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Extreme temperatures can intensify predator–prey interactions

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Extreme temperatures and heatwave events present challenging conditions for wildlife and are increasing in frequency and intensity in many regions due to climate change. High daily temperatures increase physiological stress and cause mortality in susceptible individuals (e.g. from poor health or exposure) but may also drive behavioural changes as individuals seek to thermoregulate (e.g. seeking shelter or water). As daily high temperatures accumulate into heatwave events, the ability of wildlife to tolerate conditions can diminish and exacerbate stress. Although climate change is well known to decouple species interactions, here we examined how extreme conditions may intensify interactions between predators and prey. In particular, we explored whether predators can exploit the thermoregulatory requirements of prey as they increasingly require access to water. We presented evidence from the use of artificial waterpoints by dingoes, *Canis dingo*, and eastern grey kangaroos, *Macropus giganteus*, on a wildlife property in Australia's semiarid drylands, asking whether high temperatures and heatwaves alter species behaviour and interactions between them. Both species increasingly accessed waterpoints as daily maximum temperatures increased; however, the degree of co-occurrence at waterpoints increased significantly as the temperatures became extreme and resulted in heatwaves. Not only did waterpoints become increasingly important for both species during heatwaves, but dingo hunting attempts on kangaroos at these times were significantly higher than expected based on the number of days when heat anomalies occurred. Additionally, dingoes relaxed their predisposition to hunt kangaroos in poor body condition, making kangaroo hunting opportunistic during these times. Our findings emphasize the potential for climate change to exacerbate predator–prey interactions, which may have an impact on species persistence if prey is unable to adapt to predators that exploit their thermoregulatory demands.

Anthropogenic climate change is recognized as one of the major threats to global biodiversity (IPCC, 2022). It can exacerbate existing threats such as habitat loss and fragmentation, overexploitation, pollution and agricultural expansion and has been predicted to increase species extinction rates this century (Cahill et al., 2013). Climate change can drive geographical range shifts (Monzón et al., 2011), challenge species to physiologically adapt to a warming climate (Acevedo-Whitehouse & Duffus, 2009), and create phenological mismatches in species that heavily rely on environmental cues (Wilmers et al., 2007). Furthermore, as the global climate warms above 1.5 °C preindustrial levels because of the increasing intensity of climate patterns such as El Niño and La Niña (Cai et al., 2021), as well as shifts in the Indian Ocean Dipole, North Atlantic Oscillation, Arctic Oscillation and other similar patterns (Cai et al., 2009; Delworth et al., 2016; Hamouda et al., 2021), phenomena such as extreme temperatures and heatwaves are expected to increase in both intensity and frequency (Dosio et al., 2018; Trancoso et al., 2020). The current rate at which the climate is changing may be too rapid for many species to adapt, driving biodiversity loss via radical shifts in biotic interactions (Acevedo-Whitehouse & Duffus, 2009; Blois et al., 2013). Efforts to counteract and anticipate biodiversity loss driven by climate change require detailed knowledge of the shifts in biotic interactions to mitigate extinction risk where possible (Urban, 2015).

Biotic interactions play a critical role in ensuring optimal ecosystem functioning (Bascompte, 2009). Mutualistic relationships can help sustain ecosystem productivity and biodiversity (Dehling et al., 2022), while competitive interactions can push species to

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adapt and occupy narrower ecological niches, leading to specialization (Armbruster, 2017). Likewise, parasitic relationships are key structural components of ecosystems because they influence the behaviour, health and population size of the hosts (Brown, 2022; Preston & Johnson, 2010). These interactions are critical in shaping trophic food webs and ultimately biodiversity (Brown, 2022). Equally important in this regard are the interactions that occur between predators and prey. Predators can regulate prey populations through effects like hunting and killing and by inspiring fear in prey, creating hotspots in the landscape of fear (Gaynor et al., 2019; Ripple et al., 2014). Both the consumptive and nonconsumptive effects of predators shape the ecology and behaviour of prey, with effects sometimes able to cascade to influence lower trophic levels and vegetation communities (Lundgren et al., 2022; Wallach et al., 2010). While relationships between temperature and predation rates are well studied, knowledge of how extreme temperatures and heatwaves shape the dynamic spatiotemporal interactions of predators and prey as they seek to mitigate heat stress remains limited. Not only may access to water become a contested space under extreme conditions, but predators may also be able to exploit prey that use behavioural strategies to reduce heat stress.

Weather conditions are known to play a large role in shaping the mechanisms and outcomes of predator–prey interactions, especially extreme temperature conditions exacerbated by climatic change (Romero et al., 2018; Schemske et al., 2009). Importantly, subtle deviations in the nature of predator–prey interactions may occur because of variance in species heat tolerance, thermoregulatory requirements, behavioural and competitive adaptation and cognition (for individuals and social groups), attributes that may alter the survival and persistence of species (Guiden et al., 2019; Soravia et al., 2021; Wooster et al., 2023). Deviations can lead to biotic decoupling, where co-occurrences and resulting dependencies are unfavourable because of phenological shifts in seasonality. For example, while predation by ladybeetle larvae on aphids increases with warming temperatures, it decreases rapidly when a temperature threshold is reached (Sentis et al., 2012). In contrast, coupling effects that promote the intensification of direct interactions between predators and prey may also occur, for example, through behavioural adjustments that intensify their spatiotemporal overlap. For example, Rafiq et al. (2023) found that large African carnivores became more nocturnal and had decreased activity levels when temperatures increased. However, in doing so, competition for space among predators can intensify, as temporal overlap can increase during extreme temperature events (Rafiq et al., 2023). Weather conditions can also directly impact the ability of prey species to avoid predators, affecting their vulnerability to predation and potentially increasing predation rate. For example, reduced snow cover due to climate change allows coyotes, *Canis latrans*, which are poorly adapted to walk through deep snow, to hunt snowshoe hares, *Lepus americanus*, more effectively (Peers et al., 2020). These impacts can then lead to changes in the survival and persistence of species by increasing predation pressure.

As climate change increases the frequency and intensity of extreme temperature events, like heatwaves, wildlife's access to water may become an increasingly critical requirement to avoid death for many species. When temperatures exceed the thermal neutral zone (TNZ) of an individual, a favourable temperature range, often species-specific, within which body temperature regulation is optimal (Norris & Kunz, 2012), the metabolic rate of the affected individual is forced to increase to maintain an optimal body temperature (Norris & Kunz, 2012). Consequently, metabolic water will evaporate at a quicker rate, pushing the individual further towards dehydration and overheating, and, if unable to replace the lost metabolic water (e.g. by drinking), physiological impairments linked to such impacts are likely to be triggered (Acevedo-Whitehouse & Duffus, 2009; Costa et al., 2013). The main physiological impacts linked to overheating or dehydration will often involve impairments of the reproductive and immune systems, as well as cognitive abilities, among others (Acevedo-Whitehouse & Duffus, 2009; Costa et al., 2013; Norris & Kunz, 2012). The intensification of weather events like heatwaves could lead to wild animals in affected regions relying on water sources more often than they usually would for thermoregulatory purposes (Fuller et al., 2021). Thus, savvy predators may use waterpoints to actively predate on weaker prey. This is particularly the case for interactions between predators and prey in arid and semiarid drylands, where water is a sparse yet vital resource.

Globally, rangelands constitute about 54 % of all land cover and are found on most continents, with arid and semiarid ecosystems constituting the majority (ILRI et al., 2021). Water, or lack thereof, is one of the key features of dryland systems influencing mammal communities (Smit et al., 2007), with predators in dryland systems often focusing their activity around water (Makin et al., 2017; Valeix, Fritz, et al., 2009; Wallach et al., 2009; Wooster et al., 2021). For dryland wildlife, water availability can promote behaviours that affect predator–prey interactions (McCluney & Sabo, 2009; Valeix et al., 2008). For example, in arid and semiarid areas of Africa, such as Hwange National Park and the Serengeti, water location is known to be a crucial factor in lion habitat selection (Davidson et al., 2012; Mosser et al., 2009). Similarly, for herbivores in those regions, distance to water is crucial for habitat selection (Bergström & Skarpe, 1999; Thrash et al., 1995; Valeix, Loveridge, et al., 2009) and can constrain foraging activities, particularly in dry seasons (Redfern et al., 2003; Thrash et al., 1995). While drinking locations strongly influence habitat selection for predators in drylands, prey abundance also shapes selection and behavioural patterns (Davidson et al., 2012; Spong, 2002). Indeed, extreme weather conditions may intensify predator–prey interactions in regions with scarce water availability, particularly when herbivores are not only physiologically required to access water more often but may also be more limited in their choice of waterpoints. Recent evidence suggests that these conditions provide predators with more and easier hunting opportunities (Davidson et al., 2012, 2013; Harris et al., 2015).

Here, we hypothesized that high temperatures and heatwaves can intensify predator–prey interactions at waterpoints in Australia's semiarid drylands, a biodiversity hotspot vulnerable to climate change (Urban, 2015). To test this idea, we monitored the temporal patterns of a prey species, eastern grey kangaroos, *Macropus giganteus,* and a predator, dingoes, *Canis dingo*, and documented hunting attempts that occurred at waterpoints on a large dryland reserve in South-western Queensland, Australia. While eastern grey kangaroos are a mesic species (Dawson et al., 2007), part of their range extends into more arid regions, potentially making individuals in such regions more vulnerable to intensifying temperatures. In Australia, dingoes are a widespread and large predator capable of predating on macropods (e.g. kangaroos *Macropus* spp.; Letnic et al., 2012), using ambush hunting strategies as well as engaging in pack and chase behaviour (Pollock et al., 2022; Purcell, 2010; Thomson, 1992; Wooster et al., 2024). As a canid, dingoes require daily access to water for hydration and thermoregulation and are also known to use waterpoints as social hubs (Wallach & O'Neill, 2009). For prey species like kangaroos, waterpoints and their environs are also used for hydration and thermoregulation at times, obliging them to navigate these requirements alongside recognition that waterpoints can be places of risk (Wooster et al., 2022).

