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Thermoregulation strategies differ for large macropods during high temperatures

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ABSTRACT

In semi-arid drylands, landscape features such as water and trees are vital for individuals when reducing heat stress. In Australia, such landscapes have witnessed widespread canopy loss and considerable shifts in water availability due to anthropogenic processes, and are subject to greater frequencies of extreme temperatures. We explored the use of dammed watercourses and excavated earth tanks, and tree shade in two large macropod species, eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Osphranter rufus*) in the semi-arid drylands of south-western Queensland. Using a thermal drone, camera traps, and temperature sensors, we examined the relationship between temperature, and water and canopy shade use by both species. The likelihood of kangaroos being observed in the sun was negatively correlated with temperature, with the likelihood of observing eastern grey kangaroos in the sun dropping below 50 % when temperatures exceeded 28 °C, and 17 °C for red kangaroos. Probability of detecting kangaroos in the shade was positively correlated with temperature, with red kangaroos more strongly selecting shade than eastern grey kangaroos. For eastern grey kangaroos, we observed greatly increased activity at waterpoints when daily maximum temperatures exceeded 28 °C, with a preference for dammed watercourses over excavated earth tanks. Only a weak trend of using dammed watercourses at high temperatures (>36 °C) was detected for red kangaroos. As higher temperatures become more frequent due to climate change, our results suggest that the capacity of wildlife to persist may increasingly depend on the provision and maintenance of landscape features such as water and canopy shade.

1. Introduction

The mechanisms by which body temperature is regulated are critical factors in biological and ecological processes. Endotherms have temperature ranges within which basal metabolic rate is maintained constant particularly when resting, called the thermoneutral zone (Angilletta et al., 2010; Mitchell et al., 2018). Within the thermoneutral zone, maintenance of body temperature is possible without increasing evaporative water loss or engaging in energy-intensive behaviours to cool down or heat up. As temperatures exceed the upper critical limit of the thermoneutral zone, increases in evaporative water loss become the primary mechanism to dissipate heat (Mitchell et al., 2018). Endothermic species are then likely to rely more on behavioural and physiological adaptations, such as seeking cooler environments or using evaporative cooling, to maintain thermal balance (Angilletta et al., 2010; Mitchell et al., 2018). Not maintaining optimal body temperature for sustained periods can lead to overheating and potential heat stroke (Norris and Kunz, 2012), severe physiological issues from metabolic stress including fatigue, and organ stress, as well as decline in cognitive and immune function which can affect survival (Acevedo-Whitehouse and Duffus, 2009; Soravia et al., 2021). With increasing attention given to thermal tolerance of species under global warming, the ability of species to adapt and maintain optimal thermoregulatory conditions has been highlighted as a critical factor in shaping species persistence (Buchholz et al., 2019; Li and Chen, 2024).

Thermoregulatory strategies are likely to become increasingly important survival mechanisms for many wild animals as higher mean and maximum daily temperatures become more frequent. Susceptibility of many species to population collapse during heatwaves is increasingly being noted, for example in populations of flying-foxes in Australia (Welbergen et al., 2008), and knowledge of the behavioural and physiological adaptations that enable individuals to mitigate heat stress and resultant morbidities is already well established. For example, individuals can alter their daily activity patterns to be more active during cooler times of the day, with diurnal species sometimes becoming nocturnal to escape the heat (Rafiq et al., 2023). Species with the ability

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to manipulate their environment, like fennec foxes (*Vulpes zerda*), burrow underground when temperatures reach levels too high (Geffen and Girard, 2003), while African elephants (*Loxodonta africana*) and many other large mammals use mud and dust baths to dissipate heat via evaporative cooling, and protect themselves from solar radiations (Dunkin et al., 2013). While the ability to manipulate the environment to reduce heat stress is a successful adaptive behavioural strategy for many species, others must rely on existing environmental structures in their efforts to stay within appropriate ambient temperatures including abiotic (e.g., caves, anthropogenic structures, water) (Cain et al., 2008) and biotic (e.g., trees) features (Briscoe et al., 2014).

Many land-based mammal species seek shelter from solar radiation by using the shade provided by trees (Terrien et al., 2011). Tree canopies also provide significant respite from high temperatures, with temperatures often orders of magnitude lower under trees than in the open (Ashcroft et al., 2012; De Frenne et al., 2019). While entire microclimates are altered by canopy trees in systems like forests (De Frenne et al., 2019), dryland ecosystems often only have sparse tree and shrub coverage, reducing the overall footprint of their mitigating potential. The sparse nature of tree cover in dryland systems, compared to ecosystems where trees are abundant and temperatures cooler, is likely to further turn their shade into essential thermal refuges for dryland fauna seeking to thermoregulate. Understanding how these microclimates shape thermal landscapes is increasingly recognised as vital for predicting resilience to climate change (De Frenne et al., 2021, 2025). This may be of particular value in drylands, as despite dryland fauna being adapted to high temperatures, their thermal physiology may be put at risk due to climate change increasing the risk of overheating (Fuller et al., 2016).

