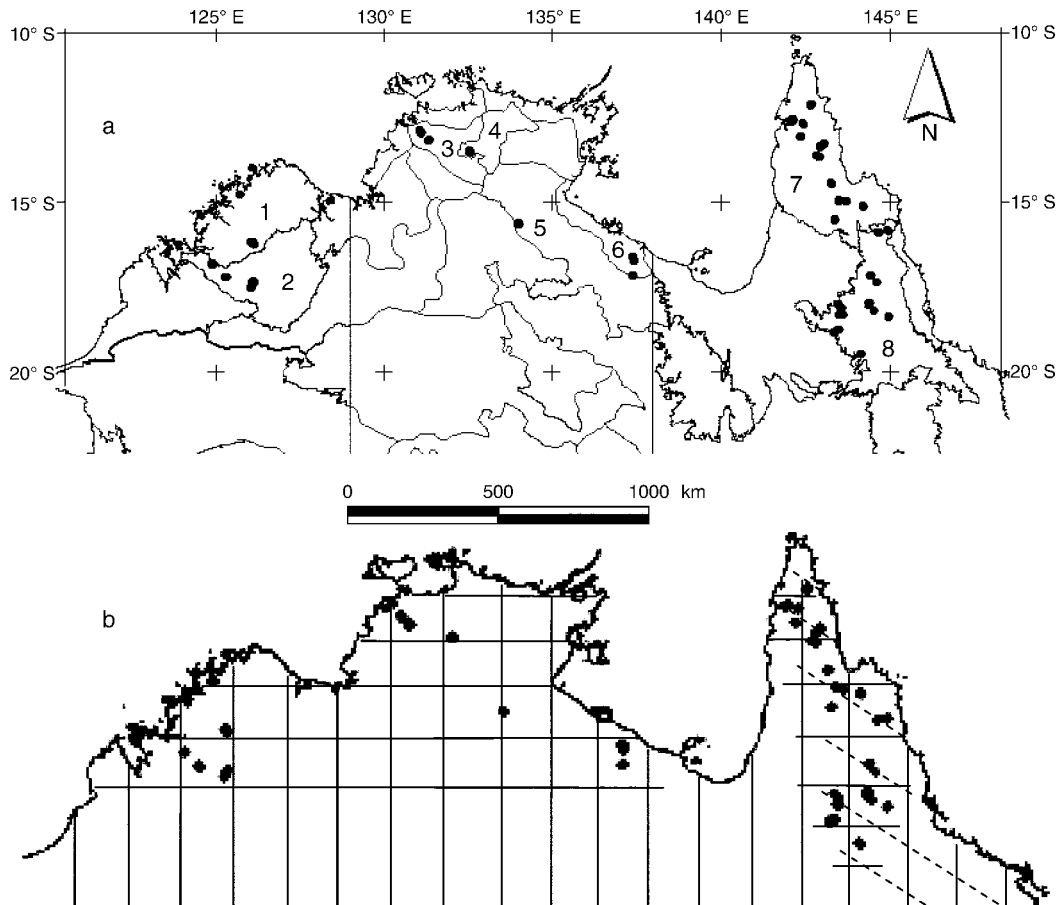


FIG. 2. (a) Map of the study region in northern Australia. Bioregion boundaries are represented by lines, numbers 1–8 indicate bioregions where surveys were conducted, and solid dots indicate survey sites. State boundaries are shown with thin straight black lines from left to right as follows: Western Australia, the Northern Territory, and Queensland. Bioregions are: 1, Northern Kimberley; 2, Central Kimberley; 3, Pine Creek; 4, Arnhem Plateau; 5, Gulf Fall and Uplands; 6, Gulf Coastal; 7, Cape York; 8, Einasleigh Uplands. (b) Map of the study region showing the distributions and areas of overlap between the antilopine wallaroo *Macropus antilopinus* (solid horizontal lines), the eastern grey kangaroo *M. giganteus* (dashed diagonal lines), and the common wallaroo *M. robustus* (solid vertical lines). Solid dots indicate survey sites.

Subsequently, many habitats burn due to direct human-caused fires or lightning strikes associated with frequent storms in the later dry season (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 2008) and the northern distributions of the common wallaroo and eastern grey kangaroo (Strahan 1995) (Fig. 2a, b). Sites were stratified by bioregion and identified by their underlying geology (basalt, granite, and sandstone) and land management (conservation or grazing). We then randomly selected sites from 1:100 000 topographic maps, provided that they offered four-wheel-drive vehicle access. Due to the logistical constraints of traveling between sites, we chose more sites in Queensland than in the Northern Territory and Western Australia. 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 5-km transect at each site, to assess seasonal variation in macropod abundance. 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 (05:30–08:30 hours) and two afternoon surveys (16:30–18:30 hours), 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 traveling 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 relative density estimates for each species. We used the mean density of all surveys of each transect (site) to calculate relative density estimates of species.

We conducted surveys by driving a vehicle along each transect at 10–15 km/h, 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), distance from the beginning of the transect (m), and the distance and angle of the individual(s) from the observer (m) (using a laser range finder). A group was defined as animals within visual contact of each other and no more than 50 m apart (Johnson 1983). We also kept a running tally of the number of cattle (*Bos indicus*), pigs (*Sus scrofa*), horses (*Equus caballus*), and dingoes (*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 relative density estimates for each macropod species according to standard line transect methodology (Grigg et al. 1989).