As a series of cascading predictions from a study system including dingoes and eastern grey kangaroos, we first predicted that waterpoint visits from both species would increase with rising temperatures as they seek to hydrate and thermoregulate. We then predicted that the presence of kangaroos at water points on hotter days would coincide with greater dingo activity than on similar hot days without kangaroos. We expected that where possible, eastern grey kangaroos would attempt to avoid access of waterpoints at times when dingoes were present, but that extreme conditions (both temperatures and heatwaves) would decrease the ability of eastern grey kangaroos to temporally avoid dingoes. For eastern grey kangaroos this represents a trade-off between accessing waterpoints and the thermoregulatory opportunities this provides while risking being hunted by dingoes, or else avoiding dingoes but risking dehydration and overheating by staying away from waterpoints. We also predicted that as opportunities for hunting increase, dingoes may shift from targeting hunting activities towards weaker individuals, a behaviour engaged in by many predators (e.g. Clements et al., 2016; Genovart et al., 2010), to being more opportunistic during high heat anomalies.

METHODS

Study Site

This research was conducted on the 480 km^2 Mourachan conservation property (MCP) in southwestern Queensland, near the township of St George. This private semiarid dryland 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 and other wildlife are protected from persecution. Eastern grey kangaroos, red kangaroos, *Osphranter rufus*, black wallabies, *Wallabia bicolor*, red-necked wallabies, *Notamacropus rufogriseus* and black-striped wallabies, *Notamacropus dorsalis*, are the only macropod species present on the property, while dingoes are the main predatory species. Southern Queensland and most of Australia suffered from a severe drought and heatwaves for the majority of 2019 and part of 2020 because of a major El Niño event (BOM, 2020).

Camera Traps

Kangaroos and dingoes were recorded using camera traps (Browning Strike Force HD Pro X) deployed from November 2019 to April 2021. As our primary goal was to understand how interactions at resource points are affected, we deployed the cameras ($N = 35$) at 16 waterpoints distributed across the property (Fig. 1). We selected the waterpoints as they were the only water sources on the property when we set up the cameras in November 2019. We deployed two cameras per waterpoint for 13 of the waterpoints because of their smaller size; however, the remaining three waterpoints required three cameras each to cover their area. We set up the cameras so that they would cover much of the ground near the water while also having part of the water visible in the frame (Fig. 2), allowing us to observe both predator−prey interactions that may occur when kangaroos are at the water (e.g. when drinking) and when approaching the water. We gathered a total of 10 736 camera trap days; however, some cameras were lost due to being completely submerged during flooding in early 2020.

Kangaroo and Dingo Activity Rate

We measured the activity rate of kangaroos and dingoes to determine how often they accessed water points. To do so, we recorded the total number of kangaroo and dingo events per day per waterpoint, defining an event as a series of camera trap images captured within 5 min of each other. Hunting attempts were identified as every event where kangaroos and dingoes were seen interacting agonistically; for example, kangaroos were chased by dingoes, there was physical contact (such as dingoes biting a kangaroo), or kangaroos were using defensive behaviours against dingoes (Fig. 2). Some of the defensive behaviours used by kangaroos when interacting with dingoes include both fight behaviours, such as adopting an upright stance in an attempt to make themselves more intimidating (Fig. 2, top), hopping in the direction of the dingo while remaining in an upright posture, and actively kicking at the predator, and flight behaviours, such as fleeing away

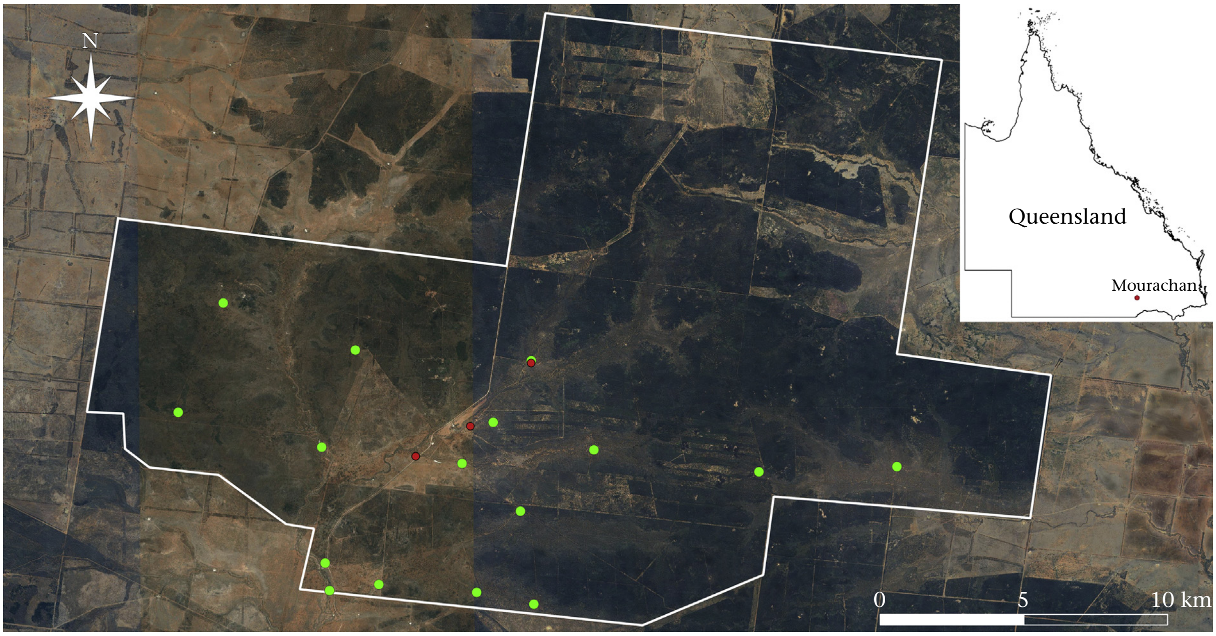

Figure 1. Map of the 480 km^2 Mourachan Conservation Property and location within Queensland, Australia. The locations of waterpoints (green circles) and iButton temperature sensors (red circles) are highlighted on the property.

Figure 2. Example of predation attempts observed at the waterpoints of the Mourachan property. Both events were part of the 67 predation attempts recorded during the study period. (Top) 22 November 2019, maximum temperature: 43.39 °C, mean daily temperature: 32.84 °C. (Bottom) 1 January 2020, maximum temperature: 44.05 °C, mean daily temperature: 35.98 °C.

from the waterpoints and fleeing towards water (Fig. 2, bottom; Jarman & Wright, 1993; Purcell, 2010; Wright, 1993).

We ran logged negative binomial regression models to measure the effect of maximum daily temperature on the daily visits of kangaroos and dingoes at waterpoints and calculated R squares to measure correlation between temperature and number of visits. We conducted negative binomial regressions to investigate the relationship between maximal daily temperature and dingo visits at waterpoints when kangaroos were absent and present. This analysis was done to determine whether dingo activity at waterpoints was solely influenced by temperature or whether kangaroo presence had an impact.

Temperature of the MCP

To determine the daily temperature of the MCP and identify heatwaves, we established 15 iButton temperature sensors (DS1922L-F5# Thermochron, Maxim Integrated, San Jose, CA, U.S.A.) at three locations across the property. Each site was split into five ground cover types to capture the full temperature spectrum of the property with one iButton per ground cover: bare ground with no trees (no shade), grass field with no trees (no shade), bare ground with trees (full shade), grass with trees (full shade), and shrub cover (limited shade). We placed the iButtons in mini-Stevenson screens made using inverted white PVC jars perforated to allow airflow (Ashcroft et al., 2012), which we then attached to star pickets. The iButtons were placed 50 cm above ground to better represent the average height of kangaroos and dingoes. To allow airflow to reach the iButtons, we placed them in fine mesh bags attached to the top of the jar, allowing the temperature sensors to hang directly in front of the holes. We then used the temperature recorded at all iButton sites to calculate the mean temperature, mean maximum temperature and mean minimum temperature across the property. The iButtons recorded temperatures half-hourly from 24 January 2023 to 21 October 2023.

To obtain site-calibrated temperature data for the entire study period, we combined the in situ iButton data with local weather station temperatures recorded by the Australian Bureau of Meteorology (BOM) for St George, QLD, the nearest town to the MCP with weather stations, approximately 52 km from the MCP (BOM, 2023). We used a linear regression model to adjust the BOM data based on the iButton temperature data. We calibrated three BOM temperature variables: the daily minimum temperature, the daily maximum temperature, and the mean temperature using the minimum and maximum temperatures. We then applied the model to BOM daily maximum and minimum temperatures from 1 February 1913 to the end of the study period 18 April 2021. BOM station 043034 was used for temperatures from January 1913 to April 1997 and station 043109 from May 1997 to April 2021 (BOM, 2023). All statistical analyses were carried out in R v4.1.1 (R Core Team, 2023).