Coupled with this is the fact that many dryland ecosystems around the world have undergone substantial canopy loss over the last few decades. Canopy removal of vast amounts of land for agriculture reduces the critical services trees provide, including shelter from the sun and heat (Abera et al., 2020; Albert et al., 2023; Ellwanger et al., 2020). Of drylands globally, 10–20 % have already been cleared or degraded with a rate of 12 million hectares degraded per year (Yirdaw et al., 2017). Land clearing has many negative impacts on the environment including loss of biodiversity, habitat fragmentation and destruction, and even intensifying extreme weather events (Ellwanger et al., 2020). However, while land clearing has many ecosystem level impacts, it also brings challenges on an individual level. The removal of trees brings challenges in the ability of wild animals to thermoregulate (Giroux et al., 2022). Shade seeking behaviour in dryland ecosystems is likely to also be coupled with water seeking behaviour during periods of high temperatures (Fuller et al., 2021). Water facilitates rehydration but also enables animals to reduce body temperature through immersion (Rogers et al., 2021). However, similar to the presence of trees, the presence of water sources in many areas, particularly drylands, is rapidly decreasing due to increasing rates of desertification (Huang et al., 2017), driven by climate change, river regulation, and vegetation clearance. Furthermore, in dryland ecosystems used for animal agriculture, which can include up to 60–70 % of Australian drylands (Williams et al., 2021), water access is often reserved for livestock and not always accessible to wildlife (Croft et al., 2007). Additionally, fencing off waterpoints has also been recommended to landholders to reduce the local population density of kangaroos in an effort to manage populations, as it is often believed that this would create unsuitable sites for kangaroos, stopping them from aggregating in specific areas (NSW Biodiversity Conservation Trust, 2020). However, there is no evidence suggesting that water presence affects the density or abundance of kangaroo populations (Croft and Witte, 2021; Lavery et al., 2018; Montague-Drake and Croft, 2004). When accessible to wildlife, whether the design of artificial waterpoints, like excavated earth tanks (herein tanks) enable the full range of use that wildlife would gain from natural water sources (soaks, lakes, creeks, floodplains) is currently unknown. Tanks are often small and deep, lacking in shallow areas that promote immersion for cooling off or vegetation growth for food.

Here we explored the use of water and shade at varying temperatures by eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Osphranter rufus*) in the semi-arid rangelands of south-western Queensland, Australia. Kangaroos use various methods of thermoregulation, for example licking of the forelimbs to cool down through evaporative cooling (Croft, 1980), or digging hip holes before lying down, with the newly exposed layer of soil offering a cooler surface to lay on (Croft, 1980). Additionally, one of the most effective ways for kangaroos to thermoregulate when temperatures are high is to rest in the shade (Fig. S1) (Dawson et al., 2006). Use of water is also a key strategy, and while kangaroos have considerably lower drinking water requirements than placental mammals (Dawson et al., 2006), access to water also enables cooling through immersion. Given that climate warming is already driving increases in temperature extremes in Australia's drylands, coupled with continuing canopy clearance across this system (Hernandez et al., 2024), our aim was to assess how kangaroos behaviourally adjust to increasing heat stress in field conditions. To achieve this, we monitored shade and water use in eastern grey and red kangaroos over two seasons – winter and summer – by recording how individuals of the more temperate eastern grey kangaroos and arid-tolerant red kangaroos adjusted their exposure to the sun by using trees, and how often they accessed tanks and natural dammed waterpoints at various temperatures. Based on knowledge of the thermoregulation strategies of macropods (Croft, 1980; Dawson et al., 2006), we predicted that 1) at higher temperatures eastern grey kangaroos would rely more on access to water than shade, while red kangaroos would be more likely to remain in the shade, and that 2) both species would use natural dammed watercourses more than tanks.

