The influence of extreme weather on the ecology and welfare of eastern grey kangaroos in semi-arid rangelands

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Under the supervision of Assoc. Prof. Daniel Ramp, Dr. Andrea M. Harvey, Dr. Eamonn I.F. Wooster

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CERTIFICATE OF ORIGINAL AUTHORSHIP

I, Loic Quentin Juillard, declare that this thesis is submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the TD School, at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

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LIST OF PAPERS AND STATEMENTS OF AUTHOR CONTRIBUTION

This thesis is a compilation of chapters including 4 published/publishable manuscripts. Each manuscript is formatted for its destination journal, except for referencing styles which were standardised throughout.

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ETHICS APPROVALS

All field work for this project was approved and conducted under a University of Technology Sydney Animal Ethics permit titled: “Predator-prey interactions in an anthropogenically warmed future”, permit number: ACEC ETH21-6640.

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THESIS ABSTRACT

Eastern grey kangaroos (*Macropus giganteus*) are one of the most iconic species in Australia. Despite being a mesic species, part of their range extends in drylands. Furthermore, like most wild animals today, they must also navigate the impacts of an intensifying climate. Due to drylands covering the majority of Australia's land mass, the main terrestrial impacts of climate change in Australia include more frequent and intense heatwaves and droughts. Impacts of such extreme weather events may be particularly severe for eastern grey kangaroos living in drylands. With Australian drylands expected to expand via aridification, we can expect more eastern grey kangaroos to be facing similar extreme conditions in the future. Therefore, knowing how eastern grey kangaroos currently living in drylands are being impacted by extreme weather is of urgent concern.

I aimed to assess some of the challenges faced by eastern grey kangaroos in drylands during heatwaves and droughts by focusing on a population in south-western Queensland. Chapter 1 introduces the main topics and objectives of this thesis, while chapter 2 reviews the literature relevant to the thesis. In chapter 3 I assess the impacts of drought on the health and demography of eastern grey kangaroos finding that the drought caused a significant decline in body condition. The demography of the population was impacted, with fewer juveniles and fewer males observed. Using drone transects, I show in chapter 4 that eastern grey kangaroos were more likely to access waterpoints at high temperatures, while red kangaroos were more likely to access shade, highlighting a difference in thermoregulation strategy between the two species. In chapter 5, I show that during periods of extreme temperatures kangaroos were unable to avoid aggregating with dingoes at waterpoints, leading to an intensification of predator-prey interactions as both species increase their use of water. I then use the findings from chapters 3-5 to build a list of potential thermoregulatory and predation-related welfare indicators/behaviours in eastern grey kangaroos during heat anomalies. Thermoregulation indicators and behaviours (e.g., kangaroos standing in water, drinking) were significantly more prevalent during heat anomalies. Predation-related indicators were significantly more prevalent during heat anomalies, and at artificial waterpoints compared to dammed natural watercourses. My work suggests that protecting natural watercourses in drylands, including natural dammed watercourses, and improving access to water may assist eastern grey kangaroos by improving their welfare and survival as they attempt to navigate the impacts of an increasingly warming world.

CHAPTER 1: INTRODUCTION

1.1. GENERAL INTRODUCTION AND OBJECTIVES

Today, most living organisms on the planet are being impacted by climate change, with IPCC reports now highlighting increasingly rapid rates of extinctions in various ecosystems (IPCC, 2023). While the Earth's climate has always experienced variations, it has now entered a period of changes so rapid living organisms stand little chance of evolving any resistance to them (Acevedo-Whitehouse & Duffus, 2009; Fuller et al., 2021). Indeed, global surface temperatures have risen faster over the past 50-year period since the 1970s than any other 50-year period in the last 2000 years (IPCC, 2023). Today's changes in the Earth's climate are mainly due to anthropogenic activities over the past century (IOM, 2023; IPCC, 2021, 2022, 2023).

As a consequence of climate change, extreme events such as heatwaves and droughts in many parts of the world are now lasting longer and are increasing in frequency and intensity (Dosio et al., 2018; Kirono et al., 2020; Trancoso et al., 2020; Vicente-Serrano et al., 2019). In Australia, heatwaves as well as droughts are expected to become more frequent and intense, particularly for the eastern part of the country (Kirono et al., 2020; Trancoso et al., 2020). Droughts in Australia are a pseudo-cyclic phenomenon and have occurred for millennia (Kiem et al., 2016). However, similar to climate change in other parts of the world, the rate at which these events are intensifying is now too rapid for species to evolve much resistance to them, be it behaviourally or physiologically (Acevedo-Whitehouse & Duffus, 2009). Similar trends are seen for heatwaves, with Trancoso et al. (2020) finding that multiple characteristics of heatwaves in Australia were intensifying including peak temperature, duration, and frequency. In the worst case scenarios, by combining extreme temperatures, high quantities of dry vegetation, and an overall lack of moisture and water in the environment, droughts and heatwaves can work together to create the perfect conditions for mega-fires (Sharples et al., 2021). Mega-fires such as the "Black Summer" fires of 2019-2020 are now reaching such intensities that even plant species normally relying on fires to germinate are being destroyed (Dickman, 2021). The most heavily felt impact of the

"Black Summer" fires being on wild animals, with an estimated 3 billion vertebrates and 240 trillion invertebrates killed (Dickman, 2021).

When it comes to heatwaves and droughts, reduced resource availability, lower body condition leading to impaired immune system as well as cognitive abilities, and increased predation rate on herbivores are only some of the impacts expected to befall wild animals (Acevedo-Whitehouse & Duffus, 2009; Becker et al., 2015). Not only are such impacts said to become more prevalent with changing climatic and environmental conditions, they directly impact the welfare of affected individuals (Harvey et al., 2020). Poor welfare can reduce the reproduction rate of individuals and their overall fitness (Harvey et al., 2020). This is likely to compromise the survival and viability of populations where the majority of individuals find themselves affected by a poorer welfare status. Consequently, such populations could become weaker, more susceptible to changes in the climate, and more prone to extinctions. Across the world, climate change has already been implicated in extinctions (Pounds et al., 1999), with many species also experiencing various levels of local extinctions (Román-Palacios & Wiens, 2020). Perhaps more alarming, it is predicted that by 2070, a third of all wildlife and plant species globally could be lost due to climate change (Román-Palacios & Wiens, 2020). Ecosystems where multiple species are either affected by poor welfare or become locally extinct, may eventually be brought to the brink of collapse when the natural equilibrium once maintained by healthy individuals and populations is lost (Thomas et al., 2004). Such predictions emphasise the significance of truly understanding how wild animals are impacted by changes in the climate for us to better protect nature.

Compared to all terrestrial ecosystems, semi-arid and arid rangelands cover the largest area of land and are found on most continents (Olson et al., 2001). In Australia, rangelands make up 81% of the country's land mass, with roughly 90% of that represented by semi-arid and arid rangelands (Australian Department of Agriculture Water and the Environment, 2021). These ecosystems are crucial to wildlife and biodiversity conservation due to the wide variety of species they harbour (Hasselerharm et al., 2021). Dryland systems, by nature, create challenging living conditions for wildlife due to lower water availability and the patchy distribution of resources like vegetation (Stokes et al., 2006). The drier and warmer conditions brought by climate change are likely to further reduce the availability of resources, and push species to the limit of their survival abilities. However, new environmental and climate extremes are not the only factors influencing life in drylands, Australian rangelands are mainly used by pastoralism, with approximately 6000 companies using 58% of the total surface covered by such ecosystems (Australian Department of Agriculture Water and the Environment, 2021). The clearing of land for animal agriculture is one of the main causes of aridification, which is further exacerbated by increasing droughts and heatwaves (Hasselerharm et al., 2021). Similar to other rangelands internationally, this is likely to aggravate the impacts felt by wild animals inhabiting these ecosystems.

In Australia, the wide variety of species found in rangelands includes the eastern grey kangaroo (*Macropus giganteus*), one of Australia's largest herbivore species. Despite eastern grey kangaroos being a mesic species, part of their range extends in semi-arid and arid rangelands (Dawson et al., 2007) (Figure 1). With processes such as aridification the range of eastern grey kangaroos is likely to become increasingly arid, exposing more individuals to extreme weather events. However, very few studies focus specifically on the impacts of extreme events like droughts and heatwaves on kangaroos, with some of the most easily found research published pre-2000 (Robertson, 1986). However, with the rapid rate of climate change, extreme events today are likely more extreme than they were in the late 1900s.

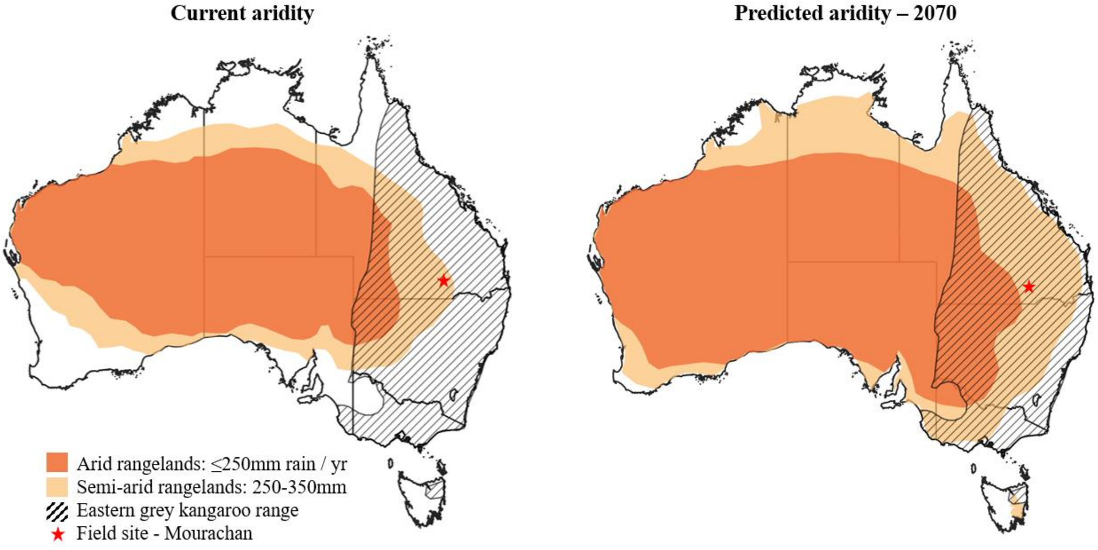

Figure 1. Map of the current extent of semi-arid and arid rangelands in Australia, showing the range of eastern grey kangaroos and location of the field site for this PhD (red star). The predicted extent of semi-arid and arid rangelands for the year 2070 is also shown (Larkin et al., 2020), showing the majority of the eastern grey kangaroo range impacted.

Kangaroos now face threats from both climate change and commercial killing programs aimed at managing their impacts on agricultural production, and for use in the meat industry (Ben-Ami et al., 2014). As the main wild herbivore species in Australia, kangaroos provide crucial ecosystem functions including nutrient cycling (Iles et al., 2010), vegetation dynamics (Pringle et al., 2023), as well as being an important resource to apex predators such as dingoes (Thomson, 1992). However, with climate change increasingly affecting species worldwide, the extent to which these changes are impacting kangaroos remains unclear. This PhD project therefore set to explore how eastern grey kangaroos in semi-arid rangelands are impacted by extreme weather events. To do so, factors including health and demography, how kangaroos use shade during high temperature events, and interactions with their predator, the dingo (*Canis dingo*), at waterpoints were measured on a semi-arid wildlife reserve in the rangelands of south-western Queensland. Data collection began in November 2019 during the driest year on record for the region, while the summer of 2019-2020 was the hottest season, with a mean seasonal temperature more than 2˚C hotter than a long-term average (BOM, 2020). Data collection, mainly using camera traps, was focused near waterpoints as I suspected that eastern grey kangaroos, being a mesic species (Dawson et al., 2007), may need to increase their activity rate at such resource points during hotter and drier times. This allowed me to also observe potential changes in thermoregulation methods used, for example from a more passive, slower method through hydration or shade use to a quicker more active method of thermoregulation such as immersion in water, while also observing interactions with predators. The findings are then used to build a list of potential indicators of welfare challenges related to thermoregulation and predation in eastern grey kangaroos.

1.2. THE MOURACHAN CONSERVATION PROPERTY

The field site used during this PhD is a property called Mourachan. Mourachan is a 480 km² conservation property owned by Australia Zoo located in the semi-arid rangelands of south-western Queensland on the Brigalow Belt (Figure 2). Extensive parts of Mourachan had previously been cleared by farmers for agricultural activities (Figure 3), but the property was then established by Australia Zoo in the early 2000s as a conservation property when woma pythons (*Aspidites ramsayi*) were found to be living on the land. Since then, the property has not only been expanded to its current size, it has rapidly been gaining biodiversity back, with plants and wild animals reclaiming their habitats (Australia Zoo, nd). As of today, Mourachan is home to at least 26 mammal species, 17 amphibians, 52 reptiles, and 102 birds, as well as many more invertebrates (Australia Zoo, nd). Some of the more notable species include woma pythons, mulga snakes (*Pseudechis australis*), yakka skink (*Egernia rugosa*), emus (*Dromaius novaehollandiae*), pink cockatoos (*Lophocroa leadbeateria*), and short-beaked echidnas (*Tachyglossus aculeatus*) (Figure 4). The macropods of the property are split into five species: eastern grey kangaroos, red kangaroos (*Osphranter rufus*), black wallabies (*Wallabia bicolor*), red-necked wallabies (*Macropus rufogriseus*), and black-striped wallabies (*Notamacropus dorsalis*), with the main predator present being the dingo (*Canis dingo*). As Mourachan is surrounded by sheep and cattle farms and is one of the only fully protected zones in the region, it acts as an oasis to most wild animals, and is one of the few areas in Australia where both kangaroos and dingoes are safe from human persecution, as long as they remain on the property.

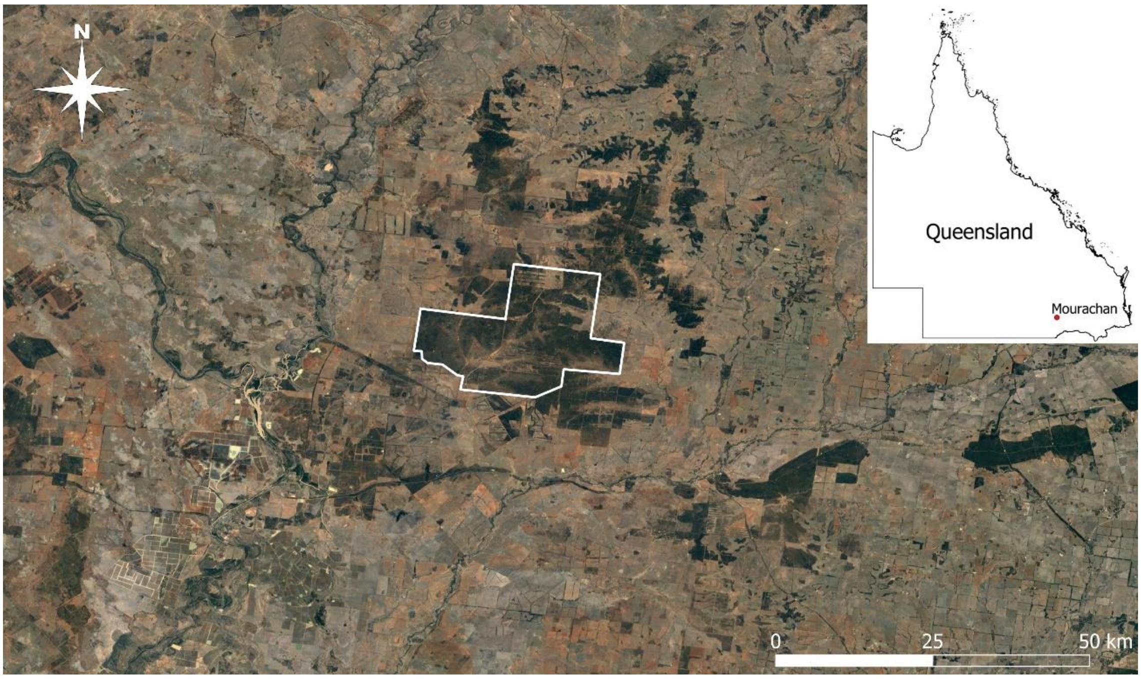

Figure 2. Satellite image showing the Mourachan property and the surrounding region. Note the clear contrast in vegetation with most surrounding properties. The location of Mourachan within Queensland is also shown.

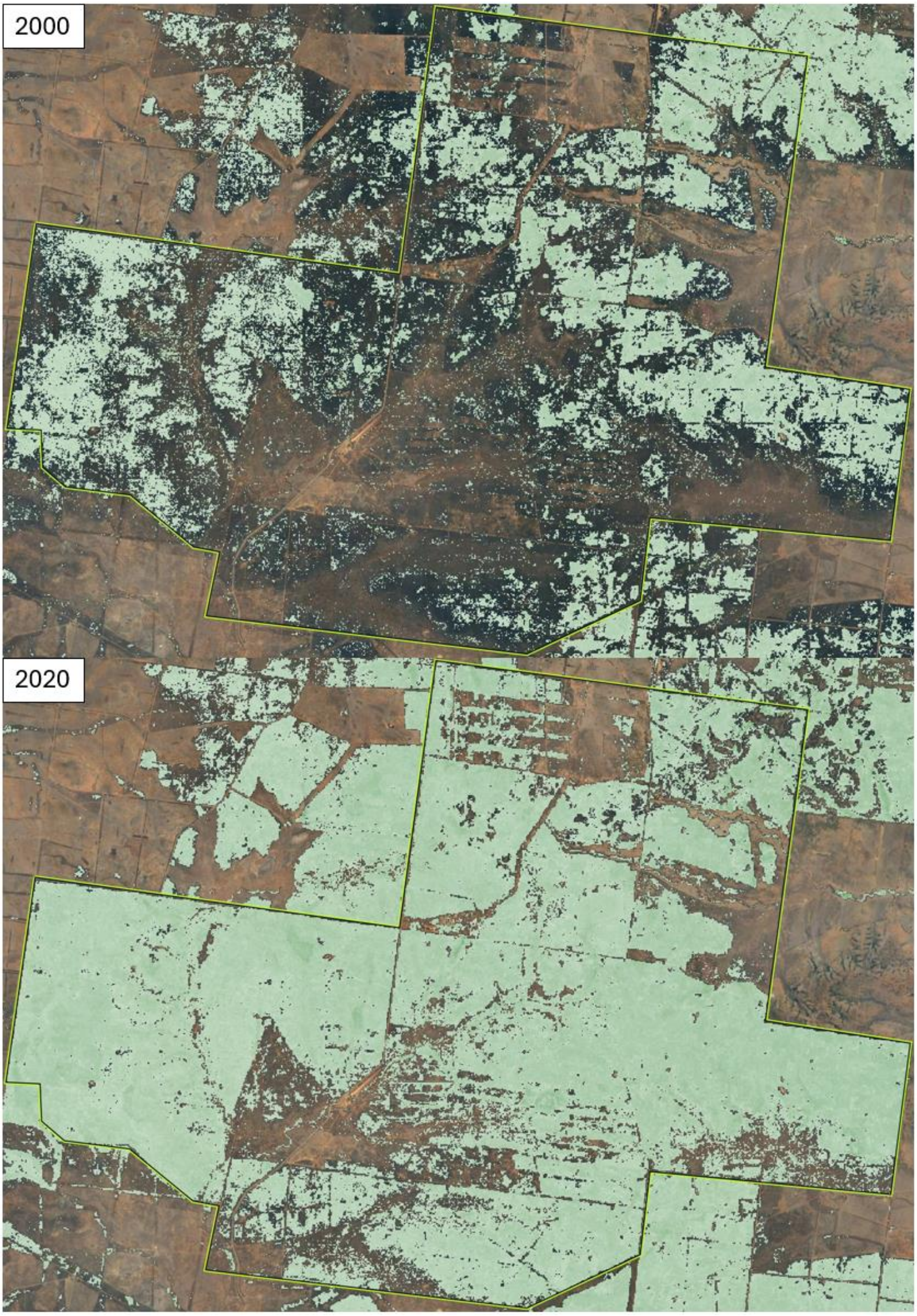

Figure 3. Area of the Mourachan property covered by trees with a canopy height of >7m increased since conversion to a conservation property in the early 2000s. 30-m spatial

resolution forest canopy height maps of the Mourachan property for canopy height >7m (green colour) for the year 2000 (top) and 2020 (bottom) (Potapov et al., 2021).