Site descriptions and vegetation surveys

We surveyed five 1.2-ha plots (6 ha total effort) spaced 1.25 km apart along each transect, recorded each plot's location with a handheld Garmin GPS (Magellan GPS 72, Garmin, Olathe, Kansas, USA) and took photo references. At each plot we recorded the following: elevation; boulders, rocks, pebbles, sand, dead trees, logs, grasses, vines, and scalds (bare surfaces, without vegetation, from which soil has been eroded or excavated), all on individual scales from 0 to 5; height of the canopy (m), measured with laser range finder (Bushnell Yardage Pro Sport 450, Bushnell, Overland, Kansas, USA); percent cover of projected foliage and percentage crown separation of canopy; percent cover of projected foliage and percentage crown separation of trees >5 m to canopy height; percent cover of projected foliage and percentage crown separation of plants >2 m and ≤5 m; percent cover of plants >1 m and ≤2 m; percent cover of plants 0 to ≤1 m. To measure fine-scale pasture composition at each plot, we placed three pairs of 1-m² quadrats along a 60-m transect, spaced at 20-m intervals. In each quadrat we recorded the following information: grass species present; percentage of bare ground; grass clump width (cm) and grass clump height (cm); greenness of grass (on a scale from 0 to 4); seeding index of grass (on a scale from 0 to 4); percent cover of grass; percent cover of non-grass; and the dry (oven-dried at 60°C for 24 h) biomass of grass (g). Lastly, at each interval we recorded the circumference at breast height of the 10

closest trees ≥2 m in height. Soil type (massive earth, sand, loam, duplex) was recorded from spatial data and ground-truthed by visual inspection (spatial data from Bureau of Rural Studies, *available online*).⁶ Water availability (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]), was assessed within a 5 km radius of each transect, and was determined by interviews with landowners, visual inspection, and spatial data from Geoscience Australia (*available online*).⁷

Fire history

We compiled the fire history of all sites using ArcView 3.3 (ESRI 1999–2002) and MODIS- and NOAA-derived digital satellite fire scar images provided by the Cape York Peninsula Development Association and the Bushfire Council of the Northern Territory through the Department of Land Information, Western Australia (*available online*).⁸ 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 percentage of the transect (0–25%, 26–50%, 51–75%, and 76–100%) burned 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, because a zero value was recorded for all sites.

Statistical analyses

Species co-occurrence.—To test for nonrandom patterns of co-occurrence of the three macropod species, we calculated C-scores in EcoSim 7.72 (Gotelli and Entsminger 2001). The C-score measures the mean number of checkerboard units between all possible pairs

⁶ (<http://www.daff.gov.au/brs>)

⁷ (<http://www.ga.gov.au>)

⁸ (<http://www.firenorth.org.au/nafi/app/init.jsp>)

TABLE 1. Principal components (rotated varimax) of climate in northern Australia.

Climate variables, northern Australia	PC 1	PC 2	PC 3
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
Variance	5.31	3.11	1.08
Variation (%)	53.15	31.13	10.77
Cumulative variation (%)	53.15	84.28	95.05

Notes: Values in bold represent factor loadings contributing the 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.

of species, as outlined in Stone and Roberts (1990). In a competitively structured community, the observed C-score should be significantly larger than expected by chance (Gotelli and Entsminger 2001). As recommended in Gotelli and Entsminger (2001), we used the fixed-rows and equiprobable-column simulation, which randomizes the occurrence of each species among the sites, assuming that the sites are equiprobable. This equates to a simple model of community assembly in which species colonize sites independently of one another. For each species-pair combination, only sites where range distributions indicated the potential for overlap were considered (see Fig. 2b). Fifty sites were compared for the antilopine wallaroo and common wallaroo combination. For the remaining combinations, 29 sites were considered.

Modeling approach.—Due to the high number of variables that might predict macropod abundance, we used a combination of correlation analysis and principal

TABLE 2. Principal components (rotated varimax) of climate in North Queensland, Australia.

Climate variables, North Queensland	PC 1	PC 2
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
Variance	5.89	3.23
Variation (%)	58.88	32.32
Cumulative variation (%)	58.88	91.20

Notes: Values in bold represent factor loadings contributing the 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.

TABLE 3. Principal components (rotated varimax) of vegetation structure in northern Australia.

Vegetation structure variable	PC 1	PC 2	PC 3
Canopy height	-0.25	0.60	-0.28
Canopy cover	-0.21	0.95	0.04
Tree circumference	0.13	0.00	-0.98
Canopy coverage >5 m	-0.60	0.30	0.09
Canopy coverage 2–5 m	-0.86	0.13	0.11
Canopy coverage 1–2 m	-0.93	0.24	0.11
Variance	2.09	1.42	1.08
Variation (%)	34.85	23.75	18.05
Cumulative variation (%)	34.85	58.60	76.65

Notes: Values in bold represent factor loadings contributing the most to each axis. PC1 describes a gradient of decreased cover for midstory, understorey, and shrub layers. PC2 describes a gradient of increased canopy cover and height. PC3 describes a gradient of smaller trees.

components analysis either to exclude variables that showed little relationship with abundance ($r \leq 0.3$), or to reduce multiple variables likely to be intercorrelated into principal component axes, before being used in the final set for the construction of models, as recommended by Quinn and Keough (2002). We plotted the relationships of abundance with the categorical variables of geology and soil type to examine their importance, and they were subsequently maintained as predictor variables in the models. Principal components (rotated varimax) were constructed for climate (Tables 1 and 2), vegetation structure (Table 3), grass layer (Table 4), and substratum (Table 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) in Statistica 6.0 (StatSoft 2003), which has the ability to include both continuous and categorical variables in such analyses. Only antilopine wallaroo abundance could be modeled across all levels,

TABLE 4. Principal components (rotated varimax) of the grass layer in northern Australia.