Heatwave Metrics

We then used the locally corrected temperatures to calculate heatwave metrics. We first calculated the monthly mean temperature for each month in a long-term reference period (1971–2000) and identified the maximum monthly mean (MMM). The MMM represents the typical highest mean temperatures that organisms experience in a location. We calculated the MMM for the study site, which was of 32.1 °C. We could then calculate temperature anomalies as the difference between the observed temperature on a given day (mean daily temperature) and the MMM plus a threshold value, for example, MMM + 0 °C, where positive values indicate likely heat stress. Negative values indicate cooler conditions. While previous uses of MMM-based anomalies have set all negative anomaly values to zero, here we retained the negative values for two reasons; the first is that cool periods following hot periods provide physiological respite from heat stress, not just an absence of heat stress (Ma et al., 2018). The second reason was statistical, as clipping all negative values to zero would induce nonlinearity into the model. Furthermore, because the camera trap data used covers all seasons, the anomalies we calculated cover all days in a year rather than a specific season.

We summed anomaly values over a 13 day window to provide a heatwave index over time. We selected the a 13 day window and MMM + 0 °C heat threshold after testing multiple accumulation window and heat threshold combinations to identify the combination best suited to explaining the relationship between heat stress and kangaroo activity using Akaike information criterion (AIC, Aho et al., 2014). We then used a generalized linear model with a Poisson distribution to model eastern grey kangaroo activity as a function of the interaction between heat anomalies and dingo activity rates. The model was then visualized using the R package 'visreg' (v2.7.0; Breheny & Burchett, 2017).

A heatwave can be determined as a prolonged period of temperatures higher than the long-term average (Robinson, 2001), which in this work refers to periods where temperatures exceed the local MMM for the long-term period of 1971–2000. Physiologically, heat stress can occur when temperatures exceed the TNZ of an animal (often species-specific) and when an individual is no longer able to maintain thermal balance (Norris & Kunz, 2012). Phenological and genetic adaptations mean that different temperatures may be considered heat stress depending on the individual animal, even within species (Hoffmann & Sgrò, 2011). For example, an eastern grey kangaroo living in the semiarid drylands of Australia will be exposed to average temperatures higher than a conspecific living along the southern coasts of the country and could, therefore, be expected to have a higher TNZ. Hence, the use of a local MMM instead of a single threshold, as a single threshold may not be semiarid dryland specific or accurately represent relationships between kangaroos in semiarid drylands and temperature.

To ascertain whether heatwaves for the study period were more intense than a long-term average and that heatwaves at the MCP are intensifying, we calculated the normal annual average heatwave metric for a benchmark period from 1971 to 2000. We then calculated differences in the annual mean heatwave metric between the benchmark value (−134.89) and all years from 1913 to 2021. We also calculated the number of days above the MMM for each year from 1913 to 2021.

Kangaroo Demographic Characteristic and Body Condition

We classified the kangaroos captured by the camera traps by demography classes: large adult, medium adult, small adult, subadult, young-at-foot and pouch young (Austin & Ramp, 2019). A single researcher (L.Q.J.) gave a body condition score (BCS) to each individual using the chart described in Juillard and Ramp (2022). The choice of a single researcher giving BCSs was made to avoid potential confusion between BCSs given by multiple people owing to the subjectivity of BCS assessments and to remain consistent throughout scoring. The scores given by the chart are as follows: 1: emaciated, 2: very thin, 3: thin, 4: optimal, 5: muscular. While the chart uses five score levels, no kangaroo with a BCS of 5 was observed throughout the period of the study; therefore, only scores 1–4 appear in our results.

Temporal Co-occurrence

We calculated the temporal patterns of kangaroos and dingoes by estimating kernel densities in R packages ‘overlap’ (v0.3.3) and ‘circular’ (v0.4-93). We used the Δ4 overlap statistic, which is regarded as reliable for measuring overlap of activity patterns when sample sizes are > 75 detections (Ridout & Linkie, 2009). To calculate the Δ_4 overlap statistic and 95 % CIs, we generated 10 000 bootstrapped detections for both kangaroo and dingo (Wooster et al., 2021). We used the ‘Basic0’ approach to adjust the 2.5 % and 97.5 % percentiles, taking into account bootstrap bias. We divided detections into heat anomaly and nonheat anomaly bins to assess how much the overlap between kangaroos and dingoes varied in response to the maximum daily temperature. Heat anomaly bins represent days when the temperature rises over the MMM threshold, whereas nonheat anomaly bins represent days when the temperature falls below the MMM. We generated the Δ4 overlap statistic for both temperature groups (heat anomaly and nonheat anomaly) and assessed significance based on the overlapping 95 % CIs.

Dingo Prey Selectivity

We explored the difference in hunting attempts between heat anomaly days (where temperature exceeded the MMM) and days of nonheat anomalies (where temperature was below the MMM) by calculating the number of events per day at waterpoints through the study period. We then used Manly's selectivity measure to find selection ratios based on the number of days available during both heat anomaly periods and nonheat anomaly periods and the number of hunting attempts observed in each period, using the package ‘adehabitatHS’ (v0.3.15) in R v4.1.1 (R Core Team, 2023). Selection ratios (Wi) greater than 1 imply hunting attempts were significantly more likely to occur relative to the number of days available, while ratios lower than 1 imply hunting attempts were significantly less likely to occur relative to the number of days available. To understand if dingoes select kangaroos based on body condition, we also used Manly's selectivity measure for each kangaroo BCS where interactions occurred with dingoes during periods of heat anomaly and periods of nonheat anomaly. Here, selection ratios (Wi) for BCS greater than 1 imply preferential selection by dingoes, while ratios lower than 1 imply that dingoes avoid interacting with kangaroos with those BCS relative to availability.

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.

RESULTS

Site-calibrated Temperature

Upon combining in situ iButton data with local weather station temperatures recorded by BOM to obtain site-calibrated temperature data for the MCP from 1913 to April 2021 (end of study), we found that the temperature of the MCP varies significantly from the location of the BOM weather station (St George Airport, QLD). While the maximum temperature recorded by BOM reached 40.1 °C, that of the MCP reached 50.69 °C (Fig. 3a). Similarly, the MCP minimum temperature was colder than St George, with the coldest temperature of the MCP recorded being −6.0 °C compared to a temperature of −1.2 °C for the BOM data (Fig. 3b).

Heatwave Metrics

Based on the average annual heat anomaly of a benchmark period from 1971 to 2000 of −134.89, the year 2019 had the second most intense heatwave on record with a heat anomaly 16.79 above the benchmark period, while 2020 was still abnormally high with an anomaly 7.93 above the benchmark (Fig. 4a). The year with the highest annual heat anomaly was 1973, with an anomaly 18.07 higher than the benchmark. A linear regression model also revealed an increasing anomaly trend, with heatwaves becoming more intense over time (Fig. 4a). A similar trend to heatwave intensity was revealed with the annual number of days above the MMM. The mean number of days per year above the MMM for the benchmark period between 1971 and 2000 was 7.39. The MCP experienced 48 days above the MMM in 2019 and 41 days in 2020 (Fig. 4b). The year 2017 had the highest number of days above the MMM (53 days). A gradual increase in the annual number of days above the MMM was also identified (Fig. 4b).

Activity Responses to Rising Temperatures

The activity rate of kangaroos at waterpoints significantly increased with increasing daily maximum temperature ($R^2 = 0.225$, $z = 31.98$, $P \leq 0.001$; Fig. 5a). The same pattern was found for dingoes, with activity rate increasing significantly as temperatures rose ($R^2 = 0.204$, $z = 17.92$, $P \leq 0.001$; Fig. 5b). The number of daily dingo visits at waterpoints increased significantly when kangaroos were absent and when kangaroos were present, with a slightly stronger effect when kangaroos were present (kangaroos absent: $R^2 = 0.125$, $z = 9.235$, $P \leq 0.001$; kangaroos present: $R^2 = 0.172$, $z = 12.850$, $P \leq 0.001$; Figs. S1 and S2).

Although kangaroo activity rates significantly increased with increasing temperatures, rates also increased with both higher heat

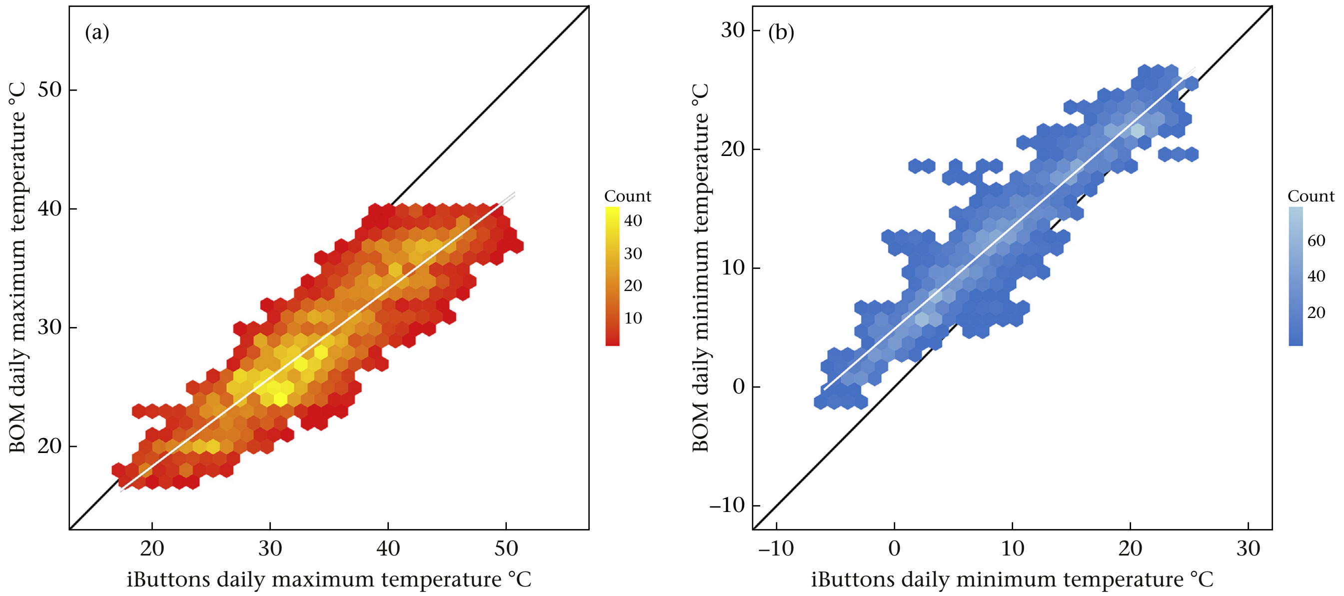

Figure 3. Temperature recorded by iButton sensors deployed at the Mourachan conservation property (MCP) compared to the Bureau of Meteorology (BOM) temperature recorded for the town of St George. (a) Maximum temperature, (b) minimum temperature. The white line in both graphs represents a linear trend, while the black line represents the identity line where BOM and iButton temperatures match.

anomalies and higher dingo activity (kangaroo ~ heat anomaly × dingo: $z = 3.621$ $P \leq 0.001$; Fig. 6a). These results suggest that kangaroos are unable to avoid aggregating with dingoes when both heat anomalies and dingo activity rates are high, creating potentially dangerous situations for the kangaroos during heat anomalies.