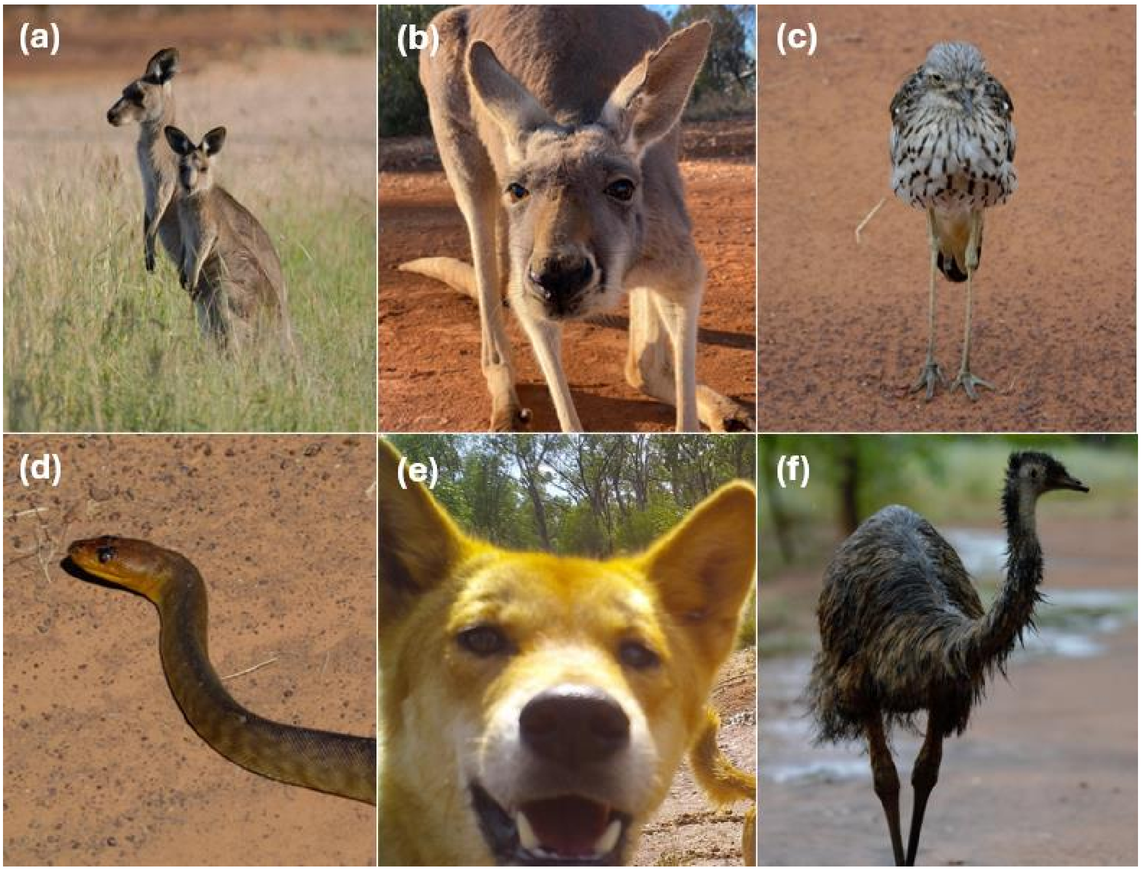

Figure 4. Some of the species present on the Mourachan property include **(a)** eastern grey kangaroos (*M. giganteus*), **(b)** red kangaroos (*O. rufus*), **(c)** bush stone-curlews (*Burhinus grallarius*), **(d)** Woma python (*A. ramsayi*), **(e)** dingoes (*C. dingo*), and **(f)** emus (*D. novaehollandiae*). (*Photo credits: a, c, d, f: L.Q. Juillard; b: Taylor McEvoy; e: CfCC*)

The landscape found on Mourachan varies, with flat rocky outcrops dominated by bendee (*Acacia catenulate)* woodlands, alluvial clay floodplains dominated by poplar box (*Eucalyptus populnae*) woodlands with small stands of brigalow (*Acacia harpophylla*), slopes dominated by mulga (*Acacia aneura*) woodlands with scattered silver-leafed ironbark (*Eucalyptus melanophloia*), as well as open grassland areas dominated by species such as buffel grass (*Cenchrus ciliaris*), grey copper burr (*Sclerolaena diacantha*), and wilga (*Geijera parviflora*). The property is relatively flat with very little elevation difference throughout its area.

COVID-19 impact on research

Gaining access to more sites would have been beneficial to my research, however, the unique conditions for wildlife offered by Mourachan are only present on a minority of other properties around the country, properties often found outside of New South Wales. With the majority of the data collection happening during the COVID-19 pandemic, opportunities to access new sites outside of New South Wales were made volatile due to border closures between states. The time between border closures where I was able to travel outside of the state often left me with only enough time to conduct Mourachan field trips before the borders closed again, leaving no time for other sites. Despite these limitations, Mourachan offered a study area of 48000 ha with sites of interest for camera traps evenly spread across the property. Furthermore, with eastern grey kangaroo home ranges estimated to be on average approximately 23.2 – 70.4 ha for males and 20.5 – 83 ha for females (Jaremovic, 1987; Jaremovic & Croft, 1987; Moore et al., 2002; Neaves et al., 2017) this offered the opportunity to study multiple subpopulations of kangaroos on the property as opposed to significantly smaller properties that may only offer enough space for a single population.

1.3. THESIS STRUCTURE AND CHAPTERS

This PhD thesis is separated into seven chapters including four data chapters. **Chapter 1** is a broad introduction to the topic researched throughout this PhD. **Chapter 2** consists of a literature review of the main topics included in this PhD. **Chapter 3** (Published – (2022) *Animals MDPI*) set off to explore how droughts affect health and population parameters of eastern grey kangaroos. The health parameters focused on are body condition, and parasite load, while the population parameters are demography (both age groups and sex ratio), and activity rate of kangaroos at artificial water points. While demography, activity rate, and parasite load have all been used by a wide range of research in the past, body condition scores (BCS) remain a relatively novel idea for macropod species, with this chapter describing in detail an eastern grey kangaroo body condition chart for the first time. **Chapter 4** explores thermoregulatory methods used by kangaroos during increasing temperatures. To do so, 2km long drone transects using both TIR infrared and RGB footage were used to count the number of individual kangaroos using shade cover and those exposed to the sun. The activity rate of kangaroos at both dammed watercourses and excavated earth tanks of the property was also measured. This chapter also briefly mentions some of the limitations that may arise when using drones. **Chapter 5** of this thesis (Published – (2025) *Animal Behaviour*) assesses how temperature affects interactions between eastern grey kangaroos and their predator, dingoes, at waterpoints, and discusses ecological and evolutionary consequences of aggregation with dingoes on kangaroo populations. I then combine the findings from chapters 3 to 5 in **chapter 6** to build a list of potential indicators of welfare challenges related to thermoregulation, predation, as well as more general indicators in eastern grey kangaroos. The aim of this chapter is to show which indicators were observable using camera traps and describe what potential mental experience could be cautiously inferred from such indicators. In this chapter I also assess the difference in prevalence for each indicator and behaviour between tanks and dammed watercourses during periods of heat anomaly and periods of non-heat anomaly. Finally, **chapter 7** forms a final discussion of this PhD project through which the findings made throughout previous chapters and future directions are discussed.

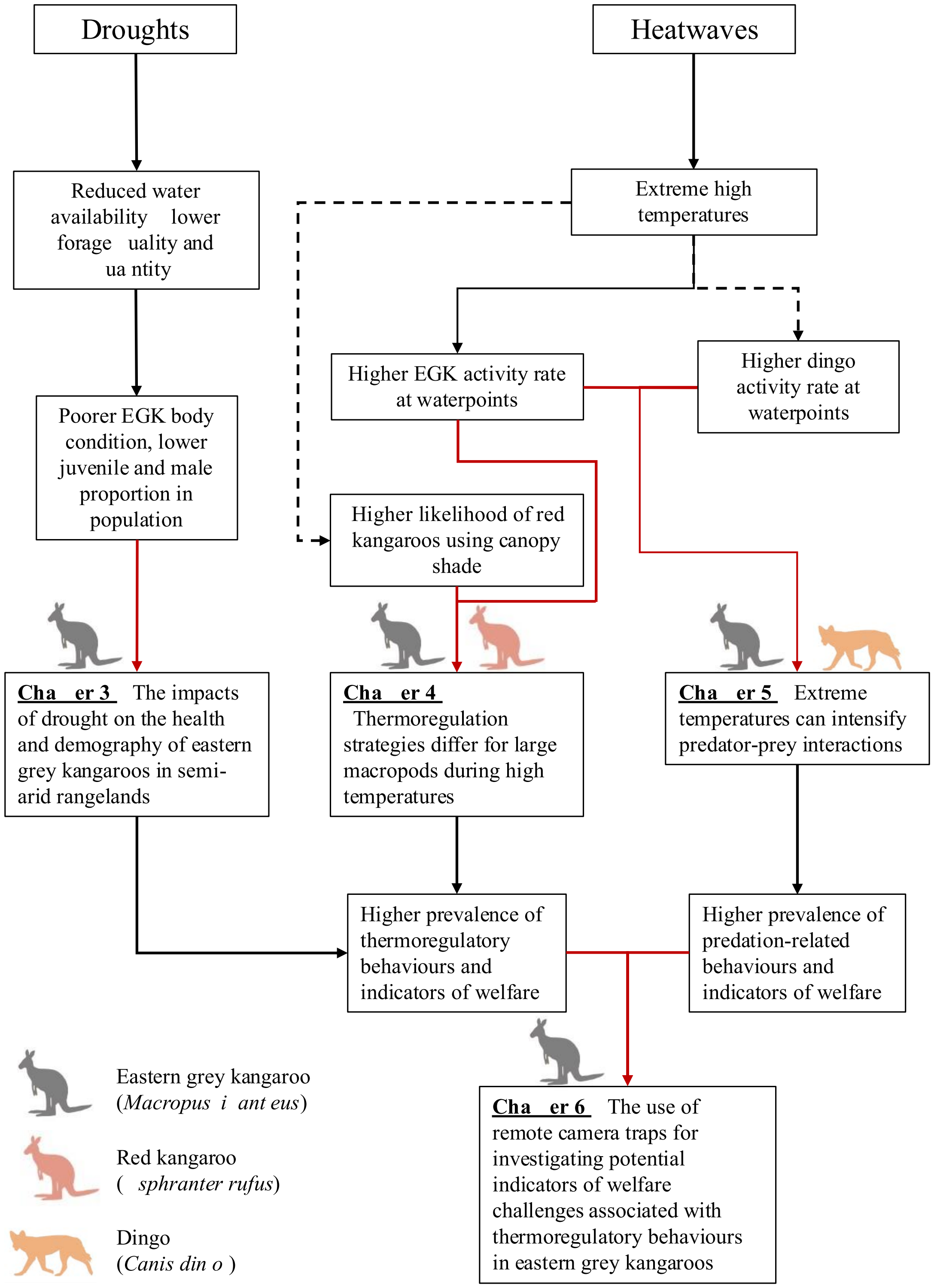

Figure 5. Framework showing some of the impacts of droughts and heatwaves on eastern grey kangaroos (EGK) and the data chapters the impacts shape. Dotted lines represent impacts on species other than eastern grey kangaroos, red lines show chapters related to the impacts. Silhouettes represent species present in each chapter.

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CHAPTER 2: LITERATURE REVIEW

2.1. CLIMATE CHANGE AND EXTREME WEATHER EVENTS

While the Earth's climate has always experienced variations, it is now going through a period of rapid changes, mainly due to anthropogenic activities over the past century (Inkley et al., 2004). These rapid changes are causing shifts in weather and climate patterns such as El Niño and La Niña events (Kirono et al., 2020; Vicente-Serrano et al., 2019), which further warm the world above 1.5˚C pre-industrial levels (Cai et al., 2021), impacting both fauna and flora, as well as humans. Shifts in weather patterns such as the ones mentioned have led to a rise in the frequency and intensity of daily temperature extremes, with increasing extreme high temperatures and decreasing extreme low temperatures, while also causing an intensification in precipitation extremes (Stott, 2016). In semi-arid and arid regions such as the semi-arid rangelands of Australia, heatwaves and droughts are the most prominent extreme weather events intensifying over time. Knowing this, this thesis focuses specifically on the impacts of heatwaves and droughts on eastern grey kangaroos.

2.1.1. Heatwaves

The exact definition of a heatwave varies depending on factors such as location or simply context, however, a general description of heatwaves tends to be a period of abnormally hot weather, where temperatures exceed a long-term average for the specific location where the heatwave is occurring (Disher et al., 2021; Dosio et al., 2018). The Australian Bureau of Meteorology, for example, states that a heat event needs to encompass at least 3 days of abnormally hot weather to register as a heatwave (BOM, 2024). Research focusing on heatwaves uses a wide variety of indices to measure factors such as intensity, duration or frequency (Disher et al., 2021; Dosio et al., 2018). In fact, so many indices exist that Disher et al. (2021), which describes 26 different indices still does not mention all of them. Those indices vary in how they measure heatwaves and what parameters they use. For example, the Excess heat factor (EHF) assesses the intensity of a heatwave using cumulative changes in high temperature over a 3-day period compared to the previous 30 days (Scalley et al., 2015), the Three-day maximum temperature (3DMT) uses the lowest maximum temperature over a 3-day period (Scalley et al., 2015). Often, multiple indices must be used to measure different characteristics of heatwaves. For example, Fischer and Schär (2010) quantified shifts in different aspects of heatwaves by differentiating them using indices including: HWF90 (day frequency) for the mean frequency of days that reach a specific heatwave criteria, HWN90 (number of heatwaves) for the mean number of heatwave events over a given summer season, HWA90 (amplitude) for the mean highest temperature for the hottest event in a given summer, and finally HWD90 (max duration) for the average length of the longest heatwave in summer.

Heatwaves under a 1.5°C warming are expected to intensify and become more frequent for large regions of the world, should we fail to limit global temperatures to 1.5°C as set by the Paris Agreements (UNFCCC, 2015). In a world where global temperatures exceed a 1.5°C warming around 1 billion people are expected to experience severe heatwaves every 5 years, and 700 million to be exposed to extreme heatwaves every 20 years (Dosio et al., 2018; Hoegh Guldberg et al., 2018; IPCC, 2022). However, if global temperatures were to exceed a 2°C limit, close to 3 billion people are expected to face severe heatwaves every 5 years, and more than 2 billion face extreme heatwaves every 20 years (Dosio et al., 2018; Hoegh Guldberg et al., 2018; IPCC, 2022).

Australia is no stranger to heatwaves with much of the land cover being semi-arid to arid, including deserts. Trancoso et al. (2020), who studied Australian heatwaves over a 67-year period, revealed that heatwave characteristics including peak temperature, frequency, and duration were all increasing. Furthermore, by focusing on regional trends, they showed that not only did heatwave characteristics increase in all states and territories, they did so at a faster rate on the south-eastern part of the country especially for New South Wales, Victoria, and the Australian Capital Territory (Trancoso et al., 2020). When looking at future trends Trancoso et al. (2020) focused on Queensland (where the study site for this thesis is located), showing severe increases in heatwaves with projections suggesting that single heatwave events may sometimes last up to

40 days, an eight-fold increase in frequency of heatwave days compared to current conditions. However, Trancoso et al. (2020) suggested that while tropic areas of Queensland are predicted to experience significant rises in the frequency and duration of heatwaves, arid regions may be more impacted by rises in the peak temperature of heatwaves. Such findings are directly relevant to this thesis as the research site presented in later chapters is located in the semi-arid rangelands of south-western Queensland.

2.1.2. Droughts

Similar to heatwaves, the definition of a drought is not as straight forward as it might seem. Due to the vast number of systems affected, be it environmental, structural or economic, measuring the severity and impacts of droughts is difficult (Vicente-Serrano et al., 2019). However, droughts can usually be described as periods of abnormally low water availability (Naumann et al., 2018). Some of the methods used to measure intensity of droughts such as the Standardised Precipitation Index (SPI) are precipitation-based indices that measure how extreme precipitations relate to the long-term average of a specific location (Vicente-Serrano et al., 2010). However, the SPI does not take in consideration other key variables that may influence droughts, for example temperature, wind, water holding capacity of soil, and evapotranspiration (Vicente-Serrano et al., 2010). The Standardised Precipitation Evapotranspiration Index (SPEI) extends the Standardised Precipitation Index (SPI) by integrating both measures of precipitation and potential evapotranspiration (PET) (Vicente-Serrano et al., 2010). Furthermore, the SPEI can be calculated over various timescales from 1 to 48 months (Vicente-Serrano et al., 2010). The different timescales as well as the variables the SPEI considers allow researchers to not only detect and monitor droughts, but also study the influence of global warming on droughts (Vicente-Serrano et al., 2010). The SPEI was used to measure drought intensity at the Mourachan Property and how it influenced the health of eastern grey kangaroos in chapter 3.

Similar to current and future trends in heatwaves, droughts are expected to become more intense, frequent, and last longer in many regions of the world (Kirono et al., 2020; Naumann et al., 2018;

Vicente-Serrano et al., 2019). Under a 1.5°C warming, while droughts in general are expected to increase in severity, changes will be moderate when compared to higher warming scenarios (Naumann et al., 2018). Indeed, should we breach the 1.5°C limit, the global average durations of droughts will shift from 9 months under 1.5°C to 11 months under 2°C, and 18 months under a 3°C warming (Naumann et al., 2018). Naumann et al. (2018) go on to mention that in today's conditions, Australia, parts of South America, and Eastern Africa are experiencing the worst drought magnitudes. However, under a 1.5°C, 2°C, and 3°C warming, drought magnitude worldwide is expected to increase by 30%, 38%, and 51% respectively, with shifts in the duration and magnitude of droughts being strongly correlated (Naumann et al., 2018). With increasingly rapid rates of warming rare and extreme droughts such as the "Millenium drought" in Australia or "dust bowl" in the United States could become more frequent (Fye et al., 2003; Naumann et al., 2018; Van Dijk et al., 2013).

Predictions of droughts the magnitude of the "Millenium drought" becoming more common in countries like Australia have already been proven. From 2017 to 2019 parts of Australia, including New South Wales, experienced their lowest levels of rainfall on record, and all years from 2017 to 2020 were in the warmest on record (DPIE, 2021). The 2017-2020 drought and accompanying extreme temperature events were major factors in the severity of the 2019-2020 bushfires, which killed approximately 3 billion wild animals, bringing many including koalas (*Phascolarctos cinereus*) closer to extinction while causing extensive welfare challenges to many of the surviving individuals (UNEP, 2020; WWF, 2020). Over 18 million hectares of land were burnt and 5,900 buildings including more than 2,800 homes were destroyed, as well as human lives lost (UNEP, 2020).

2.2. CLIMATE CHANGE AND WILDLIFE

While most wildlife species have evolved along with their habitats, the persistence of individuals and populations may depend on their ability to adapt to extreme climatic and weather events (Milligan et al., 2009), particularly as environments become increasingly arid. Extreme climatic events often impact the abundance and dynamics of populations (Ratnayake et al., 2019). The health of wildlife, however, is also impacted, with extreme events such as heatwaves, for example, creating challenges in the physiological ability of wild animals to survive such conditions (Acevedo-Whitehouse & Duffus, 2009). Wild animals have always been subjected to climatic changes and have, to some extent, evolved the necessary requirements to survive them (Acevedo-Whitehouse & Duffus, 2009; Reusch & Wood, 2007). However, the rate at which our global climate is now changing is far more rapid than evolution, leading to many species not having time to adapt to more extreme conditions before suffering the consequences (Thomas et al., 2004).

2.2.1. Population ranges

The distribution range of species is closely linked to environmental and climatic conditions (Aspinall & Matthews, 1994). This, in turn, can lead to changes in the distribution, abundance, and density of species (Seabrook et al., 2011; Thomas et al., 2006). While some species may be able to adapt to the changing conditions within their range, others will be forced to migrate to more suitable areas if they are to survive (Seabrook et al., 2011). The range of snowshoe hares (*Lepus americanus*) in Wisconsin, USA, for example, has been shifting north for the past 30 years (Sultaire et al., 2016). Sultaire et al. (2016) stated that the more recent shifts were mainly due to a loss of snow cover caused by warmer winter temperatures. The rate at which snowshoe hares are able to adapt their coat colour to match their environment is slower than the rate at which snow cover is decreasing (Sultaire et al., 2016). This then leads to hares with a winter coat becoming fully exposed in the absence of snow, making them highly vulnerable to predators (Sultaire et al., 2016). Another example of range shift due to climate change can be seen in the distribution of the Adélie penguin (*Pygoscelis adeliae*) populations along the Antarctic Peninsula. In recent decades, Adélie penguins have been moving further south as their usual habitats are impacted by rising temperatures and reduced sea ice (Cimino et al., 2016). The loss of sea ice has not only affected their breeding grounds but has also reduced their access to krill, a key food source that depends on the ice for habitat. Consequently, Adélie penguins have been gradually shifting their range to areas with more stable sea ice conditions to sustain their populations (Cimino et al., 2016). Shifts in ranges can often cause wild animals to collide with towns and cities, or other human infrastructures (Abrahms, 2021). This usually leads to conflicts with humans if wildlife enters agricultural properties, for example, a species not previously found in an area may be branded an "invasive" species or "pest", in which case the changing environmental conditions pushing such species to shift range is no longer the main threat they will face. People will often see these species as "invaders", an idea often supported by the media (Milman, 2021). Once a species has been branded a "pest", programs will sometimes be organised to lethally control said species, sometimes even involving the practice of using bounties, where hunters are paid for each animal killed, as is the case in some regions of Australia with dingoes (Wallach et al., 2009).