Grass layer variable	PC 1	PC 2	PC 3
Percent cover, 0–1 m	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
Percentage grass	-0.05	0.97	-0.12
Percentage non-grass	0.03	-0.98	0.06
Variance	2.15	2.12	1.06
Variation (%)	30.71	30.33	15.17
Cumulative variation (%)	30.71	61.04	76.21

Notes: Values in bold represent factor loadings contributing the 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.

TABLE 5. Principal components (rotated varimax) of substratum in northern Australia.

Substratum variable	PC 1	PC 2
Boulders	0.47	0.41
Rocks	0.67	-0.14
Pebbles	0.29	0.68
Sand	-0.50	0.59
Variance	1.87	1.22
Variation (%)	46.63	30.44
Cumulative variation (%)	46.63	77.06

Notes: Values in bold represent factor loadings contributing the most to each axis. PC1 describes a gradient of increased rockiness. PC2 describes a gradient of increased pebbles and sandiness.

because 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 that this had on AIC (Akaike information criterion) 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 overdispersion as recommended by Burnham and Anderson (2002) for studies using count data; however, no models showed evidence of overdispersion 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 and Anderson 2002). We examined the relationship between abundance and species at the three different spatial scales mentioned (see Figs. 1 and 2): 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 northeastern 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).

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 (Table 6). Within North Queensland, 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 individuals/km² (all values reported as mean \pm SE;

TABLE 6. Relative density of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*), and eastern grey kangaroos (*M. giganteus*) across northern Australia and between bioregions.

Region, site no., and bioregion	Relative density (no. individuals/km ²)		
	Antilopine wallaroo	Common wallaroo	Eastern grey kangaroo
Western Australia			
1, Central Kimberley	0.33	0.17	
2, Central Kimberley	1.17	0.17	
3, Central Kimberley	0.00	0.00	
4, Northern Kimberley	0.00	0.00	
5, Central Kimberley	0.00	0.00	
6, Central Kimberley	3.75	0.38	
7, Central Kimberley	0.00	0.17	
8, Northern Kimberley	7.38	0.00	
9, Northern Kimberley	5.13	0.00	
10, Northern Kimberley	3.33	0.00	
Northern Territory			
1, Gulf Fall and Uplands	0.25	3.25	
2, Pine Creek	1.25	0.00	
3, Pine Creek	4.17	0.00	
4, Arnhem Plateau	3.50	0.00	
5, Arnhem Plateau	0.00	0.00	
6, Pine Creek	0.00	0.00	
7, Pine Creek	1.00	0.00	
8, Pine Creek	2.00	0.00	
9, Gulf Fall and Uplands	12.88	0.38	
10, Gulf Coastal	0.17	0.00	
11, Gulf Coastal	1.00	0.00	
Queensland			
1, Cape York	1.43	0.00	0.00
2, Einasleigh Uplands	0.00	0.38	1.81
3, Einasleigh Uplands	1.60	1.58	0.00
4, Cape York	0.00	0.00	0.00
5, Cape York	0.00	0.00	0.25
6, Einasleigh Uplands	0.00	0.00	0.00
7, Einasleigh Uplands	0.88	2.75	0.00
8, Cape York	6.25	3.06	0.00
9, Einasleigh Uplands	5.00	0.00	0.00
10, Cape York	0.00	2.00	5.81
11, Einasleigh Uplands	1.38	0.00	0.13
12, Einasleigh Uplands	2.63	2.06	0.00
13, Cape York	1.56	0.06	0.00
14, Cape York	0.00	0.00	0.13
15, Cape York	0.75	0.00	0.25
16, Cape York	0.88	0.00	0.00
17, Einasleigh Uplands	9.81	0.00	0.00
18, Einasleigh Uplands	0.67	1.67	0.00
19, Cape York	0.25	0.38	0.00
20, Cape York	0.00	0.00	0.50
21, Cape York	0.88	0.00	0.00
22, Cape York	4.13	0.00	0.00
23, Einasleigh Uplands	8.38	0.19	0.00
24, Einasleigh Uplands	0.00	0.94	0.06
25, Cape York	0.00	0.25	0.25
26, Einasleigh Uplands	5.17	0.90	0.00
27, Cape York	1.44	0.00	0.00
28, Einasleigh Uplands	3.17	0.48	0.94
29, Cape York	0.00	0.00	0.38

Notes: Refer to Fig. 2a for geographic positions of bioregions. Relative density estimates were calculated according to standard line-transect methodology detailed in Grigg et al. (1989).

