

RESEARCH PAPER

 OPEN ACCESS

A continent-wide analysis of the shade requirements of red and western grey kangaroos*

J. A. Roberts^a, G. Coulson^a, A. J. Munn^{b,c}, and M. R. Kearney^a

^aSchool of BioSciences, The University of Melbourne, Melbourne Victoria, Australia; ^bSchool of Biological, Earth, and Environmental Sciences, The University of New South Wales, New South Wales, Australia; ^cFaculty of Veterinary Sciences, The University of Sydney, New South Wales, Australia

ABSTRACT

Foraging time may be constrained by a suite of phenomena including weather, which can restrict a species' activity and energy intake. This is recognized as pivotal for many species whose distributions are known to correlate with climate, including kangaroos, although such impacts are rarely quantified. We explore how differences in shade seeking, a thermoregulatory behavior, of 2 closely-related kangaroo species, *Macropus rufus* (red kangaroos) and *M. fuliginosus* (western grey kangaroos), might reflect differences in their distributions across Australia. We observed foraging and shade-seeking behavior in the field and, together with local weather observations, calculated threshold radiant temperatures (based on solar and infrared radiant heat loads) over which the kangaroos retreated to shade. We apply these calculated tolerance thresholds to hourly microclimatic estimates derived from daily-gridded weather data to predict activity constraints across the Australian continent over a 10-year period. *M. fuliginosus* spent more time than *M. rufus* in the shade (7.6 ± 0.7 h versus 6.4 ± 0.9 h) and more time foraging (11.8 ± 0.5 h vs. 10.0 ± 0.6 h), although total time resting was equivalent (~ 8.2 h). *M. rufus* tolerated 19°C higher radiant temperatures than *M. fuliginosus* (89°C versus 70°C radiant temperature). Across Australia, we predicted *M. fuliginosus* to be more restricted to shade than *M. rufus*, with higher absolute shade requirements farther north. These results corroborate previous findings that *M. rufus* is more adept at dealing with heat than *M. fuliginosus* and indicate that *M. rufus* is less dependent on shade on a continental scale.

ARTICLE HISTORY

Received 15 February 2016

Revised 4 March 2016

Accepted 4 March 2016

KEYWORDS

activity budget; endotherm; time budget; marsupial; range limits; shade-seeking behavior; thermoregulation; temperature tolerance

Introduction

Weather plays a key role in restricting foraging activity, which has important implications for species' distributions.¹ Shade can provide protection against adverse weather, including solar radiation loads during the day and high infra-red radiation losses at night.² Although shade selection is well-recognized and quantified as a thermoregulatory mechanism for ectotherms, endotherms also require shade to reduce their expenditure of energy and water for physiological thermoregulation.^{3,4} Shade use during the day can reduce exposure of large mammals to incoming solar radiation by up to 80% in desert environments.⁵ Grazing animals typically need to feed for long periods in open habitats and are thus particularly vulnerable to such

constraints imposed by weather. A lack of suitable shade may, therefore, affect a grazing endotherm's ability to balance its energy and water budgets.

A species' response to its environment depends both on the properties of the environment (physical conditions and biotic factors) and of the animal itself (behavior, physiology, and morphology). As such, related species with divergent adaptations may occupy markedly different geographical habitats, but they may also use the same habitat differently and thus experience different activity restrictions under the same climatic conditions. A species' shade requirement, which results from interactions between the environment and the animal, differs from shade availability. Therefore, if shade is present, the extent of shade-seeking behavior may

CONTACT Jessica Anne Roberts  jessroberts09@gmail.com  School of BioSciences, The University of Melbourne, Melbourne Victoria, 3010, Australia.

*This paper was accepted through Accelerated Track.

© 2016 J. A. Roberts, G. Coulson, A. J. Munn, and M. R. Kearney. Published with license by Taylor & Francis.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-Non-Commercial License (<http://creativecommons.org/licenses/by-nc/3.0/>), which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited. The moral rights of the named author(s) have been asserted.

provide an index for comparing how weather constrains the foraging activity of related species.

To unravel which climatic factors may drive species' distributions, many studies correlate the occurrence of species across the landscape with environmental predictors.⁶⁻⁹ Caughley *et al.*⁶ showed that Australia's three largest kangaroo species (*Macropus rufus*, *M. giganteus*, and *M. fuliginosus*) occupy different climatic environments, which potentially reflects divergent adaptations. These three large kangaroo species (Marsupialia: Macropodidae) are all broadly distributed grazers with similar maximum body sizes,¹⁰ body temperatures,¹¹⁻¹³ and activity patterns,^{10,14-17} but they have different geographic ranges. *M. rufus* (the red kangaroo) occupies climates that are both hotter (with mean annual temperatures up to 10°C higher) and drier than those occupied by either *M. fuliginosus* (the western grey kangaroo) or *M. giganteus* (the eastern grey kangaroo).¹⁸ In contrast, differences between grey kangaroo distributions appear related to rainfall seasonality.¹⁸ Walker¹⁹ found that the distribution of *M. rufus* was more strongly associated with higher temperatures than either grey kangaroo species, and Ritchie *et al.*²⁰ found that *M. giganteus* was strongly associated with lower temperatures (and reduced rainfall-seasonality). Such correlative studies imply that adaptive differences exist between these macropod species and affect their ability to deal with and survive in different environments.

Previous physiological and behavioral studies suggest that *M. giganteus* is not as adept at coping with higher temperatures in dry climates as *M. rufus*. In field conditions, *M. giganteus* uses significantly more water (72.0 ± 2.6 vs. 56.0 ± 7.6 mL/kg/day) and seeks more shade during the day to reduce heat load than does *M. rufus*.²¹⁻²³ Behavior (specifically behavioral avoidance) is recognized to be a relatively plastic response and is a species' first overt line of defense against adverse environmental conditions.²⁴ In the arid rangelands of Australia, *M. giganteus* crouches more frequently than does *M. rufus*, a posture that apparently facilitates heat loss by exposing the inside of limbs to free and forced convection.²³ In addition, *M. rufus* can maintain its body temperature approximately 2°C higher than *M. giganteus* during hot days, to minimize the temperature gradient for heat gain.²⁵ Together, these results suggest that significant adaptive differences exist between *M. rufus* and *M. giganteus*, affecting their abilities to cope in hot, arid environments. However, much less is known about how the other large kangaroo species that

inhabits Australia's arid regions – *M. fuliginosus* (the western grey kangaroo) – responds to climate, other than that it exhibits similar general activity patterns^{14,15,26} and similar body temperature variation to *M. rufus*.²⁵ Moreover, no studies have quantified the exact conditions under which these species require shade.

In this study, we directly compare the behavior of *M. fuliginosus* and *M. rufus* to address two key questions. First, do presumed adaptive differences – based on differences in the climatic environments occupied by these species – translate to differences in foraging and shade seeking behavior at a given site? Foraging and shade use are often mutually exclusive for kangaroos, as shade trees in Australia's arid zone are typically small and do not offer many opportunities for grazing in shade; thus, we expect foraging time to generally decrease with increased shade use. While we expect that both species would show similar overall patterns of daily activity, as reported in previous studies, we also predict that the activity of these species will cease at different thresholds of radiant heat load. To assess this, we use behavioral observations and measured climatic conditions to calculate radiant heat tolerance thresholds, above which kangaroos are constrained to enter and remain in shade. We assume that kangaroos require and retreat to shade to escape high heat loads, as has been demonstrated previously,^{5,27,28} and we aim to quantify the thresholds at which these two kangaroo species seek shade. Because the range of *M. rufus* extends into hotter and drier areas than *M. fuliginosus*, we predict that *M. rufus* will be less sensitive to increased heat loads and will remain active in direct sun for longer periods compared to *M. fuliginosus*.

Second, how do shade requirements (i.e. activity constraints) of *M. rufus* and *M. fuliginosus* compare across the Australian landscape? We apply the calculated radiant temperature thresholds to daily weather data across Australia to estimate shade requirements (i.e., constraints on activity) and evaluate whether they reflect differences in the distribution limits of *M. rufus* and *M. fuliginosus*. We also examine shade availability across Australia and hypothesize where physiological, morphological, and behavioral differences between the two macropod species might have the greatest influence on their distribution limits.