The range of eastern grey kangaroos is also being impacted by changing climatic conditions along with aridification, however, this is also combined with increasing urbanisation. As aridification reduces the availability of water and forage in more remote inland areas, kangaroos can become increasingly drawn toward urban and peri-urban environments, where artificial water sources and green spaces provide more consistent resources particularly during periods of droughts (Herbert et al., 2021). This shift in range towards human-dominated landscapes has led to more frequent human-wildlife interactions, sometimes resulting in vehicle collisions (Brunton et al., 2018) or conflicts with agricultural activities due to the livestock industry often controlling most of the water available in remote areas (Croft et al., 2007). While trade-offs are part of any animal species life, be it for resources or safety from predators, the combination of climate-driven habitat changes and expanding urban areas creates new trade-offs as kangaroos, and other species, navigate the balance between resource availability and the dangers of human proximity.

2.2.2. Health

Wildlife health can also be affected by shifts in climatic and weather conditions (Acevedo-Whitehouse & Duffus, 2009). In times of drought, for example, when resources like food are lacking, a decrease in the body condition of herbivores can often be observed, showing a clear poor nutritional status. A significant and rapid loss of weight can create further physiological challenges for the affected individual, including lower immune responses, increasing the likelihood of infections (Acevedo-Whitehouse & Duffus, 2009). This increased risk of infection can potentially lead to individuals developing serious complications due to small, usually insignificant injuries such as superficial cuts (Acevedo-Whitehouse & Duffus, 2009). Other physiological processes influenced by poorer nutrition include growth rate, self-maintenance, and even reproductive success (Acevedo-Whitehouse & Duffus, 2009; Houston et al., 2007). While a lower reproductive rate can be due to physiological impairments, it is often exacerbated by changes in behaviour, with individuals spending more of their energy on vital activities like foraging to lower starvation risk (Acevedo-Whitehouse & Duffus, 2009).

During extreme events like heatwaves wild animals can be challenged by temperatures exceeding their physiological limits, in particular, their thermoneutral zone (Norris & Kunz, 2012). The thermoneutral zone (TNZ) is a range of temperature (species specific) within which the body is able to maintain an optimal body temperature (T_B) by spending a minimal amount of energy (Norris & Kunz, 2012). However, should ambient temperatures exceed the TNZ of an individual, their body will be pushed to spend more energy to keep T_B at an ideal level (Norris & Kunz, 2012). One of the responses triggered by such an increase in energy spent, is a more rapid rate of evaporation of metabolic water. Should water be available nearby an animal can then easily replace the lost metabolic water by drinking. However, replacing lost metabolic water alone is not enough, most land-based mammals will therefore seek shelter from the sun to thermoregulate and lower their rising T_B (Terrien et al., 2011). Wild animals also possess various techniques that allow them to cool down, for example the licking of forearms by kangaroos which lowers T_B via evaporative cooling (Croft, 1980). Should wild animals fail to both replace lost metabolic water (leading to dehydration) and thermoregulate sufficiently, the affected individuals will begin to overheat (Acevedo-Whitehouse & Duffus, 2009; Norris & Kunz, 2012). Overheating can then trigger physiological impairments impacting the reproductive and immune systems as well as cognitive abilities (Acevedo-Whitehouse & Duffus, 2009; Costa et al., 2013; Norris & Kunz, 2012; Soravia et al., 2021).

Trondrud et al. (2023) studied reindeer in Northern Finland during one of the most severe heatwaves faced by the region. They found that reindeer that became inactive at higher temperatures had higher sub-cutaneous temperatures as well as lower heart rates, which may have been caused by the reindeer feeding less at higher temperatures. While some of the reduced food intake could be compensated by reindeer becoming more active during cooler parts of the day, when temperatures exceeded 20°C this shift in activity pattern was not enough to replace the lost opportunity to forage (Trondrud et al., 2023). The inactivity caused by the higher temperatures, therefore, led to lower body mass for the affected individuals (Trondrud et al., 2023). This example further reveals some of the intricate ways in which extreme events like heatwaves can affect the health of wild animals, including through changes in body temperature among other impacts.

2.2.3. Sexual dimorphism

In many species climate change can impact females and males differently. This is especially true for sexually dimorphic species, where one sex may be larger in size than the other (Isaac, 2009). A larger individual will naturally require more food to meet the energy demand of their body (Isaac, 2005). When resources are scarce, individuals with smaller body sizes and lower energy requirements, should, therefore, fare better than their larger counterparts (Isaac, 2009). Peeters et al. (2017) found that severe precipitations during harsh winters had a more significant effect on the mortality of male Svalbard reindeers than on females. The difference in body size between males and females of dimorphic species can often be due to a polygynous mating system (Toïgo & Gaillard, 2003). In polygynous species the males will usually compete to mate with multiple females. The larger and stronger the male, the higher the chances of securing a mate. While being larger than other males may be beneficial, it comes at a price. The energetic costs required to successfully compete against other males can be high and increase male mortality, especially during periods of low resources where more energy is spent than is gained (Clutton-Brock et al., 1988; Toïgo & Gaillard, 2003). Males of many species also have a lower fat content than females, potentially pushing them faster towards starvation when food sources are unavailable as they are unable to tap into their fat reserves as much as females (Glucksmann, 1974). Such an issue can lead to an imbalance in the sex ratio of populations.

Sex ratio in wildlife can also be affected by environmental variables at birth or during early life stages (Barros et al., 2013). The sex ratio of European shag fledglings was found to be in favour of females during periods of positive Northern Atlantic Oscillation (NAO), while more male fledglings were present during periods of negative NAO (Barros et al., 2013). The effect of variables like temperature on offspring sex ratio are especially significant on species with temperature-dependent sex determination, such as green sea turtles (*Chelonia mydas*) (Blechschmidt et al., 2020). At a specific temperature, known as the pivotal temperature, both sexes will represent 50% of the green sea turtle hatchlings (Blechschmidt et al., 2020). However, a study on the northern Great Barrier Reef found that a 1˚C increase can lead to 80% of hatchlings being females (Limpus, 2008). For crocodilian species like the American alligator (*Alligator mississippiensis*), hatchling sex ratios are likely to be female skewed at both low and high temperatures (Bock et al., 2020). Bock et al. (2020) predicts that the temperature of nests may increase by 1.6-3.7˚C by 2100. As a result, predictions show that regions with the highest temperature increases might see nests with hatchling sex ratios reaching nearly 100% females (Bock et al., 2020).

Such impacts may lead to local populations being unable to reproduce with one sex becoming absent (Braun McNeill et al., 2016). For populations significantly skewed towards one sex, males and females will likely experience different types of pressure. However, exactly how populations will be impacted by imbalanced sex ratios is not yet fully understood (Dunne, 2017). Temperature-dependent species may be at greater risks of extinction than many others as the health, sex, and future of their clutches directly depend on the temperature of the environment in which their eggs were laid, making them highly vulnerable to environmental changes (Bock et al., 2020).

2.2.4. Fauna in Australia

Wild animals in Australia, much like the rest of the world, have not been spared from the impacts of climate change. From 1960 to 2009, the temperature in the country had already risen by 0.7˚C, and is expected to rise by another 0.6-1.5˚C by the year 2030 (CSIRO & BOM, 2010). This has led, and will continue to lead, to an increasing number of challenges for Australia's wild animals. As another consequence of climate change, droughts and heatwaves in Australia are expected to become more intense and last longer, especially in the eastern and southern parts of the country (Kirono et al., 2020). Such changes in droughts will likely impact many of the species found within the impacted regions. A study by Seabrook et al. (2011) on the effects of drought on koalas, observed an 80% decline in their study population between 1995 and 2009. Adams-Hosking et al. (2012) stated that the range of trees that koalas use as food sources is predicted to shrink with rising temperatures and decreasing rainfall. Furthermore, Mella et al. (2020) showed that koalas may be more reliant on water sources to drink than previously believed, suggesting better access to water would assist koalas, particularly through extreme weather such as droughts and heatwaves. Similar to the range of koalas, that of the greater glider (*Petauroides volans*) was found to be significantly correlated to high temperatures and aridity, with parts of their range becoming more arid (Wagner et al., 2020).

Physiological and behavioural change caused by environmental changes can also occur. Such changes have occurred in koalas in times of unusually high temperatures, with reports of koalas too weak to climb trees or willing to risk drinking from private pools in backyards (Adams-Hosking et al., 2011). This change in behaviour, along with shifts in distribution pushes koalas, and other species closer to human proximity. While some individuals may be lucky and stumble upon people willing to help them, whether by providing water or bringing injured ones to veterinarians or wildlife organisations, others might not be so lucky. Animals struck by vehicles make up the majority of human caused injuries or deaths, however, other dangers exist such as people inclined to harm wildlife, or conflicts with domestic dogs for example (Taylor-Brown et al., 2019).

Globally, climate change has already been linked to extinctions in the past, particularly at local scales (Román-Palacios & Wiens, 2020). It is predicted that due to climate change, one third of all wildlife and plant species could face extinction by 2070 (Román-Palacios & Wiens, 2020). Perhaps more alarming is the fact that these predictions are expected to increase to half of all species, should we fail to reduce our impact on the climate (Román-Palacios & Wiens, 2020). Such an outcome will undoubtedly have catastrophic consequences on the global biodiversity and health of our planet, with various ecosystems potentially becoming no longer compatible with life for many species. While climate change is a major threat to wildlife, it occurs in a world where wild animals already face increasing pressure from anthropogenic activities, including overexploitation, habitat destruction and fragmentation, and urban expansion due to an ever-growing human population (Ripple et al., 2019). Some of these impacts alone would be enough to bring species to the brink of extinction, making it paramount to understand how climate change increases the pressure suffered by wild animals.

2.3. RANGELANDS

Rangelands are found all over the world and are important on international, national, and local scales (Lund, 2007). Although multiple definitions of rangelands exist, they are often referred to as ecosystems where grazing (whether from wildlife or livestock) is the main land use, making rangelands the largest type of land cover (Briske, 2017). While a large number of ecosystems fall into this category, the main systems found in rangelands are generally grasslands, shrublands, woodlands, wetlands, savannas, and deserts (Briske, 2017). Solely from a human perspective, the importance of rangelands mainly lies on their ability to ensure food security for millions of people (Lund, 2007). This is due in part to rangelands providing nearly 70% of the food necessary to raise livestock in many parts of the world (Lund, 2007). As of 1999, rangelands were responsible for feeding approximately 360 million cattle, and more than 600 million sheep and goats, or 9% of beef and 30% of sheep and goat meat worldwide (Blench & Sommer, 1999). Rangelands can even provide the human population with ecosystem services such as vegetation containing medicinal properties, recreational opportunities, and timber (Lund, 2007).

While the impacts of rangelands on the human population, whether from a cultural, social, economic, or recreational perspective, are highly significant, their environmental significance is just as, if not more important. Indeed, rangelands cover such an extensive area of land across the world that they harbour a wide range of both fauna and flora species and are crucial to conservation (West, 1993). Since rangelands are such important assets for livestock production, wildlife is often controlled to minimise interactions with livestock, often pushing species to the edge of their range (du Toit et al., 2017). Some of the main reasons used for the management of wildlife on rangelands include competition between wildlife and livestock, transmission of diseases, and predation from wild predators (du Toit et al., 2017). Much of the livestock-wildlife competition comes from the vast areas of land made favourable to livestock production by people (du Toit et al., 2017). While these vast areas once harboured a wide range of wildlife species, they are now occupied by only a few species of livestock (Du Toit & Cumming, 1999).

As a consequence of the replacement of wildlife with livestock, wildlife populations in rangelands, particularly herbivores, have severely declined over the last few generations (Ripple et al., 2015). While the replacement of large herbivores with livestock has had a major impact on the overall biodiversity of rangelands (Brown, 2001), other human factors have come into play, such as fencing, altering migratory routes, and locking wildlife away from resource points (Muir-Leresche & Nelson, 2000; Ripple et al., 2015). After the removal of large wild herbivores, some of their functions such as breaking up soil crust and promoting nutrient cycling were lost (Fornara & Du Toit, 2008). Consequently, this altered the nutrient cycling (Lundgren et al., 2020), compaction of soil, and trophic cascades throughout the ecosystem (Wallach et al., 2017a). Such impacts have and continue to reduce the resilience of rangelands to drier conditions, making them more vulnerable to climate change and increased rates of aridification (Silcock & Fensham, 2019; Walker et al., 2018).

For the reasons stated above, climate change has now become a significant threat to rangelands. Due to a warming climate and reduced precipitations, it is predicted that the soil water availability in rangelands, particularly semi-arid and arid ones, will decrease, leading to further aridification (Polley et al., 2017). Organisms like plants directly rely on soil water availability, and a loss of it could, therefore, lead to a decrease in plant species richness and composition (Polley et al., 2017). Multiple climate scenarios for rangelands have been produced by Polley et al. (2017), including that of a warmer, drier climate for areas such as south, south-western, and south-eastern Australia, Central and North America, southern Africa, and central Asia (Polley et al., 2017). This scenario is expected to cause impacts such as drier soils due to a low soil water availability, consequently leading to lower rates of plant productivity, and forage quality (Polley et al., 2017; Xu et al., 2013). The lower amount, and quality of forage available will likely reduce livestock production (Polley et al., 2017). While livestock will be impacted, so will the remaining wildlife in such areas as they too rely on forage quality and availability. While herbivores will be directly impacted by the lack of vegetation, their predators will be impacted through the potential decrease in the number of prey, making it more difficult for wildlife to find suitable resources.

In Australia, rangelands cover various ecosystems from semi-arid and arid regions to wetter, more tropical areas in the north (Smyth & James, 2004). They make up approximately 81% of Australia's total land cover (Australian Department of Agriculture Water and the Environment, 2021). Similar to other countries, Australian rangelands are mainly used by pastoralism, with approximately 6000 companies using 58% of the total surface covered by rangelands (Australian Department of Agriculture Water and the Environment, 2021). However, other large industries use these systems, including mining, and tourism (Australian Department of Agriculture Water and the Environment, 2021). According to the Australian Department of Agriculture Water and the Environment (2021), the annual revenue from rangelands is more than $12b through mining,

$2b through tourism, and was $2.4b in 2001 through pastoralism and agriculture together (Australian Department of Agriculture Water and the Environment, 2021). While Australian rangelands cover a number of ecosystems, the majority of their area is made of semi-arid, and arid ecosystems (Stokes et al., 2006). These systems have naturally low levels of resources available to both flora and fauna (Stokes et al., 2006). The low levels of resources, along with their patchy distribution across the landscape makes it challenging for organisms to survive in such habitats. Many wildlife species, especially herbivores, developed migratory behaviours to move from one favourable resource point to another (Stokes et al., 2006). After the colonisation of Australia and the implementation of western style pastoralism bringing in intensive land use, such behaviours were disrupted by the fragmentation of rangelands into parcels of land (Boone & Hobbs, 2004; Stokes et al., 2006).

The increase in pastoralism in Australia, like much of the world, has been and continues to be the source of conflicts between people and wild animals (Machovina et al., 2015; Wallach et al., 2017). Carnivore species especially, like dingoes (*Canis dingo*), are the perpetual target of persecution through so-called “control” programs (Wallach et al., 2017). In Australia, campaigns to remove predators from rangeland properties often include shooting, baiting, and poisoning (1080 poison), combined with bounty systems in some parts of the country to financially encourage the culling of dingoes (Wallach et al., 2009). Similarly, large herbivore species such as the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Osphranter rufus*) are also culled and actively removed from properties (Ramp, 2013). It is estimated that nearly 3 million kangaroos are killed every year in rangelands (Boom et al., 2012). The culling of kangaroos began shortly after European colonisation, when farmers began to view macropods as “pests” that were eating and destroying the resources needed to feed their livestock (Boom et al., 2012). The removal of species like kangaroos, however, can lead to a further loss of biodiversity in rangelands due to their important roles as ecosystem engineers, and in maintaining biodiversity (Iles et al., 2010). Treatments such as the ones suffered by dingoes and kangaroos, are the cause of extensive wild animal welfare crises, as the brand of “pest” will simply nullify any consideration for the welfare of the targeted individuals by devaluing them (Boronyak et al., 2023).

Rangelands could be strongholds of wildlife conservation, which farming properties could benefit from under wildlife-friendly principles (Hasselerharm et al., 2021). Wildlife friendly farming seeks to foster the cohabitation of wildlife and humans through the non-lethal management of wild predators (Wallach et al., 2017) and herbivores (Kinnaird & O'brien, 2012), as well as by removing the use of exclusion methods such as exclusion fencing (Western et al., 2009). Unfortunately, many of the farming methods employed are not compatible with the protection of wildlife and are leading to further declines in the biodiversity of rangelands (Hasselerharm et al., 2021).

2.4. EASTERN GREY KANGAROO

Eastern grey kangaroos are the second largest macropod species found in Australia, red kangaroos (*Osphranter rufus*) being the largest. Eastern grey kangaroos have a relatively slow reproductive rate, with males reaching maturity at 18 months and females at 48 (Dawson, 1995). While gestation is only 36 days, the newborn joey is going to remain in the mother's pouch until it takes its first steps outside, approximately 9 months later (Dawson, 1995). Finally, juveniles reach the weaning stage about 540 days after birth (Dawson, 1995). Compared to other mammals that may have multiple offspring at a time, eastern grey kangaroos will usually only have one, and while they may give birth to multiple joeys through their lifetime, only 2-3 will make it past the weaning stage due to high juvenile mortality (Bilton & Croft, 2004; Dawson, 1995). This slow reproductive rate makes the species particularly vulnerable to changes in environmental and climatic conditions. As a mesic species, the range of eastern grey kangaroos is located on the eastern side of Australia, in forests, grasslands, and woodlands, however, part of their range also extends into semi-arid and arid areas (Garnick et al., 2010). While red kangaroos are arid adapted (Moss & Croft, 1999), eastern grey kangaroos are not, meaning individuals living in the more arid parts of their range run higher risks of being exposed to extreme conditions brought by the naturally lower water availability and warmer temperatures of arid rangelands. Therefore, understanding how changes in weather patterns known to intensify extreme events like droughts and heatwaves in the semi-arid and arid rangelands may influence eastern grey kangaroos is of urgent concern.

In Australia, dingoes are a widespread and large predator capable of predating on kangaroos (Letnic et al., 2012) through ambush as well as by engaging in pack and chase behaviour (Pollock et al., 2022; Purcell, 2010; Thomson, 1992). Predation by dingoes can limit kangaroo recruitment, with hunting preferences believed to be directed mainly towards adult females and juveniles as well as generally weaker individuals (Letnic et al., 2012). Where dingoes are absent or have been lethally removed by humans, primary productivity and food sources become the main factors driving kangaroo population dynamics and density (Montague-Drake & Croft, 2004). While resource availability (e.g., plants) and primary productivity can affect populations, evidence suggests that waterpoints do not influence the density and abundance of kangaroos as previously believed (Montague-Drake & Croft, 2004). Rather, kangaroos will only access water points to drink before returning to their preferred foraging and resting sites (Montague-Drake & Croft, 2004). While kangaroos can obtain much of their hydration through the moisture contained in plants they eat (Ayliffe & Chivas, 1990), increasing temperatures and aridity can lead to forage containing little to no moisture, forcing kangaroos to rely more on waterpoints for hydration and thermoregulation.

When temperatures rise, kangaroos can use various thermoregulatory methods to keep an optimal body temperature. As is the case for most land-based mammals, seeking shade to shelter from the sun's harsh radiations remains the most common method via which kangaroos thermoregulate (Dawson et al., 2006). However, kangaroos can also use other methods. When looking at a kangaroo, one can easily notice the thin appearance of their forearms. This plays a major role in thermoregulation as it causes blood vessels passing through the forearms of the kangaroos to be closer to the skin. At higher temperatures kangaroos will sometimes lick their forearms, allowing their saliva to then evaporate and cool down the blood passing through their forearms via evaporative cooling (Croft, 1980; Dawson et al., 2006) (Figures 1 and 2), however, the licking of forearms can also occur as a stress response. Kangaroos are also known to dig hip holes before lying down, with the newly exposed layer of soil offering a cooler surface to lay on (Croft, 1980).

Figure 1. Eastern grey kangaroos can thermoregulate by licking their forearms. Camera trap image from the Mourachan property (*Photo credits: CfCC*)

Figure 2. Eastern grey kangaroos standing in the shade of a tree on the Mourachan property. Their wet forearms also show evidence of forearm licking (*Photo credits: Loic Q. Juillard*).