2. Methods

2.1. Study site

This research was conducted on the 480 km^2 Mourachan Conservation Property (herein Mourachan) in south-western Queensland, near the township of St George (Fig. 1). This private semi-arid rangeland reserve, owned by Australia Zoo, is surrounded by cattle and sheep farms. While a small number of cattle are run on one section of the property under wildlife friendly principles (Hasselerharm et al., 2021), the remainder is maintained as a conservation reserve where kangaroos, dingoes (*Canis dingo*), and other wildlife are protected from persecution. Eastern grey kangaroos, red kangaroos, black wallabies (*Wallabia bicolor*), red-necked wallabies (*Macropus rufogriseus*), and black-striped wallabies (*Notamacropus dorsalis*) are the only macropod species present on the property. Waterpoints present at Mourachan include tanks, and dammed watercourses. Tanks are artificially constructed depressions – often referred to as farm dams or excavated earth tanks – designed to capture and store water including from rain and runoff (DPIRD, 2022). They are typically dug into the ground in areas of natural runoff and may have compacted dirt or clay walls to hold larger volumes of water (DPIRD, 2022). However, while tanks can support a range of wildlife during drier periods by providing water for hydration, they are often small and deep, lacking in shallow areas that promote immersion for cooling off, while also offering less vegetation growth for food than natural watercourses (Westgate et al., 2021). In contrast to tanks, here we called "dammed watercourses" naturally occurring watercourses that have been blocked by a constructed dam wall to control water flow and create a reservoir. These waterpoints tend to support more complex ecosystems, supporting a greater variety of aquatic and terrestrial species due to their connection with natural waterways (Fig. 1). The vegetation around dammed watercourses tends to be more established, contributing to better water quality and more stable habitats for wildlife (Malerba et al., 2023).

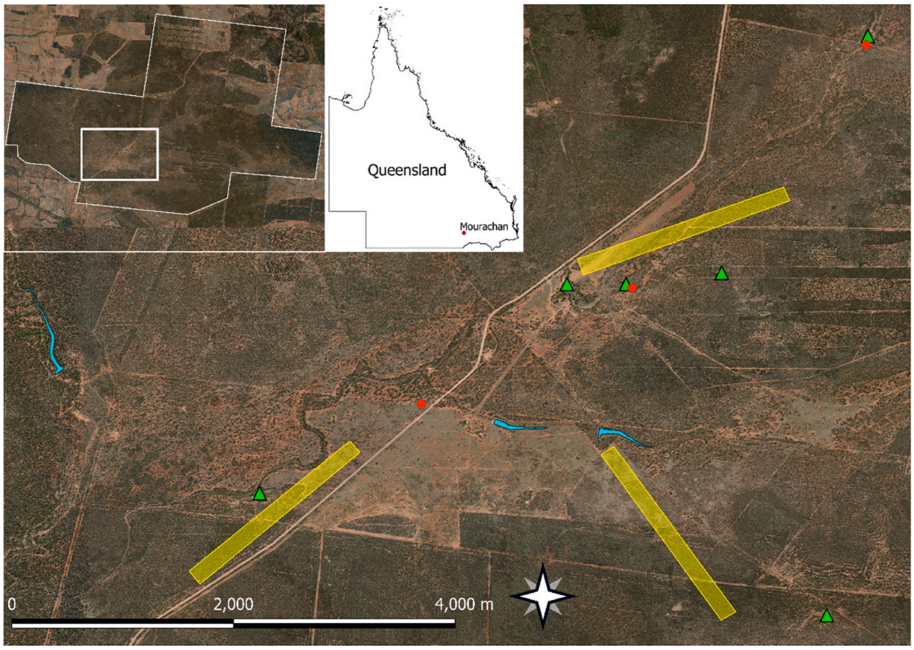

Fig. 1. Zoomed-in drone transect zone with satellite imagery of the Mourachan property where the study was conducted showing its location within Queensland, Australia. The red dots represent the locations of iButton sites. The yellow rectangles represent the area covered by each 2 km long transect (28.4 ha). Blue polygons show the location and area of three of the four dammed watercourses of the property, while green triangles show the location of six of the 13 tanks of the property. Tanks are not shown as polygons due to their size being too small to be visible on the presented map.

2.2. *Temperature ranges*

To measure the ambient temperatures being experienced by kangaroos, we established 12 iButton temperature sensors (DS1922L-F5# Thermochron, Maxim Integrated, San Jose, CA, USA) at three locations across Mourachan from January 2023 to October 2023 with four iButtons at each site (Fig. 1). With grasses usually being the preferred food source of kangaroos (Montague-Drake and Croft, 2004), and kangaroos being known to use shade under trees to shelter from the sun (Dawson et al., 2006) we chose natural open grasslands with sparse canopy cover as the sites of deployment for the iButtons. This allowed us to split each iButton site into two ground cover types: open grassland (exposed to the sun), and tree cover (sheltering from the sun), deploying a total of six iButtons per cover type. Tussock grasses composed the majority of grasslands with the dominant grass species being buffel grass (*Cenchrus* spp.). Dominant tree species scattered throughout the open grasslands included brigalow (*Acacia harpophylla*), poplar box (*Eucalyptus populnae*), mulga (*Acacia aneura*), and bendee (*Acacia catenulata*).

We placed the iButtons 50 cm above ground in mini-Stevenson screens made using inverted white PVC jars perforated to allow air flow (Ashcroft et al., 2012), which we then attached to star pickets (Fig. S2). To allow airflow to reach the iButtons, we placed the iButtons in fine mesh bags attached to the top of the jar allowing the temperature sensors to hang directly in front of the holes (Fig. S2). While such research would benefit from measuring the impact of solar radiation on individuals standing in the sun, iButtons made of metal would not be representative of the ways in which the fur and skin of kangaroos absorb solar radiation, hence we placed all iButtons in Stevenson screens to measure differences in ambient temperature under trees and in the sun. By placing all iButtons in screens we also protected them from potential rain events. Temperature was recorded half-hourly.