Materials and methods

We compared the foraging behavior and shade use of *M. rufus* and *M. fuliginosus* at the University of

New South Wales Fowlers Gap Arid Zone Research Station, NSW (31°05'25"S, 141°42'30"E), which is located 112 km north of Broken Hill, NSW, Australia. In January 2009 we captured five *M. rufus* and nine *M. fuliginosus* from wild populations living on the station property, using a dart gun (Pneu-Dart^{inc.} X-Caliber CO₂ rifle, Williamsport, PA, USA) with 1.0 mL darts containing 375–400 mg (~15 mg/kg) of Zoletil 100 (Virbac, Milperra, NSW, Australia). All kangaroos captured were adult females. After initial capture, kangaroos were given an intra-muscular injection of penicillin to minimize risk of infection (2 mL; VET TEK, Blue Springs, MO, USA), administered Lacri-lube (Refresh lubricant eye ointment, Allergan, Irvine, CA, USA) to keep their eyes moist, and had their dart wound treated with anti-septic spray (Cetrigen, Virbac Milperra, NSW, Australia). Body mass of *M. fuliginosus* ranged from 15.4 to 26.4 kg (average 22.3 ± 1.5 kg), while *M. rufus* ranged from 21.1 to 25.6 kg (average $22.8 \text{ kg} \pm 1.1$ kg). All except three had pouch young, which were all furless and <10 cm in length. These young were removed to synchronize reproductive state and to reduce variation in energy or water use associated with lactation and were euthanized according to ethical guidelines. Each kangaroo was given a unique combination of ear tag colors (Allflex button tags; Allflex Australia, Capalaba, QLD, Australia) and a distinctive symbol in their fur (Super Blonde hair dye, L'Oreal Paris, New York, NY, USA) to facilitate individual identification. All kangaroos were closely monitored during recovery (1–2 h) in a semi-natural enclosure where they remained for the duration of the study.

The enclosure was approximately 8 ha and surrounded by a kangaroo-proof fence, which excluded grazing by stock and feral and native herbivores. At the time of the study, extensive plant growth due to recent summer rains covered the enclosure with green native vegetation, namely grasses (which comprise most of the kangaroos' native diet), numerous small forbs, and low woody shrubs (mostly halophytes of the family Chenopodiaceae, including the bladder saltbush, *Atriplex vesicaria*).²⁹ A trough provided a constant drinking water supply, and small scattered trees provided shade and shelter. The kangaroos were allowed to acclimate to the enclosure for 3 to 5 weeks

(depending on capture date) before behavior observations began.

All behavior observations were made from a 7-m tall tower located in the center of the enclosure. This setup enabled detailed observations using scan sampling to monitor the behavior, posture, and shade use of individual kangaroos. Blocks of time were randomly selected for scan sampling, with each time interval sampled at least three times during the study period. Scans were conducted at 10-min intervals during the day and at 15-min intervals at night. Scans at night were made using a 100-W spotlight with an incandescent globe (which was also used on randomly selected nights throughout the acclimation period). Behavior observations were not conducted during or immediately after rainstorms, due to risks associated with lightning strikes and flooding creeks. The weather during the study period was variable, ranging from cooler cloudy and/or rainy days (<20°C) to hot, dry days with clear skies (>40°C; Fig. 1).

Behaviors were classed according to the activity, posture and shade use of the kangaroo when first sighted, under the following categories: lying, crouching (associated with non-foraging behaviors), standing, foraging (either moving between foraging patches or chewing food while crouching), walking not associated with foraging behavior, hopping, interacting with others, licking, drinking, grooming (either itself or another individual), and 'other' (which comprised <2 % of observations). Shade selected by kangaroos was estimated as patches in full sun, partially shaded (~ 1/4 shaded), half sun/half shade, partially sunlit (~ 3/4 shade), and full shade.

Cloud cover was estimated as the proportion of the sky (divided into eighths) covered by cloud at the time of behavioral observations, while all other weather variables were recorded by data loggers. A 6-channel portable weather station (Signature Series 916, WeatherHawk, Logan, UT, USA) recorded six variables every 5 min for the duration of the study: air temperature, wind speed, wind direction, solar radiation, relative humidity, and rainfall. iButton data loggers (Thermochron, Maxim, Sunnyvale, CA, USA) recorded soil temperatures at two depths (2 cm and 10 cm), in each of three levels of shade (full sun, 70% shade, and 90% shade; the latter two were measured under tents made of 70% and 90% UV block shade cloth; Coolaroo, Braeside, Victoria,

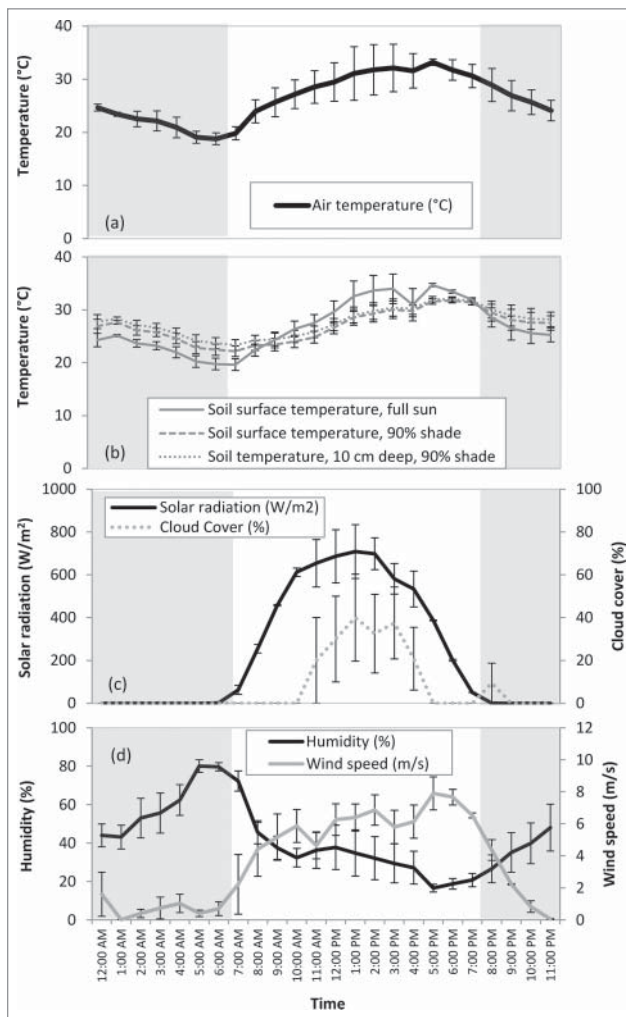


Figure 1. Weather data recorded during the study period: (a) Air temperatures (°C, black line); (b) soil temperatures (°C) on the surface in full sun (solid gray line), on the surface in 90% shade (dashed gray line) and 10 cm deep in 90% shade (dotted gray line); (c) Solar radiation (W/m², black line) and percentage cloud cover (%) (gray dotted line); and (d) Relative humidity (%) and wind speed (m/s). Data is \pm standard error, and pale shaded gray indicates night, with sunrise and sunset at \sim 7 AM and 8 PM, respectively.

Australia). Average weather conditions recorded during the study period are presented in Fig. 1.

Analysis of average hourly activity and shade use

Prior to analysis, behavior observations were converted to binomial scores (1 = performing, 0 = not performing the behavior) and shade use was converted to the percentage of shade selected (full sun = 0, partial shade = 0.25, half sun/half shade = 0.5, partial sun = 0.75, and full shade = 1). For each hour, the average proportion of time each individual spent foraging, resting (lying + crouching) and using shade

was calculated. Individual identification made it possible to combine data per individual, allowing us to control for variation in individual behavior and to avoid pseudo-replication because not all individuals were sampled in every scan.

After checking that the arcsine-transformed data conformed to the assumptions of normality (Shapiro-Wilk) and homogeneity of variance, the proportions of kangaroos foraging and seeking shade were each analyzed using factorial ANOVAs. Each ANOVA examined the effect of *species* (red versus western grey kangaroo) and *hour* (each hour during the day, i.e. Three-4 AM, etc.), and the interaction term (*species*hour*), with *body mass* as a covariate. Note that this analysis does not relate the behavioral observations to concurrently measured weather conditions. If either *species* or *species*hour* was statistically significant, post-hoc Tukey's tests were used to explore differences between species at each hourly interval.

