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

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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.

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. Shade can provide protection against adverse weather, including solar radiation loads during the day and high infra-red radiation losses at night. 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. Shade use during the day can reduce exposure of large mammals to incoming solar radiation by up to 80% in desert environments. 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

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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.\(^18\) Walker\(^19\) 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 (%22.3 mg), while *M. rufus* ranged from 21.1 to 25.6 kg (average 22.8 kg ± 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*). 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 (~ ¼ shaded), half sun/half shade, partially sunlit (~ ⅛ shade), and full shade.

Cloud cover was estimated as the proportion of the sky (divided into eightths) 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,
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 ($T_{\text{rad}}$, in °C) was calculated as:

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

(1)

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

$$S_{\text{refl}} = S_{\text{sky}} \cdot R_{\text{grad}} \cdot |cos(\psi)| \quad (2)$$

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 (dotted 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 ± standard error, and pale shaded gray indicates night, with sunrise and sunset at ~7 AM and 8 PM, respectively.
with \( \text{Ref}_{\text{grnd}} \) as the reflectivity (or albedo) of the ground and \( \psi \) 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 \( (\varepsilon, \text{of the sky or ground}) \), the Stefan-Boltzmann constant \( (\sigma) \), and the air temperature \( (T_A, ^\circ \text{C}) \):

\[
IR_{\text{direct}} = \varepsilon_{\text{sky}} \sigma (T_A + 273.16)^4 \tag{3}
\]

\[
IR_{\text{indirect}} = \varepsilon_{\text{grnd}} \sigma (T_A + 273.16)^4 \tag{4}
\]

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

\[
\varepsilon_{\text{sky}} = \left( 1 - 0.84C \right) \varepsilon_{\text{clearsky}} + 0.84C \tag{5}
\]

with

\[
\varepsilon_{\text{clear sky}} = \left( 9.6 \times 10^{-6} \right) (T_A + 273.16)^2 \tag{6}
\]

After calculating the radiant temperature \( (T_{\text{rad}}) \) associated with each binomial observation of shade use \( (1 = \text{in shade}, 0 = \text{not in shade}) \), 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 Excel\textsuperscript{TM} 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 \( 1^\circ \) latitude intervals across the continent from a resolution of \( 0.05^\circ \). 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 model \(^{34}\) 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 \( M. \text{fuliginosus} \) naturally occurs), Alice Springs (where only \( M. \text{rufus} \) 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 ± standard error of the mean (SEM).

### Results

Compared with \( M. \text{rufus} \), \( M. \text{fuliginosus} \) foraged for longer from dusk until dawn (Tables 1-3, Fig. 3a). In addition, \( M. \text{fuliginosus} \) spent more time foraging
overall, 49.3% ± 2.1 (ANOVA, Tables 1-3), compared with *M. rufus*, 41.6% ± 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% (± 2.7; ANOVA, Tables 1-3, Fig. 3b), were observed in shade compared with *M. rufus*, 49.4% (± 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.

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

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 |
| **Proportion seeking shade** |     |       |       |       |
| species             | 1,150 | 0.4831 | 6.571 | 0.0113 |
| 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 |
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, 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 | Percentage (%) resting | Percentage in shade (%) |
|--------|-------------------------|------------------------|-------------------------|
|        | *M. rufus* | *M. fuliginosus* | *M. rufus* | *M. fuliginosus* | *M. rufus* | *M. fuliginosus* |
| 12:00AM | 7.7541 | 0.005674 | - | - |
| 1:00AM | 0.0903 | 0.763996 | - | - |
| 2:00AM | 6.2659 | 0.012800 | - | - |
| 3:00AM | 7.0009 | 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 | 0.8609 |
| 8:00AM | 2.0430 | 0.09762 | 0.60712 | 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 | 0.2294 |
| 2:00PM | 0.0043 | 0.947962 | 0.0887 | 0.7661 |
| 3:00PM | 0.1086 | 0.741933 | 0.1643 | 0.6858 |
| 4:00PM | 0.5753 | 0.484726 | 0.0263 | 0.8714 |
| 5:00PM | 2.2598 | 0.133746 | 0.022 | 0.8823 |
| 6:00PM | 0.5449 | 0.469045 | 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 | - | - |
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.\(^6,38\)

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 digestion;\(^ {43}\) 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,
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 (°C) above which there is a ≥50% and ≥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.

| Df | 1,1694 | 1,900 |
|---|---|---|
| Binominal logit link GLM equation | $\Pi(x) = \frac{e^{-7.23174 + 0.13466x}}{1 + e^{-7.23174 + 0.13466x}}$ | $\Pi(x) = \frac{e^{-5.55757 + 0.08693x}}{1 + e^{-5.55757 + 0.08693x}}$ |
| Std. Error (Intercept) | 0.361 | 0.347 |
| Std. Error (Radiant temp.) | 0.0066 | 0.0054 |
| Radiant temp. z value | 16.97 | 10.58 |
| 50% threshold (°C radiant temperature) | 53.71 | 63.93 |
| 90% threshold (°C radiant temperature) | 70.07 | 89.12 |
| AIC | 691.9 | 563.1 |
| $r^2$ | 0.694 | 0.563 |
| Test Brier scores | 0.058 (n = 1696) | 0.067 (n = 1687) |
| Train Brier scores | 0.099 (n = 902) | 0.089 (n = 882) |
(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...
conditions and a species’ behavior, morphology, and physiology alter mass and energy balance. 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. 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
- \(IR_{\text{direct}}\): direct infrared radiant heat flux, \(W/m^2\)
- \(IR_{\text{indirect}}\): indirect infrared radiant heat flux, \(W/m^2\)
- \(Refl_{\text{grnd}}\): reflectivity or albedo of the ground
- \(Solar_{\text{sky}}\): direct and indirect solar radiation from the sky, \(W/m^2\)
- \(Solar_{\text{refl}}\): solar radiation reflected from the ground, \(W/m^2\)
- \(T_A\): air temperature, \(^\circ C\)
- \(T_{\text{rad}}\): radiant temperature, \(^\circ C\)
- \(\epsilon_{\text{grnd}}\): emissivity of the ground
- \(\epsilon_{\text{clearsky}}\): emissivity of the sky without cloud
- \(\epsilon_{\text{sky}}\): emissivity of the sky with cloud
- \(\psi\): zenith angle of the sun
- \(\sigma\): Stefan-Boltzmann constant

**Disclosure of potential conflicts of interest**

No potential conflicts of interest were disclosed.

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