2.5. HUMAN-KANGAROO CONFLICTS

While kangaroos living on Mourachan are safe from human persecution, for many kangaroos in the rest of their range the situation is significantly different. Kangaroos have been a part of the Australian landscape for about 20 million years (Kangaroos Alive, 2021). They are also a crucial part of First Nations peoples cultures and ceremonies, including as a food source and as a totem animal (Kangaroos Alive, 2021). However, Europeans started hunting kangaroos for meat soon after the colonisation of Australia in 1788 (Boom et al., 2012). However, they were mostly used as a supplement to resources imported from overseas, and traded with First Nations People (Boom et al., 2012). When enough livestock was imported and raised to meet the need of people for meat, the kangaroo hunt became more recreational (Croft, 2005). In the late 1800s however, farmers began to see kangaroos as a "pest" and argued that their numbers had increased as a result of the removal of dingoes and First Nations People (Boom et al., 2012). Kangaroos were officially branded as a "pest" in the 1870s (Pople & Grigg, 1999). All of eastern Australia had introduced laws in favour of the destruction of kangaroos in the 1880s, even going as far as offering bounties for the head of marsupials (Boom et al., 2012). As a result, the brush-tailed rock-wallaby was nearly pushed to extinction, when more than 640,000 bounties were received for the species between 1884 and 1914 (Short & Milkovits, 1990). Between 1877 and 1907, hunters in Queensland killed close to 8 million kangaroos and wallaroos, a number which grew to 65 million by 1987 (Robertshaw & Harden, 1989). Even with legislations such as the "*Animals Protection Act 1879 (NSW)*" put in place, which aimed to stop the culling of native wildlife during their breeding season, extensive exploitation continued (Boom et al., 2012). The trade for kangaroo meat truly began in the 1950s when it was sold as pet food, before also being sold as human food from 1955 onwards (Corrigan, 1988).

Today, the use of land for agriculture and livestock production is pushed to the limits to meet the needs of an ever-growing human population. As a result, more wildlife habitat is destroyed, and the landscape is becoming increasingly fragmented, creating more conflicts between people and species like kangaroos (Austin, 2020). The four large macropod species: eastern grey kangaroos, red kangaroos, western grey kangaroos (*M. fuliginosus*) and wallaroos (*M. robustus*), are thus still part of management programs aimed at reducing their impacts on agricultural endeavours (Ben-Ami et al., 2014; Ramp, 2013), with some hunters also shooting them for recreational purposes (Ramp, 2013). During the decade from 2000 to 2009, a total of approximately 30 million kangaroos (all four species combined) were shot, including nearly 8.5 million females with 75% of them having pouch young and 25% having dependent young-at-foot (Ben-Ami et al., 2014).

While the said aim is to reduce the kangaroo's impacts on agricultural lands and the environment, they are also hunted for their meat. The kangaroo industry is the world's largest slaughter of mammals, even surpassing the number of harp seals harvested in Canada by tenfold (Boom et al., 2012), although this statement is in no way meant to make a competition out of which wildlife slaughter is worse, only to put into perspective the scale of the lesser known kangaroo slaughter by using the scale of a well-known one such as harp seals. Welfare issues related to the killing of kangaroos are mainly focused on juveniles that still depend on their mother (Ramp, 2013). Juveniles such as pouch young and young-at-foot are usually left behind by the shooter (Ramp, 2013), rather than killed as legally required (by shot, blunt trauma, or beheading depending on size). As a result, these juveniles die of dehydration, predation, or exposure (Ramp, 2013). When it comes to the welfare of adults, kangaroo shooters are instructed to shoot individuals in the brain to reduce the likelihood of suffering experienced before death (Boom et al., 2012). However, this is far from always being the case. Of the 30 million kangaroos killed from 2000 to 2010, 1.3 million were not instantly killed and suffered prior to death (Ramp, 2013). Despite the obvious impacts on the kangaroos' population and welfare, these practices occur on a daily basis, with officials often turning a blind eye on them (Ben-Ami et al., 2014; Boom et al., 2012; Ramp, 2013). Furthermore, in many cases the killing of kangaroos occurs on large remote private properties too far from any town or city or the public eye, and takes place at night (Ben-Ami et al., 2014; Boom et al., 2012; Ramp, 2013). When a population is subjected to shooting, its individuals will generally flee the area (Ramp, 2013). This can lead to social ties within groups being broken, disrupting the social learning networks linked to foraging and predation that are vital to ensure the survival of juveniles into adulthood (Higginbottom & Croft, 1999; Ramp, 2013). Due to their slow growth and reproductive rate (Croft & Boom, 2011), as well as their dependence on environmental conditions, kangaroos are relatively slow at repopulating an area where shooting previously occurred (Ramp, 2013). Furthermore, while governing bodies claim that large management zones have quotas for the number of kangaroos commercially shot set on a sustainable basis, the crash of populations at a local scale still occurs (Ramp, 2013), potentially leading to local extinctions.

In addition to being hunted, kangaroos face other threats in areas like rangelands where livestock production occurs. One of these threats comes from fences cutting through the landscape (Ens et al., 2016). Studies on fences have found that they impact wildlife both directly and indirectly (Rey et al., 2012). Some of the direct impacts include entanglement, injuries when trying to cross, starvation when entangled, separation of young from mothers, and death (Rey et al., 2012).

Indirect effects include habitat fragmentation, restricted access to resources (Mbaiwa & Mbaiwa, 2006), heightened stress levels when navigating around the fences (Islam et al., 2010), and increased vulnerability to predators (Mbaiwa & Mbaiwa, 2006). All these impacts lead to lower welfare levels for the species involved, which ultimately decreases the survival and viability of populations (Harvey et al., 2020).

In Australia, landholders have shown a growing interest in exclusion fences within the last few years. Exclusion fences were created to be impossible to cross for large to medium sized species, with a focus on kangaroos, dingoes, and emus (Ens et al., 2016). The fences are generally 1.5-1.8m in height or higher, with wires running both vertically and horizontally and a top layer made of barbed wires (Ens et al., 2016). In addition, a horizontal part of the fence, or “skirt”, extends directly on the ground to stop animals from digging underneath (Ens et al., 2016). The fences are usually set up in a way that allows neighbouring properties to come together to create exclusion clusters that cover thousands of hectares of land (Ens et al., 2016). This method of setting up exclusion fences is known as cluster fencing. Exclusion fences are generally implemented by owners of agricultural or livestock farms to keep wildlife out of their properties. Once the fences have been set up, kangaroos as well as dingoes still on the property are shot, either by the landholder or hired shooters (Giumelli & White, 2016). The focus on killing all kangaroos found within the fence means that entire populations trapped will eventually be wiped out, leading to numerous local extinctions.

2.6. BODY CONDITION SCORE

With extreme weather events intensifying due to climate change, more research on their impacts on wild animals are being conducted, with many focusing on parameters such as species distribution and abundance (Hale et al., 2016; Seabrook et al., 2011), health (Chandranaik et al., 2022; Trondrud et al., 2023), behaviour (Abernathy et al., 2019; Buchholz et al., 2019), or biotic interactions (Brivio et al., 2024; Gauzens et al., 2024; Rafiq et al., 2023; Romero et al., 2018). Part of this thesis focuses on health parameters of eastern grey kangaroos through droughts and heatwaves. Health assessments often include the measurement of indicators such as physical condition. A variety of methods can be used to measure the physical condition of animals, including the bone marrow fat index, kidney fat index, bioelectrical impedance analysis, as well as more general ones such as weight and size, body mass, and length of specific limbs (Schiffmann et al., 2017). Live animal handling can not only cause stress in the animals handled, but also put them and the handlers at risk of injuries, however, non-invasive and more ethical methods do exist, such as Body Condition Scores, the measurement used in this thesis. While Body Condition Scores can be measured by handling the animals, they can also be used to estimate the nutritional status and physical condition of individuals non-invasively (Harvey et al., 2020; Pérez-Flores et al., 2016). BCS systems are particularly popular and important to industries working with animals, from cattle farms to zoos, and veterinarian clinics (Schiffmann et al., 2017).

While BCSs are generally used to ensure animals are in a healthy state, their use may be motivated by different factors from one field to another, for example, in the meat or dairy industry it may be motivated by an economic factor, while avoiding serious health complications motivates pet owners and veterinarians (Laflamme, 2012). In scientific research BCSs have been used by various studies to analyse the effects of resource fluctuations and overall changes in the environment on wild animals (Lane et al., 2014; McWilliams & Wilson, 2015). Unfortunately, BCS does have limitations, for example, the feathers of birds make it difficult, if not impossible, to observe crucial body features such as muscle definition (Schiffmann et al., 2017). Similarly, the body of mammals found in colder climate such as in the high arctic will often be covered by a thick insulating layer of fur, making the use of BCS challenging (Gerhart et al., 1996). When it can be used, BCS has proven to be a practical and low-cost method. Furthermore, it also allows better communication and sharing of important information related to animal health between scientists, veterinarians or animal keepers in zoos (Bray & Edwards, 2001; Clements & Sanchez, 2015).

Today, body condition scoring systems exist for a vast array of species, from cheetahs (*Acinonyx jubatus*) (Reppert et al., 2011), to mountain chicken frogs (*Leptodactylus fallax*) (Jayson et al., 2018), and from spiders (Jakob et al., 1996), to bottlenose dolphins (*Tursiops truncatus*) (Gryzbek, 2013), and African and Asian elephants (*Loxodonta spp.*) (Morfeld et al., 2016). Body condition scoring systems are generally made up of five levels, or categories, 1 being the poorest and 5 the highest condition (Schiffmann et al., 2017). BCS charts generally describe the muscle mass or fat deposit of specific body parts like the hips, ribs, base of the tail, and back bone (Schiffmann et al., 2017). While most BCS charts have levels from 1 to 5, some are more detailed and implement higher levels. Reppert et al. (2011) described body condition scores for cheetahs using 9 categories, while Clark et al. (2016) described a BCS system for ant-eating mammals using scores from 1 to 5, while having seven categories by adding the scores 2.5 and 3.5, giving them their own descriptions.

While the most popular method to visually score body condition is by using direct observations, studies are now also using material such as camera trap images. Harvey et al. (2021), sought to assess the use of camera traps to measure various indicators of welfare, including body condition, in wild free-roaming horses. They reported that BCS of horses was assessable for 73% of observation events from camera trap images, and 79% from videos (Harvey et al., 2021). Some limitations were found, notably images taken at night where it may be too dark to observe crucial body parts, images where the full body of an animal may not be visible (e.g., only the tail or a leg in the frame), the position of the individual altering the shape of the body (e.g., crouching, image captured mid-scratch), or images where an individual may be too far or moving too fast to allow for high quality footage to be recorded (Harvey et al., 2021) (Figure 3).

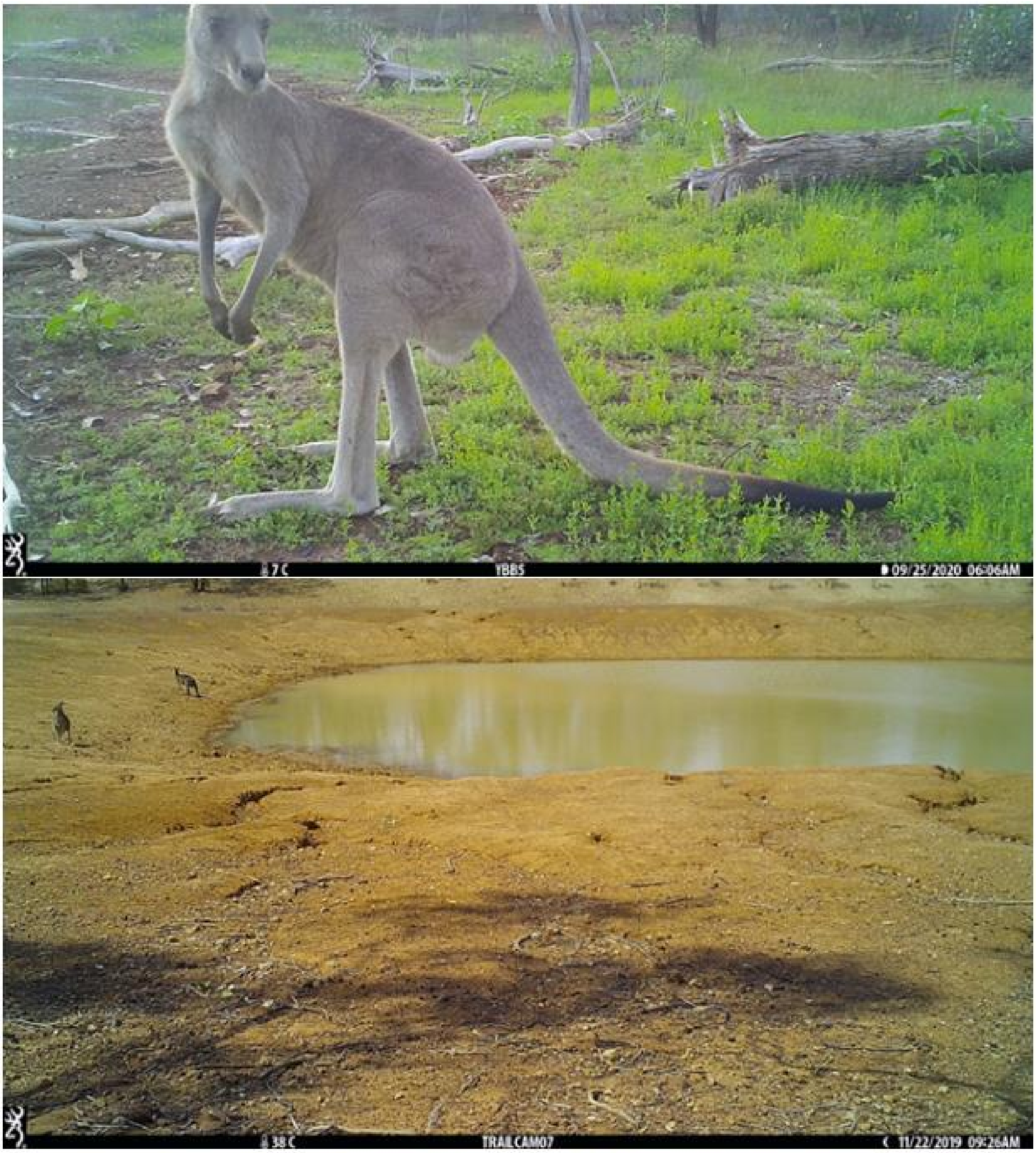

Figure 3. Example of camera trap images of eastern grey kangaroos taken as part of this PhD research. (Top) The kangaroo is fully visible and the image is clear, and can therefore be used for BCS assessment. (Bottom) The two kangaroos are too far for their body condition to be scored. (*Photo credits: CfCC)*

A number of other studies have also used camera traps to assess wildlife body condition. Pérez-Flores et al. (2016) used camera traps to assess the body condition of the Baird's tapir (*Tapirus bairdii*) using water points in the Calakmul region of Mexico. Studies using BCS with wildlife species often focus on how environmental changes affect body condition. Laidre et al. (2020)

studied how sea-ice loss due to climate change over a 20-year period affected the movement, seasonal range use, reproduction, and body condition of polar bears (*Ursus maritimus*) in Kane Basin, Canada. They found that the BCS of the bears was higher during spring when the number of seals available to hunt increased, while at the southern end of the study area (Kane Basin), the body condition of the bears was associated with the loss of sea-ice cover (Laidre et al., 2020). Bradford et al. (2012) studied how the body condition of western grey whales (*Eschrichtius robustus*) changed within-season and interannually, while focusing mainly on the BCS of females with calves. Lactating females with calves had lower body conditions than both females without calves and males (Bradford et al., 2012). This is thought to be due to the high energy cost that comes with lactation for most mammal species (Young, 1976). On the other hand, the body condition of the calves accompanying the females was found to remain at a constantly high level, which is thought to be caused by an energetic buffer created by the mother at her own expense, partly explaining the lactating females lower BCS (Bradford et al., 2012).

Studies on BCS such as the ones by Bradford et al. (2012), and Laidre et al. (2020), emphasise the importance of knowing how the body condition of wild animals changes depending on the life history of the species and environmental factors. However, while poor BCS can be caused by external, as well as internal factors (e.g., lactation), low body condition itself can be a potential factor of health issues in wildlife (Sánchez et al., 2018). Indeed, individuals with poor body condition often suffer from impaired immune and reproductive systems, while also showing lower levels of maintenance or self-care (Acevedo-Whitehouse & Duffus, 2009; Sánchez et al., 2018). While limitations to the use of BCS exist, they are by far outweighed by the advantages brought by camera traps when assessing body condition and other welfare indicators of wildlife (Harvey et al., 2021). The non-invasive, visual method of measuring body condition (e.g., through the use of camera traps) has proven its usefulness in measuring wildlife body condition in a manner that does not cause stress, whether physical or psychological, on the individuals studied.

2.7. WILD ANIMAL WELFARE

Very few studies directly assess wild animal welfare, despite the direct link between welfare and the survival of individuals (Beausoleil et al., 2018; Boys, Beausoleil, Pawley, Betty, et al., 2022; Paquet & Darimont, 2010). While its direct assessment may still be rare for wild animals, wild animal welfare is receiving an increasing amount of attention in the conservation world (Beausoleil et al., 2018; Boys, Beausoleil, Pawley, Betty, et al., 2022; Dubois et al., 2017; Paquet & Darimont, 2010). This could largely be due to the relatively new emergence of the field of conservation welfare, which combines principles from both conservation and animal welfare science (Beausoleil et al., 2018). Animal welfare science emerged in response to growing concerns about the treatment of animals in agriculture, research, and captivity (Fragoso et al., 2023). These concerns and growing interest in animal welfare led to the development of the Five Freedoms, which emphasised the animals' needs to express natural behaviours and be free from suffering (Mellor, 2016). Over time, welfare assessment frameworks evolved and became parts of new fields of research, including conservation welfare, and are now able to be applied to wild animals. Conservation welfare emphasises the importance of considering both the physical fitness and the emotional or mental state of animals (Beausoleil et al., 2018; Harvey et al., 2020), rather than focusing solely on one aspect. This holistic approach, summarised by Beausoleil et al. (2018) as "fitness and feelings, not fitness or feelings" recognizes that an animal's physical health and mental state are linked and both crucial to their overall welfare, with the mental state and experience of an animal representing how they may be experiencing life (Harvey et al., 2020). While mental state is important to an animal’s welfare, due to its subjectivity it cannot be directly measured, however, it can be inferred using measurable indirect indices as part of welfare assessment frameworks (Harvey et al., 2020).

One of the frameworks that allows detailed assessments to be made is the Five Domains Model for assessing animal welfare (Mellor & Beausoleil, 2015; Mellor et al., 2020; Mellor & Reid, 1994). The Five Domains Model was first created in 1994 with the purpose of analysing negative impacts suffered by animals used for research, teaching, and testing (Mellor et al., 2020; Mellor & Reid, 1994). However, it has since been updated and improved a number of times to include new welfare knowledge, including positive welfare rather than only negative (Mellor et al., 2009; Mellor & Stafford, 2001; Mellor, 2004, 2012, 2017; Mellor & Beausoleil, 2015; Mellor et al., 2020). The framework is made up of four physical/functional domains; 1) nutrition, 2) physical environment, 3) health, 4) behavioural interactions which each include specific animal-based indicators related to those domains (Mellor & Reid, 1994). Once those indicators have been assessed, the expected affective consequences, whether positive or negative, are allocated to the fifth domain, mental state (Mellor & Reid, 1994). However, due to the still novel nature of the Five Domains Model in the context of wild animals and conservation, many free-roaming wild species still do not have welfare indicators assigned to them. The first step or phase in research to study the welfare of a species, before affective consequences can be assigned to domain 5, is to identify which indicators (in domains 1-4) can be confidently identified (Harvey et al., 2021). Furthermore, indicators should be species and often context specific (Boys, Beausoleil, Pawley, Betty, et al., 2022). Once a list of observable indicators has been created and scientifically validated, it is then possible to use it to assess welfare.

With the recent increase in attention wild animal welfare for conservation has been receiving, the range of wild animal species covered has been continuously expanding, with research focusing on species including a variety of equid species (Harvey et al., 2023; Mellish et al., 2023; Viksten et al., 2023), and cetacean species (Boys et al., 2023; Boys, Beausoleil, Pawley, Littlewood, et al., 2022; Rae et al., 2023; Serres et al., 2024), as well as octopus (Andrade et al., 2023) and penguins (Nicol et al., 2021). However, in the case of eastern grey kangaroos no study has yet focused on assessing the welfare of wild individuals using frameworks like the Five Domains Model. The welfare of kangaroos is most often mentioned in a management context due to the vast amount of welfare concerns and issues related to programs aimed at controlling kangaroo populations through lethal means (Ben-Ami et al., 2014; Boom & Ben-Ami, 2011; Clarke & Ng, 2006; Descovich et al., 2015; Hampton & Forsyth, 2016; Hing et al., 2019; Ramp, 2013;

Thompson et al., 2022; Wilson & Edwards, 2019). This aligns perfectly with Simmonds (2017) who suggests that wild animal welfare is likely to be given more consideration where direct impacts of human activities can be observed, including through hunting or lethal management, as such impacts are often obvious and easy to see. Hence it is no surprise that wild animal welfare in a climate change context is as of yet given little consideration, however, this consideration is slowly increasing. Detailed welfare assessments can not only provide information to political and ethical debates, they also inform about the ways in which we interact with wildlife (Harvey et al., 2021). Such information may, therefore, be crucial to improve the ways in which kangaroos are perceived and treated. Kangaroos are also known to be susceptible to capture myopathy, indicating a heightened "fight or flight" stress response, highlighting the importance of welfare considerations (Green-Barber et al., 2017). Furthermore, direct welfare assessments will undoubtedly provide vital information about the ways kangaroos and other wild animal species, including threatened and endangered ones, are coping with extreme weather events, particularly with intensifying droughts and heatwaves (Kirono et al., 2020; Trancoso et al., 2020).