Calculating radiant heat thresholds

To investigate the effect of heat on shade use selected by the kangaroos, each observation of shade use was converted into a binomial measure (1 = selected shade, 0 = did not select shade) and radiant temperature in the sun was calculated from measured environmental conditions. All of the following equations (1–6) were sourced from and based on the principles outlined by Campbell and Norman.³⁰ Radiant temperature (T_{rad} , in °C) was calculated as:

$$T_{rad} = \left(\frac{\frac{1}{2} (Solar_{sky} + Solar_{refl} + IR_{direct} + IR_{indirect})}{\sigma} \right)^{\frac{1}{4}} - 273.16 \quad (1)$$

where σ is the Stefan-Boltzmann constant (5.67×10^{-8} W/m²K⁴), $Solar_{sky}$ is the direct and indirect solar radiation from the sky (W/m²), $Solar_{refl}$ is the solar radiation reflected from the ground (W/m²), and IR_{direct} and $IR_{indirect}$ are the direct and indirect infrared radiant heat fluxes respectively (W/m²). Although the equation for T_{rad} is based upon radiant heat components, it converts these measures into a radiant temperature (°C). While direct and indirect solar radiation in $Solar_{sky}$ were measured together directly using the portable weather station, the solar radiation reflected from the ground $Solar_{grnd}$ was calculated as follows:

$$Solar_{refl} = Solar_{sky} \cdot Refl_{grnd} |\cos(\psi)| \quad (2)$$

with $Refl_{grnd}$ as the reflectivity (or albedo) of the ground and ψ is equal to the zenith angle of the sun (where the sun directly overhead means $\psi = 0^\circ$ and the sun at the horizon means $\psi = 90^\circ$). Infrared radiant heat calculations were based on the Stefan-Boltzmann equation and incorporated the emissivity (ϵ , of the sky or ground), the Stefan-Boltzmann constant (σ), and the air temperature (T_A , $^\circ\text{C}$):

$$IR_{direct} = \epsilon_{sky}\sigma(T_A + 273.16)^4 \quad (3)$$

$$IR_{indirect} = \epsilon_{grnd}\sigma(T_A + 273.16)^4 \quad (4)$$

The emissivity of the ground, ϵ_{grnd} , was assumed equal to 1 (though it normally ranges from 0.95 to 1), while ϵ_{sky} , the emissivity of the sky (with or without cloud), was calculated based on the proportion of sky covered by cloud (C , estimated at the time of behavior observations) and the air temperature (T_A , $^\circ\text{C}$):

$$\epsilon_{sky} = ((1 - 0.84C)\epsilon_{clearsky} + 0.84C) \quad (5)$$

with

$$\epsilon_{clear\ sky} = (9.6 \times 10^{-6})(T_A + 273.16)^2 \quad (6)$$

After calculating the radiant temperature (T_{rad}) associated with each binomial observation of shade use (1 = in shade, 0 = not in shade), we developed a binomial logit link generalized linear model (GLM) for each species. This relates the observed shade-seeking behavior to a single representative environmental variable. We assumed that kangaroos did not retreat from heat into the shade at night (where it would be warmer due to a higher effective 'sky temperature'). The GLMs were used to predict the probability that a kangaroo (of each species) would be observed in shade at a given level of radiant heat. The GLMs were based on a training set of data ($\sim 35\%$ of observations), which was selected using random numbers generated in Microsoft ExcelTM with the RAND function, and tested on the remainder. The performance of the model was tested using Brier's Score, which measures the accuracy of a set of probability assessments and is commonly used to evaluate the predictive power of probabilistic weather forecasting e.g. "will it rain or not?".³¹ Using the binomial logit link GLM equations, we calculated two radiant temperature thresholds, above which $\geq 50\%$ and $\geq 90\%$ of kangaroos would be in shade; as the results were consistent when

applying the 50% and 90% thresholds, we only present the results from applying 90% thresholds.

Applying the radiant temperature thresholds across Australia

Radiant temperature thresholds for each species were used to calculate the number of hours per day that the activity of each kangaroo species was constrained, i.e., that kangaroos were forced to be in shade. This was calculated on a continent-wide scale, by sampling weather data at 1° latitude intervals across the continent from a resolution of 0.05° . Radiant temperatures at each location were calculated for every hour of every day over a 10-year period (2000 to 2009). Daily minimum and maximum temperatures, vapor pressure, rainfall, and daily solar radiation (from which cloud cover was derived), were obtained from the Australian Water Availability Project, AWAP.^{32,33}

Using a microclimate model³⁴ recently tested extensively throughout Australia,³⁵ daily weather data were converted to hourly microclimate data at the height of a female kangaroo (50 cm). The radiant temperature in full sun for each hour was calculated to determine the average number of hours per year that each kangaroo species could be restricted to shade across Australia. For visualization of temporal patterns, we also present the activity constraint predictions for each hour of the year at the field site (Fowlers Gap Research Station, where both species occur) and three Australian cities which vary in latitude: Adelaide (where *M. fuliginosus* naturally occurs), Alice Springs (where only *M. rufus* occurs), and Katherine (where neither species occurs).

All statistical analyses (ANOVAs and GLMs) were performed in R.^{36,37} Shade availability data was sourced for visual comparison (Fig. 2), based on monthly FAPAR remote-sensed measurements (fraction of available photosynthetically active radiation, long term averaged: 1998-2005) which represent the proportion of a pixel covered in vegetation from the Australian Water Availability Project, AWAP.^{32,33} All data in text is presented as means \pm standard error of the mean (SEM).

Results

Compared with *M. rufus*, *M. fuliginosus* foraged for longer from dusk until dawn (Tables 1-3, Fig. 3a). In addition, *M. fuliginosus* spent more time foraging

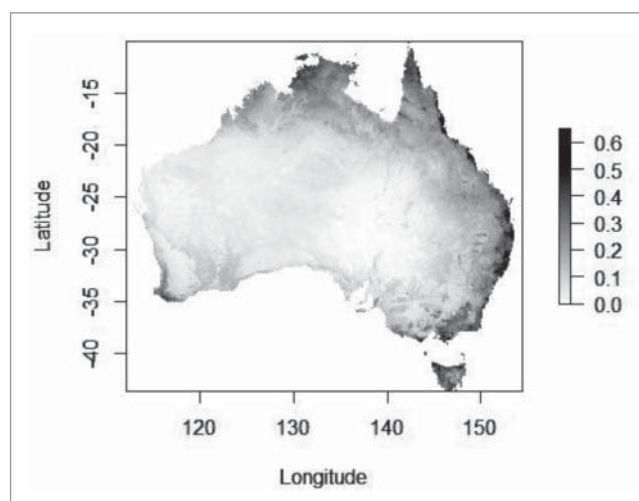


Figure 2. Availability of shade across Australia (in decimal percentages of each pixel covered in shade). This measurement is based on monthly fractions of available photosynthetically active radiation, which indicates the proportion of a pixel covered in vegetation. This data is long-term averaged (1998–2005), satellite derived, and sourced from the Australian Water Availability Project.³³

overall, $49.3\% \pm 2.1$ (ANOVA, Tables 1–3), compared with *M. rufus*, $41.6\% \pm 2.6$ (SEM), but equivalent time resting (34%, ANOVA, Table 1), though both responses varied through time and were affected by body mass (Table 1, Table 3). This equates to *M. fuliginosus* spending (on average) a total of 11.8 h/day (± 0.5) foraging and 8.2 h/day (± 0.6) resting, while *M. rufus* spent 10.0 h/day (± 0.6) foraging and 8.2 h/day (± 0.7) resting.

Despite equivalent time resting, a significantly higher proportion of *M. fuliginosus*, $58.5\% (\pm 2.7)$; ANOVA, Tables 1–3, Fig. 3b), were observed in shade compared with *M. rufus*, $49.4\% (\pm 3.8)$ during daylight hours. The significant differences were primarily observed before 14:00 hours, although the trend was consistent throughout daylight hours (Table 3,

Fig. 3b). Converted to time, this is equivalent to *M. fuliginosus* spending 7.6 h/day (± 0.7) in shade compared to 6.4 h/day (± 0.9) for *M. rufus*. In addition, *M. fuliginosus* retreated to the shade at a lower radiant temperature, 70.1°C , compared with *M. rufus*, 89.1°C (Fig. 4), according to the binomial logit link GLMs (Table 4).

Across Australia, the predicted activity of *M. rufus* was much less restricted than that of *M. fuliginosus* at almost every site (Figs. 5–6). Neither *M. rufus* nor *M. fuliginosus* currently persist where they would be constrained to the shade for more than ~ 1800 h per year (averaged over 10 years, Fig. 6). The northern range limit of *M. fuliginosus* closely matched this calculated activity constraint (i.e. average number of hours in shade per year per site; Fig. 6b), while *M. rufus* did not

Table 1. Results of factorial ANOVAs from comparisons of red and western grey kangaroos (*Macropus rufus* and *M. fuliginosus*; ‘species’) by time (‘hour’), with body mass as a covariate. Bold font indicates significant differences. The results remain statically significant when the models are reduced to the simplest versions without losing explanatory power (i.e., when non-significant factors are removed).