Temporal Co-occurrence and Hunting Attempts

Kangaroos shifted their activity pattern from crepuscular to diurnal during the presence of heat anomalies, with much of their activity focused in the early afternoon (Fig. 7). A similar trend can be observed for dingoes, with their activity shifting towards mid to late afternoon as well. The shift in activity pattern for both species during periods of heat anomalies drove a significant 7.8 % increase in temporal overlap (nonheat anomaly $\Delta^4 = 0.791 \pm 0.742–0.821$, Fig. 7a; heat anomaly: $\Delta^4 = 0.853 \pm 0.826–0.861$, Fig. 7b). Days experiencing heat anomalies represented only 10.68 % ($N = 55$) of the total number of days in our 18 months study period. Although 74.63 % ($N = 50$) of 67 documented hunting attempts at waterpoints occurred during those days, and there was an increase in overlap between the two species during periods of heat anomalies, we found that 73.9 % of interactions between kangaroos and dingoes resulted in hunting attempts outside of heat anomalies, compared to 64.1 % during heat anomalies. This implies that while interactions were higher during heat anomalies and hunting attempts occurred significantly more than would be expected during heat anomalies based on the number of days available during that period, in proportion to the number of interactions, hunting attempts were lower; outcomes of such events (e.g. kangaroo mortality), however, remain unknown due to the hunting attempts generally ending out of frame. It is therefore impossible to conclude whether hunting success is higher during heat anomalies or outside of them (heat anomaly: $Wi = 6.99 \pm 2.06$; nonheat anomaly: $Wi = 0.28 \pm 0.05$; Fig. S3). Quantifying the BCS of each individual recorded in the study revealed that on days with temperatures below MMM, dingoes preferred hunting of kangaroos with low BCS (BCS 1: $Wi = 12.64 \pm 7.51$; BCS 2: $Wi = 1.55 \pm 0.331$; Fig. 8b, Table S1). However, dingoes abandoned these preferences during heat anomalies, instead hunting all kangaroos relative to their prevalence at waterpoints on those days (Table S1, Fig. 8a).

DISCUSSION

Understanding how an increasing prevalence of extreme temperatures and heatwaves shape predator−prey interactions is an urgent conservation concern in the face of rapid climate change. We predicted that as temperature increased, so would the predation pressure exerted on kangaroos by dingoes at shared waterpoints, given their increasing water dependence. We found that during periods of nonanomalous conditions, kangaroos were able to avoid waterpoints where dingoes were present by avoiding times of dingo activity. However, as heat anomalies became more severe, both the activity and temporal overlap of kangaroos and dingoes increased. Similar effects have been observed for other species where the number of visits at waterpoints increased with increasing temperatures (Lundgren et al., 2022). Such an increase in kangaroo activity rate at waterpoints meant that kangaroos were no longer able to avoid dingoes at water, instead significantly aggregating with them, particularly when dingoes concurrently increased their activity rate at the waterpoints. Similarly, ibex, *Capra ibex*, increase their nocturnal activity following days with high temperatures despite a higher likelihood of predation by wolves, *Canis lupus* (Brivio et al., 2024). Our results confirm that prolonged periods of extreme temperatures can increase the temporal overlap of predators and prey as they mitigate the effects of heat stress. Additionally, our research provides evidence that while this overlap did not result in a higher proportion of hunting attempts compared to the number of interactions between the two species, hunting attempts still occurred significantly more than expected based on the number of days during which heat anomalies occurred, and that predators may have access to a wider array of prey than the weaker individuals they may typically hunt (Genovart et al., 2010). Since all predation attempts observed here ended outside of the frame of our camera traps, it is impossible to conclude whether they were more successful during heat

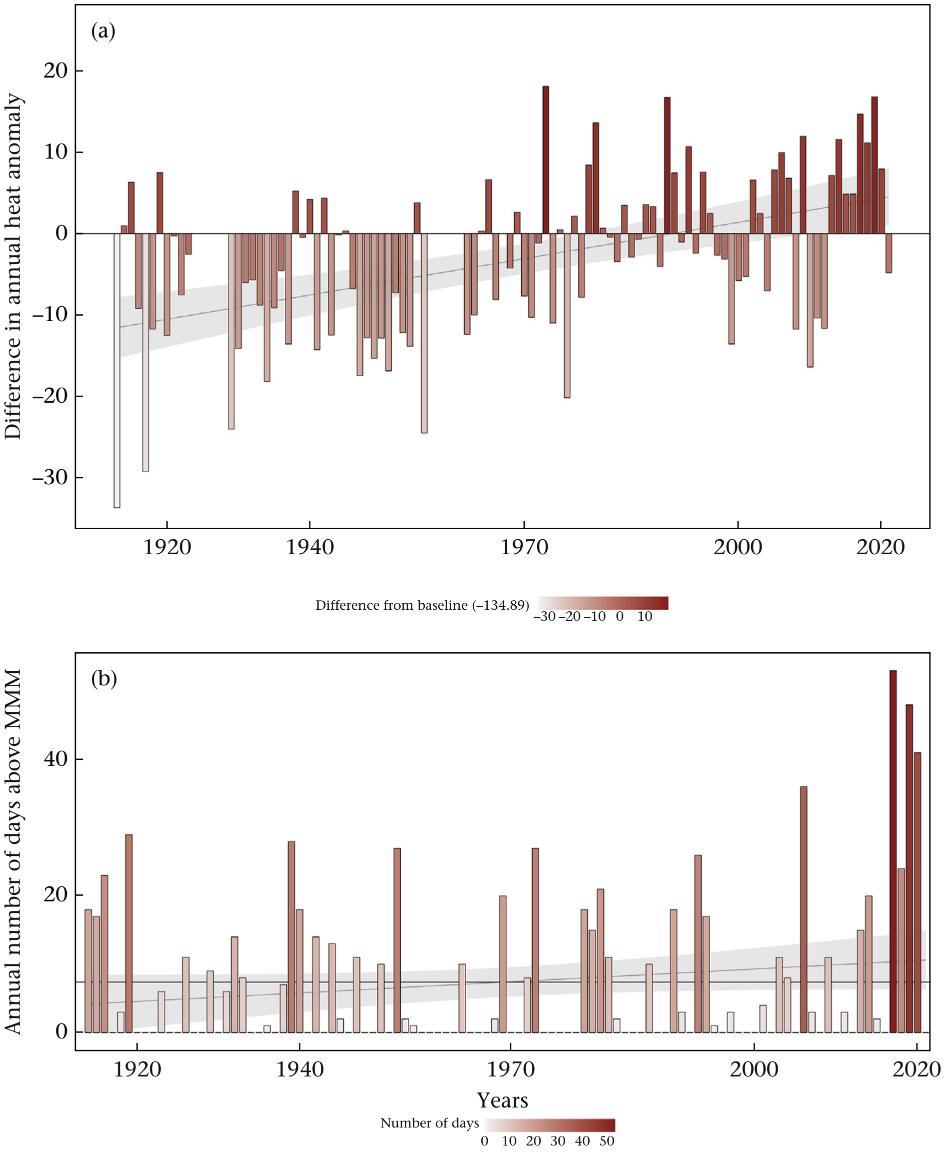

Figure 4. (a) Difference in average annual heat anomalies at the Mourachan conservation property (MCP) from 1913 to 2021 from the average annual heat anomaly for a benchmark period from 1971 to 2000 (−134.89). The trend line represents an increase in heatwave intensity over time using a linear regression. The grey confidence intervals on the trend line represent a 95 % confidence interval. (b) Annual number of days at the MCP exceeding the MMM of 32.1 °C. The black horizontal line represents the average annual number of days for a benchmark period from 1971 to 2000 (7.39). Years without a column had no days above the MMM. The trend line represents an increase in the number of days over time using a linear regression. The grey confidence intervals on the trend line represent a 95 % confidence interval.

anomalies. More work is needed to study dingo hunting success during heatwaves.