We then used hexbin plots to compare open grassland temperatures and tree canopy temperatures to visualise differences between the two cover types using the geom_hex function in the “ggplot2” package (Wickham, 2016). We chose hexbin plots to visualise differences as such plots group data points in bins and use colour intensity to represent the number of observations within each bin, providing a clear way to visualise the density and distribution of large datasets without overplotting (Lewin-Koh, 2011).

2.3. *Kangaroo presence in the shade*

The use of Unmanned Aerial Vehicles (UAVs), or drones, has gained rapid popularity in wildlife research (Hodgson et al., 2018). In many situations, using drones can save time and resources and offers safer means to monitor species on dangerous terrain (Francis et al., 2020). Drones in wildlife research have been used in a wide variety of applications, including estimating the body mass of cetaceans (Christiansen et al., 2019), observing wild animal behaviour for both terrestrial and marine species (Jagielski et al., 2022; Pollock et al., 2022; Torres et al., 2018), building photographic identification catalogue of endangered whale populations (Ryan et al., 2022), and for surveys of African elephants (*Loxodonta africana*) (Vermeulen et al., 2013). In many cases drones offer a significantly more accurate method of monitoring wild animals as opposed to ground-based observations by humans (Hodgson et al., 2018), and the addition of features such as thermal infrared cameras further improves the quality and accuracy of the data collected (Brunton et al., 2020).

We surveyed three drone transects using a DJI Mavic 2 Enterprise with a thermal camera (M2ED Thermal Camera; sensor: Uncooled VOx Microbolometer; sensor resolution: 160x120) between the 27th and July 29, 2023 and 20th and October 22, 2023. The altitude of the drone was selected according to Brunton et al. (2019), who reported that kangaroos were most likely to flee from the area when flying at an altitude below 30m. To further minimise the risk of kangaroos fleeing we added a buffer of 10m and flew the drone 40m above ground level. We flew the transects at a speed of 5 m per second with the camera positioned at a 30-degree angle (Fig. S3). The transects were 2 km long and covered an area of 28.4 ha (Fig. 1). Placement of the transects was targeted towards open grasslands with sparse canopy cover to match the landcover represented by the iButtons.

Each transect was flown every 2 h from sunrise to sunset to cover most of the daily temperature spectrum, resulting in a total of 36 flights. We recorded each transect as a video using both thermal infrared (TIR) and true-colour (RGB) imagery. We counted kangaroos along the transects using TIR footage due to the TIR higher success rate at detecting kangaroos (Brunton et al., 2020), and used the RGB videos simultaneously for species identification, and recorded whether the kangaroos were in the shade or exposed to the sun.

2.4. *Activity rate at waterpoints*

After analysing how kangaroos use shade at various temperatures, we decided to also measure the potential differences in the activity of eastern grey kangaroos and red kangaroos at waterpoints. We also focused on the difference in activity at tanks and dammed watercourses within each species. However, here instead of using drones we used camera traps (Browning Strike Force HD Pro X) previously deployed at waterpoints of the Mourachan property from January 2023 to October 2023 (Fig. 1). We deployed 2 cameras per tank ($n = 13$) and 3 cameras to each dammed watercourse of Mourachan ($n = 4$) due to their larger size, ensuring more comparable detection coverage across waterpoint types. We measured the activity rate of kangaroos to analyse how often they accessed waterpoints based on maximum daily temperature. To do so we recorded the total number of kangaroo events per day per waterpoint, defining events as a series of camera trap images captured within 5 min of the previous image.

2.5. *Statistical analysis*

We used a generalised linear mixed model (GLMM) with a Binomial distribution in R v4.3.2 (R Core Team, 2023) to model the probability of detecting a kangaroo in the sun at various temperatures. Transect location and date of flights were added to the models as random variables, which accounted for repeated measures and reduced the risk of pseudo-replication. To assess the relationship between maximum daily temperature and kangaroo activity at waterpoints we fit Generalised Additive Models (GAMs) using the “mgcv” package (v1.9-1) (Wood, 2015). A separate model was fit for each species rather than adding species as a factor to a single model to capture species-specific responses to temperature and dam type, including potentially different thresholds in the smoothing terms, however, the model outputs were then plotted together for comparison purposes. We modelled the number of visits by eastern grey kangaroos and red kangaroos at both waterpoint types (tanks, dammed watercourses) as a function of maximum daily temperature using a Poisson distribution. To determine the maximum daily temperature at which rapid increases in kangaroo activity rates began, we calculated the derivatives of the GAM predictions, which represent the rate of change in activity as temperature increases. We applied a 95 % confidence interval to the derivatives and focused on points where the lower bound of this interval was positive, indicating a significant increase in activity. We then examined the rate of change in the derivative to identify the specific temperature where the rate of change was highest. This temperature was recorded as the point where kangaroo activity started to increase significantly. All statistical analyses for our work were carried out in R v4.3.2 (R Core Team, 2023).