		Df	MS	F	P
Proportion foraging	species	1,278	0.7981	11.647	0.000993
	hour	23,278	1.6198	23.640	<0.0001
	mass	1,278	0.5252	7.665	0.007364
	species:hour	23,278	0.1513	2.208	0.002844
	species:mass	1,278	0.3853	5.623	0.021495
	hour:mass	23,278	0.0429	0.595	0.931033
	species:hour:mass	23,278	0.0514	0.714	0.831074
	species	1,150	0.4831	6.571	0.0113
Proportion seeking shade	hour	12,150	1.8923	25.737	<0.0001
	mass	1,150	0.2366	3.218	0.0749
	species:hour	12,150	0.0368	0.501	0.9114
	species:mass	1,150	0.0050	0.068	0.7943
	hour:mass	12,150	0.0602	0.819	0.6305
	species:hour:mass	12,150	0.0291	0.396	0.9632

Table 2. Proportions of *Macropus rufus* and *M. fuliginosus* (red and western grey kangaroos) foraging, lying down or crouching, and seeking shade throughout the day. All data is \pm standard deviation with sample size (n) in parenthesis.

Hour	Percentage (%) foraging		Percentage (%) resting		Percentage in shade (%)	
	<i>M. rufus</i>	<i>M. fuliginosus</i>	<i>M. rufus</i>	<i>M. fuliginosus</i>	<i>M. rufus</i>	<i>M. fuliginosus</i>
12:00AM	41.2 \pm 12.84 (6)	72.9 \pm 23.31 (10)	19.0 \pm 24.81 (6)	9.3 \pm 13.05 (10)	—	—
1:00AM	74.1 \pm 25.68 (6)	73.4 \pm 17.87 (10)	4.2 \pm 6.51 (6)	6.1 \pm 8.05 (10)	—	—
2:00AM	54.9 \pm 31.01 (5)	84.5 \pm 10.91 (10)	2.5 \pm 5.59 (5)	5.2 \pm 5.19 (10)	—	—
3:00AM	41.0 \pm 34.95 (6)	75.4 \pm 14.16 (10)	21.0 \pm 38.93 (6)	2.1 \pm 4.50 (10)	—	—
4:00AM	50.3 \pm 33.82 (6)	66.9 \pm 18.16 (10)	13.5 \pm 14.28 (6)	3.3 \pm 8.05 (10)	—	—
5:00AM	68.3 \pm 10.87 (5)	59.9 \pm 15.80 (10)	7.8 \pm 4.56 (5)	1.1 \pm 3.51 (10)	—	—
6:00AM	64.9 \pm 11.56 (5)	42.3 \pm 18.81 (10)	4.7 \pm 7.30 (5)	12.8 \pm 13.28 (10)	—	—
7:00AM	68.9 \pm 20.53 (5)	45.6 \pm 31.16 (10)	8.6 \pm 12.56 (5)	14.8 \pm 16.06 (10)	0.0 \pm 0.0 (5)	0.6 \pm 1.76 (10)
8:00AM	51.3 \pm 27.79 (5)	57.9 \pm 25.96 (10)	23.5 \pm 24.88 (5)	19.3 \pm 19.76 (10)	11.6 \pm 11.03 (5)	21.4 \pm 19.60 (10)
9:00AM	39.4 \pm 19.18 (6)	24.0 \pm 17.91 (10)	46.4 \pm 27.07 (6)	65.4 \pm 19.17 (10)	52.1 \pm 32.37 (6)	74.7 \pm 14.10 (10)
10:00AM	6.5 \pm 13.34 (6)	21.1 \pm 19.96 (10)	66.5 \pm 33.89 (6)	72.8 \pm 20.55 (10)	53.9 \pm 33.36 (6)	75 \pm 25.11 (10)
11:00AM	25.9 \pm 20.37 (6)	29.5 \pm 15.77 (10)	47.2 \pm 33.10 (6)	63.8 \pm 22.10 (10)	45.8 \pm 26.74 (6)	64.9 \pm 10.93 (10)
12:00PM	25.2 \pm 15.26 (6)	21.9 \pm 11.82 (10)	61.6 \pm 22.44 (6)	74.7 \pm 12.98 (10)	58.3 \pm 25.90 (6)	74.5 \pm 11.84 (10)
1:00PM	14.9 \pm 12.06 (6)	12.0 \pm 9.85 (10)	74.5 \pm 17.61 (6)	82.7 \pm 15.32 (10)	64.8 \pm 20.26 (6)	80.2 \pm 8.18 (10)
2:00PM	10.8 \pm 8.52 (6)	10.5 \pm 8.73 (10)	76.5 \pm 12.89 (6)	86.4 \pm 8.68 (10)	71.2 \pm 15.61 (6)	77.7 \pm 9.16 (10)
3:00PM	10.3 \pm 11.18 (5)	6 \pm 4.92 (10)	73.0 \pm 4.50 (5)	90.4 \pm 7.88 (10)	71.6 \pm 9.54 (5)	76.7 \pm 9.69 (10)
4:00PM	16.6 \pm 20.36 (6)	9.3 \pm 11.42 (10)	64.0 \pm 15.36 (6)	82.4 \pm 13.07 (10)	71.8 \pm 19.19 (6)	77.3 \pm 9.12 (10)
5:00PM	5.4 \pm 5.90 (6)	19.1 \pm 21.79 (10)	66.3 \pm 33.74 (6)	72.1 \pm 25.88 (10)	75.9 \pm 39.39 (6)	78.5 \pm 20.69 (10)
6:00PM	55.9 \pm 25.79 (5)	66.0 \pm 18.62 (10)	29.6 \pm 22.43 (5)	26.2 \pm 19.41 (10)	28.3 \pm 18.62 (5)	33.6 \pm 19.95 (10)
7:00PM	81.1 \pm 15.01 (5)	86.2 \pm 23.93 (9)	10.0 \pm 12.04 (5)	8.6 \pm 21.89 (9)	17.8 \pm 9.94 (5)	21.4 \pm 15.97 (9)
8:00PM	72.8 \pm 10.85 (5)	71.0 \pm 23.57 (10)	6.4 \pm 8.55 (5)	3.8 \pm 5.4 (10)	—	—
9:00PM	50.1 \pm 23.87 (6)	71.1 \pm 20.25 (10)	19.4 \pm 12.92 (6)	6.2 \pm 10.62 (10)	—	—
10:00PM	40.3 \pm 22.89 (6)	77.5 \pm 20.16 (10)	30.2 \pm 24.32 (6)	2.2 \pm 5.37 (10)	—	—
11:00PM	54.4 \pm 25.03 (6)	83.3 \pm 10.69 (10)	22.7 \pm 13.82 (6)	0.8 \pm 2.64 (10)	—	—
Overall	41.6 \pm 29.71(135)	49.3 \pm 32.46(239)	34.3 \pm 32.11(135)	34.0 \pm 36.78(239)	49.4 \pm 32.17 (73)	58.5 \pm 30.52(129)

reach equivalent levels of activity constraint anywhere across the continent (Fig. 6a). *M. rufus* was required to be in shade for fewer hours at all sites compared with *M. fuliginosus*, and relatively consistent differences in activity constraints were predicted across the continent (Fig. 6).

Site-specific predictions illustrate how shade requirements vary both temporally and spatially for each species (Fig. 5), as well as demonstrating the extent of weather data required for every site to generate predictions across Australia (Fig. 6). From these samples of site-specific predictions, the greatest activity constraints for both species appear to occur in winter in the far north (Katherine, July/August, the dry season; Fig. 5a) and in the summer in the south (Adelaide, January/February, also the dry season, Fig. 5c, d).

Discussion

Relative heat tolerances of *M. rufus* and *M. fuliginosus*

Female *M. fuliginosus* appear less able to deal with high external heat loads than *M. rufus*, which corroborates the correlative study of Caughley *et al.* (1987). *M. fuliginosus* spent more time resting in the shade

during the day (Fig. 3) and moved into the shade at lower levels of radiant heat (up to 19°C lower) than *M. rufus* (Fig. 4). This behavioral evidence indicates

Table 3. Results of planned main effects tests,³⁷ comparing the difference between species at each hour for the proportion of kangaroos foraging and seeking shade. Values in bold indicate significance <0.05.