Our results concur with a rapidly growing body of research demonstrating that increasing temperatures under climate change are likely to alter the nature of predator–prey interactions (Brivio et al., 2024; Gauzens et al., 2024; Rafiq et al., 2023; Romero et al., 2018). Both prey and predators are being found to change in ways that affect the nature of their interactions; some prey species shift their activity patterns to nocturnality despite higher predation risks (Brivio et al., 2024), while some predators also shift to more nocturnal patterns despite higher activity overlaps with more dominant predator species (Rafiq et al., 2023). However, here we also show that predation impacts may be felt across the population, rather than just by those in poorer body condition. Our results show that dingoes hunted kangaroos of all body conditions during high heat anomalies. This shift in prey selectivity could be due to most kangaroos being weakened by heat stress, making them easier prey, including those with higher body conditions that dingoes may generally avoid. Despite being weakened by heat stress, stronger kangaroos would likely stand more of a chance to survive periods of extreme temperatures than those in poorer conditions (Juillard & Ramp, 2022). It is likely that the loss of individuals of greater fitness may have long-term impacts on population growth and genetic diversity.

Additionally, eastern grey kangaroos are a mesic species, with a portion of their range extending into semiarid and arid drylands, as is the case with our study site As a result, individuals in drier regions encounter conditions to which they lack complete adaptation (Dawson et al., 2007; Dawson et al., 2007). Compared to the other large macropod species of the MCP, the red kangaroo, a more arid adapted species (Moss & Croft, 1999), eastern grey kangaroos were the only species observed during the hunting attempts. We can speculate that the adaptation of red kangaroos to hotter and drier conditions may allow them to avoid waterpoints during extreme

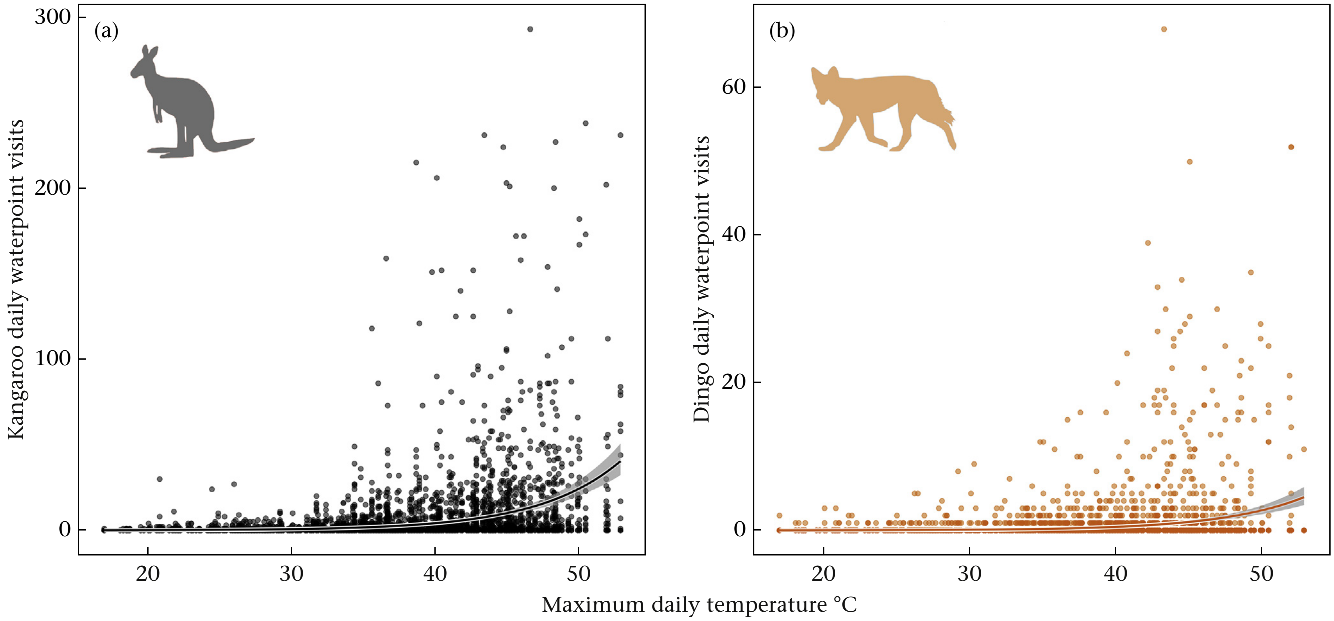

Figure 5. Total daily number of (a) eastern grey kangaroo and (b) dingo visits at waterpoints on the Mourachan conservation property (MCP) by daily maximum temperature (°C). Each point represents a day. The lines represent the relationship between maximum temperature and number of events obtained from a logged negative binomial regression.

temperatures when predators are present (Dawson et al., 2007). Indeed, when temperatures exceed the TNZ of individuals, metabolic rates increase to maintain an optimal body temperature, increasing the rate of metabolic water loss (Norris & Kunz, 2012). If not replaced in time (e.g. by drinking), extensive loss of metabolic water exacerbates physiological impairments already triggered by general heat stress because of dehydration and overheating (Acevedo-Whitehouse & Duffus, 2009; Costa et al., 2013; Norris &

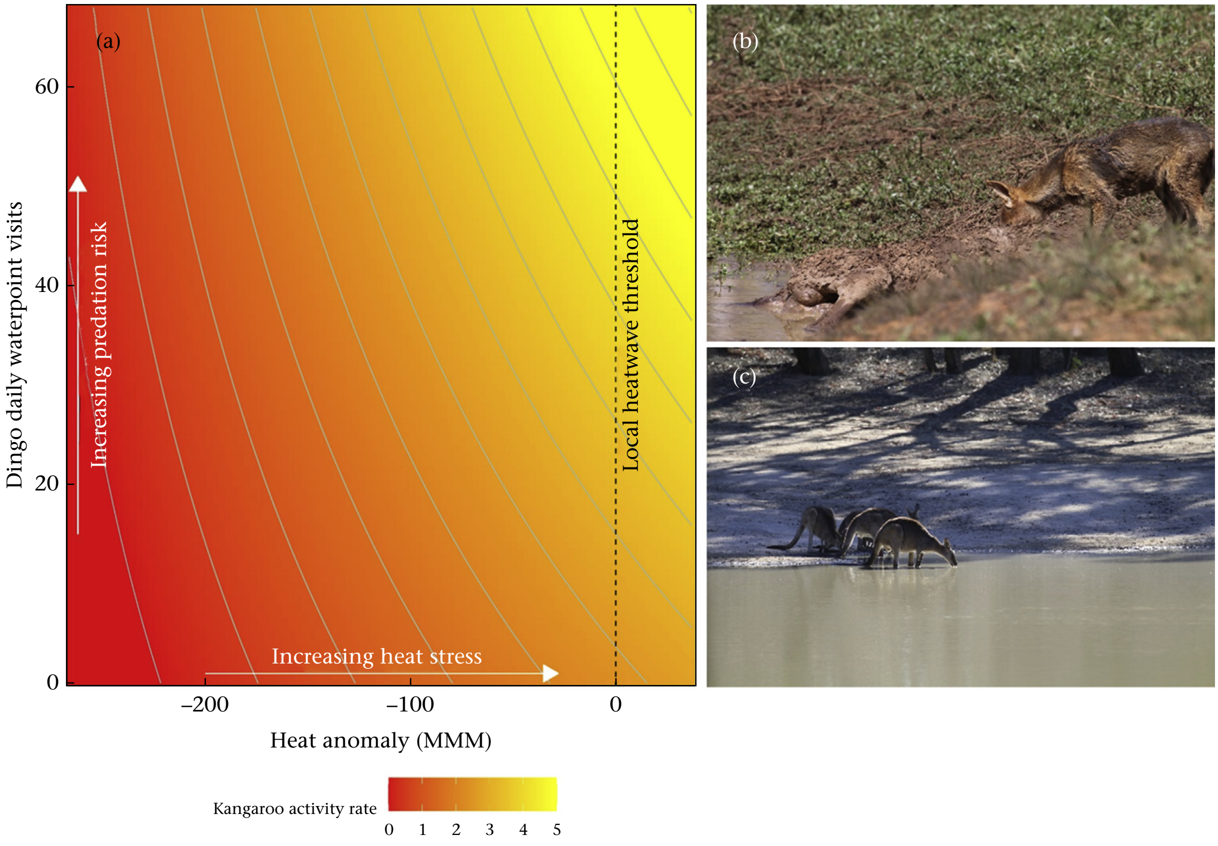

Figure 6. (a) Eastern grey kangaroo activity rate at waterpoints as a function of dingo activity and heat anomalies. The vertical line represents the local heatwave threshold for the Mourachan conservation property (MCP) based on the MMM of 32.1 °C; *X* axis values greater than the threshold represent heat anomalies, while values lower represent cooler periods. (b) A juvenile dingo feeding on an eastern grey kangaroo carcass at a waterpoint. Photo: L. M. Ashby. (c) Eastern grey kangaroos drinking at a waterpoint. Photo: T. J. McEvoy.