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CHAPTER 3: THE IMPACTS OF DROUGHT ON THE HEALTH AND DEMOGRAPHY OF EASTERN GREY KANGAROOS

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Chapter 3 preamble

In chapter 3 I explore the effects of drought on the health and demography of eastern grey kangaroos. Following chapter 2 (literature review), which highlights some of the broader impacts of climate change and extreme weather events on wildlife, here I begin to focus on specific consequences of droughts for eastern grey kangaroos living in semi-arid rangelands. I do so by assessing the impacts of drought on body condition scores, population parameters such as age class and sex, as well as activity rate at waterpoints.

SIMPLE SUMMARY

Eastern grey kangaroos, like most wildlife, are facing an increasingly uncertain future under rapid climate change. How individuals and populations cope with extreme climatic events will influence their capacity to adapt and persist. Here, we analysed how drought impacted eastern grey kangaroo populations by focusing on their body condition, demography, activity rates at water points, and the likelihood of parasitic infections. We found that body condition was lower as environmental conditions became more extreme and that fewer males in the population were observed. The proportion of juveniles within the population increased as more favourable conditions returned. Higher parasite egg burdens in scats occurred in autumn. Our study has shown that the impacts eastern grey kangaroos face during climatic events such as drought can be severe and may have long-term consequences.

ABSTRACT

Extreme climatic events such as droughts and floods are expected to become more intense and severe under climate change, especially in the southern and eastern parts of Australia. We aimed to quantify the relationship between body condition scores (BCS), demography, activity rate, and parasitic infections of eastern grey kangaroos on a large conservation property under different climate extremes by employing camera traps established at artificial water points (AWPs). The survey period (November 2019 to April 2021) included a severe drought, broken by a significant flooding event. Climatic and environmental conditions were documented using remotely sensed indices of moisture availability and vegetation productivity. These conditions were found to affect all health and population parameters measured. BCS, juvenile proportions, and sex ratios were most correlated with 6-month lags in climatic conditions, while the activity rate of kangaroos at AWPs was most correlated with vegetation productivity. The concentration of parasitic eggs in faeces was higher in autumn than in spring. Our study offers a glimpse into some of the impacts of drought on eastern grey kangaroo populations and their health, information that may become increasingly important in today's climate. It further emphasises the importance of this knowledge for wildlife conservation efforts appropriate to managing the impact of climate change alongside other threats.

Keywords: Eastern grey kangaroo; Body condition; Demography; Drought; Climate change; SPEI; NDVI; Parasites

3.1. INTRODUCTION

The global climate is changing at an unprecedented rate, leading to an increase in the frequency and intensity of extreme climatic events and posing significant threat to many wildlife species (Hoffmann & Sgrò, 2011). Natural phenomena such as droughts and floods are expected to become more intense and frequent as the world warms above 1.5 °C pre-industrial levels (Kirono et al., 2020; Vicente-Serrano et al., 2019), due to an intensification of El Niño and La Niña events in many parts of the world (Cai et al., 2021). On top of this, climate change is occurring in a world where wildlife are already facing mounting pressure from a range of anthropogenic activities, including habitat destruction and fragmentation, pollution, pathogens, and overexploitation (Ripple et al., 2019). The persistence of individuals and populations may hinge on their ability to adapt to extreme weather events caused by a changing climate (Milligan et al., 2009), particularly as environments increase in aridity. The capacity for adaptation may disfavour species of temperate or mesic regions rather than species that are already arid-adapted. This may be especially noticeable for species in temperate regions with narrow climatic niches (Ashcroft et al., 2012; Gollan et al., 2014), but extreme events may also have an impact on the ranges of such species that currently extend into semi-arid regions (Seabrook et al., 2011). Furthermore, the global climate is now changing so rapidly that many species simply do not have time to evolve resistance to it (Acevedo-Whitehouse & Duffus, 2009). Understanding how wildlife are affected by events such as droughts and floods is therefore essential for addressing future issues in conservation (Foley et al., 2008).

While population abundance and ecological dynamics are often impacted by environmental change and climate, so are the health and welfare of wildlife (Acevedo-Whitehouse & Duffus, 2009). Direct impacts during heatwaves can result in mass death events (Ratnayake et al., 2019; Welbergen et al., 2008), but the long-term and gradual impacts of drought can lead to immunosuppression, disease susceptibility, and reproductive and developmental decline (Milligan et al., 2009). Reduced health and welfare can lead to a decline in the reproduction rate, skewing demography towards older populations as individuals become more likely to reach advanced life stages without successfully reproducing (Marealle et al., 2010). While extreme conditions are more likely to affect a population, conditions with lower intensity repeated over longer periods can also affect the body condition of individuals (Gardner et al., 2018). Body condition is known to be closely linked to the survival and reproduction rate of many species (Bassano et al., 2003; Pérez-Flores et al., 2016). Poor body condition can impair the immune system, putting individuals at risk of pathogenic and parasitic infections (Acevedo-Whitehouse & Duffus, 2009). Individuals with lower body conditions can also become more vulnerable to predation as they become too weak to flee from predators, or choose to trade costly behaviours such as vigilance for more vital ones such as feeding (Pérez-Flores et al., 2016). While parasite infections are often the cause of poorer body conditions, poor body condition can also make individuals more susceptible to parasite infection (Sánchez et al., 2018). Furthermore, as body condition declines, individuals can suffer from defective immune systems as well as lower levels of maintenance and overall function, further increasing the likelihood of parasitic infection (Klasing, 2007; Sánchez et al., 2018). When food and water become scarce during drought, wildlife will often congregate at resource points in larger numbers than usual, increasing the risk of parasite transmission and outbreaks (Becker et al., 2015; Murray et al., 2016).

In Australia, drought is a pseudo-cyclic phenomenon that has occurred for millennia (Kiem et al., 2016). Under climate change, droughts in Australia are becoming more intense and lasting longer in southern and eastern parts of the country (Kirono et al., 2020). These temperate environments are likely to experience more frequent droughts and increasing aridity. While most anthropogenic structures exert pressure on wildlife, artificial water points (AWPs) may offer much-needed water (Epaphras et al., 2007; Letnic & Crowther, 2013). Similar effects have been observed for water points dug by wildlife themselves (Lundgren et al., 2021). Large herbivores, such as kangaroos, have been observed using AWPs, particularly during hot periods when the vegetation is drier (Montague-Drake & Croft, 2004). However, even though kangaroos may utilize AWPs to drink, there is no evidence that AWPs influence densities or assist with population growth (Lavery et al., 2018; Montague-Drake & Croft, 2004). While dingoes can suppress kangaroo populations through top-down regulation (Wallach et al., 2010), in the absence of dingoes, kangaroo abundance and population dynamics are driven by primary productivity and the availability of food sources (Caughley et al., 1984; Croft & Witte, 2021; Short, 1985). Despite this, access to water from AWPs and natural water sources is likely important for individuals in managing their health during drought (Caughley et al., 1984).

Here, we aimed to detect changes in populations and health parameters of eastern grey kangaroos (*Macropus giganteus*) during two extreme weather events, namely, drought followed by flooding. To do so, we monitored body condition, demography, presence of parasites, and activity rates of eastern grey kangaroos at AWPs on a wildlife reserve in semi-arid south-western Queensland over a period of 18 months. Long-term changes in weather conditions were captured using the standardized precipitation evapotranspiration index (SPEI), which measures the driving effects of temperature on water demand by taking into account the potential evapotranspiration as well as precipitation to determine droughts (Vicente-Serrano et al., 2010), while shorter-term changes in the amount of live green vegetation were captured using the normalized difference vegetation index (NDVI) (Pettorelli et al., 2005). NDVI can quantify vegetation density by using differences in spectrometric data including near-infrared and visible red light reflectance (Pettorelli, 2013), and has previously been used to analyse the relationship between vegetation and wildlife performance (Pettorelli et al., 2011). Eastern grey kangaroos are grazers, and will often select open areas such as grasslands for foraging purposes (Moore et al., 2002; Taylor, 1984), therefore, NDVI should act as a good proxy for the availability and quality of forage used by that species (Pettorelli et al., 2011; Ryan, 2006; Ryan et al., 2012).

We expected that the body condition of individuals would be lower during drier months (i.e., drought), and the use of AWPs would increase due to the lack of moisture in forage. We also predicted that higher body conditions would be observed in times of higher SPEI and NDVI, and that demographic shifts would occur as juvenile kangaroos become more frequent under favourable conditions due to increases in survival rates. Eastern grey kangaroos are seasonal breeders and although they have the capacity to use embryonic diapause – similar to their arid cousin the red kangaroo when environmental conditions decline – they rarely make use of it, meaning they are more likely to wait until conditions become favorable to breed (Dawson, 2012). Despite this, a peak in juvenile proportion in populations is usually observed during the warmer summer months (Lucas et al., 2021), therefore, we also expected that the more favorable summer of 2020-2021 would have a higher proportion of juveniles than the 2019-2020 summer drought.

3.2. MATERIALS AND METHODS

3.2.1. Study Site

The study was conducted on the 480 km^2 Mourachan Conservation Property (MCP) in south-western Queensland, near the township of St George. This private semi-arid rangeland reserve, managed by Australia Zoo, is surrounded by cattle and sheep farms. Although 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 and other wildlife are protected from persecution (Zemanova & Ramp, 2021). The MCP includes four macropod species: eastern grey kangaroos, red kangaroos (*Osphranter rufus*), black wallabies (*Wallabia bicolor*), and red-necked wallabies (*Macropus rufogriseus*). Eastern grey kangaroos are distinguished from the only other large macropod, the red kangaroo, by body color and facial markings. Southern Queensland and most of Australia was in drought for the majority of 2019 due to El Niño, but weather conditions changed at the beginning of 2020, and the MCP was inundated with flood waters in late January 2020. Furthermore, 2019 was the driest year on record for the MCP (Figure 1).

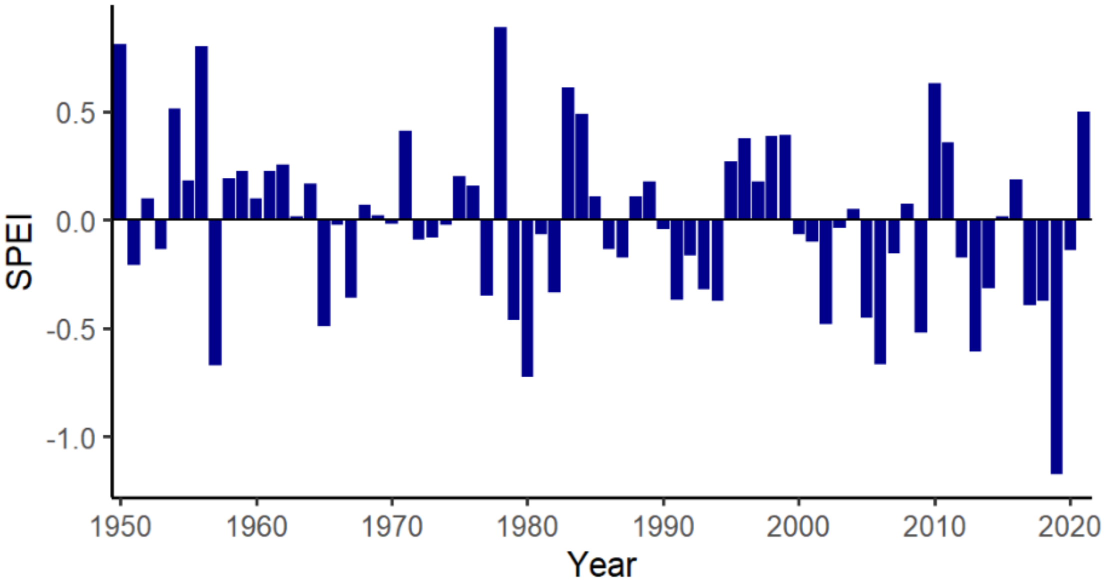

Figure 1. Yearly standardized precipitation evapotranspiration index (SPEI) average for the Mourachan Conservation Property from 1950 to 2021, showing 2019 as the driest year on record. SPEI values can be sorted into five classes: 1. non-drought (>−0.5), 2. mild (between −0.5 and −1), 3. moderate (between −1 and −1.5), 4. severe (between −1.5 and −2), and 5. extreme (<−2) (Paulo et al., 2012).

3.2.2. Camera traps

Camera traps (Strike Force HD Pro X, Browning, Morgan USA) were setup in November 2019 at 15 AWPs distributed across the property (Figure 2). At the time of installation, they were the only available sources of water on the reserve. A total of 40 cameras were used to capture motion-sensed photos from November 2019 to April 2021, leading to a total of 10,736 camera trap days. Some cameras were lost due to being completely submerged during flooding, while some temporal breaks in data capture occurred because of COVID-19 border restrictions that limited access to the site.

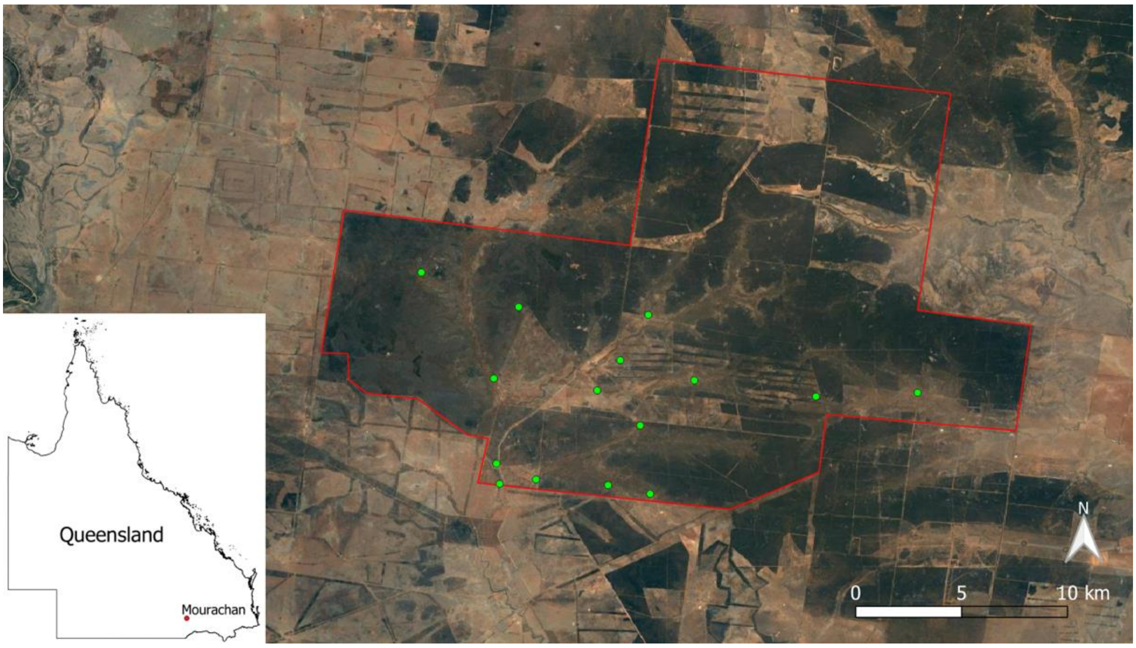

Figure 2. Location of the MCP within Queensland, showing the location of each artificial water point used within the property (green dots).

3.2.3. Body condition score and demography

Eastern grey kangaroos were given a BCS score between 1 and 5, depending on their visual body condition, using a similar method described by Johnston et al. (Johnston et al., 1997). A subjective body condition scoring system was developed using images of eastern grey kangaroos obtained from camera traps by the CfCC over multiple projects (Austin, 2020; Austin & Ramp, 2019) and across different ecosystems from semi-arid to temperate. This allowed the scoring system to not be limited to the current project, or semi-arid nature of the MCP which might skew kangaroos to have a lower body condition due to lower food availability in such ecosystems. Example photos of each score can be found in Appendix A Table A1. Scores were described as: 1 (emaciated), 2 (very thin), 3 (average/thin), 4 (optimal), and 5 (muscular). Images used to score BC were selected based on their quality, mainly relying on the full or most of the body being clearly visible. If more than one individual was present on an image, all kangaroos were scored. Only one image per event (pictures taken within 5 min of each other) was scored. A total of 3993 camera trap images were used. The demographic class of each scored kangaroo was also recorded using the classification references described by Austin and Ramp (2019), using the following categories: pouch young, young-at-foot, sub-adult, small adult, medium adult, and large adult. The sex of each individual was determined using the description in Jarman et al. (1989).

3.2.4. Activity rate

The activity rate of kangaroos was measured to analyse how often they use artificial water points, both during drought and under more favorable conditions. We recorded the total number of daily kangaroo events, defining events as a series of camera trap images captured within 5 min of the previous image, where one or more kangaroos were visible. The number of kangaroos visible on an image did not influence the number of events (i.e., images within 5 min of each other with more than one kangaroo were still counted as a single event). The activity rate here, therefore, does not represent the number of individuals within the population, only how often kangaroos were observed using the AWPs.

3.2.5. Parasitology

Kangaroo scat samples were used to estimate the average Faecal Egg Count (FEC) of the population during drought (2019) and post-flood (2021). Where possible, fresh scat samples were collected directly after observing foraging eastern grey kangaroos. When no kangaroos were present, samples were collected based on the size and shape of the scat (Power et al., 2005). We validated that the scats collected in November 2019 were from eastern grey kangaroos through genetic analysis (Zemanova & Ramp, 2021). Samples were collected from each AWP in November 2019 (spring) and stored at −20 °C. It should be noted that storage at −20 °C can lead to some loss of eggs in the scats due to biological degradation (Nielsen et al., 2010). Samples were also collected in April 2021 (autumn). FECs were performed by mixing 3 g of a scat sample in 60 mL of saturated salt solution. Eggs were counted using a Whitlock Universal 4 chamber worm egg counting slide (J.A. Whitlock and Co, Eastwood, Australia), following the methods described by Gordon and Whitlock (Gordon & Whitlock, 1939).

3.2.6. Statistical analysis

Generalised linear mixed models (GLMM) were used to analyse the effects of climatic conditions and primary productivity on the body condition, demographic classes, and activity rate of the population. Models for body condition and activity rate used a Poisson distribution, while demography used a binomial distribution as demography was measured as presence/absence of male and juvenile for each event observed, all models used camera trap location as a random variable. GLMMs were used due to their flexibility when handling random variables present in our data collection (camera location) and for their ability to work with data not normally distributed as is often the case in ecological studies (Bono et al., 2021), and test the relationship between variables: kangaroo based data (BCS, demography) and environmental data (SPEI, NDVI). SPEI values were used to represent long-term trends and were, therefore, used with lags of 3, 6, and 12 months to represent a quarter of a year, half of a year, and a full year. NDVI was used to represent more immediate and short-term changes in health and population parameters related to primary productivity and was, therefore, used with a monthly lag. SPEI time series was downloaded from the SPEI Global Drought Monitor using the MCP as a single grid cell (Begueria et al.). We used a polygon of the MCP as a mask to select tiles and obtain monthly NDVI values from the MODIS Terra NDVI composites (Didan, 2015). We calculated R squares to measure the correlation between environmental conditions (SPEI, NDVI) and activity rate at waterpoints, demographic classes, and BCS. A t-test was performed to compare the Fecal Egg Count from scats between November 2019 and April 2021.

All GLMMs were performed in R v4.1.1 (R Foundation for Statistical Computing, Vienna, Austria) (R Core Team, 2023) using the "glmer" function of the "lme4" package (Version 1.1-27.1) (Bates et al., 2015).

3.3. RESULTS

3.3.1. BCS and demography

There was a moderately strong positive relationship between SPEI and BCS, with the 3-month lag (SE = 0.011, z = 13.93, *p* = <0.001, and r = 0.6) and 12-month lag (SE = 0.009, z = 14.86, *p* = <0.001, and r = 0.57) showing similar patterns (Figure 3). However, a stronger relationship was observed between BCS and SPEI with a 6-month lag (SE = 0.013, z = 15.35, *p* = <0.001, and r = 0.87). Similarly, NDVI was also shown as being significantly correlated with BCS (SE = 0.156, z = 12.046, *p* = <0.001, r = 0.8) (Figure 3).

SPEI with a 3-month lag (SE = 0.047, z = 8.612, *p* = <0.001, and r = 0.54) and a 12-month lag (SE = 0.037, z = 10.11, *p* = <0.001, and r = 0.62) were found to have the strongest effect on the sex ratio of the population, with fewer males observed using AWPs during drier conditions. SPEI values with a 6-month lag (SE = 0.051, z = 7.527, *p* = <0.001, and r = 0.14), and NDVI values (SE = 0.634, z = 5.643, *p* = <0.001, and r = 0.21) were found to have the weakest relationships with sex ratio. The sex ratio balanced out with the return of more favorable conditions (Figure 4A, B).