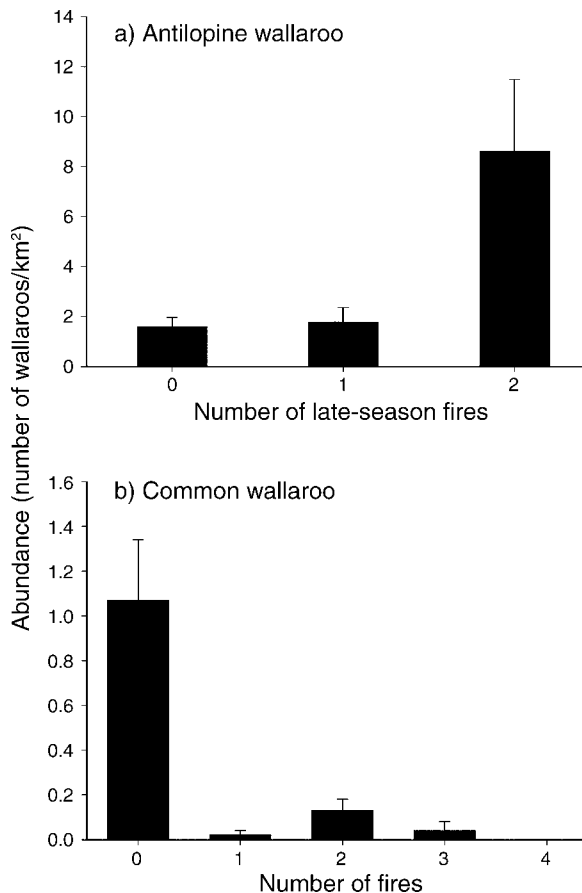


FIG. 3. (a) Relationship between the abundance (mean \pm SE) of antilopine wallaroos and the number of times sites were burned (by late-season fires) for northern Australia between 2002 and 2005. (b) Relationship between the abundance (mean \pm SE) of common wallaroos and the number of times sites were burned between 2002 and 2005 for northern Australia.

range 0.2–12.9) 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 Fig. 2a for bioregion locations). Common wallaroos occurred at an average density of 1.1 ± 0.2 individuals/km² (range 0.1–3.3) across northern Australia, and were significantly less abundant than antilopine wallaroos across this region (t test, $t_{98} = 3.9$; $P < 0.001$; Table 6). Within North Queensland, common wallaroos occurred at an average density of 1.2 ± 0.3 individuals/km² (range 0.1–3.1) and eastern grey kangaroos at 1.0 ± 0.5 individuals/km² (range 0.1–5.8). Antilopine wallaroos were significantly more abundant than common wallaroos and eastern grey kangaroos in North Queensland (ANOVA, $F_{2,84} = 7.0$; $P = 0.002$; Table 6).

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 ($C = 100.0$, $P = 0.8$) and eastern grey kangaroos and common wallaroos ($C = 50$, $P = 0.5$) were neither positively nor negatively associated.

Fire frequency and regime

In total, 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 burned 1.5 ± 0.2 times (mean \pm SE; range 0–4); an average of $31\% \pm 4.4\%$ of its area was affected by each fire; 18 sites (36%) were not burned. Early-season fires were more common than late-season fires in the Northern Territory (early-season, 2.1 ± 0.4 fires [all values mean \pm SE]; late-season, 0.4 ± 0.2 fires) and Western Australia (early-season, 1.2 ± 0.2 fires; late-season, 0.6 ± 0.2 fires), but nearly equal in frequency in Queensland (early-season, 0.5 ± 0.2 fires; late-season, 0.4 ± 0.1 fires). Across northern Australia, antilopine wallaroos were significantly more abundant at sites that were burned more than once by late-season fires between 2002 and 2005 (ANOVA, $F_{2,47} = 12.2$, $P < 0.001$; Fig. 3a). Common wallaroos were significantly more abundant on unburned sites across northern Australia (ANOVA, $F_{4,45} = 5.6$, $P = 0.001$; Fig. 3b). Within North Queensland, there was no significant effect of fire frequency on eastern grey kangaroo abundance (Kruskal-Wallis, $\chi^2 = 3.5$, $df = 3$, $P = 0.32$).

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 (Tables 7a–d and 8a–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 (Tables 7a and 8a), 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 (Tables 7b and 8b). At the smallest scale (bioregional: Cape York and Einasleigh Uplands), vegetation structure and grass layer composition were important predictors of antilopine wallaroo abundance (Tables 7c, d and 8c, d). An interaction between geology and land management affected antilopine wallaroo abundance across the species' range (Tables 7a and 8a). Antilopine wallaroos were most abundant on cattle-grazing sites with basaltic geology (Fig. 4) and showed a highly significant positive trend with increased availability of permanent water (Fig. 5). The abundance of common wallaroos showed a weaker positive correlation with water availability, and eastern grey kangaroos showed a weak negative correlation with water avail-

TABLE 7. Summary habitat models of antilopine wallaroo (*Macropus antilopinus*) abundance across (a) northern Australia, (b) North Queensland, (c) Cape York, and (d) Einasleigh Uplands bioregions.