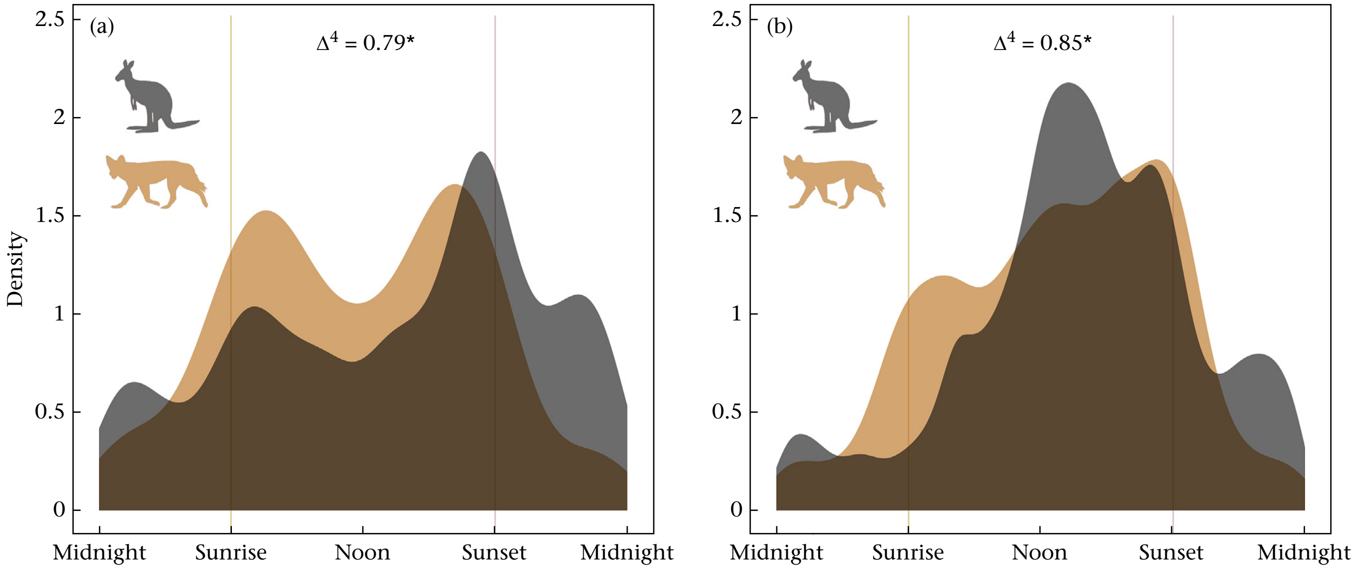

Figure 7. Overlap in the temporal activity density of kangaroos and dingoes for (a) nonheat anomaly and (b) heat anomaly periods. Asterisks indicate significance inferred by the nonoverlapping of bootstrapped 95 % confidence intervals.

Kunz, 2012). Such impairments are likely to be driving forces of behavioural change, particularly during heatwaves and in less arid-adapted species like eastern grey kangaroos because of the increased need for thermoregulation (Acevedo-Whitehouse & Duffus, 2009). Our findings indicate that under these conditions, prey may face impossible choices between accessing water and avoiding predation (Wallach & O'Neill, 2009; Wooster et al., 2022). This evidence supports the concept of state-dependent risk-taking, where the physical state of the prey, such as its hydration levels, influences its behaviour (Clark, 1994). Heat anomalies serve as a key stressor affecting physical conditions, pushing prey species, such as eastern grey kangaroos, to make potentially dangerous decisions and prioritizing physiological needs over predator avoidance. This creates a link between how predators and prey interact, implying that water-dependent prey species, which may already be in decline, may face major population issues (Fuller et al., 2021).

Herbivores in semiarid and arid environments often aggregate around water points, making such locations reliable sources of prey for predators (Valeix et al., 2010). Water availability in semiarid drylands is naturally low (Stokes et al., 2006), and it is likely to fall even further in a warming future as heatwaves and droughts deepen (Kiem et al., 2016; Kirono et al., 2020). As a result,

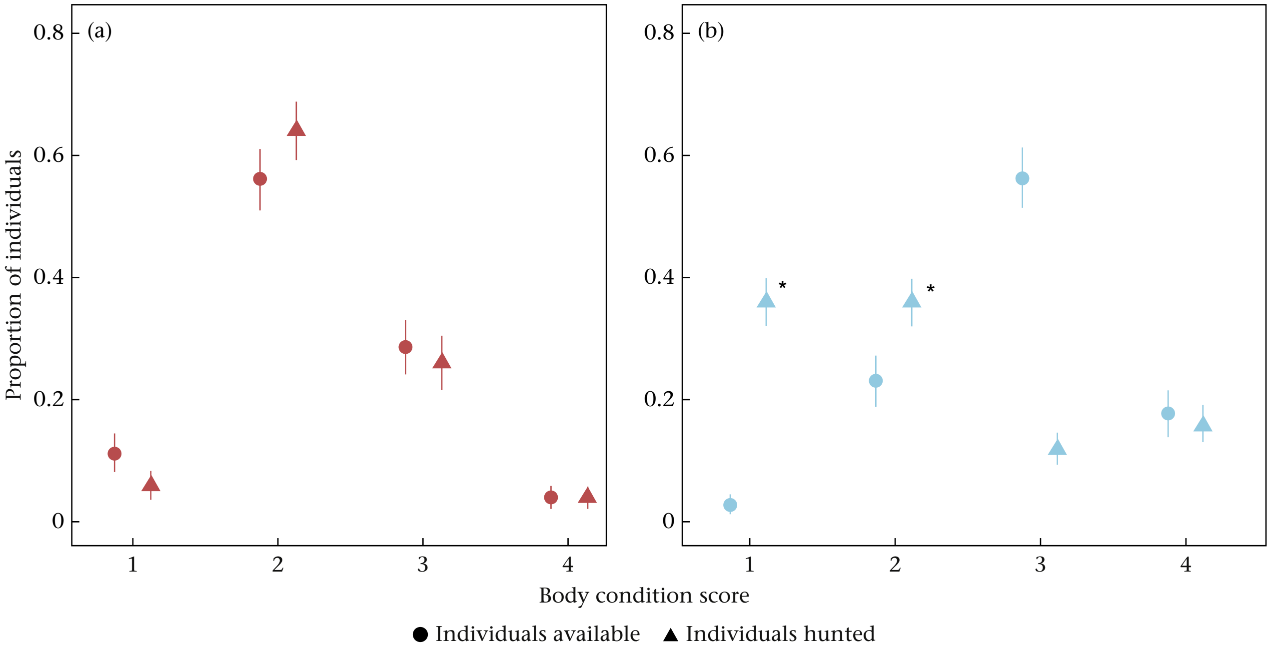

Figure 8. The proportion of individuals from each body condition score available in the population and observed being hunted by dingoes during (a) heat anomaly and (b) nonheat anomaly periods, as calculated by the Manly selection measure. Asterisks indicate that individuals were hunted significantly more or less than would be expected by their prevalence in the population.

waterpoint selection will be constrained, causing prey species to congregate in greater numbers and access areas with higher predator activity rates (Sutherland et al., 2018; Western, 1975). Valeix, Fritz, et al. (2009) explored, for example, how the risk of encountering lions influences African herbivore behaviour at water points. They discovered that when buffalo, *Syncerus caffer*, did not avoid problematic waterpoints (high predator density), it was during a severe drought, indicating that their need for water outweighed their instinct to avoid predators (Valeix, Fritz, et al., 2009). Additionally, Destefano et al. (2000) provided evidence that coyote, *Canis latrans*, activity was seven times higher at sites with water than at sites without water in southern Arizona, U.S.A. Here, dingoes significantly increased their activity at waterpoints when temperatures increased and kangaroos were absent; however, when kangaroos were present, the increase in dingo activity was stronger. This could suggest that the increase in dingo activity rate we observed at waterpoints with increasing temperatures could in part be due to the dingoes exploiting the increased physiological need for water of the kangaroos and not only for their own physiological requirements. We also show that dingo's preference for hunting weaker kangaroos was abandoned during these climatic events, that heatwaves at the MCP are intensifying, and that the number of days above the MMM per year is increasing. These findings imply that, as these weather extremes continue to intensify across Australia (Kirono et al., 2020), so might kangaroo–dingo interactions; however, more work is needed to fully confirm this trend across the kangaroos range. We can also speculate that increased temporal overlap between kangaroos and dingoes further results in a coupling effect of predator–prey interactions and that dingoes will hunt any individual during these times.

Our findings indicate that the intensification of heatwaves under climate change may be a key player in the coupling of predator–prey interactions in semiarid drylands by causing thermoregulation needs of prey to take over their predator avoidance instincts. Water availability is a major driving factor in dryland ecology (Stokes et al., 2006); however, water availability is being greatly influenced by both climate change and human activity (McCluney et al., 2012). Understanding how that influence might play out in dryland ecosystems is particularly important due to the vast areas of land they cover and the biodiversity they support globally (Rija et al., 2013). As temperatures continue to rise and water becomes increasingly scarce, our work suggests that water points may become increasingly contested spaces. This issue could be a more concerning matter for mesic species like eastern grey kangaroos with ranges extending into drier regions (Coghlan et al., 2015). Individuals living in the more arid parts of their range could have the potential to be more vulnerable to intensifying events like heatwaves followed by increased interactions with predators, unless they can adapt to such conditions. Further, this phenomenon is likely to affect more populations in the future as processes such as aridification expand drylands in Australia (Larkin et al., 2020). Our results highlight the urgency of continuing to explore how a warmer future might alter key biotic interactions and their roles in the functioning of ecosystems.

Author Contributions

Daniel Ramp: Writing – review & editing, Visualization, Investigation, Formal analysis, Conceptualization. **Eamonn I.F. Wooster:** Writing – review & editing, Visualization, Investigation, Formal analysis, Conceptualization. **Gavin T. Bonsen:** Investigation, Formal analysis. **Kyle J.A. Zawada:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Loic Q. Juillard:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization.

Data Availability

Data used in this research are available at https://doi.org/10.6084/m9.figshare.25815319.v1.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123242.