Hour	Percentage (%) Foraging Df = (1, 326)		Percentage (%) in Shade Df = (1, 176)	
	F	P	F	P
12:00AM	7.7541	0.005674	—	—
1:00AM	0.0903	0.763996	—	—
2:00AM	6.2659	0.012800	—	—
3:00AM	7.7009	0.005840	—	—
4:00AM	1.0457	0.307252	—	—
5:00AM	0.3684	0.544286	—	—
6:00AM	2.7580	0.097736	—	—
7:00AM	4.2358	0.040379	0.0269	0.8699
8:00AM	0.2596	0.610712	1.3454	0.2477
9:00AM	2.6458	0.104794	3.9666	0.04796
10:00AM	3.3751	0.067104	4.6518	0.03238
11:00AM	0.6445	0.422668	3.2277	0.07412
12:00PM	0.0296	0.863511	1.0794	0.3003
1:00PM	0.0428	0.836294	1.1774	0.2794
2:00PM	0.0043	0.947962	0.0887	0.7661
3:00PM	0.1086	0.741933	0.1643	0.6858
4:00PM	0.5753	0.448726	0.0263	0.8714
5:00PM	2.2598	0.133746	0.022	0.8823
6:00PM	0.5449	0.460945	0.238	0.6263
7:00PM	1.2284	0.268539	0.0744	0.7854
8:00PM	0.0019	0.965351	—	—
9:00PM	3.8531	0.050510	—	—
10:00PM	9.9741	0.001737	—	—
11:00PM	5.0499	0.025300	—	—

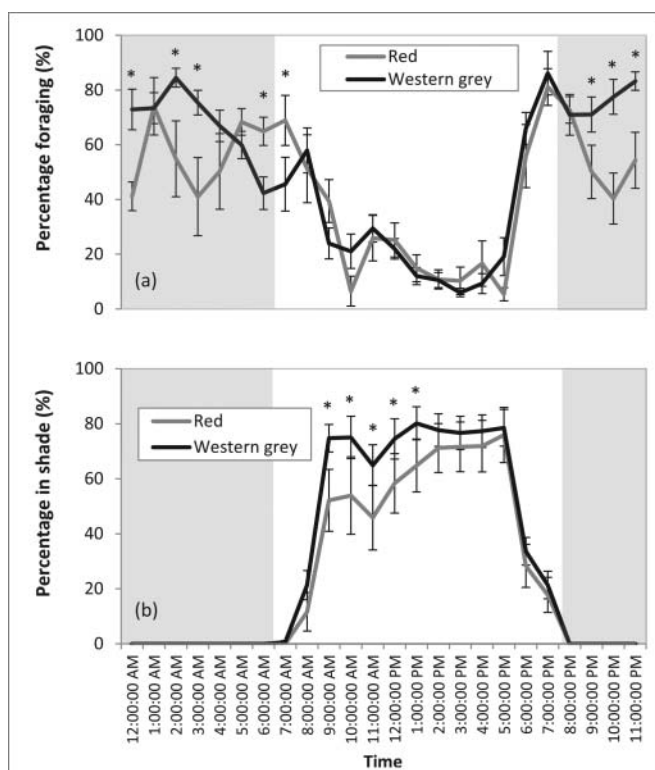


Figure 3. Percentage of kangaroos (a) foraging and (b) seeking shade at Fowlers Gap Research Station in February 2009. *Macropus fuliginosus* (western grey kangaroos, 'Western grey') are represented by black lines and *M. rufus* (red kangaroos, 'Red') by grey lines. Pale shaded gray indicates night, with sunrise and sunset at ~7 AM and 8 PM, respectively. All data is mean \pm SEM (Table 2), and significance is denoted by asterisks (*, refer to Table 3).

that heat constrains the activity of *M. fuliginosus* more than that of *M. rufus*. It also mirrors the previously observed lower heat tolerance of *M. giganteus*, the eastern grey kangaroo^{22,23}; *M. giganteus* is a close relative of *M. fuliginosus*, but typically occupies more mesic regions of eastern and southern Australia, though populations do extend into arid regions.^{6,38} While it could be argued that both grey kangaroo species have adapted to deal with heat equally well but in different ways, assuming ample shade and drinking water, these results demonstrate that *M. rufus* has a greater ability to remain exposed to solar radiation. Moving to the shade (i.e., behavioral avoidance of the conditions) may be a behavioral water-saving strategy for kangaroos in arid environments, where water conservation is crucial; shade use by *M. rufus* can reduce incoming solar inputs by up to 80%.⁵ Compared with *M. rufus*, higher shade use by both *M. giganteus* and *M. fuliginosus* may reflect adaptive differences in properties such as fur insulation.^{5,39}

In addition to seeking more shade, *M. fuliginosus* appears to require more time foraging than *M. rufus*. This is possibly because *M. fuliginosus* is more selective and does not browse as widely on arid zone species, avoiding native lily *Bulbinopsis semibarbata* and chenopod *Sclerolaena diacantha* (Short 1986). Indeed, more recent studies have revealed that *M. fuliginosus* forage mostly on grasses (with monocot grasses comprising at least 44% and up to 81% of forestomach contents)^{14,40} while *M. rufus* can subsist on fewer grasses but more chenopods (c. Fifteen% and c. 63% respectively).¹⁶ While differences in grazing behavior between species may vary with pasture abundance,²⁶ increased foraging time by *M. fuliginosus* may compound issues associated with being restricted to the shade, although they rested for an equivalent amount of time.

That both kangaroo species foraged in the open when radiant temperatures were lower and on cloudier days, suggesting that they seize opportunities to forage – if possible – during the day. Although the degree to which foraging increases during cloudy days requires further quantification, this motivation may arise from several factors, all of which would have consequences for restriction to shade during the day. First, a diel change in forage quality may heighten the drive for kangaroos to feed in daylight hours, particularly in the afternoon.⁴¹ Herbivores typically prefer afternoon vs. morning harvested forage because the soluble carbohydrate concentrations of pasture are highest at or after mid-day, after being photosynthetically active for a number of hours.⁴¹ In contrast, the water content of some grasses is highest at night until around dawn.⁴² Second, restriction to the shade for consecutive hours throughout the day could impact gut refill time and thus digestion⁴³; gut filling allows kangaroos to focus their feeding at thermally-favorable times.¹⁶ Third, by foraging during the day, the kangaroos would be able to seek shelter at night to avoid heat losses under clear night sky.^{2,44} Furthermore, both kangaroo species might forage during the day to reduce risks associated with night-time predation, though vigilance behavior of *M. giganteus* actually decreases after dark.⁴⁵ Finally, kangaroos obtain less food per unit time after dark (i.e. they have slower foraging rates), as they spend more time searching between bites.⁴⁵ However, the degree to which kangaroos engage in cathermerality, or shift their periods of activity, and to what extent diurnal activity restriction impacts night-time foraging,

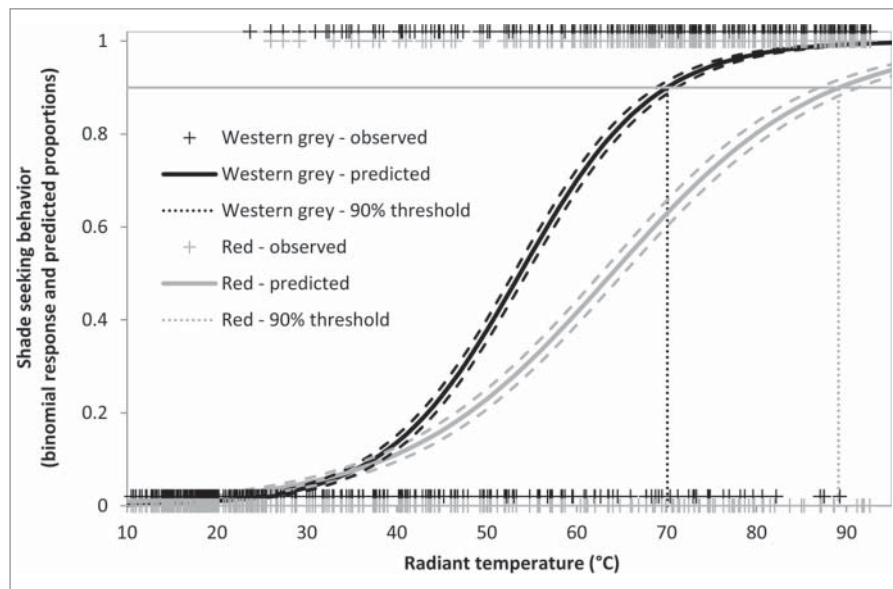


Figure 4. Observed shade use and modeled probability of observing *M. rufus* and *M. fuliginosus* in shade with respect to radiant heat load ($^{\circ}\text{C}$) throughout the study period. Raw observations (binomial response: “in shade” = 1 and “in sun” = 0) are plotted with black and gray crosses for *M. fuliginosus* (western grey kangaroos) and *M. rufus* (red kangaroos), respectively. Generalized linear models (GLMs, binomial logit link, Table 4) show the predicted probability that kangaroos are seeking shade at a given level of solar radiation, plotted \pm 95% confidence intervals (dashed lines), with *M. fuliginosus* in black (‘Western grey’, $r^2 = 0.487$; Table 4) and *M. rufus* in grey (‘Red’, $r^2 = 0.694$; Table 4). The vertical dotted lines (and thin horizontal line) indicate the 90% thresholds for each species, above which there is a $\geq 90\%$ probability of observing that species in shade.

require further investigation. Indeed, while restriction to shade may or may not impact total time spent foraging, being restricted to shade may still impact kangaroos in a variety of indirect, and potentially more subtle, ways.