Model, by region	Permanent water (total)	No. late- season fires	Geol- ogy	Land manage- ment	Geology × land manage- ment†	Eastern grey kangaroo abundance	Soil type	PC2 (vegetation structure)	PC1 (vegetation structure)	PC2 (grass layer)	AIC _c	Δ _i	w _i
a) Northern Australia													
1	x	x	x	x	x						163.02	0.00	0.52
2	x	x	x								165.15	2.13	0.18
3	x	x		x	x						166.02	3.00	0.12
4	x	x	x	x							166.28	3.26	0.10
5	x	x			x						166.91	3.89	0.08
b) North Queensland													
1	x	x				x	x				73.22	0.00	0.61
2	x	x				x					75.30	2.08	0.22
3	x	x					x				77.10	3.88	0.09
4	x	x									77.11	3.89	0.09
c) Cape York													
1	x	x						x			43.88	0.00	0.37
2	x	x						x			44.66	0.78	0.25
3	x							x			46.86	2.98	0.08
4	x						x	x			47.02	3.14	0.08
5	x	x					x				47.11	3.24	0.07
6		x					x	x			47.15	3.27	0.07
7	x						x				47.41	3.53	0.06
d) Einasleigh Uplands													
1						x			x	x	32.41	0.00	0.31
2									x	x	33.21	0.81	0.21
3	x								x	x	33.30	0.89	0.20
4	x					x			x	x	34.37	1.96	0.12
5	x									x	34.76	2.35	0.10
6	x										35.38	2.98	0.07

Notes: Parameters included in each model are denoted by "x." PC is the principal component axis (refer to Tables 3 and 4). AIC_c is the corrected Akaike Information Criterion model score; models with lower scores are better than models with higher scores. Δ_i is the model score difference; 0 is the "best" model; values between 0 and 2 have substantial support; values >2 have considerably less support. The Akaike model weight, w_i, is the weight of evidence for model *i* being the best model given that one model in the set must be the best model. Models in boldface have substantial support (Δ_i < 2).

† Interaction of factors.

ability. The availability and sources of water varied between regions, with approximately twice as many permanent natural sources present in Western Australia and the Northern Territory as in Queensland, whereas there were 10 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 (Fig. 6). Eastern grey kangaroos were also more abundant on massive earths, and common wallaroos on loams and sandy soils (Fig. 6).

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 (Tables 7b–d and 8b–d). There were key differences in the factors affecting antilopine wallaroo abundance between bioregions within North Queensland (Tables 7c, d and 8c, 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 understory 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.

Common wallaroo.—Across northern Australia, the frequency of fire (–), climate (+), and geology (+) were the best predictors of common wallaroo abundance (Tables 9a, b and 10a, b). Common wallaroo abundance was lower at sites that were burned and in conservation areas (Figs. 3b and 4), and higher on cattle-grazing sites of granitic geology (Fig. 4). Common wallaroos were also more abundant in areas of increased temperature variation and decreased rainfall and rockier habitats (Tables 1 and 5). Within North Queensland, common wallaroos were less abundant in areas of higher temperature and increased rainfall and more abundant in open habitats (Tables 2, 9b, and 10b).

Eastern grey kangaroo.—The abundance of eastern grey kangaroos in North Queensland was correlated

TABLE 8. Parameter estimates and their relative importance for summary habitat models of antilopine wallaroo (*Macropus antilopinus*) abundance.

Parameter, by bioregion	Level of effect	Parameter estimate	Relative importance
a) Northern Australia (intercept: -3.65)			
Permanent water (total)		3.20	1.00
No. 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 (intercept: -1.70)			
Permanent water (total)		3.42	1.00
No. 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 (intercept: -2.17)			
Permanent water (total)		4.58	0.93
PC 2 (vegetation structure)		0.48	0.86
No. late-season fires		0.48	0.77
Eastern grey kangaroo abundance		-1.88	0.54
d) Einasleigh Uplands (intercept: 1.58)			
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

Notes: Level of effect refers to categorical variables and the extent to which levels within these variables contributed to models. The parameter estimate, calculated during the modeling process, indicates how much influence each variable has on abundance. The relative importance of parameters 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 and Anderson (2002).

with the abundance of antilopine wallaroos (-), geology (+ and -), and climate (-) (Tables 2, 11, and 12). Eastern grey kangaroos were most abundant on sites of basaltic geology, and, unlike common wallaroos, were less abundant at sites with granitic geology (Fig. 4).

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

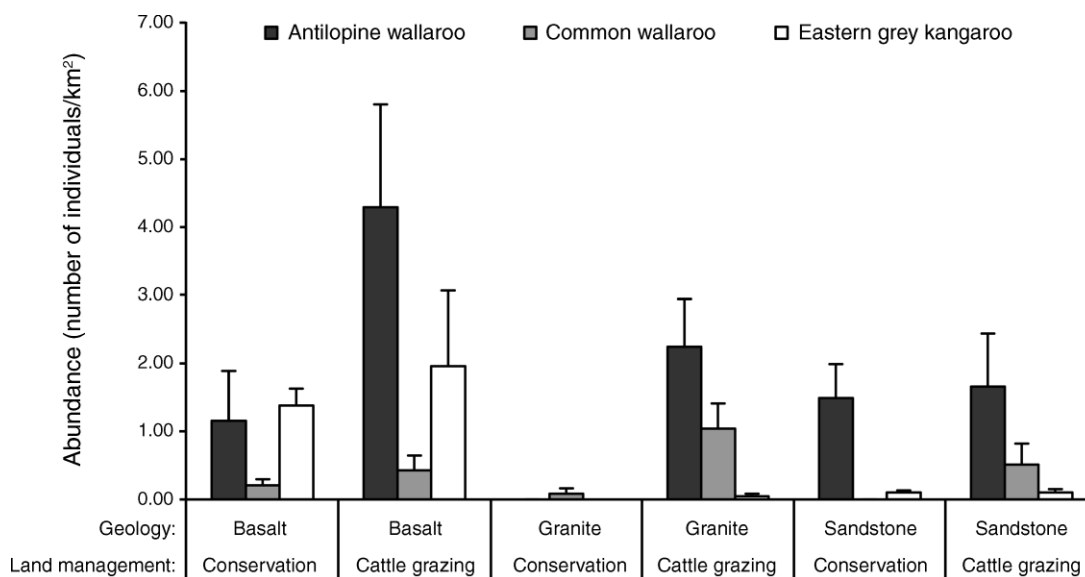


FIG. 4. Abundance (mean + SE) of antilopine wallaroos (*Macropus antilopinus*), common wallaroos (*M. robustus*), and eastern grey kangaroos (*M. giganteus*) in relation to geology and land management across northern Australia.