The monthly juvenile to adult ratio of the MCP population visiting AWPs had a relatively weak relationship with SPEI at 3-month lags (SE = 0.065, z = 7.896, *p* = <0.001, and r = 0.18), and NDVI (SE = 0.863, z = 5.48, *p* = <0.001, and r = 0.14). Stronger effects came from SPEI with longer term lags, as shown by values with a 6-month lag (SE = 0.079, z = 11.824, *p* = <0.001, and r = 0.23) and a 12-month lag (SE = 0.081, z = 14.767, *p* = <0.001, r = 0.31).

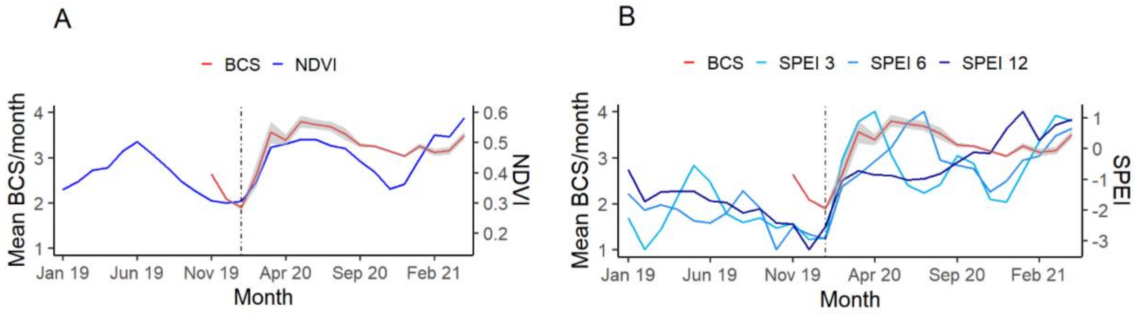

Figure 3. Temporal changes in the mean body condition score (BCS) of eastern grey kangaroos; environmental conditions represented by the Normalized Difference Vegetation Index (NDVI) (**A**); and standardized precipitation evapotranspiration index (SPEI) with a 3, 6, and 12-month lag (**B**). The black reference line represents the January 2020 floods and the end of the 2019-2020 drought. The shaded confidence interval around BCS represents the standard error of the mean.

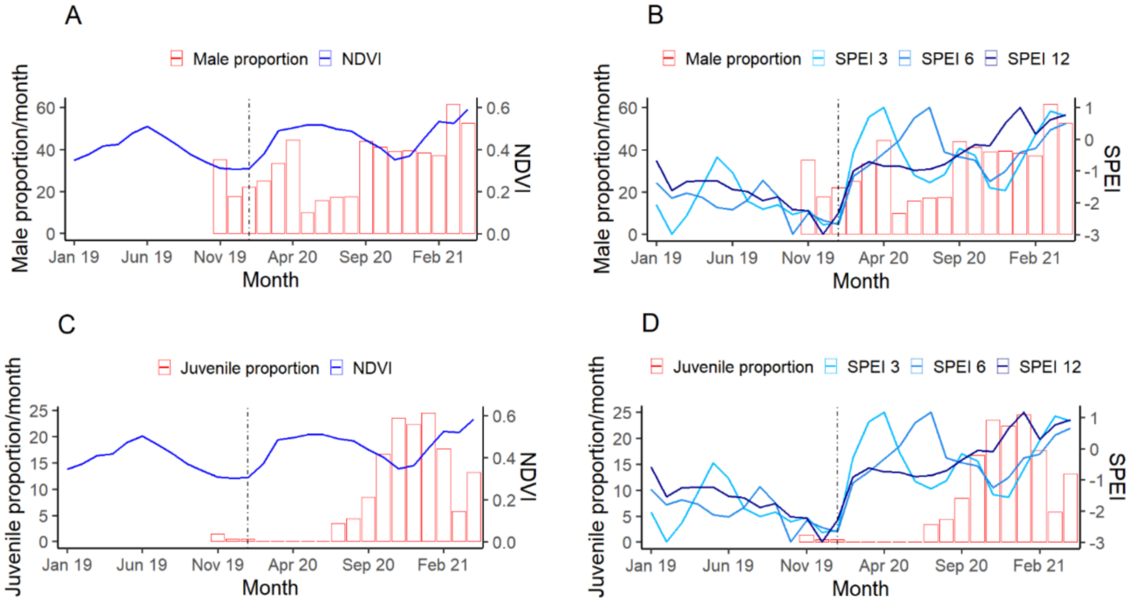

Figure 4. Temporal changes in the monthly proportion of male eastern grey kangaroos within the observed population compared to the normalized difference vegetation index (NDVI) **(A)**; standardized precipitation evapotranspiration index (SPEI) with a 3, 6, and 12-month lag **(B)**; and proportion of juvenile kangaroos compared to NDVI (**C**) and (SPEI) (**D**). The black reference line represents the January 2020 floods and the end of the 2019 drought.

3.3.2. Activity rate

Activity rates of eastern grey kangaroos significantly declined at AWPs as weather and vegetation indices increased after the drought broke (SPEI with a 3-month lag SE = 0.013, z = −72.00, p = <0.001, r = −0.72, a 6-month lag SE = 0.013, z = −71.286, p = <0.001, r = −0.75, a 12-month lag SE = 0.01, z = −63.667, p = <0.001, r = −0.59 and NDVI SE = 0.194, z = −69.01, p = <0.001, and r = −0.77). This shows that drier conditions increased the likelihood of kangaroos accessing AWPs (Figure 5A, B).

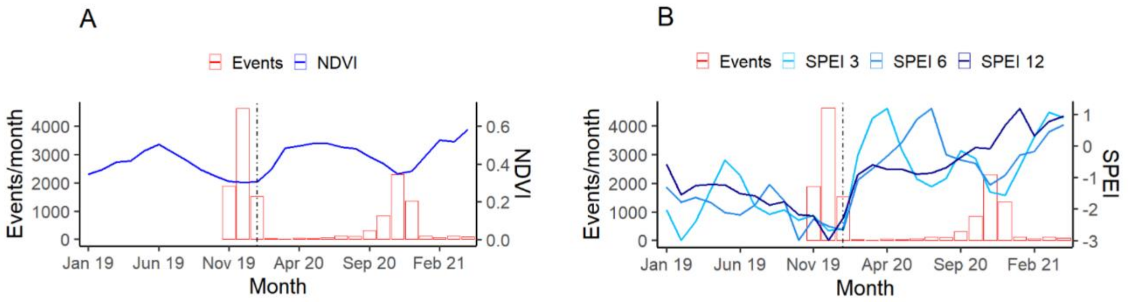

Figure 5. Temporal changes in the number of eastern grey kangaroo events per month compared to shifts in environmental conditions represented by **(a)** the normalized difference vegetation index (NDVI), and **(b)** standardized precipitation evapotranspiration index (SPEI) with a 3, 6, and 12-month lag. The black reference line represents the January 2020 floods and the end of the 2019 drought.

3.3.3. Parasitology

Fecal egg counts for April 2021 (post-flood) were found to be significantly higher than November 2019 (drought) (df; degrees of freedom = 41.971, t = −3.644, *p* = 0.001) (Figure 6). All eggs observed were identified as *Strongyle* eggs.

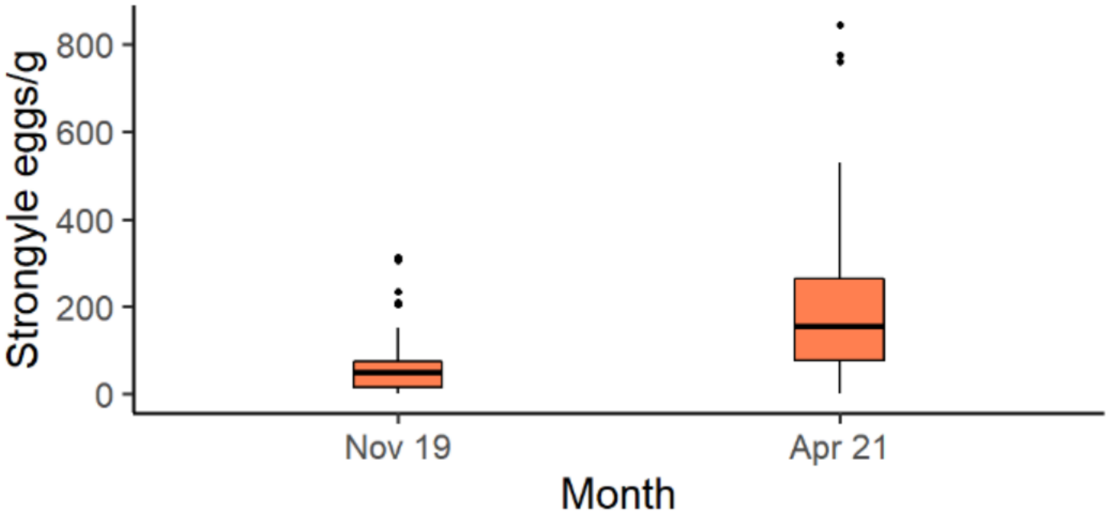

Figure 6. Number of Strongyle eggs per gram of kangaroo feces for samples collected in November 2019 during the drought ($n = 82$), and in April 2021 ($n = 42$). Outliers are represented by dots. BCS: body condition score

3.4. DISCUSSION

We found that the body condition of eastern grey kangaroos was negatively correlated with environmental factors measured using SPEI and NDVI. As both SPEI and NDVI increased, leading to more favorable conditions, the body condition of kangaroos increased. We also found that the SPEI data with a 6-month lag had the strongest relationship with BCS. However, this does not suggest that NDVI values cannot be used to predict a relationship between BCS and primary productivity since a correlation of r = 0.8 was found between NDVI and BCS. In other species, such as the roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), NDVI was found to be a strong predictor of body mass (Pettorelli et al., 2006; Pettorelli et al., 2011). NDVI has also been shown to influence the body condition and reproductive timing of the African buffalo (*Syncerus caffer*) and African elephant (*Loxodonta africana*) (Ryan et al., 2012). Poor body condition of animals during drought is thought to be one of the major causes of deaths (Knight, 1995). For example, Knight (Knight, 1995) found that 90% of fresh carcasses (of four species of ungulates) found during droughts in the southern Kalahari had poor body conditions. In Australia, the body condition of the southern hairy-nosed wombat (*Lasiorhinus latifrons*) is closely related to food availability and quality (Gaughwin et al., 1984). Kangaroos often choose greener, more nutritious vegetation, resulting in high mortality rates during drought when such resources are not available (Moss & Croft, 1999). Poor body condition often leads to adverse health effects such as lower immune responses due to impaired immune systems, increasing infection likelihood while lowering resistance (Acevedo-Whitehouse & Duffus, 2009). This can also impair nutrient uptake and lead to poor nutritional status (Katona & Katona-Apte, 2008). Nutritional and hydrological stresses, such as drought, are known to affect other processes such as growth and reproduction, over and above increased mortality during these events (Houston et al., 2007).

The sex ratio of eastern grey kangaroos visiting AWPs at Mourachan shifted during drier months, with fewer males being observed when environmental conditions were poorer (Figure 4A, B). However, the increase in males observed post flood did not result from juvenile male births but from the adult individuals. This could suggest that some of the males were alive during the drought but simply did not use the water points as much as the females did. Previous studies on the mortality of kangaroos during droughts have reported that males had a higher mortality rate than females (Norbury et al., 1988; Robertson, 1986), which manifested itself through all age classes and is thought to have been caused by the differences in energetic costs, body size, and mobility between the sexes (Norbury et al., 1988). As the sex ratio of eastern grey kangaroos in our study returned quickly to parity and was not driven by recruitment, it is likely that behavioral decisions may explain this trend. However, observations over multiple dry seasons would be needed to confirm this trend, and whether abnormally dry periods like the 2019 drought are more likely to be the cause.

The proportion of juvenile kangaroos within the population increased as environmental conditions improved post drought and exhibited a stronger relationship with longer-term data (SPEI 6 and 12) than short-term (Figure 4D). Reproduction in kangaroos is driven by biological and ecological constraints. Gestation period in this species is approximately 36 days (Poole & Catling, 1974) and is influenced by the mother's health and climatic conditions. Reproduction is more successful when females have a high BCS (Moss & Croft, 1999). Juvenile kangaroos represented less than 2% of observations at the height of the drought and were absent until July 2020, four months after the floods (Figure 1). For many mammal species, the energy requirements of reproduction can lead to a reduction in female body mass (Clutton-Brock et al., 1982), requiring females to feed more to compensate for the energy allocated towards reproducing (Jönsson, 1997). Further, eastern grey kangaroos are seasonal breeders and embryonic diapause is rare (Dawson, 2012), meaning that response to favorable conditions may be delayed as individuals take time to improve body condition and synchronize with typical reproductive cycles. Under the favorable conditions at Mourachan that began in autumn 2020, the proportion of juveniles gradually increased and peaked at the beginning of summer 2020/2021, where they comprised around 25% of observations, matching with the findings by Lucas et al. (2021) who reported the highest proportion of eastern grey juveniles for their study between the months of September and December. However, despite generally good conditions in the summer of 2020/2021, observations of juveniles declined to around 5% as summer progressed, possibly due to juvenile mortality as they are more vulnerable to higher temperatures and a lack of moisture in vegetation than adults (Ben-Ami et al., 2014; Shepherd, 1987). In previous studies, juveniles and older kangaroos have been shown to be the first to die during droughts (Robertson, 1986).

For arid-adapted macropod species, such as the red kangaroo (*Osphranter rufus*), rearing juveniles can cost the mother as much as 50% of her own daily energy requirement for maintenance near the end of the juvenile's pouch stage (Moss & Croft, 1999). If environmental conditions are favorable and the condition of mothers is high, up to 85% of pouch young can make it to the weaning stage (Frith & Sharman, 1964; Moss & Croft, 1999). During drought, the costs of caring for young can often surpass the daily energy intake of the mother, leading to higher rates of juvenile mortality (Renfree & Tyndale-Biscoe, 1973). Red kangaroo mothers have the adaptive advantage of suspending embryonic development (embryonic diapause) while environmental conditions are poor (Moss & Croft, 1999), a trait that has evolved to promote survival under arid conditions (Dawson, 2012). Without this advantage, grey kangaroos are less resilient to drought conditions. It remains to be seen whether eastern grey kangaroos under increasing aridification can utilize diapause more commonly than current evidence suggests. What is apparent, however, is that red kangaroos may be physiologically better suited to survive droughts than eastern grey kangaroos (Dawson et al., 2007).

We also found that environmental conditions affect the activity rate of kangaroos at artificial water points, with more events occurring during the 2019 drought when significantly less water and live green vegetation was available across Mourachan (Figure 5). Eastern grey kangaroos access water points to drink before returning to a more favorable grazing site (Montague-Drake & Croft, 2004), while food availability is a greater driver of dispersion and density. Kangaroos living in rangelands often drink at AWPs, especially during summer when vegetation availability and moisture content are low. As growing vegetation became available after the flood, we found that kangaroos spread out and were less reliant on AWPs. Wildlife activity in semi-arid and arid ecosystems is often focused around sources of water, but while AWPs were originally thought to increase the abundance and density of kangaroos (Dawson et al., 1975), it has now been accepted that AWPs do not influence their density (Letnic & Crowther, 2013). In accordance with this, we suggest that changes in activity rates at AWPs at Mourachan were likely a response of changing physiological requirements due to the lack of moisture in vegetation, a circumstance that may become more challenging as droughts are predicted to become more frequent and intense.

The fecal egg count data revealed that the number of eggs per gram of scat was significantly higher in autumn than in spring, suggesting cooler, wetter conditions could be more favorable to parasites such as strongyles (Figure 6B). Kangaroos naturally carry a variety of gastrointestinal parasites (Cripps et al., 2013); however, strongylid nematodes are the most abundant in eastern grey kangaroos (Beveridge & Arundel, 1979; Cripps et al., 2013). Juvenile kangaroos are the most at-risk, especially from trichostrongylid nematodes such as *Globocephaloides trifidospicularis*. Parasite infections in eastern grey kangaroos are more prevalent in winter during wetter conditions (Cripps et al., 2015). While the post-flood samples were not collected in winter, the flood would have created conditions more suited to parasites than the drought (Beveridge & Spratt, 2015). Floods can also bring in more parasites such as *Fasciola hepatica*, which use freshwater snails as intermediate hosts (Beveridge & Spratt, 2015). While we cannot attribute differences in parasite load to drought/flood cycles because we were unable to replicate sampling to accommodate seasonal or annual trends, we nevertheless note the potential for changes in patterns of parasite prevalence to impact on the parasite burden of kangaroos, which may be heightened by increasing extreme conditions.

3.5. CONCLUSION

The impacts on the health and demography of eastern grey kangaroos identified in this study are only some of the effects caused by environmental events such as droughts. While droughts have been a part of Australia's climate for thousands of years (Kiem et al., 2016), predictions of increasing prevalence are concerning. Droughts in the southern and eastern regions of the country are expected to last longer, while reaching more extreme intensities due to the intensification of El Niño and La Niña events (Cai et al., 2021). Much of the wildlife in Australia has evolved with droughts; however, rapid changes in global climate may reduce the resistance of many species to droughts (Acevedo-Whitehouse & Duffus, 2009). Species such as kangaroos may suffer from poorer body conditions, leading to an increased risk of infections by parasites (Sánchez et al., 2018). Lower body condition could also lead to lower birth rates due to the poor fitness of females, while juveniles may have higher mortality rates (Moss & Croft, 1999). These challenges, along with current threats from human activities (Ben-Ami et al., 2014; Ramp, 2013), may contribute to further declines in kangaroo populations. From a global perspective, climate change causes new challenges for wildlife conservation. It is therefore essential to understand how wildlife is affected by climate change to address this issue (Foley et al., 2008). To improve our knowledge of the impacts of climate change on eastern grey kangaroos, longer term studies located in different ecosystems would be required to cover more populations. While our study showed a contrast between drought and flood, it only covered one drought/flood cycle; a longer project would, therefore, allow for the comparison of multiple cycles and could further clarify patterns we have found. Studies covering a longer period would also allow for the collection of data on parameters such as the growth rate and survival of juvenile kangaroos, while also enabling yearly comparisons of the reproduction rate, BCS, and demography of populations.

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3.6. APPENDIX A

Table A1. Descriptions and examples of the Body Condition Scores used in the study.

BCS	Description	Example camera trap photos
5 (Muscular)	Thick tail with a large base. Moderate fat cover on body. Muscle definition highly visible across most of the body, especially biceps and forearms, chest, and legs.	
4 (Optimal)	Thick base of tail. Hips covered by fatty tissue. Ribs not visible. Hips well covered with no visibly sunken area or bones protruding. Muscle mass well developed with generally minimal fat cover on the body.	

3 (Average/Thin)	Tail appears thin but no caudal vertebrae are visible. Some ribs may be visible, but rib cage area mostly covered. Hips generally well covered. Muscle mass somewhat visible. No visible fat cover across the body.	
2 (Very thin)	Most caudal vertebrae visible, giving the tail a bony appearance. Tail base skinny. Hip region mostly without fat or muscle tissue cover, creating sunken appearance above the femur (as seen in the visual example). Most ribs visible (easily distinguishable on individuals with shorter fur as pictured here).	
1 (Emaciated)	Caudal vertebrae visible, giving the tail a bony appearance. Base of tail appears skinny. Hip region not covered by fatty tissue and sunken in appearance. All ribs visible (may be difficult to distinguish if the individual has longer fur as pictured here).	