2.6. *Ethical note*

The study was approved by the Ethics Committee of the University of Technology Sydney (ACEC ETH21-6640). All animal-based data were collected using camera traps, no animal was therefore handled for the purpose of this study and no welfare concern arose throughout the study.

3. Results

Maximum ambient air temperatures recorded in the open grasslands of Mourachan were consistently warmer on average by 2.4 °C than those recorded under tree cover, becoming slightly more elevated at higher maximum temperatures with open grasslands reaching a maximum of 47.8 °C in the sun compared to 43.8 °C under tree cover (Fig. 2a). In contrast minimum ambient air temperatures recorded in open grasslands were consistently cooler on average by 1.9 °C than those recorded under tree cover, with minimum temperatures at the two canopy cover types becoming more similar the higher they became (Fig. 2b).

As temperatures in open grassland (exposed to the sun) warmed, the probability of observing eastern grey kangaroos in the sun significantly decreased ($SE = 0.022$, $z = -4.438$, $p = <0.001$; Fig. 3a, Table S1), with a similar pattern found for red kangaroos ($SE = 0.035$, $z = -3.998$, $p = <0.001$; Fig. 3a–Table S1). However, the likelihood of detecting red kangaroos in the sun decreased at double the rate for eastern greys, with the models showing 50 % probabilities of reds being detected at only 17 °C versus 28 °C for eastern grey kangaroos. Almost no red kangaroos were detected in the sun on transects above 30 °C, whereas eastern grey kangaroos were still detected in the sun above 40 °C.

As the probability of observing kangaroos in the sun decreased with rising temperature we estimated the probability of observing kangaroos in the shade across the same temperature range. As actual temperatures during surveys warmed, the likelihood of detecting eastern grey kangaroos in the shade under trees increased moderately, from 15 % at 10 °C to 35 % at 40 °C on average (eastern grey kangaroos: $SE = 0.02$, $z = 2.04$, $p = 0.041$; Fig. 3b–Table S1). Red kangaroos were also more likely to be detected in the shade as temperatures increased, however, detection probability increased at a faster rate than for eastern grey kangaroos, from 10 % at 10 °C to 50 % at 40 °C (red kangaroos: $SE = 0.027$, $z = 2.291$, $p = 0.022$; Fig. 3b–Table S1).

While the probability of detecting red kangaroos in the shade as temperatures increased was stronger than for eastern grey kangaroos, eastern grey kangaroos were more likely to be detected at water points. Using generalised additive models, we found that the predicted number of visits of eastern grey kangaroos at both dammed watercourses and tanks increased significantly with rising maximum daily temperatures (Dammed: $X^2 = 7982$, $p = <0.001$; Tanks: $X^2 = 1046$, $p = <0.001$; Fig. 4a, Table S2). We found that the rate of change in predicted activity of eastern grey kangaroos at the two types of waterpoints did not increase equally, with the rate of visits at dammed watercourses significantly increasing on days when maximum temperatures reached 27.6 °C, compared to 36.8 °C for tanks; a 9.2 °C difference (Fig. 4a). Red kangaroo predicted visits at waterpoints increased significantly at dammed watercourses only, with the predicted rate of change in activity significantly increasing on days when maximum temperatures were above 35.6 °C, 8 °C higher than that of eastern grey kangaroos (Dammed: $X^2 = 15.114$, $p = <0.001$; Tanks: $X^2 = 0.497$, $p = 0.779$; Fig. 4b).

4. Discussion

We found that the probability of observing both eastern grey and red kangaroos in the sun decreased significantly with rising temperatures, however, red kangaroos were less likely to be observed in the sun than eastern grey kangaroos. Further, by tracking the location of kangaroos using a thermal drone, we were able to show that the use of tree canopy was affected by temperature, potentially due to the lower ambient temperature and shade canopies provide (Dawson et al., 2006). We predicted that the probability of observing kangaroos in the shade would be more pronounced for red kangaroos than eastern grey kangaroos, which modelled responses confirmed. By utilising data on activity rates of these species at waterpoints at different maximum daily temperatures, we were also able to ascertain that eastern grey kangaroos favoured significantly the riparian habitats of dammed watercourses as temperatures increased, providing a possible explanation for why their use of shade was lower than red kangaroos. In contrast, red kangaroos showed only a weak increase in their use of waterpoints during high temperatures.