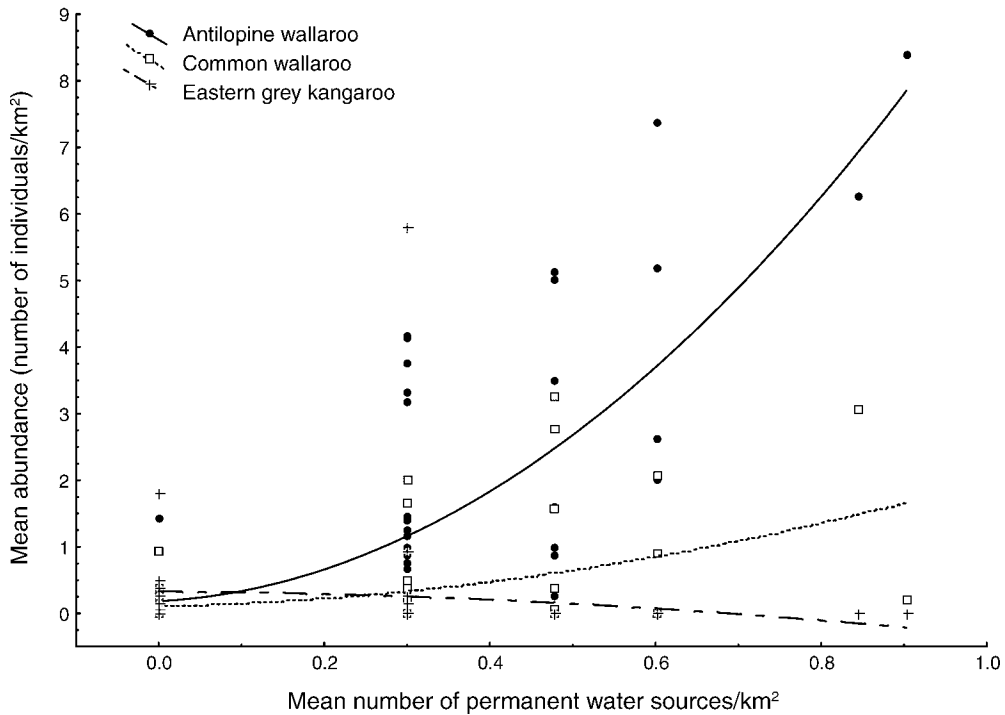


FIG. 5. Relationship between the abundance of large macropods and the availability of permanent water in northern Australia. For antilopine wallaroos, $r = 0.68$, $P < 0.001$; for common wallaroos, $r = 0.36$, $P = 0.01$; for eastern grey kangaroos, $r = -0.12$, $P = 0.41$.

complete distributions and at smaller spatial scales (Peterson and Holt 2003, Murphy and Lovett-Doust 2007). 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 Peterson et al. 2001, Hughes 2003,

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 modeling the abundance of one species, the antilopine wallaroo, across its geo-

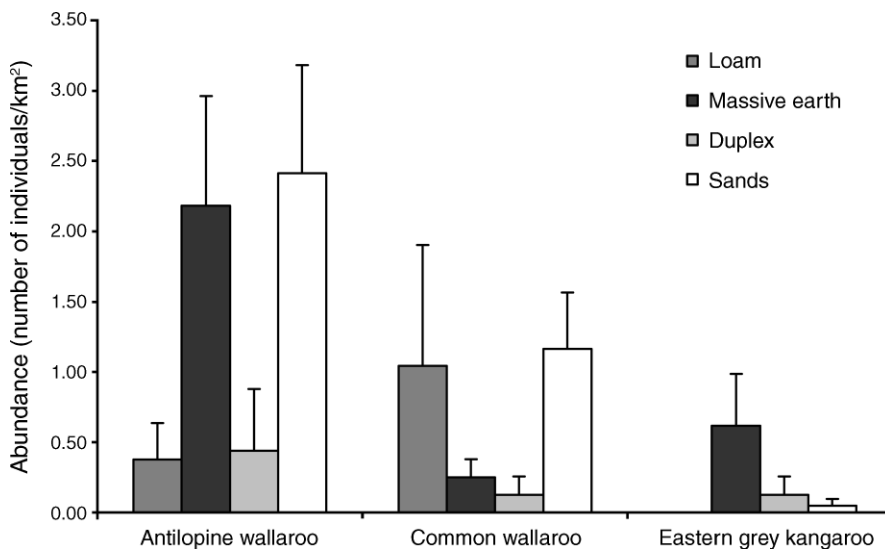


FIG. 6. Abundance (mean \pm SE) of antilopine wallaroos, common wallaroos, and eastern grey kangaroos in relation to soil type across North Queensland, Australia.