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CHAPTER 4: THERMOREGULATION STRATEGIES DIFFER FOR LARGE MACROPODS DURING HIGH TEMPERATURES

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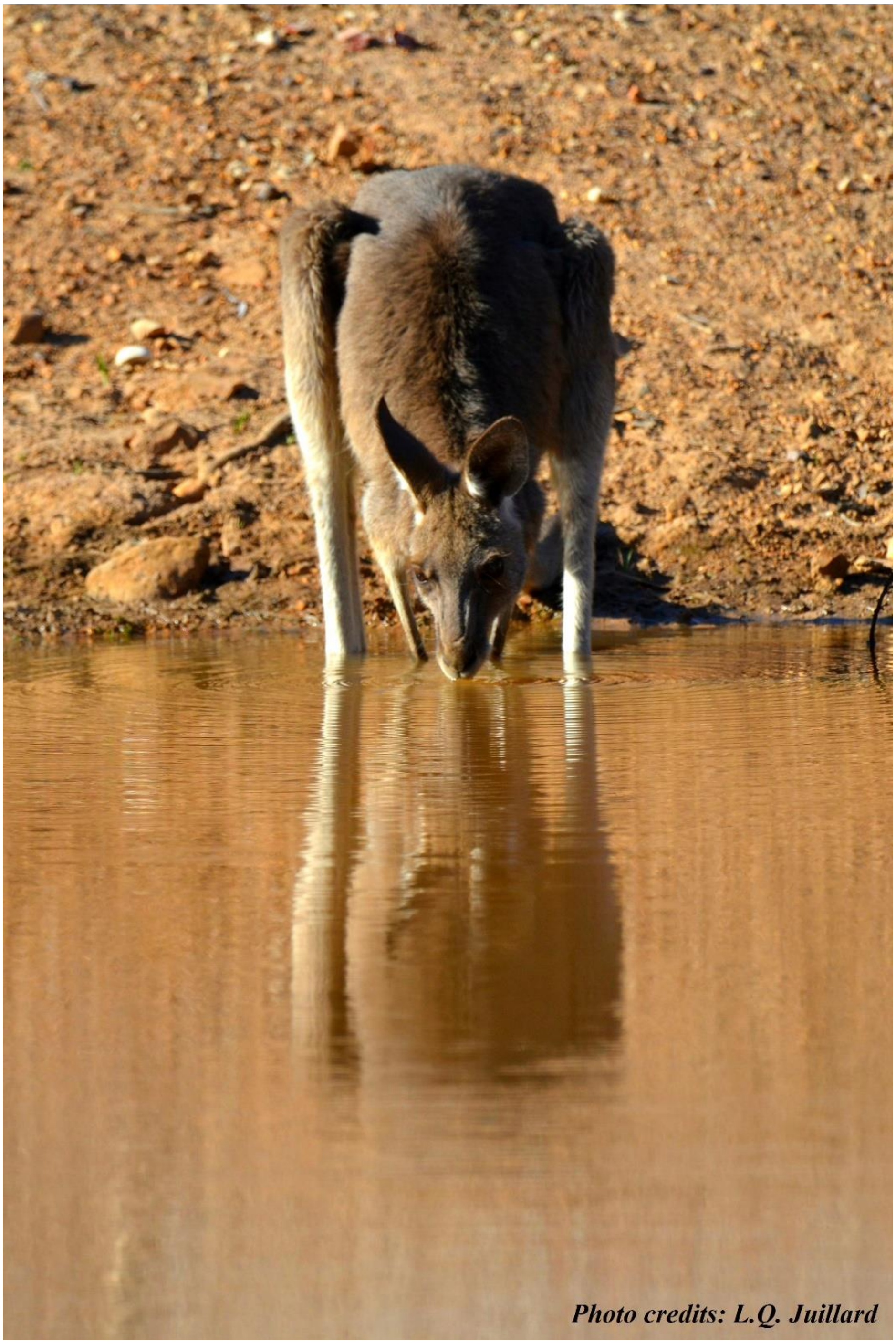

Chapter 4 preamble

While in chapter 3 I focused on the impacts of drought on eastern grey kangaroos, in this chapter I focus on daily temperatures (i.e., maximum daily temperature) and the presence of eastern grey kangaroos in shade and at waterpoints during days of high heat, also comparing them to the red kangaroos of Mourachan due to red kangaroos being a more arid adapted species. I show that eastern grey kangaroos significantly increased their activity at waterpoints, showing a preference for dammed natural watercourses compared to artificial waterpoints. Red kangaroos had a much weaker relationship between activity at waterpoints and heat, however, were more likely to be found in the shade than eastern grey kangaroos. The findings here are then used in chapter 5 to understand how increasing temperatures affect kangaroo-dingo interactions at waterpoints.

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 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 depend on the provision and maintenance of landscape features such as water and canopy shade.

4.1. INTRODUCTION

The mechanisms by which body temperature (T_B) is regulated are critical factors in biological and ecological processes. Homeothermic animals have a range of ambient temperatures within which they function optimally, called the Thermoneutral Zone (TNZ) (Norris & Kunz, 2012). Within the TNZ, maintenance of T_B is possible without increasing metabolic heat production or engaging in energy-intensive behaviours to cool down or heat up. As temperatures exceed the TNZ, significant increases in metabolic energy are required to maintain T_B through physiological and behavioural adaptations, including sweating, seeking cooler external environments, and reducing engagement in activities that would otherwise expend additional metabolic energy. Not maintaining optimal T_B for sustained periods can lead to overheating and potential heat stroke (Norris & Kunz, 2012), severe physiological issues from metabolic stress including nutrient depletion, fatigue, and organ stress, as well as decline in cognitive function which can affect survival and reproduction (Soravia et al., 2021). Chronic heat stress can also compromise immune function, lowering the ability to respond to infection and illness (Acevedo-Whitehouse & Duffus, 2009). 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 across their range (Buchholz et al., 2019; Li & Chen, 2024).

Thermoregulatory strategies are likely to become increasingly indispensable survival mechanisms for many wild animals as higher mean and maximum daily temperatures become more frequent. While the susceptibility of many species population to collapse during extreme heat is increasingly being noted, for example in populations of flying-foxes in Australia (Welbergen et al., 2008), less is known about the behavioural and physiological adaptations that enable individual kangaroos to remain within their thermoneutral zone, mitigating heat stress and resultant morbidities. 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 to manipulate their environment, like fennec foxes (*Vulpes zerda*), burrow underground when temperatures reach levels too high (Geffen & 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). Accessing below-ground water sources is a strategy that many species utilise to obtain drinking water, particularly equids, when water is scarce (Lundgren et al., 2021). 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).

Habitat features that provide shade enable animals to avoid direct solar radiation and select cooler microclimatic conditions, helping to manage heat stress and assist the body in maintaining an optimal T_B. Indeed, many land-based mammal species seek shelter from solar radiation by using the shade provided by trees (Terrien et al., 2011), while for species such as koalas (*Phascolarctos cinereus*) trees can act as crucial microhabitats through the provision of shelter against the sun, of food, water, and surfaces cool enough to support thermoregulation (Briscoe et al., 2014; Crowther et al., 2014; Mella et al., 2024; Mella et al., 2020). The presence of trees and green spaces in urban landscapes are increasingly being recognised as important features in reducing heat island effects, brought on by energy storage from heat in artificial surfaces, like concrete and bitumen (Gunawardena et al., 2017). Human health and wellbeing in cities are intrinsically linked to mitigation of heat buildup (Jay et al., 2021). Similarly, tree canopies provide significant respite from high temperatures, with temperatures often orders of magnitude lower (Ashcroft et al., 2012). Loss of shading from trees resulting from disturbance not only affects individuals as they are unable to seek respite from solar radiation, but also alters how communities of individuals (both within and between species) adjust to the loss (Testard et al., 2024). While entire microclimates are altered by canopy trees in ecosystems like rainforests , dryland ecosystems often only have sparse tree and shrub coverage, reducing the overall footprint of their mitigating potential. For dryland fauna the importance of tree canopies in enabling thermoregulatory behavioural strategies is relatively unknown.

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 (Albert et al., 2023; Ellwanger et al., 2020). Of drylands globally, 10 to 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 T_B through immersion. 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). When accessible, 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 (Figure 1) (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 bathing and immersion.

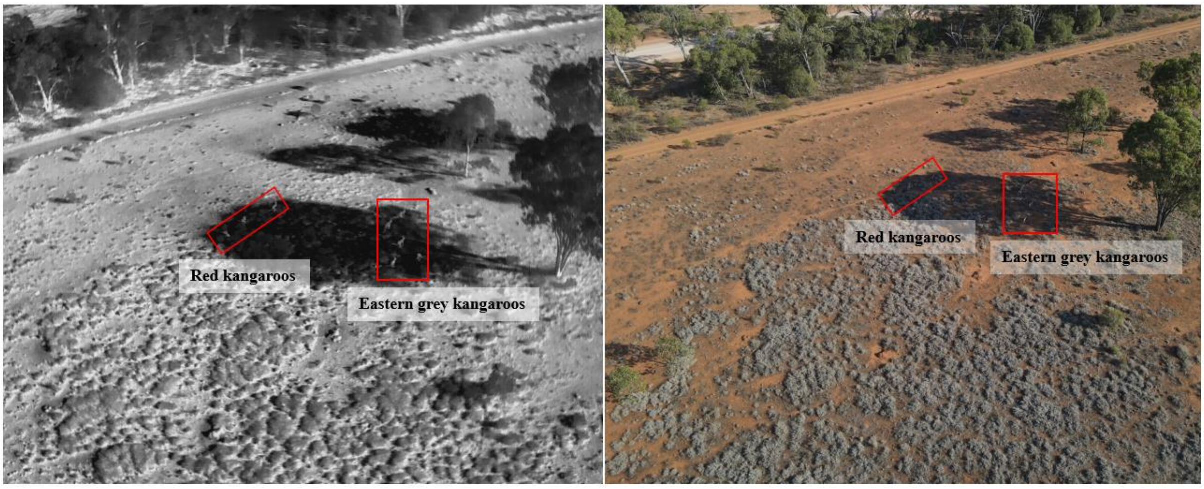

Figure 1. Left: TIR, and **right:** RGB image of red kangaroos and eastern grey kangaroos standing in the shade of a tree of the Mourachan property (*photo credits: L.Q. Juillard*).

Despite these behavioural adaptations, past research on exploring the TNZ of kangaroos has found that individuals were relatively tolerant of short-term increases in temperature during controlled captive experiments (Dawson, Blaney, et al., 2000; Dawson, Munn, et al., 2000). Given that climate warming is already driving increases in temperature extremes in Australia's drylands, coupled with continuing canopy clearance across this ecosystem (Hernandez et al., 2024), our goal was to assess how kangaroos behaviourally adjust to high temperatures in field conditions. To achieve this, we monitored shade and water use in kangaroos over two seasons – winter and summer – to record how individuals of the more temperate eastern grey kangaroos and arid-tolerant red kangaroos adjusted their exposure to the sun by using trees at various temperatures. It appeared reasonable to assume, based on knowledge of the thermoregulation strategies of macropods (Croft, 1980; Dawson et al., 2006), that eastern grey kangaroo may rely more on tree canopies for shade than red kangaroos (Dawson et al., 2007). However, we were also aware from our past research that eastern grey kangaroos increase use of waterpoints in higher temperatures (Juillard & Ramp, 2022), which may alter their reliance on canopy shade as temperatures increase. Hence, we also recorded the use of waterpoints by kangaroos throughout the study while also measuring differences in activity rate between dammed watercourses and tanks of the property.

4.2. METHODS

4.2.1. Study site

This research was conducted on the 480 km^2 Mourachan Conservation Property (MCP) in south-western Queensland, near the township of St George (Figure 2). 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 familiaris 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 hotter 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 (Figure 3). 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).

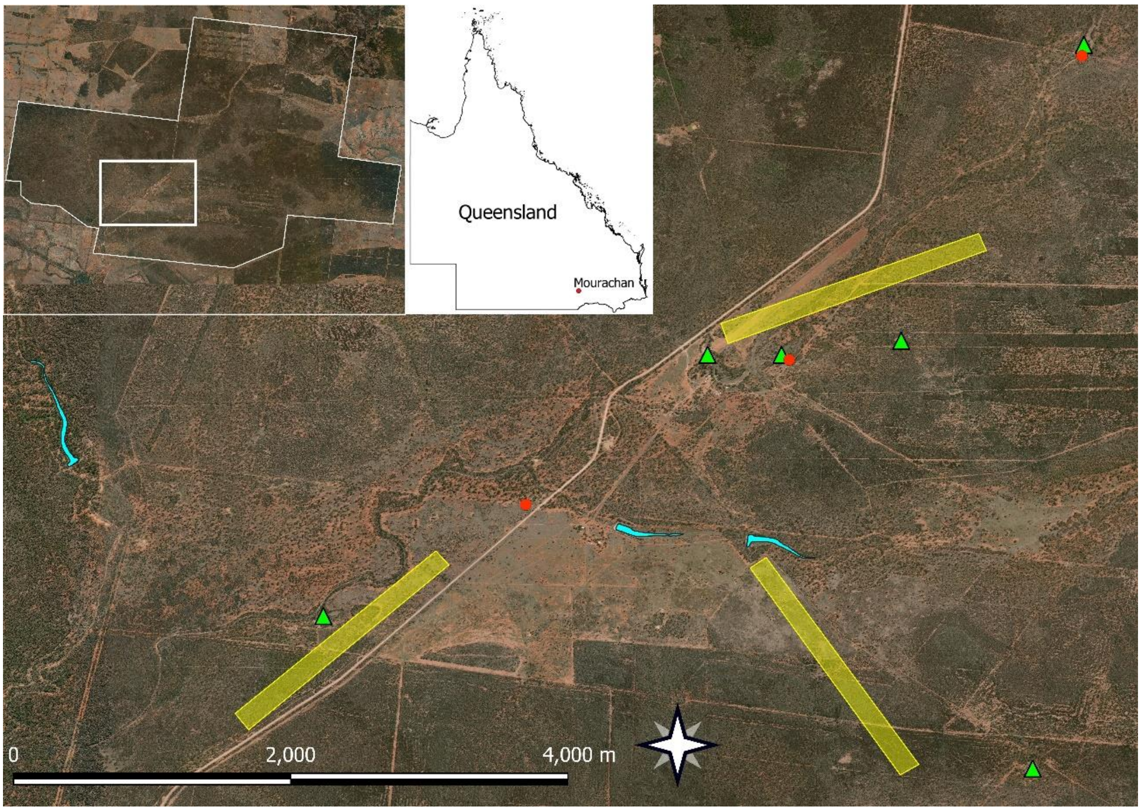

Figure 2. Zoomed-in transect zone with satellite imagery of the Mourachan property where the study was conducted showing its location within Queensland, Australia. The yellow rectangles represent the area covered by each 2km long drone transect (28.4 ha). Blue polygons show the location and area of dammed watercourses with camera traps, while green triangles show the location of tanks with camera traps. Tanks are not shown as polygons due to their size being too

small to be visible on the presented map. The red dots show the location of the three sites where iButtons were deployed.

Figure 3. Drone photograph of a dammed watercourse at the Mourachan property, the dam wall is visible at the bottom of the picture and marked by a red line. The natural "tail" of the waterpoint can clearly be seen extending away from the dam wall with flat ground on the sides covered in grass giving wild animals easy access to the water as well as food (*photo credits: Loic Q. Juillard*).

4.2.2. 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 the property from January 2023 to October 2023 with four iButtons at each site. With grasses usually being the preferred food source of kangaroos (Montague-Drake & 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 grass (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 (Figure 4). 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 (Figure 4). 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.

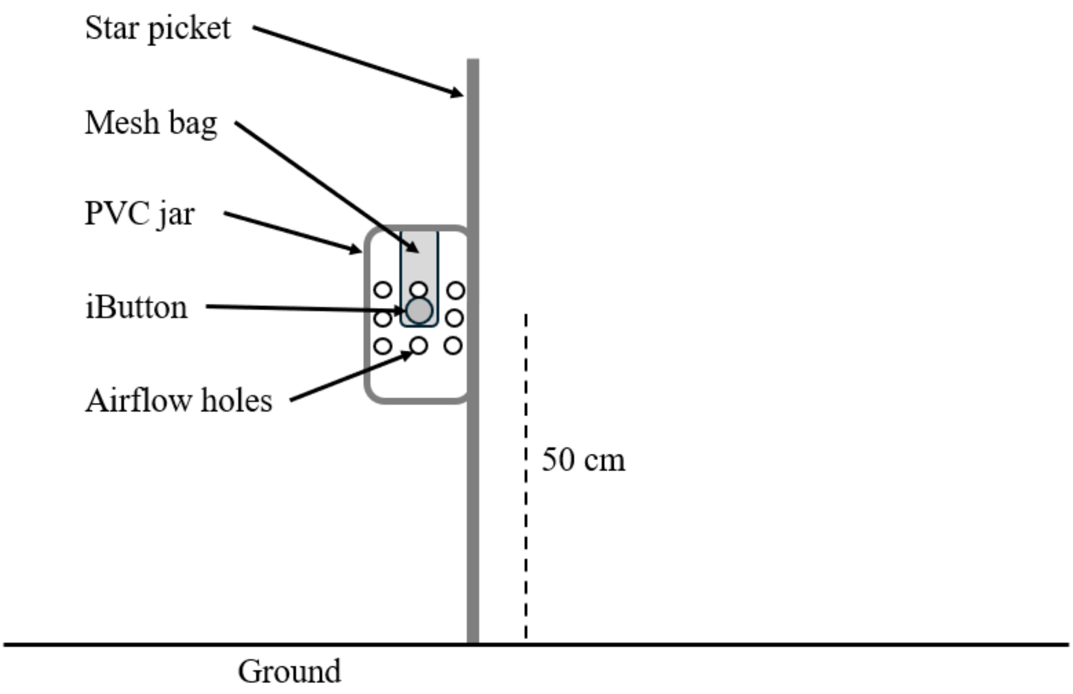

Figure 4. Diagram of iButton setup, showing the perforated PVC jar containing the iButton. The iButtons were deployed 50cm above the ground. The iButtons were placed in a fine mesh bag attached to the top of the jar so that they would hang in front of the holes, allowing airflow to reach the sensors.

4.2.3. Kangaroo surveys

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 infrared camera between the 27th and 29th of July 2023 (July mean daily temperature = 12.2°C, mean daily maximum temperature = 23.3°C) and 20th and 22nd of October 2023 (October mean daily temperature = 22.8°C, mean daily maximum temperature = 34.5°C). 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 metres per second with the camera positioned at a 30-degree angle (Figure 5). The transects were 2km long and covered an area of 28.4 hectares (Figure 2). Placement of the transects was targeted towards open grasslands with sparse canopy cover to match the landcover represented by the iButtons (Figure 6).

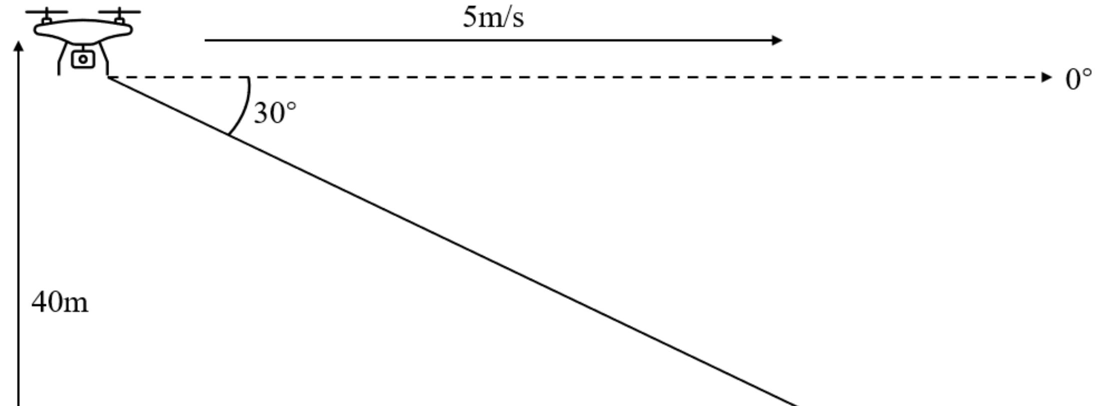

Figure 5. Diagram of drone transect settings

Each transect was flown every 2 hours from sunrise to sunset to cover most of the daily temperature spectrum, resulting in a total of 36 flights. We flew the drone manually and 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. We then 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, with kangaroos in the sun measured as binary data (presence/absence) for both species. Transect location and date of flights were added to the models as random variables.

Figure 6. Grassland of the Mourachan property composed mainly of tussock grasses such as buffel grass (*Cenchrus spp.*), trees are scattered throughout offering shade cover to wildlife (*photo credits: Loic Q. Juillard)*.

4.2.4. Activity rate at waterpoints

Using camera traps (Browning Strike Force HD Pro X) deployed at waterpoints on the MCP from January 2023 to October 2023 (Figure 2), 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 minutes of the previous image. The property including both dammed watercourses and tanks we deployed cameras at each waterpoint type, allowing us to assess potential differences in the use of waterpoints by the kangaroos. We performed Generalised Additive Models (GAMs) to assess the relationship between maximum daily temperature and kangaroo activity at waterpoints using the "mgcv" package (v1.9-1) (Wood, 2015). We used GAMs due to their higher flexibility than other models in dealing with potential non-linearity in the data (e.g., number of kangaroo visits at waterpoints across a temperature gradient). We modelled the number of visits by eastern grey kangaroos and red kangaroos at both waterpoint types as a function of maximum daily temperature using a Poisson distribution. All statistical analyses of our work were carried out in R v4.3.2 (R Core Team, 2023).

4.3. RESULTS

Maximum ambient air temperatures recorded in open grasslands of the MCP 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 (Figure 7a). In contrast minimum ambient air temperatures recorded in open grasslands of the MCP 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 (Figure 7b).