Shade use at higher temperatures has been observed as a thermoregulatory method in many species (Crowther et al., 2014). Tourani

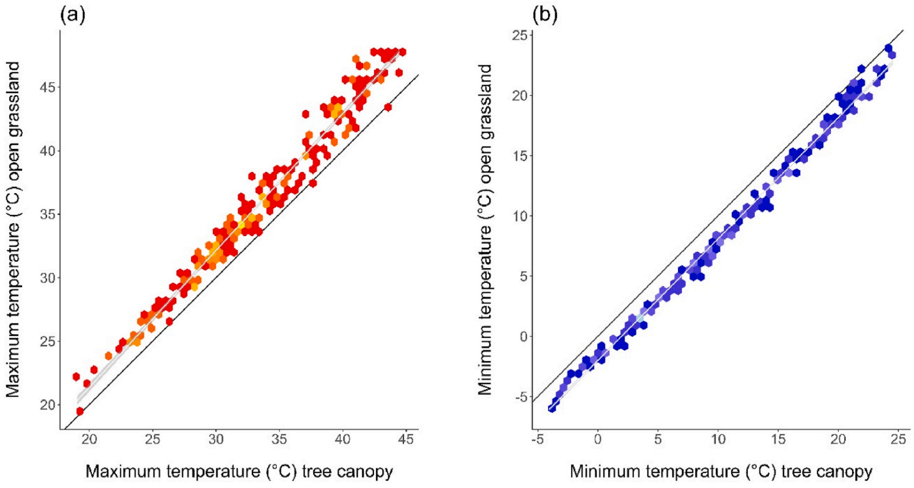

Fig. 2. **(a)** Hexbin plot showing the distribution of maximum ambient temperature (°C) measured in open grassland (no shade) and under tree canopy (shade). Each hexagon represents a spatial bin, with colour intensity showing the density of temperature measurements. Yellow colour represents higher concentration of data points while red colour represents lower concentration of data points. The black line represents the identity line where Open grassland and under tree temperatures match. **b)** Hexbin plot showing the distribution of minimum ambient temperature (°C) in open grassland and under tree canopy. Light blue colour represents higher concentration of data points, dark blue colour represents lower concentration of data points. The black line represents the identity line where Open grassland and under tree temperatures match.

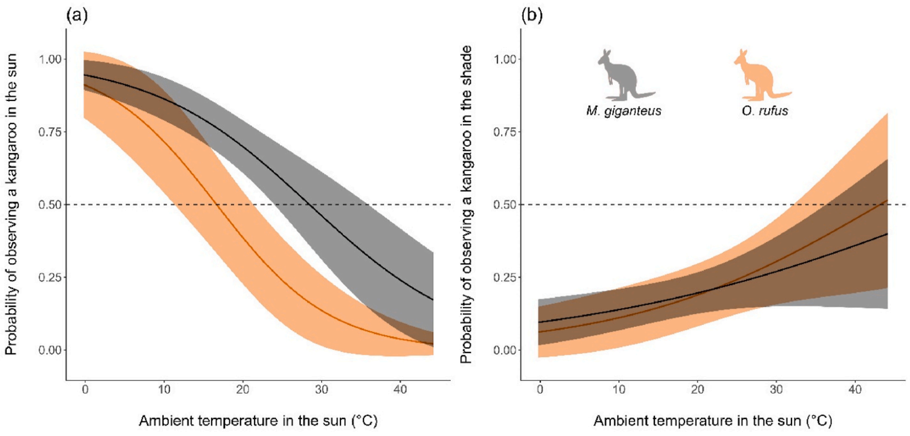

Fig. 3. **The probability of observing kangaroos decreased in the sun and increased in the shade with increasing temperatures.** Binomial model outputs for the probability of observing both eastern grey kangaroos (*M.giganteus*) and red kangaroos (*O.rufus*) in **(a)** the sun and **(b)** the shade as a function of temperature (°C) in the sun, as recorded by iButtons deployed on Mourachan. The dashed horizontal line shows 50 % probability. The dark grey lines and shaded areas represent eastern grey kangaroos while the orange colour represents red kangaroos. The shaded areas represent 95 % confidence intervals.