Activity constraints of *M. rufus* and *M. fuliginosus* across Australia

By quantifying the heat tolerance of the kangaroos, we predicted the shade requirements of each species across the Australian continent. It is evident that the pattern

of activity constraints for each species (Fig. 6) differs markedly from patterns of shade availability across the continent (Fig. 2), although we acknowledge that this comparison is limited as this figure describes the presence of vegetation rather than the definite presence of shade cover. The activity of *M. fuliginosus* is much more restricted across Australia at almost every site compared with that of *M. rufus* (Figs. 5 and 6), which reflects observed behavior and distributions. That the northern range limit of *M. fuliginosus* appears associated with a threshold of restricted activity (~ 1800 h/

Table 4. Equations and statistics for fitted binomial logit link generalized linear models (GLMs) for *Macropus fuliginosus* and *M. rufus* (western grey and red kangaroos, respectively). Calculated radiant heat was used as the only predictor variable. The 50% and 90% thresholds refer to the values of radiant heat ($^{\circ}\text{C}$) above which there is a $\geq 50\%$ and $\geq 90\%$ probability (respectively) of observing the kangaroo in shade rather than in sun. For both GLM models, P values are < 0.0001 . The performance of the model was tested using Brier’s Score, which measures the accuracy of a set of probability assessments from 0 to 1; scores closer to 0 have higher predictive power.^{1,3}

	<i>Macropus fuliginosus</i> (Western grey kangaroo)	<i>M. rufus</i> (Red kangaroo)
Df	1,1694	1,900
Binomial logit link GLM equation	$\Pi(x) = \frac{e^{-7.23274 + 0.13466x}}{1 + e^{-7.23274 + 0.13466x}}$	$\Pi(x) = \frac{e^{-5.55757 + 0.08693x}}{1 + e^{-5.55757 + 0.08693x}}$
Std. Error (Intercept)	0.361	0.347
Std. Error (Radiant temp.)	0.0066	0.0054
Radiant temp. z value	15.97	10.58
50% threshold ($^{\circ}\text{C}$ radiant temperature)	53.71	63.93
90% threshold ($^{\circ}\text{C}$ radiant temperature)	70.07	89.12
AIC	691.9	563.1
r^2	0.694	0.487
Test Brier scores	0.058 (n = 1696)	0.067 (n = 1687)
Train Brier scores	0.099 (n = 902)	0.089 (n = 882)

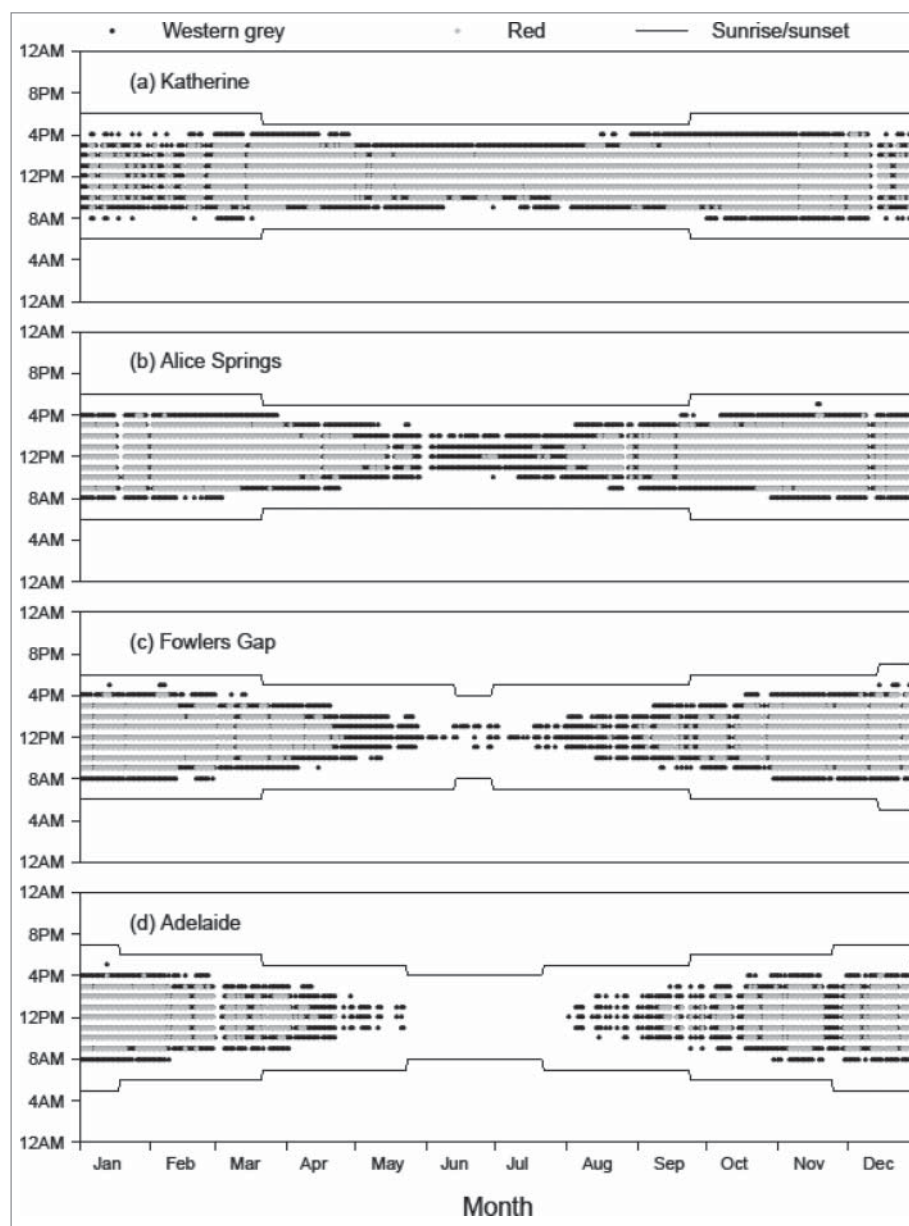


Figure 5. Hours in 2009 that *M. fuliginosus* (western grey kangaroos) and *M. rufus* (red kangaroos) are predicted to be in shade at 4 locations in Australia: (a) Katherine, NT (14.47° S, 132.27° E), (b) Alice Springs, NT (23.67° S, 133.83° E), (c) Fowlers Gap Research Station, NSW (31.09° S, 141.71° E), (d) Adelaide, SA (34.55° S, 138.35° E). Predictions were made according to the radiant heat thresholds (Fig. 4, Table 4). Shade use of *M. rufus* is represented by gray circles while that of *M. fuliginosus* is represented by both black and gray circles (gray overlaps black). Solid black lines indicate sunrise and sunset. Notably, the range of *M. rufus* does not extend to Katherine or Adelaide, and the range of *M. fuliginosus* does not extend to Katherine or Alice Springs.¹⁸

year) may explain the northern distribution limit for this species (Fig. 6). Similarly, the area of maximum advantage (and lowest activity constraints) for *M. fuliginosus* is in the south and appears to correspond with the current distribution of this species (Fig. 6). However, one notable region where low activity constraints do not reflect the observed distribution of *M. fuliginosus* is in the south-eastern corner of the Australian mainland, where inter-specific competition with *M. giganteus* may play an important role.^{20,46}

Although this paper uses an integrated environmental variable, ‘radiant temperature’, as a predictor, not all biophysical processes of heat exchange (e.g., evaporation and convective heat loss) are accounted for in this predictor; thus, our predictions should be treated with a degree of caution, especially in more humid areas near the coast. Our future work aims to develop a full heat budget model for these species using biophysics. Biophysical models describe how climate