References

Acevedo-Whitehouse, K., & Duffus, A. L. (2009). Effects of environmental change on wildlife health. *Philosophical Transactions of the Royal Society of London, 364*(1534), 3429–3438. https://doi.org/10.1098/rstb.2009.0128

Aho, K., Derryberry, D., & Peterson, T. (2014). Model selection for ecologists: The worldviews of AIC and BIC. *Ecology, 95*(3), 631–636. https://doi.org/10.1890/13-1452.1

Armbruster, W. S. (2017). The specialization continuum in pollination systems: Diversity of concepts and implications for ecology, evolution and conservation. *Functional Ecology, 31*(1), 88–100. https://doi.org/10.1111/1365-2435.12783

Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology, 18*(6), 1866–1879. https://doi.org/10.1111/j.1365-2486.2012.02661.x

Austin, C. M., & Ramp, D. (2019). Behavioural plasticity by eastern grey kangaroos in response to human behaviour. *Animals, 9*(5), 244. https://doi.org/10.3390/ani9050244

Bascompte, J. (2009). Disentangling the web of life. *Science, 325*(5939), 416–419. https://doi.org/10.1126/science.1170749

Bergström, R., & Skarpe, C. (1999). The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *African Journal of Ecology, 37*(1), 12–26. https://doi.org/10.1046/j.1365-2028.1999.00165.x

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science, 341*(6145), 499–504. https://doi.org/10.1126/science.1237184

BOM. (2020). *Climate of the 2019-20 financial year.* Australian Bureau of Meteorology. Retrieved 22.02 from http://www.bom.gov.au/climate/updates/articles/a037.shtml.

BOM. (2023). Climate data online. http://www.bom.gov.au/climate/data/.

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *R Journal, 9*(2), 56.

Brivio, F., Apollonio, M., Anderwald, P., Filli, F., Bassano, B., Bertolucci, C., & Grignolio, S. (2024). Seeking temporal refugia to heat stress: Increasing nocturnal activity despite predation risk. *Proceedings of the Royal Society B: Biological Sciences, 291*(2015), Article 20231587. https://doi.org/10.1098/rspb.2023.1587

Brown, M. J. (2022). Complex networks of parasites and pollinators: Moving towards a healthy balance. *Philosophical Transactions of the Royal Society B: Biological Sciences, 377*(1853), Article 20210161. https://doi.org/10.1098/rstb.2021.0161

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., & Warsi, O. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences, 280*(1750), Article 20121890. https://doi.org/10.1098/rspb.2012.1890

Cai, W., Santoso, A., Collins, M., Dewitte, B., Karamperidou, C., Kug, J.-S., Lengaigne, M., McPhaden, M. J., Stuecker, M. F., Taschetto, A. S., Timmermann, A., Wu, L., Yeh, S.-W., Wang, G., Ng, B., Jia, F., Yang, Y., Ying, J., Zheng, X.-T., … Zhong, W. (2021). Changing El Niño–southern Oscillation in a warming climate (2021) *Nature Reviews Earth & Environment, 2*, 628–644. https://doi.org/10.1038/s43017-021-00199-z.

Cai, W., Sullivan, A., & Cowan, T. (2009). Climate change contributes to more frequent consecutive positive Indian Ocean Dipole events. *Geophysical Research Letters, 36*, Article L23704. https://doi.org/10.1029/2009GL040163

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology, 5*(2), 159–170. https://doi.org/10.1093/beheco/5.2.159

Clements, H. S., Tambling, C. J., & Kerley, G. I. (2016). Prey morphology and predator sociality drive predator prey preferences. *Journal of Mammalogy, 97*(3), 919–927. https://doi.org/10.1093/jmammal/gyw017

Coghlan, B. A., Goldizen, A. W., Thomson, V. A., & Seddon, J. M. (2015). Phylogeography of eastern grey kangaroos, *Macropus giganteus*, suggests a mesic refugium in eastern Australia. *PLoS One, 10*(5), Article e0128160. https://doi.org/10.1371/journal.pone.0128160

Costa, D. P., Houser, D. S., & Crocker, D. E. (2013). Fundamentals of water relations and thermoregulation in animals. In *In eLS*. John Wiley & Sons. https://doi.org/10.1002/9780470015902.a0003216.pub2.

Davidson, Z., Valeix, M., Loveridge, A. J., Hunt, J. E., Johnson, P. J., Madzikanda, H., & Macdonald, D. W. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: Scale matters. *Journal of Mammalogy, 93*(3), 677–685. https://doi.org/10.1644/10-MAMM-A-424.1

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS One, 8*(2), Article e55182. https://doi.org/10.1371/journal.pone.0055182

Dawson, T. J., Blaney, C. E., McCarron, H. C., & Maloney, S. K. (2007). 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. *Journal of Comparative Physiology B, 177*, 797–807. https://doi.org/10.1007/s00360-007-0176-1

Dehling, D. M., Barreto, E., & Graham, C. H. (2022). The contribution of mutualistic interactions to functional and phylogenetic diversity. *Trends in Ecology & Evolution, 37*(9), 768–776. https://doi.org/10.1016/j.tree.2022.05.006

Delworth, T. L., Zeng, F., Vecchi, G. A., Yang, X., Zhang, L., & Zhang, R. (2016). The North Atlantic oscillation as a driver of rapid climate change in the Northern hemisphere. *Nature Geoscience, 9*(7), 509–512. https://doi.org/10.1038/ngeo2738

Destefano, S., Schmidt, S. L., & DeVos, J. C. (2000). Observations of predator activity at wildlife water developments in southern Arizona. *Rangeland Ecology & Management/Journal of Range Management Archives, 53*(3), 255–258. https://doi.org/10.2307/4003428

Dosio, A., Mentaschi, L., Fischer, E. M., & Wyser, K. (2018). Extreme heat waves under 1.5 C and 2 C global warming. *Environmental Research Letters, 13*(5), Article 054006. https://doi.org/10.1088/1748-9326/aab827

Fuller, A., Mitchell, D., Maloney, S. K., Hetem, R. S., Fonsêca, V. F., Meyer, L. C., Van de Ven, T. M., & Snelling, E. P. (2021). How dryland mammals will respond to climate change: The effects of body size, heat load and a lack of food and water. *Journal of Experimental Biology, 224*(Suppl_1), Article jeb238113. https://doi.org/10.1242/jeb.238113

Gauzens, B., Rosenbaum, B., Kalinkat, G., Boy, T., Jochum, M., Kortsch, S., O'Gorman, E. J., & Brose, U. (2024). Flexible foraging behaviour increases predator vulnerability to climate change. *Nature Climate Change, 14*(4), 387–392. https://doi.org/10.1038/s41558-024-01946-y

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution, 34*(4), 355–368. https://doi.org/10.1016/j.tree.2019.01.004

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: Evidence of natural selection by predation. *PLoS One, 5*(3), Article e9774. https://doi.org/10.1371/journal.pone.0009774

Guiden, P. W., Bartel, S. L., Byer, N. W., Shipley, A. A., & Orrock, J. L. (2019). Predator–prey interactions in the anthropocene: Reconciling multiple aspects of novelty. *Trends in Ecology & Evolution, 34*(7), 616–627. https://doi.org/10.1016/j.tree.2019.02.017

Hamouda, M. E., Pasquero, C., & Tziperman, E. (2021). Decoupling of the arctic oscillation and North Atlantic oscillation in a warmer climate. *Nature Climate Change, 11*(2), 137–142. https://doi.org/10.1038/s41558-020-00966-8

Harris, G., Sanderson, J. G., Erz, J., Lehnen, S. E., & Butler, M. J. (2015). Weather and prey predict mammals' visitation to water. *PLoS One, 10*(11), Article e0141355. https://doi.org/10.1371/journal.pone.0141355

Hasselerharm, C. D., Yanco, E., McManus, J. S., Smuts, B. H., & Ramp, D. (2021). Wildlife-friendly farming recouples grazing regimes to stimulate recovery in semi-arid rangelands. *Science of the Total Environment, 788*, Article 147602. https://doi.org/10.1016/j.scitotenv.2021.147602

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature, 470*(7335), 479–485. https://doi.org/10.1038/nature09670

ILRI, IUCN, FAO, WWF, UNEP, & ILC. (2021). *Rangelands Atlas*. ILRI.

IPCC. (2022). Climate Change 2022: Impacts, Adaptation, and Vulnerability *(Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Issue)*. C. U. Press.

Jarman, P. J., & Wright, S. M. (1993). Macropod studies at Wallaby Creek. IX Exposure and responses of eastern grey kangaroos to dingoes. *Wildlife Research, 20*(6), 833–843. https://doi.org/10.1071/WR9930833

Juillard, L. Q., & Ramp, D. (2022). The impacts of drought on the health and demography of eastern grey kangaroos. *Animals, 12*(3), 256. https://doi.org/10.3390/ani12030256

Kiem, A. S., Johnson, F., Westra, S., van Dijk, A., Evans, J. P., O'Donnell, A., Rouillard, A., Barr, C., Tyler, J., & Thyer, M. (2016). Natural hazards in Australia: Droughts. *Climatic Change, 139*(1), 37–54.

Kirono, D. G., Round, V., Heady, C., Chiew, F. H., & Osbrough, S. (2020). Drought projections for Australia: Updated results and analysis of model simulations. *Weather and Climate Extremes, 30*, Article 100280. https://doi.org/10.1016/j.wace.2020.100280

Larkin, Z. T., Ralph, T. J., Tooth, S., Fryirs, K. A., & Carthey, A. (2020). Identifying threshold responses of Australian dryland rivers to future hydroclimatic change. *Scientific Reports, 10*(1), 6653. https://doi.org/10.1038/s41598-020-63622-3

Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: The dingo *Canis lupus dingo* as a case study. *Biological Reviews (Cambridge), 87*(2), 390–413. https://doi.org/10.1111/j.1469-185X.2011.00203.x

Lundgren, E. J., Ramp, D., Middleton, O. S., Wooster, E. I., Kusch, E., Balisi, M., Ripple, W. J., Hasselerharm, C. D., Sanchez, J. N., & Mills, M. (2022). A novel trophic cascade between cougars and feral donkeys shapes desert wetlands. *Journal of Animal Ecology, 91*(12), 2348–2357.