et al. (2023) found that North American mammals increased their use of forested habitats in hotter regions, by using shaded areas to shelter from extreme temperatures. Furthermore, Shütz et al. (2024) showed that sheep provided with shade to shelter from solar radiation in a temperate climate showed reduced signs of heat stress, such as lower respiration rates and less panting, compared to those without access to shade. That eastern grey kangaroos are considered a mesic species and red kangaroos arid-adapted (Dawson, 2012) may explain the different uses of shade and waterpoints we observed between the two species. Other studies have found sympatric species using different methods to reduce the impact of heat stress. Black wildebeest (*Connochaetes gnou*) and blue wildebeest (*Connochaetes taurinus*), for example, often co-occur at the same locations yet use the landscape differently at higher temperatures (Lease et al., 2014). Lease et al. (2014) found that black wildebeest were more likely to orient their body parallel to the sun at high temperatures, while blue wildebeest were more likely to use shade. Black wildebeest are more often found in open grasslands while blue wildebeest have evolved in savannah woodland, where shade is more readily available, potentially explaining the difference in shade and sun orientation use (Lease et al., 2014). Red kangaroos have evolved in drylands and have always been exposed to higher temperatures and lower water availability, hence they are able to keep a stable body temperature and experience lower water losses at higher temperatures than eastern grey kangaroos (Dawson et al., 2000, 2007). This may explain the higher use of shade by red kangaroos and the higher use of waterpoints by eastern grey kangaroos we observed.

The increased activity rate of eastern grey kangaroos at waterpoints observed may be for hydration purposes, either through drinking or through foraging on vegetative growth surrounding waterpoints. However, it could also be that, at extreme temperatures, immersing in water might be a potentially more effective strategy to cool down than only sheltering in the shade, particularly for a mesic species like eastern grey kangaroos (Dawson et al., 2007). Using water to thermoregulate either through immersion or behaviours such as wallowing has been observed in many species (Parker and Robbins, 2018; Ruf et al., 2023). For example, black bears (*Ursus americanus*) are known to immerse themselves in water to cool down, particularly at the end of summer when temperatures are still high and their fat reserves are increasing (Sawaya

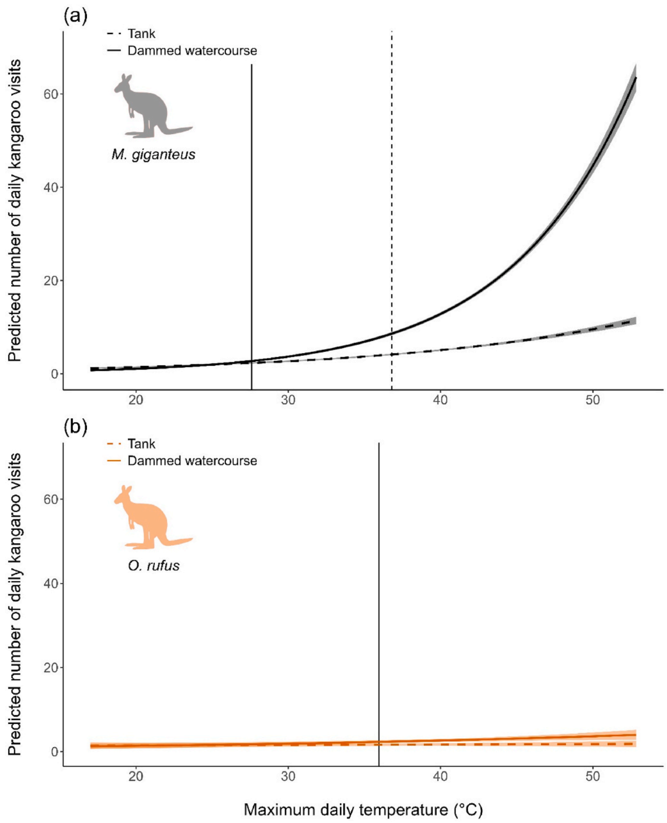

Fig. 4. Both eastern grey kangaroos and red kangaroos visited dammed watercourses significantly more at higher temperatures. Outputs of the predicted number of visits from **(a)** eastern grey kangaroos and **(b)** red kangaroos at tanks (dashed line) and dammed watercourses (solid line) as a function of maximum daily temperature of the Mourachan property obtained from a generalised additive model (GAM). Vertical lines show the temperature thresholds at which number of visits significantly increased as determined by GAMs. The temperature thresholds were obtained by calculating the rate of change in the derivative of the predicted number of visits using maximum daily temperature. The solid vertical lines represent dammed watercourses while the dashed vertical line represents tanks. The shaded areas represent 95 % confidence intervals.

et al., 2017). The use of water sources for behavioural thermoregulation was also found to be important for grizzly bears (*Ursus arctos*), particularly lactating females (Rogers et al., 2021). However, more research is needed to confirm the usefulness of water immersion for eastern grey kangaroo thermoregulation, and how often they make use of it.