TABLE 9. Summary habitat models of common wallaroo (*Macropus robustus*) abundance for (a) northern Australia and (b) North Queensland.

Model, by region	PC1 (substratum)	No. fires	PC1 (climate)	Land management	Geology	Geology × land management†	Openness	AIC _c	Δ _i	w _i
a) Northern Australia										
1	x	x	x	x				35.19	0.00	0.28
2	x	x	x	x	x			35.80	0.61	0.21
3	x	x	x	x		x		36.07	0.88	0.18
4	x	x	x	x	x	x		36.34	1.15	0.16
5	x	x	x		x	x		37.85	2.66	0.07
6		x	x	x	x			38.79	3.60	0.05
7		x	x	x		x		38.98	3.79	0.04
b) North Queensland										
1			x		x		x	39.61	0.00	0.28
2		x	x				x	40.19	0.58	0.21
3		x	x		x		x	40.89	1.28	0.15
4			x				x	41.09	1.48	0.13
5		x					x	42.14	2.54	0.08
6		x	x					42.43	2.82	0.07
7			x					43.30	3.70	0.04
8		x			x		x	43.41	3.80	0.04

graphic 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 the requirements are studied. At larger scales, broadscale 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.

Abundance of macropods in Australia

The density of large macropod species in tropical savannas was much lower than is typical for arid rangelands or the southern commercial harvest zones of Australia. Antilopine wallaroos were found at a maximum density of ~13 individuals/km², with a much lower mean density of 3 individuals/km². Common

wallaroos and eastern grey kangaroos were found at mean densities of 1 individual/km². As a comparison, in southern Australia, eastern grey kangaroos and common wallaroos have been recorded at densities above 30 individuals/km² (Southwell et al. 1999). Likewise, red kangaroos (*Macropus rufus*) have been found at similar densities in the arid southern rangelands of Australia (Caughley et al. 1977, Cairns et al. 1991). This discrepancy in the typical density of large macropods in tropical vs. temperate and arid regions is of biological and conservation significance.

There are at least three reasons why macropods may occur at lower densities in northern than in southern Australia. First, soils in northern Australia are typically low in available nutrients; therefore pastures are correspondingly nutritionally poor (Williams et al. 2005). Second, although annual rainfall is higher in

TABLE 10. Parameter estimates and their relative importance for summary habitat models of common wallaroo (*Macropus robustus*) abundance.

Parameter, by bioregion	Level of effect	Parameter estimate	Relative importance
a) Northern Australia (intercept -2.55)			
No. fires		-0.73	1.00
PC1 (climate)		0.98	1.00
Land management	conservation	-1.57	0.93
PC1 (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 (intercept -5.65)			
Openness		1.26	0.89
PC1 (climate)		-1.56	0.88
No. fires		-0.35	0.54
Geology	basalt	-0.87	0.47
Geology	granite	0.03	0.47

Notes: Level of effect refers to categorical variables and the extent to which levels within these variables contributed to models. The parameter estimate, calculated during the modeling process, indicates how much influence each variable has on abundance. The relative importance of parameters 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 and Anderson (2002).

TABLE 11. Summary habitat model of eastern grey kangaroo (*Macropus giganteus*) abundance for North Queensland.

Model	Antilopine wallaroo abundance	PC2 (climate)	Geology	AIC _c	Δ_i	w_i
1	x	x	x	29.66	0.00	0.81
2	x	x		32.61	2.94	0.19

Notes: PC is the principal component axis (refer to Table 2). AIC_c is the corrected Akaike Information Criterion model score; models with lower scores are better than models with higher scores. Δ_i is the model score difference: 0 is the “best” model; values between 0 and 2 have substantial support; values >2 have considerably less support. The Akaike model weight, w_i , is the weight of evidence for model i being the best model given that one model in the set must be the best model. Models in boldface have substantial support ($\Delta_i < 2$).

tropical than in temperate Australia, evaporation rates are much higher in the tropics, so permanent drinking water for macropods can become a patchy and often scarce resource. In southern Australia, intensive pastoralism has seen the establishment of many permanent water sources (e.g., dams and bores) across the landscape (Dawson et al. 2004). Third, dingoes and wild dogs are heavily controlled over large areas of southern Australia, and kangaroo abundance is typically highest where these predators are absent (Pople et al. 2000). Dingoes remain widespread and abundant through most of northern Australia. The lower abundance of large macropods in northern Australia requires different management to that for large macropods in southern Australia. Specifically, species in the north may be more susceptible to population declines through stochastic events and should be systematically monitored to avoid overexploitation where hunting and/or culling occur.

Niche variation in marsupial herbivores

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. At a coarse scale, geology may be considered as a good surrogate for measures of productivity and therefore is also likely to be a good predictor of the abundance of species across the landscape (Mutanga et al. 2004). A partial explanation for this relationship may be the tendency in Australia for grazing properties to be located in more productive areas and conservation reserves in less productive areas (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 et al. 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, which are an important shelter resource facilitating thermoregulation by this species and reducing its dependence on free water in areas of high temperature (Dawson and Denny 1969, Dawson 1995). In contrast, antilopine wallaroos do not use rock shelters (Ritchie 2008); 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, Olf et al. 2002). In contrast to other parts of the world, Australia's savannas are characterized 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). As mentioned previously, geology and soil type provide good proxies for soil fertility (productivity) at the coarse scale (Mutanga et al. 2004). Volcanic soils (basalt) are more

TABLE 12. Parameter estimates and their relative importance for summary habitat models of eastern grey kangaroo (*Macropus giganteus*) abundance for North Queensland (intercept = -2.04).