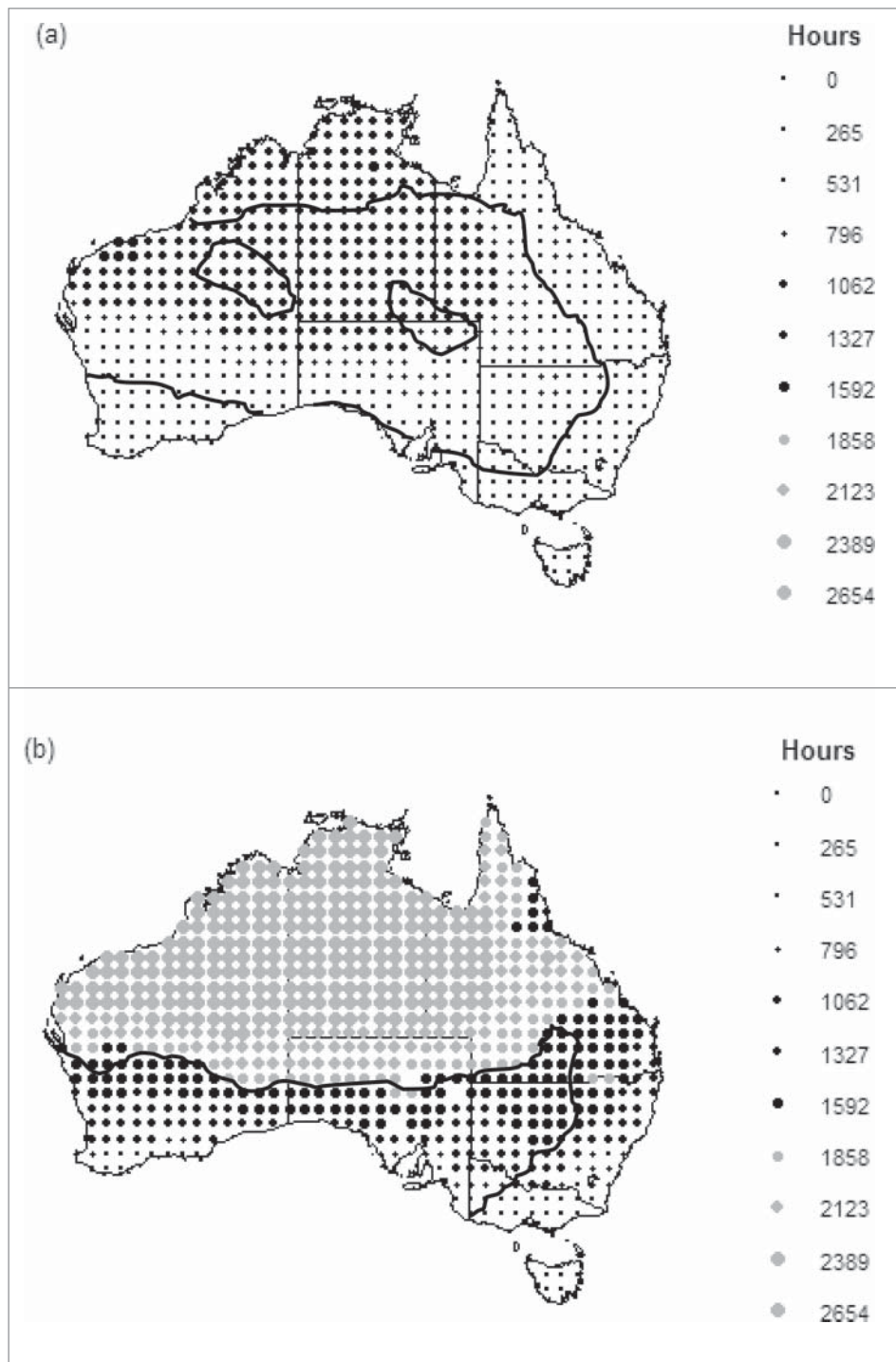


Figure 6. Average number of hours per year that (a) *M. rufus* and (b) *M. fuliginosus* are predicted to seek shade across Australia. Predictions were made based on 1° grids of climate data from 2000–2009 from the Australian Water Availability Project (AWAP).³² The AWAP data was converted into hourly climate data, and the radiant temperature in full sun was calculated for every hour (see text). The 90% radiant heat thresholds for each species (see text, Figs. 2 and 4, Table 4) were applied to determine how many hours per year each species would be restricted to shade at every site, averaged over 10 y.

conditions and a species' behavior, morphology, and physiology alter mass and energy balance.^{47–49} By predicting hourly field energy and water requirements for kangaroos, a biophysical

model would allow explicit quantification of metabolic and hydric benefits of changing activity and seeking shelter.⁵⁰ It could also be used to predict shade requirements, although simpler models

would make similar assumptions to those made here regarding shade and water availability.

By quantifying thresholds of radiant temperature tolerance, we estimated shade requirements from simple behavioral data, and this novel approach can easily be applied to other taxa. While our assessment of activity constraint does not account for the actual limits of physiological tolerance, it enables direct links to be made across temporal and spatial scales. Few other studies have quantified activity constraints across an endotherm's entire distribution, and these studies have mostly focused on species seeking shelter from cold rather than heat.⁵¹ By estimating thresholds of radiant temperature tolerance for any mammal, combined with fine-scale weather data, broad inferences can be drawn about how much shade a species would need in different habitats.

Abbreviations

AWAP	Australian Water Availability Project
C	proportion of sky covered by cloud
GLM	Generalized Linear Model
IR _{direct}	direct infrared radiant heat flux, W/m ²
IR _{indirect}	indirect infrared radiant heat flux, W/m ²
Refl _{grnd}	reflectivity or albedo of the ground
Solar _{sky}	direct and indirect solar radiation from the sky, W/m ²
Solar _{refl}	solar radiation reflected from the ground, W/m ²
T _A	air temperature, °C
T _{rad}	radiant temperature, °C
ε _{grnd}	emissivity of the ground
ε _{clearsky}	emissivity of the sky without cloud
ε _{sky}	emissivity of the sky with cloud
ψ	zenith angle of the sun
σ	Stefan-Boltzmann constant

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

Acknowledgments

This work was conducted with ethics approval from the University of New South Wales (UNSW ACEC 09/120A) and permit approval from NSW NPWS (Scientific License S13025).

Funding

This work was funded by the Holsworth Wildlife Research Endowment. The authors wish to thank the staff at Fowlers Gap Arid Zone Research Station (UNSW) for their support and the following volunteers who helped with data collection: Terry

Dawson, Steve McLeod, Trudy Sharp, Sophie Barwick, Melissa Rigby, Stephanie Phelan, Peta Skeers, and Andrew Lothian.

References

- [1] Dunbar R, Korstjens A, Lehmann J. Time as an ecological constraint. *Biol Rev* 2009; 84:413–29; PMID:19485986; <http://dx.doi.org/10.1111/j.1469-185X.2009.00080.x>
- [2] Gates DM. *Biophysical Ecology*. New York: Springer-Verlag, 1980.
- [3] Blackshaw JK, Blackshaw A. Heat stress in cattle and the effect of shade on production and behaviour: a review. *Animal Production Science* 1994; 34:285–95; <http://dx.doi.org/10.1071/EA9940285>
- [4] Bianca W, ed. *Thermoregulation*. Philadelphia: Lea and Febiger, 1968.
- [5] Dawson TJ, Brown GD. A comparison of the insulative and reflective properties of the fur of desert kangaroos. *Comparative Biochem Physiol* 1970; 37:23–38; [http://dx.doi.org/10.1016/0010-406X\(70\)90954-0](http://dx.doi.org/10.1016/0010-406X(70)90954-0)
- [6] Caughley G, Short J, Grigg GC, Nix H. Kangaroos and climate: an analysis of distribution. *J Animal Ecol* 1987; 56:751–61; <http://dx.doi.org/10.2307/4946>
- [7] Austin MP, Nicholls AO, Margules CR. Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecological Monographs* 1990; 60:161–77; <http://dx.doi.org/10.2307/1943043>
- [8] Kearney M, Porter WP. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 2004; 85:3119–31; <http://dx.doi.org/10.1890/03-0820>
- [9] Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecogeography* 2006; 29:129–51; <http://dx.doi.org/10.1111/j.2006.0906-7590.04596.x>
- [10] Dawson T. *Kangaroos*. CSIRO Publishing, 2012.
- [11] Maloney SK, Fuller A, Kamerman PR, Mitchell G, Mitchell D. Variation in body temperature in free ranging western grey kangaroos *Macropus fuliginosus*. *Australian Mammal* 2004; 26:135–44; <http://dx.doi.org/10.1071/AM04135>
- [12] McCarron HCK, Buffenstein R, Fanning FD, Dawson TJ. 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 Comparative Physiol B-Biochem Systemic Environmental Physiol* 2001; 171:401–11; <http://dx.doi.org/10.1007/s003600100189>
- [13] Brown GD, Dawson TJ. Seasonal variations in the body temperatures of unrestrained kangaroos (Marsupialia). *Comparative Biochem Physiology Part A: Physiology* 1977; 56:59–67; [http://dx.doi.org/10.1016/0300-9629\(77\)90442-X](http://dx.doi.org/10.1016/0300-9629(77)90442-X)
- [14] Munn AJ, Skeers P, Kalkman L, McLeod SR, Dawson TJ. Water use and feeding patterns of the marsupial western