When using waterpoints, both species used dammed watercourses more than tanks, despite there only being four dammed watercourses compared to 13 tanks. The higher activity rate observed at dammed watercourses despite their low number could, therefore, suggest a strong behavioural preference by kangaroos for these waterpoints. Modified natural waterpoints such as dammed watercourses offer more preferable conditions and opportunities for wildlife than tanks. They can also offer better microclimates and more extensive vegetation cover, providing cooling opportunities and protection from predators as well as foraging opportunities (Alikhanova and Bull, 2023; Maestas et al., 2023; Malerba et al., 2023). Furthermore, natural water sources, particularly in drylands, harbour a wide array of species, supporting the local biodiversity (Maestas et al., 2023). Tanks found in the Australian drylands are designed to provide water to livestock, are made of dug-up clay soils and generally do not promote much vegetation growth on their often steep sides (Croft et al., 2007). Such conditions can even create muddy or silted dams sometimes trapping and killing animals, including livestock (Wallach et al., 2017). That both species of kangaroos used tanks less than dammed watercourses may imply they only access tanks when temperatures become too extreme to ignore such water sources, or when more natural water sources, including dammed watercourses, are not available. Because we can only infer motivations for actions we can only speculate about these findings. Although artificial water points, such as tanks, have been shown to not alter the density and abundance of kangaroos in semi-arid rangelands (Croft et al., 2007; Montague-Drake and Croft, 2004), our findings show that modified natural waterpoints may play a role in helping kangaroos thermoregulate during high temperatures. We suggest that implementing modified natural water sources in dryland ecosystems may be a vital strategy for protecting the welfare and thermoregulatory needs of wildlife when designing conservation landscapes, or even wildlife-friendly production landscapes. Additionally, artificial waterpoints such as tanks can be managed in ways that promote biodiversity by creating enhanced dams – artificial waterpoints that either fully exclude livestock (when located on livestock properties) through the use of fences, or that contain a single entry point for livestock while allowing wildlife to access water freely (Westgate et al., 2021). Enhanced dams also promote vegetation diversity through re-planting of vegetation, including shrubs and trees, while also promoting higher water quality than non-managed artificial tanks (Westgate et al., 2021). Waterpoint protection could also assist coexistence between species by promoting niche-partitioning opportunities (Sandoval-Serés et al., 2025). However, more research is needed to analyse the effectiveness of such dams in a warming context, particularly their benefits for wildlife thermoregulation.

Here, due to timing constraints we only conducted drone transects over three days in July and three days in October. This was one of the main limitations of our work and future research would benefit from flights being conducted at additional dates throughout the year to produce even more robust findings. Additionally, because transects were surveyed at different times of day, it is possible that some individuals were detected more than once when the same transect was flown on multiple occasions, a potential cause for concern when it comes to pseudo-replication; however, double counting within a single flight was unlikely as no flight response from the kangaroos due to the drone presence were observed. Further, repeated detections across transects at the same time of day were highly unlikely due to the distance between transects. Any such incidental re-detections would have minimal effect on our results, other than potentially leading to a slight underestimation of variance.

The rate at which the climate is currently changing, particularly in drylands around the world, brings major physiological challenges to species affected (Acevedo-Whitehouse and Duffus, 2009; Fuller et al., 2021). Mass wildlife die-offs are known to occur during severe droughts when sources of food and water are severely diminished, a phenomenon known to affect kangaroo populations (Croft and Witte, 2021; Robertson, 1986). Access to adequate conditions to thermoregulate is vital, particularly in ecosystems with a naturally hot climate like Australia's drylands (Stokes et al., 2008). However, the practice of clearing trees from production landscapes and limiting access to waterpoints by wildlife, particularly in semi-arid and arid Australia for agricultural activities (e.g., livestock), is further limiting thermoregulation opportunities (Bradshaw, 2012; Croft et al., 2007). While state-based legislation prohibits first-time clearing of forest in many areas (DCCEE, 2011), re-clearing of regrown forest is likely to be continual (Simmons et al., 2018). This, along with remoteness of some private properties, can often lead to densely forested, "non-remnant" habitat on private properties being cleared on a large scale (State of Queensland, 2019). Furthermore, fencing off waterpoints has been recommended as a management strategy to reduce the local population density of kangaroos and mitigate grazing pressure (NSW Biodiversity Conservation Trust, 2020). However, there is no evidence that water availability directly influences kangaroo abundance or distribution (Croft and Witte, 2021; Lavery et al., 2018; Montague-Drake and Croft, 2004). One of the most significant impacts that blocking access to water may have is on the welfare of kangaroos (McLeod and Sharp, 2020), potentially pushing their vulnerability to extreme weather events such as heatwaves to limits incompatible with life. As climate warming continues to exacerbate the potential for more intense and frequent high temperatures in the drylands of Australia, the capacity of wild animals to persist may increasingly depend on the provision and maintenance of landscape features such as water and canopy shade.

CRediT authorship contribution statement

Loic Q. Juillard: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Lisa M. Ashby:** Writing – review & editing, Methodology, Investigation. **Taylor J. McEvoy:** Methodology, Investigation. **Daniel Ramp:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Data accessibility statement

The data collected and used in this work is available at https://doi.org/10.6084/m9.figshare.28181339.v1.

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Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2025.104245.

Data availability

The data collected and used in this work is available at https://doi.org/10.6084/m9.figshare.28181339.v1.

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