Parameter	Level of effect	Parameter estimate	Relative importance
Antilopine wallaroo abundance		-1.15	1.00
Geology	basalt	1.30	1.00
Geology	granite	-0.24	1.00
PC2 (climate)		-1.46	0.81

Notes: Level of effect refers to categorical variables and the extent to which levels within these variables contributed to models. The parameter estimate, calculated during the modeling process, indicates how much influence each variable has on abundance. The relative importance of parameters 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 and Anderson (2002).

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. 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 favor nutrient-rich grasses in their diets (Dawson 1995, Fossan 2005). On the other hand, the common wallaroo is a mixed feeder that includes 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 and 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 it significantly shapes ecosystem structure and function (Bowman 1998, van Langevelde et al. 2003, Bond and Keeley 2005). Antilopine wallaroos were most abundant at sites where there had been two late-dry-season fires in the previous three years, whereas common wallaroos were significantly more abundant on unburned 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 favored 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 burned habitat to feed on fresh, nutrient-rich grass (Bowman 1998, Bowman et al. 2001a, Yibarbuk et al. 2001). Our results also suggest that such an effect may be cumulative, because no difference in antilopine wallaroo abundance was found between unburned sites and sites burned only once, whereas abundance greatly increased in areas burned 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 favor more open habitats. One possible explanation is that although these fires may increase openness and grass nutrient content, 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 and Bowman 2006). Continued removal of browse by fire and increases in grass biomass within habitats may confer an advantage to more specialized grazing species such as antilopine wallaroos and eastern grey kangaroos, and disadvantage more generalist feeders such as common wallaroos. The rockier habitats typically occupied by the common wallaroo, in addition to aiding thermoregulation, also may 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 to the structuring of macropod assemblages.

Climate

Our results build on earlier work by Caughley et al. (1987, 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 et al. 2002, Ogutu and Owen-Smith 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 favored areas of lower rainfall and greater temperature variation, representative of increasing aridity. This preference by the common wallaroo may explain the sharp decrease in this species' abundance in lower (more "tropical") latitudes (which may correlate with an ecophysiological threshold). No work to date has compared the ecophysiology of sympatric antilopine wallaroos, common wallaroos, and eastern grey kangaroos, and its effects on their respective abilities to occupy tropical habitats. Antilopine wallaroos, however, do have two morphological adaptations that may be related to coping with the climatic conditions experienced in this region: a highly

vascularized 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 probably enhances evaporative cooling (through panting) in humid air (Dawson 1995, Ritchie 2008). 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 behavioral 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 absence of co-occurrence among large mammalian herbivores (Young et al. 2005, Wegge et al. 2006). 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 demonstrated. 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 (Fig. 2b), we found climate to be an important factor influencing eastern grey kangaroos, but not antilopine wallaroos. At the same level of modeling, 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 (most of northern Australia) may not. Climatic seasonality and changes in the availability of food resources may be a critical consideration when exploring the potential for competition between macropods in the monsoonal tropics. Edwards et al. (1996) found that competition was only intermittent between red kangaroos and sheep (*Ovis aries*) within the Australian arid zone (a seasonally unpredictable environment), after climatically driven resource depletion (drought). Our results further high-

light 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 broadscale 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 in areas with an understory 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 the 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 and management 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 predict not only increased temperature and possibly slightly increased annual rainfall, but also increased uncertainty of rainfall events and the possibility of longer, harsher dry seasons (Walsh et al. 2001, Hughes 2003). Even if overall rainfall increases, the availability of water in many areas may decrease as higher temperatures increase rates of evaporation, causing water loss (negative water balance) in this region (Walsh et al. 2001). Of the three species that we studied, the antilopine wallaroo is most dependent on access to water. Reduced water availability may be exacerbated if rainfall becomes less predictable. Because the breeding season of antilopine wallaroos is tightly centered around monsoonal rains (Ritchie 2008), any disturbance to, or reduction of, these rainfall events could negatively impact the breeding phenology of this species, leading to possible localized population declines.

Increased temperatures and rainfall and increased levels of CO₂ in northern Australia will also influence the structure and composition of habitats and the

frequency of fire. As we have shown, the three macropods differ in their habitat preference; thus there is potential for species to be affected in different ways under changing climate and habitat. Changes in climate may have a number of effects on the structure and composition of savanna. First, increased temperature and rainfall may result in habitat thickening due to increased numbers and/or growth of woody plants (Hughes 2003), and these plants may be favored by elevated levels of CO₂ (which is thought to favor C3 over C4 plants, and also to simply provide more carbon for plants to engineer structural tissue). A number of studies provide evidence that this may already be occurring (Archer et al. 1995, Bowman et al. 2001*b*). Second, under these conditions, rain forest may invade woodlands (Bowman et al. 2001*b*), 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, although this could be counterbalanced by a potential increase in food (woody plants). Likewise, we predict that antilopine wallaroos would be favored 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. The management of fire regimes will be a particularly important aspect of this complexity.

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 how 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 conservation and management.

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