- grey kangaroo (*Macropus fuliginosus melanops*) grazing at the edge of its range in arid Australia, as compared with the dominant local livestock, the Merino sheep (*Ovis aries*). *Mammalian Biology-Zeitschrift für Säugetierkunde* 2013; 79:1–8.
- [15] Munn A, Dawson T, McLeod S, Dennis T, Maloney S. Energy, water and space use by free-living red kangaroos *Macropus rufus* and domestic sheep *Ovis aries* in an Australian rangeland. *J Comp Physiol B* 2013; 183:843–58.
- [16] Munn A, Dawson T, McLeod S. Feeding biology of two functionally different foregut-fermenting mammals, the marsupial red kangaroo and the ruminant sheep: how physiological ecology can inform land management. *J Zool* 2010; 282:226–37; <http://dx.doi.org/10.1111/j.1469-7998.2010.00740.x>
- [17] McCullough DR, McCullough Y. Kangaroos in outback Australia: comparative ecology and behavior of three co-existing species. Columbia University Press, 2000.
- [18] Caughley G, Shepherd N, Short J. Kangaroos: their ecology and management in the sheep rangelands of Australia. Cambridge University Press, 1987.
- [19] Walker PA. Modelling wildlife distributions using a Geographic Information System: kangaroos in relation to climate. *Biogeography* 1990; 17:279–89; <http://dx.doi.org/10.2307/2845124>
- [20] Ritchie EG, Bolitho EE. Australia's savanna herbivores: bioclimatic distributions and an assessment of the potential impact of regional climate change. *Physiol Biochem Zool* 2008; 81:880–90; PMID:18937565; <http://dx.doi.org/10.1086/588171>
- [21] Caughley G. Social organization and daily activity of the red kangaroo and the grey kangaroo. *J Mammal* 1964; 45:429–36; <http://dx.doi.org/10.2307/1377416>
- [22] Dawson TJ, Denny MJS, Russell EM, Ellis B. Water usage and diet preferences of free ranging kangaroos, sheep, and feral goats in Australian arid zone during summer. *J Zool* 1975; 177:1–23; <http://dx.doi.org/10.1111/j.1469-7998.1975.tb05968.x>
- [23] Dawson TJ, McTavish KJ, Munn AJ, Holloway J. Water use and the thermoregulatory behaviour of kangaroos in arid regions: insights into the colonisation of arid rangelands in Australia by the eastern grey kangaroo (*Macropus giganteus*). *J Comparative Physiol B-Biochem Systemic Environmental Physiol* 2006; 176:45–53; <http://dx.doi.org/10.1007/s00360-005-0030-2>
- [24] Bartholomew GA. Interspecific comparison as a tool for ecological physiologists. In: Feder ME, Bennett AF, Burggren WW, Huey RB, eds. *New directions in ecological physiology*. Cambridge: Cambridge University Press, 1987:11–35.
- [25] Dawson TJ, Blaney CE, McCarron HCK, Maloney SK. Dehydration, with and without heat, in kangaroos from mesic and arid habitats: different thermal responses including varying patterns in heterothermy in the field and laboratory. *J Comparative Physiol B-Biochem Systemic Environmental Physiol* 2007; 177:797–807; <http://dx.doi.org/10.1007/s00360-007-0176-1>
- [26] Priddel D. The diurnal and seasonal patterns of grazing of the red kangaroo, *Macropus rufus*, and the western grey kangaroo, *Macropus fuliginosus*. *Wildlife Res* 1986; 13:113–20; <http://dx.doi.org/10.1071/WR9-860113>
- [27] Dawson TJ. Thermoregulatory responses of arid zone kangaroos, *Megaleia rufa* and *Macropus robustus*. *Comparative Biochem Physiol* 1973; 46:153–69; [http://dx.doi.org/10.1016/0300-9629\(73\)90568-9](http://dx.doi.org/10.1016/0300-9629(73)90568-9)
- [28] Dawson TJ, Denny MJS. A bioclimatological comparison on summer day microenvironments of two species of arid-zone kangaroo. *Ecology* 1969; 50:328–33; <http://dx.doi.org/10.2307/1934861>
- [29] Dawson TJ, McTavish KJ, Ellis BA. Diets and foraging behaviour of red and eastern grey kangaroos in arid shrub land: is feeding behaviour involved in the range expansion of the eastern grey kangaroo into the arid zone? *Australian Mammalogy* 2004; 26:169–78.
- [30] Campbell GS, Norman JM. Introduction to environmental biophysics. Springer Verlag, 1998.
- [31] Brier GW. Verification of forecasts expressed in terms of probability. *Monthly Weather Rev* 1950; 78:1–3; [http://dx.doi.org/10.1175/1520-0493\(1950\)078<0001:VOFEIT>2.0.CO;2](http://dx.doi.org/10.1175/1520-0493(1950)078<0001:VOFEIT>2.0.CO;2)
- [32] Raupach M, Briggs P, Haverd V, King E, Paget M, Trudinger C. CSIRO AWAP Run 26c Historical Monthly and Annual Model Results for 1900–2009. Canberra, Australia, Centre for Australian Weather and Climate Research (Bureau of Meteorology and CSIRO) Available at <http://www.csiro.au/awap> Accessed June 2011; 22:2011
- [33] Jones DA, Wang W, Fawcett R. High-quality spatial climate data-sets for Australia. *Australian Meteorological Oceanographic J* 2009; 58:233.
- [34] Mitchell JW, Beckman WA, Bailey RT, Porter WP. Microclimatic modeling of the desert. In: De Vries DA, Afgan NH, eds. *Heat and mass transfer in the biosphere, Part 1 Transfer processes in the plant environment* Washington, DC, USA: Scripta Book, 1975:275–86.
- [35] Kearney MR, Shamakhy A, Tingley R, Karoly DJ, Hoffmann AA, Briggs PR, Porter WP. Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods Ecol Evolution* 2014; 5:273–86.
- [36] R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing, 2013.
- [37] Logan M. Biostatistical design and analysis using R: a practical guide. Oxford, United Kingdom: Wiley-Blackwell, 2010
- [38] Caughley G, Brown B, Dostine P, Grice D. The grey kangaroo overlap zone. *Australian Wildlife Res* 1984; 11:1–10; <http://dx.doi.org/10.1071/WR9840001>
- [39] Mykytowycz R, Nay T. Studies of the cutaneous glands and hair follicles of some species of Macropodidae. *CSIRO Wildlife Res* 1964; 9:200–17; <http://dx.doi.org/10.1071/CWR9640200>
- [40] Coulson G, MacFarlane A, Parsons S, Cutter J. Evolution of sexual segregation in mammalian herbivores:

- kangaroos as marsupial models. *Australian J Zool* 2006; 54:217–24; <http://dx.doi.org/10.1071/ZO05062>
- [41] Mayland H, Mertens D, Taylor T, Burns J, Fisher D, Gregorini P, Ciavarella T, Smith K, Shewmaker G, Griggs T. Diurnal changes in forage quality and their effects on animal preference, intake, and performance. *California Alfalfa and Forage Symp*, 35th, Visalia, CA, 2005:12–4.
- [42] Underhill S, Grigg GC, Yates DJ. Daily changes in plant water content in western Queensland: Implications for red kangaroo foraging times. *Rangeland J* 2004; 26:102–10.
- [43] Jeschke JM, Tollrian R. Predicting herbivore feeding times. *Ethol* 2005; 111:187–206.
- [44] Monteith J, Unsworth M. *Principles of environmental physics: plants, animals, and the atmosphere*. Academic Press, 2013.
- [45] Clarke J, Jones M, Jarman P. Diurnal and nocturnal grouping and foraging behaviors of free-ranging eastern grey kangaroos. *Australian J Zool* 1995; 43:519–29.
- [46] Caughley G, Grice D, Barker R, Brown B. The edge of the range. *J Animal Ecol* 1988; 57:771–85.
- [47] Porter WP, Gates DM. Thermodynamic equilibria of animals with environment. *Ecological Monographs* 1969; 39:227.
- [48] Porter WP, Kearney M. Size, shape and the thermal niche of endotherms. *Proc Natl Acad Sci USA* 2009; 106:19666–72.
- [49] Porter WP, Munger JC, Stewart WE, Budaraju S, Jaeger J. Endotherm energetics: from a scalable individual-based model to ecological applications. *Australian J Zool* 1994; 42:125–62.
- [50] Roberts JA. *Energy and mass budgets of kangaroos and their implications for behaviour and life history*. Department of Zoology: University of Melbourne, 2014.
- [51] Dunbar RI, Shi J. Time as a constraint on the distribution of feral goats at high latitudes. *Oikos* 2012; 22:403–10; PMID:25914426