Ma, C. S., Wang, L., Zhang, W., & Rudolf, V. H. (2018). Resolving biological impacts of multiple heat waves: Interaction of hot and recovery days. *Oikos, 127*(4), 622–633. https://doi.org/10.1111/oik.04699

Makin, D. F., Chamaillé-Jammes, S., & Shrader, A. M. (2017). Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal Behaviour, 127*, 225–231. https://doi.org/10.1016/j.anbehav.2017.03.024

McCluney, K. E., Belnap, J., Collins, S. L., González, A. L., Hagen, E. M., Nathaniel Holland, J., Kotler, B. P., Maestre, F. T., Smith, S. D., & Wolf, B. O. (2012). Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews (Cambridge), 87*(3), 563–582. https://doi.org/10.1111/j.1469-185X.2011.00209.x

McCluney, K. E., & Sabo, J. L. (2009). Water availability directly determines per capita consumption at two trophic levels. *Ecology, 90*(6), 1463–1469. https://doi.org/10.1890/08-1626.1

Monzón, J., Moyer-Horner, L., & Palamar, M. B. (2011). Climate change and species range dynamics in protected areas. *BioScience, 61*(10), 752–761. https://doi.org/10.1525/bio.2011.61.10.5

Moss, G., & Croft, D. (1999). Body condition of the red kangaroo (*Macropus rufus*) in arid Australia: The effect of environmental condition, sex and reproduction. *Australian Journal of Ecology, 24*(2), 97–109. https://doi.org/10.1046/j.1442-9993.1999.241949.x

Mosser, A., Fryxell, J. M., Eberly, L., & Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. *Ecology Letters, 12*(10), 1050–1060. https://doi.org/10.1111/j.1461-0248.2009.01359.x

Norris, A. L., & Kunz, T. H. (2012). Effects of solar radiation on animal thermoregulation. *Solar Radiation, 1*, 195–220. https://doi.org/10.5772/34771

Peers, M. J., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., & Krebs, C. J. (2020). Climate change increases predation risk for a keystone species of the boreal forest. *Nature Climate Change, 10*(12), 1149–1153. https://doi.org/10.1038/s41558-020-00908-4

Pollock, T. I., Hunter, D. O., Hocking, D. P., & Evans, A. R. (2022). Eye in the sky: Observing wild dingo hunting behaviour using drones. *Wildlife Research, 50*(3), 212–223. https://doi.org/10.1071/WR22033

Preston, D., & Johnson, P. (2010). Ecological consequences of parasitism. *Nature Education Knowledge, 3*(10).

Purcell, B. V. (2010). A novel observation of dingoes (*Canis lupus dingo*) attacking a swimming eastern grey kangaroo (*Macropus giganteus*). *Australian Mammalogy, 32*(2), 201–204. https://doi.org/10.1071/AM10001

R Core Team. (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-Project.org/.

Rafiq, K., Jordan, N. R., Golabek, K., McNutt, J. W., Wilson, A., & Abrahms, B. (2023). Increasing ambient temperatures trigger shifts in activity patterns and temporal partitioning in a large carnivore guild. *Proceedings of the Royal Society B: Biological Sciences, 290*(2010), Article 20231938. https://doi.org/10.1098/rspb.2023.1938

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology, 84*(8), 2092–2107. https://doi.org/10.1890/01-0625

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics, 14*(3), 322–337. https://doi.org/10.1198/jabes.2009.08038

Rija, A., Kideghesho, J., Mwamende, K. A., & Selemani, I. (2013). Emerging issues and challenges in conservation of biodiversity in the rangelands of Tanzania. *Nature Conservation, 6*, 1–29. https://doi.org/10.3897/natureconservation.6.5407

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., & Nelson, M. P. (2014). Status and ecological effects of the world's largest carnivores. *Science, 343*(6167), Article 1241484. https://doi.org/10.1126/science.1241484

Robinson, P. J. (2001). On the definition of a heat wave. *Journal of Applied Meteorology and Climatology, 40*(4), 762–775. https://doi.org/10.1175/1520-0450(2001)040<0762:OTDOAH>2.0.CO;2

Romero, G. Q., Gonçalves-Souza, T., Kratina, P., Marino, N. A., Petry, W. K., Sobral-Souza, T., & Roslin, T. (2018). Global predation pressure redistribution under future climate change. *Nature Climate Change, 8*(12), 1087–1091.

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics, 40*(1), 245–269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430

Sentis, A., Hemptinne, J.-L., & Brodeur, J. (2012). Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. *Oecologia, 169*, 1117–1125. https://doi.org/10.1007/s00442-012-2255-6

Smit, I. P., Grant, C. C., & Devereux, B. J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation, 136*(1), 85–99. https://doi.org/10.1016/j.biocon.2006.11.009

Soravia, C., Ashton, B. J., Thornton, A., & Ridley, A. R. (2021). The impacts of heat stress on animal cognition: Implications for adaptation to a changing climate. *Wiley Interdisciplinary Reviews: Climate Change, 12*(4), Article e713. https://doi.org/10.1002/wcc.713

Spong, G. (2002). Space use in lions, *Panthera leo*, in the selous game reserve: Social and ecological factors. *Behavioral Ecology and Sociobiology, 52*, 303–307. https://doi.org/10.1007/s00265-002-0515-x

Stokes, C., McAllister, R. R., & Ash, A. J. (2006). Fragmentation of Australian rangelands: Processes, benefits and risks of changing patterns of land use. *Rangeland Journal, 28*(2), 83–96. https://doi.org/10.1071/RJ05026

Sutherland, K., Ndlovu, M., & Pérez-Rodríguez, A. (2018). Use of artificial waterholes by animals in the southern region of the Kruger National Park, South Africa. *African Journal of Wildlife Research, 48*(2), 1–14. https://doi.org/10.3957/056.048.023003

Thomson, P. (1992). The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. *Wildlife Research, 19*(5), 531–541. https://doi.org/10.1071/WR9920531

Thrash, I., Theron, G., & Bothma, J.d. P. (1995). Dry season herbivore densities around drinking troughs in the Kruger National Park. *Journal of Arid Environments, 29*(2), 213–219. https://doi.org/10.1016/S0140-1963(05)80091-6

Trancoso, R., Syktus, J., Toombs, N., Ahrens, D., Wong, K. K. H., & Dalla Pozza, R. (2020). Heatwaves intensification in Australia: A consistent trajectory across past, present and future. *Science of the Total Environment, 742*, Article 140521. https://doi.org/10.1016/j.scitotenv.2020.140521

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science, 348*(6234), 571–573. https://doi.org/10.1126/science.aaa4984

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2009). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology, 63*(10), 1483–1494. https://doi.org/10.1007/s00265-009-0760-3

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F., & Madzikanda, H. (2008). The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology, 46*(3), 402–410. https://doi.org/10.1111/j.1365-2028.2007.00874.x

Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology, 90*(1), 23–30. https://doi.org/10.1890/08-0606.1

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: Waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology, 25*(3), 337–351. https://doi.org/10.1007/s10980-009-9425-x

Wallach, A. D., Johnson, C. N., Ritchie, E. G., & O'Neill, A. J. (2010). Predator control promotes invasive dominated ecological states. *Ecology Letters, 13*(8), 1008–1018. https://doi.org/10.1111/j.1461-0248.2010.01492.x

Wallach, A. D., & O'Neill, A. J. (2009). Artificial water points: Hotspots of extinction or biodiversity? *Biological Conservation, 7*(142), 1253–1254. https://doi.org/10.1016/j.biocon.2009.01.011

Wallach, A. D., Ritchie, E. G., Read, J., & O'Neill, A. J. (2009). More than mere numbers: The impact of lethal control on the social stability of a top-order predator. *PLoS One, 4*(9), Article e6861.

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology, 13*(3–4), 265–286. https://doi.org/10.1111/j.1365-2028.1975.tb00139.x

Wilmers, C. C., Post, E., & Hastings, A. (2007). The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology, 76*(6), 1037–1044. https://doi.org/10.1111/j.1365-2656.2007.01289.x

Wooster, E. I., Gaynor, K. M., Carthey, A. J., Wallach, A. D., Stanton, L. A., Ramp, D., & Lundgren, E. J. (2023). Animal cognition and culture mediate predator–prey interactions. *Trends in Ecology & Evolution, 39*(1), 52–64. https://doi.org/10.1016/j.tree.2023.09.012

Wooster, E. I., Middleton, O. S., Wallach, A. D., Ramp, D., Sanisidro, O., Harris, V. K., Rowan, J., Schowanek, S. D., Gordon, C. E., & Svenning, J. C. (2024). Australia's recently established predators restore complexity to food webs simplified by extinction. *Current Biology, 34*(22), 5164–5172. https://doi.org/10.1016/j.cub.2024.09.049. e5162.

Wooster, E. I., Ramp, D., Lundgren, E. J., O'Neill, A. J., & Wallach, A. D. (2021). Red foxes avoid apex predation without increasing fear. *Behavioral Ecology, 32*(5), 895–902. https://doi.org/10.1093/beheco/arab053

Wooster, E. I. F., Ramp, D., Lundgren, E. J., O'Neill, A. J., Yanco, E., Bonsen, G. T., & Wallach, A. D. (2022). Predator protection dampens the landscape of fear. *Oikos, 2022*(11), Article e09059. https://doi.org/10.1111/oik.09059

Wright, S. (1993). Observations of the behaviour of male eastern grey kangaroos when attacked by dingoes. *Wildlife Research, 20*(6), 845–949. https://doi.org/10.1071/WR9930845