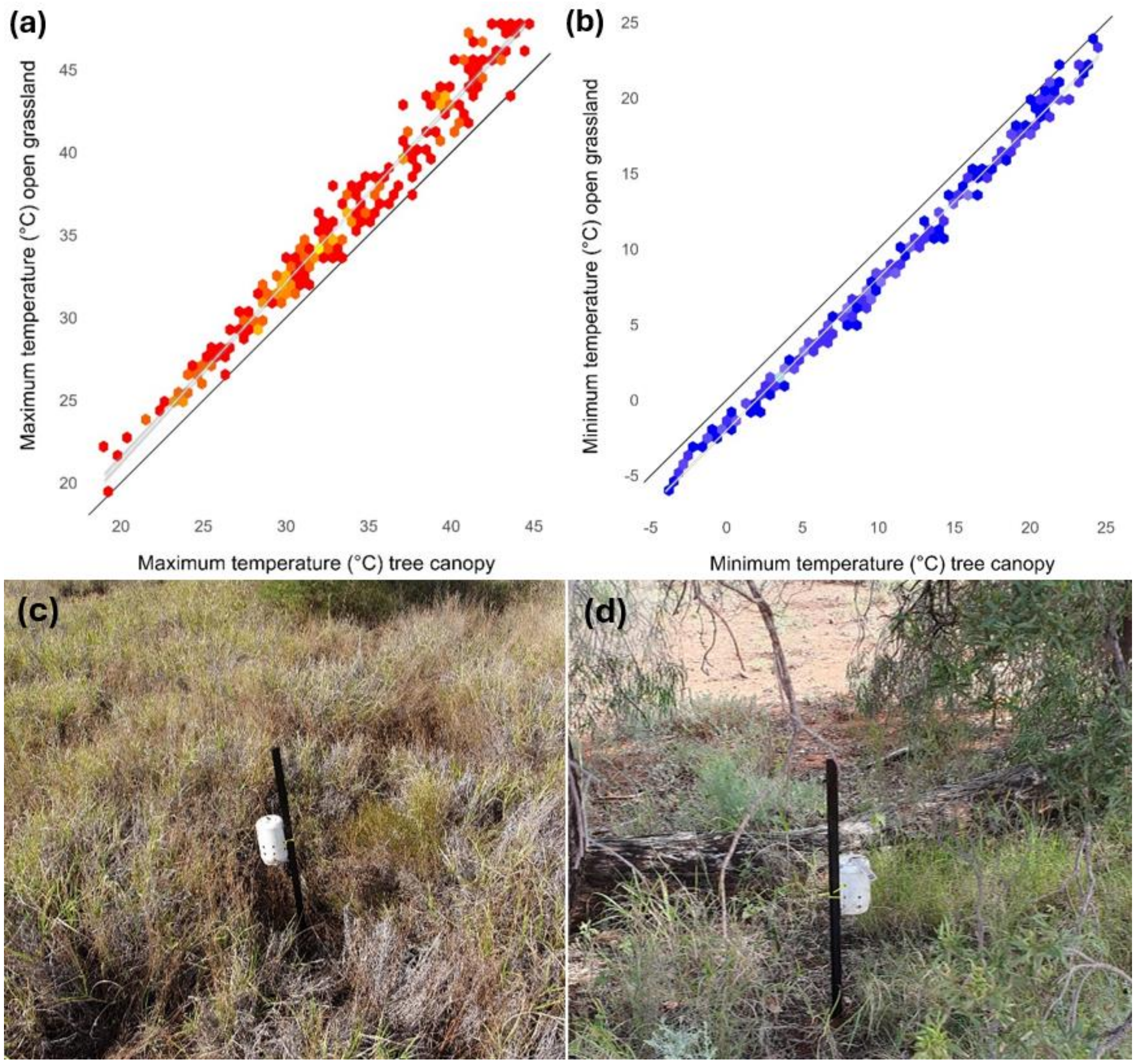

Figure 7. (a) Hexbin plot showing the distribution of maximum ambient temperature (°C) measured in open grassland (no shade) and under tree canopy (shade). Each hexagon represents a spatial bin, with colour intensity showing the density of temperature measurements. Yellow colour represents higher concentration 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. **(c)** iButton in mini-Stevenson screen deployed in open grass with no shade. **(d)** iButton in mini-Stevenson screen deployed under tree canopy of open grasslands.

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, AIC = 131.6; Figure 8), with a similar pattern found for red kangaroos (SE = 0.035, z = -3.998, p = <0.001, AIC = 58.621; Figure 8). 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.

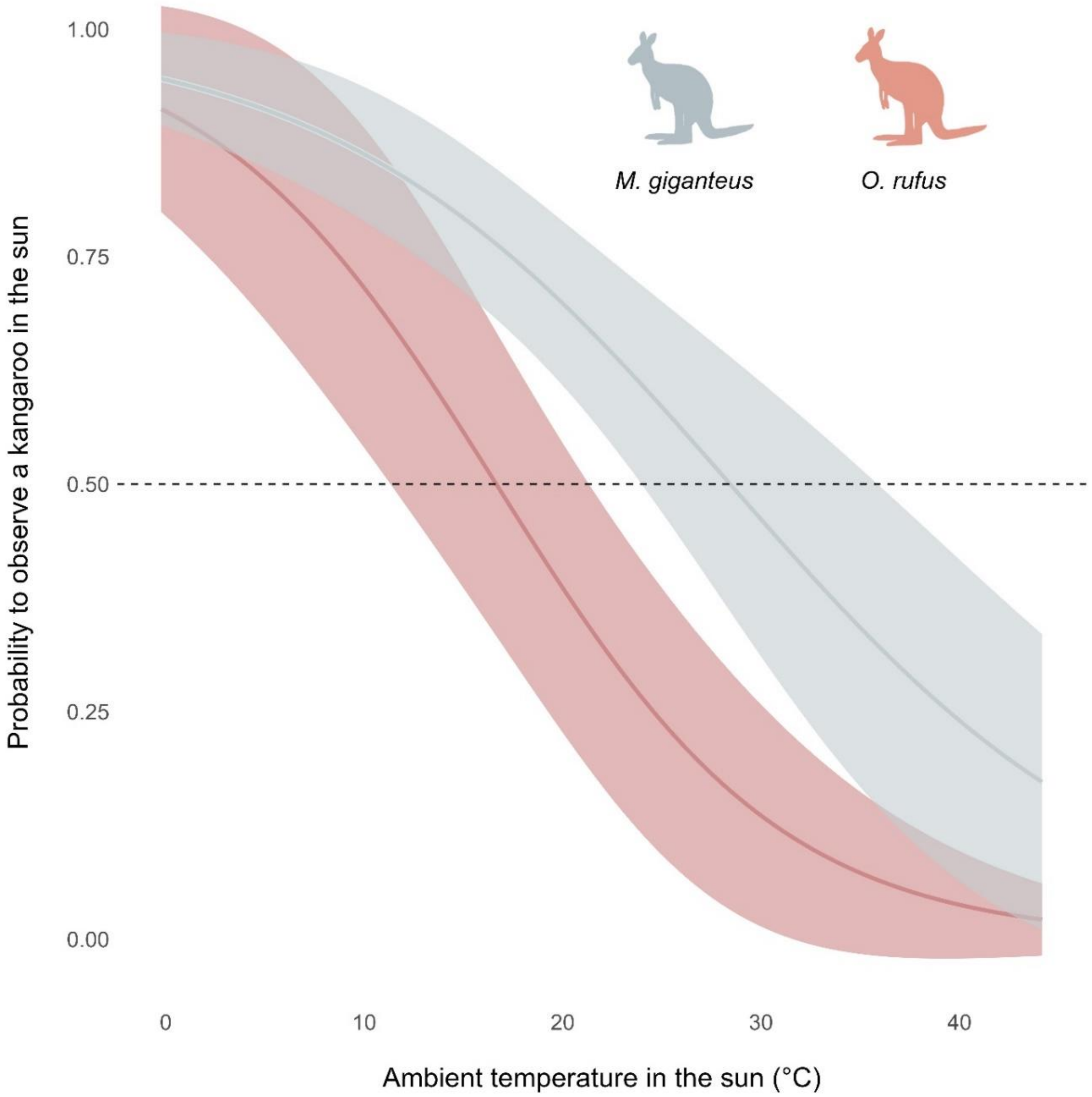

Figure 8. The probability of observing kangaroos in the sun decreased with increasing temperatures. Binomial model outputs for the probability of observing both eastern grey kangaroos and red kangaroos in the sun as a function of temperature (°C) in the sun as recorded by iButtons deployed on the MCP, showing that reds were less likely to be detected in the sun as temperatures increased than greys. The dashed horizontal line shows 50% probability.

As actual temperatures during surveys warmed, the likelihood of detecting eastern grey kangaroos in the shade under trees increased moderately, from 15% and 10 °C to 35% at 40 °C on average (eastern grey kangaroos: SE = 0.02, z = 2.04, p = 0.041, AIC = 124.11; Figure 9). In comparison, while red kangaroos were also more likely to be detected in the shade as temperatures increased, 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, AIC = 60.993; Figure 9).

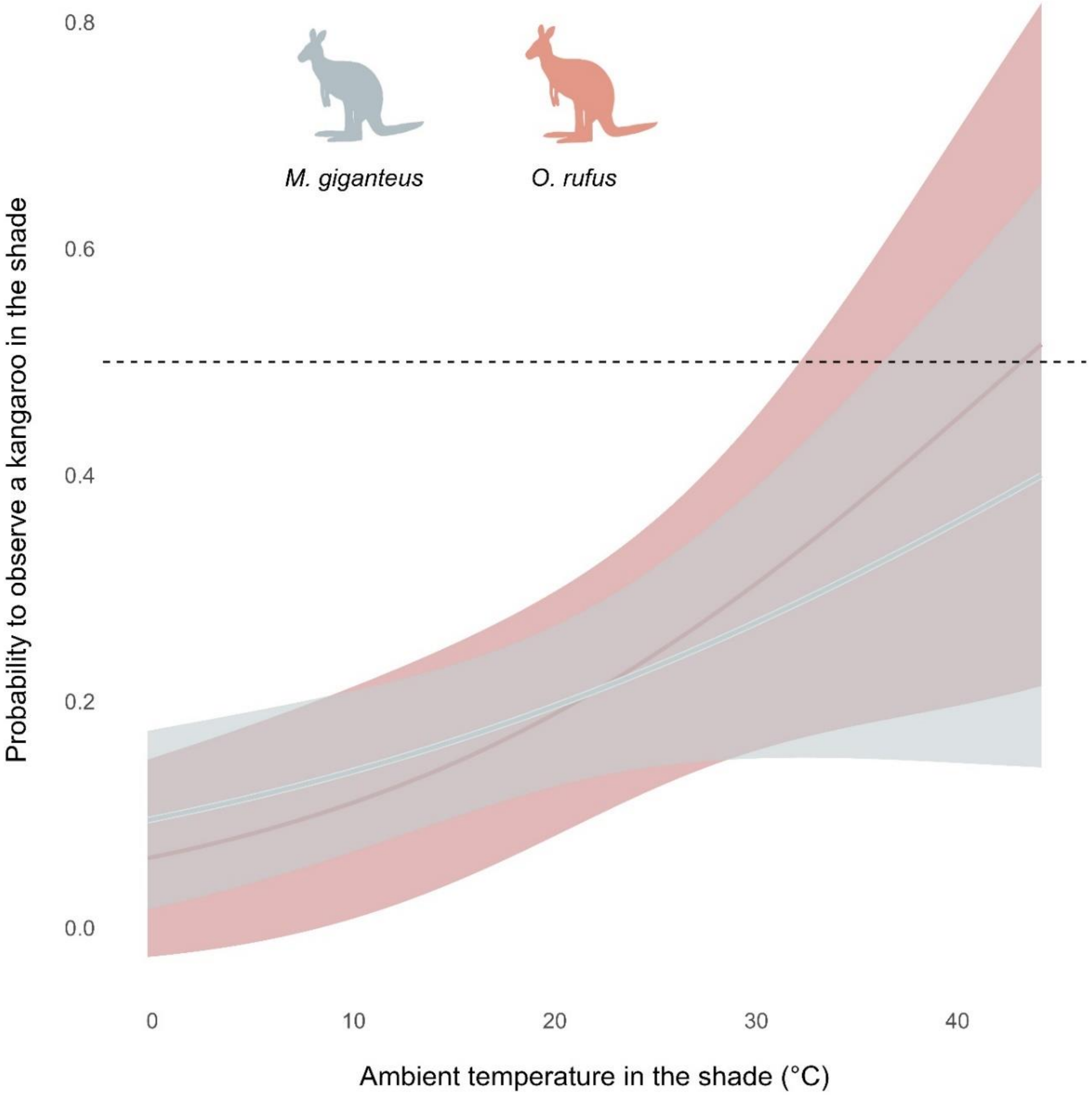

Figure 9. The probability of observing kangaroos in the shade increased with increasing temperatures. Binomial model outputs for the probability of observing both eastern grey kangaroos and red kangaroos in the shade as a function of temperature (°C) in the sun as recorded by iButtons deployed on the MCP. The dashed horizontal line shows 50% probability.

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 number of visits of eastern grey kangaroos at both dammed watercourses and tanks increased significantly with rising maximum daily temperatures (*M. giganteus* Dammed: Chi-sq = 7982, p = <0.001; *M. giganteus*

Tanks: Chi-sq = 1046, p = <0.001; Figure 10a). We found that the rate of change in activity of eastern grey kangaroos at the two types of waterpoints did not increase equally, with the rate of visits at dammed watercourses significantly increased on days when maximum temperatures reached 27.6°C, compared to 36.8°C for tanks; a 9.2°C difference (Figure 10a). Red kangaroo visits at waterpoints increased significantly at dammed watercourses only, with the 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, although while the increase was significant the effect of temperature on red kangaroo activity was still relatively weak (*O. rufus* Dammed: Chi-sq = 15.114, p = <0.001; *O. rufus* Tanks: Chi-sq = 0.497, p = 0.779; Figure 10b).

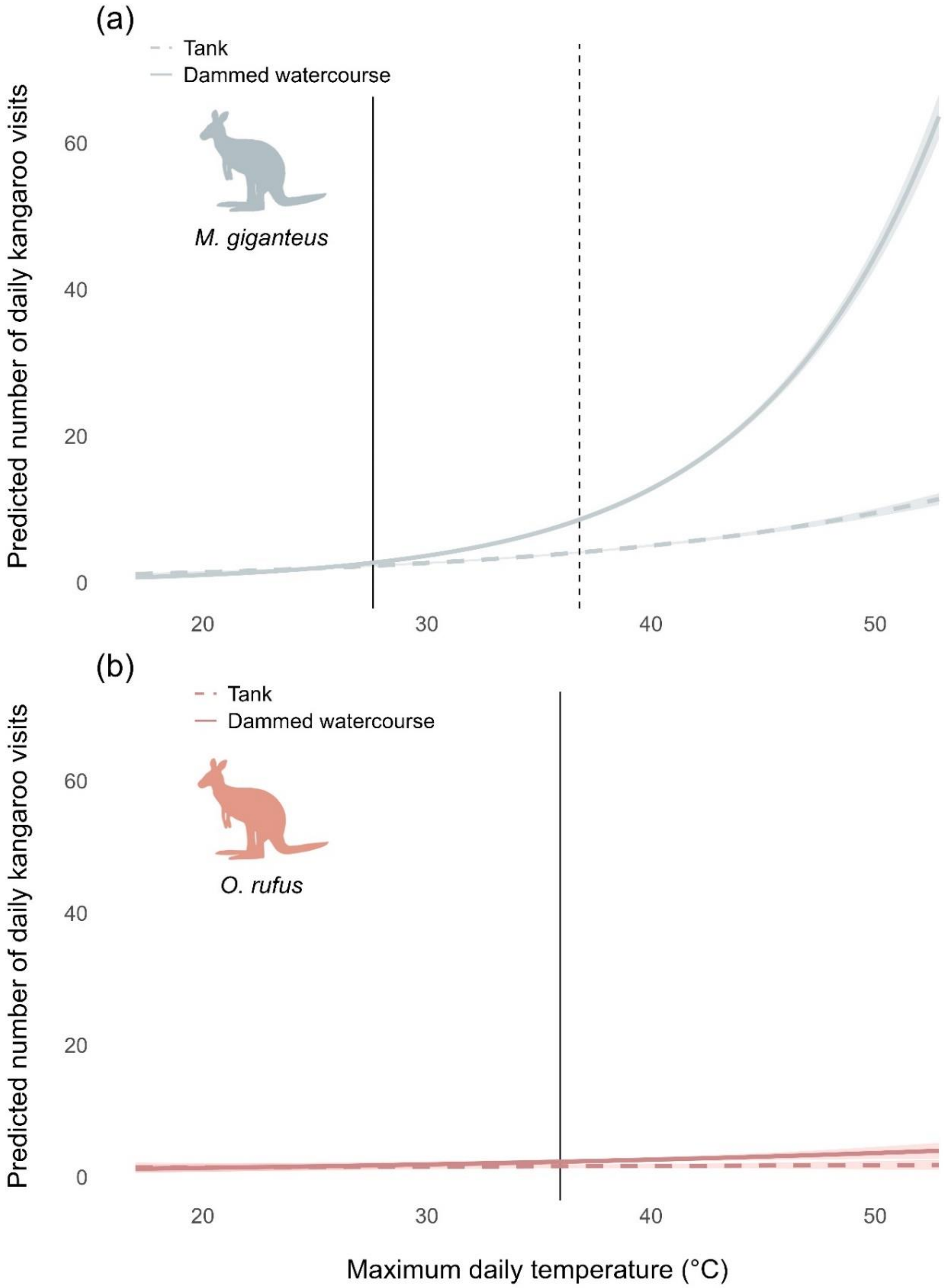

Figure 10. Both eastern grey kangaroos and red kangaroos visited dammed watercourses significantly more at higher temperatures. Outputs of the predicted number of visits from **(a)** eastern grey kangaroos and **(b)** red kangaroos at tanks (dashed line) and dammed watercourses (solid line) as a function 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.

4.4. 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. While the probability of detecting red kangaroos in the sun fell below 50% at 17°C, detecting eastern grey kangaroos only fell below 50% when temperatures reached 28°C, an 11°C difference. Our findings support the conclusion that mammals like kangaroos avoid direct solar radiation, and the radiant heat from hot surfaces, as ambient air temperatures increase. Further, by tracking the location of kangaroos using a thermal drone, we were able to show that the use of tree canopy was directly affected by temperatures, potentially due to the lower ambient temperatures and shade canopies provide from direct solar radiation (Dawson et al., 2006). Although we initially predicted that the probability of observing kangaroos in the shade would be more pronounced for eastern grey kangaroos, modelled responses showed stronger responses for red kangaroos. We also found that the likelihood of detecting red kangaroos in the sun dropped almost twice as fast as for eastern grey kangaroos. By utilising data on the number of visits of these species at waterpoints at different maximum daily temperatures, we were able to ascertain that eastern grey kangaroos greatly favoured the riparian habitats of dammed watercourses as temperatures increased, providing a possible explanation for why their reliance on canopy shade was lower than for red kangaroos. In contrast, red kangaroos showed only a mild increase in use of dammed watercourses during high temperatures.

Shade use at higher temperatures has been observed as a thermoregulatory method in many species (Crowther et al., 2014). Tourani et al. (2023) found that North American mammals increased their use of forested habitats in hotter regions, showing a preference for 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. Full exposure to solar radiation, particularly during high temperatures, can further push T_B levels near the upper critical temperature (UCT), where behaviourally led thermoregulation strategies are no longer enough to maintain optimal T_B (Norris & Kunz, 2012). The affected individual must then physiologically maintain T_B by increasing the use of metabolic energy to remove excess heat (Norris & Kunz, 2012). Norris and Kunz (2012) also explain that the temperature range from the UCT to the upper lethal temperature (ULT) (where death occurs due to overheating) is where evaporation of metabolic water is the most effective way to reduce excess heat. An increase in the rate of evaporation of metabolic water means that organisms must access water or moisture more often if they are to replace it and avoid dehydration, which can further constrain thermoregulation (Costa et al., 2013), unless shade is available offering shelter from infrared radiation.

It is likely that some of the kangaroos in the shade at high temperatures were simply not visible on either the TIR or RGB videos due to being hidden by thicker vegetation (Brunton et al., 2020). Keeping this limitation in mind, and that solely using data presented in this work we cannot confirm that the drop in kangaroo numbers was caused by kangaroos seeking water, we can speculate that some kangaroos leaving the transects could have been seeking water. Indeed, during extreme temperature events it is likely that even ambient temperature in the shade can sometimes exceed an individual's TNZ. This could cause a loss of metabolic water even when sheltered from the sun. Replacing metabolic water lost through evaporation is vital to an organism's survival (Costa et al., 2013), failure to do so can lead to impacts ranging from kidney failure to more pronounced heat stress which consequently impairs cognitive abilities and systems like reproductive and immune systems (Acevedo-Whitehouse & Duffus, 2009), and can ultimately lead to the death of the affected individual.

While an increasing activity rate of kangaroos at waterpoints may be to replace lost metabolic water, either through drinking or through foraging on vegetative growth surrounding waterpoints, 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 & Robbins, 2018; Ruf et al., 2023). For example, black bears 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 et al., 2017). However, this is not suggesting that a landscape with water and no shade is a healthy and viable option for macropods and other wild animal species, but rather that for optimal thermoregulation opportunities and survival they need a combination of both water sources and canopy cover. Even if one of the two features was to be more effective at maintaining an individual's T_B at an optimal level, water and shade provide different cooling mechanisms. For example, water might offer a quicker, more drastic way to reduce high T_B when individuals immerse themselves in it, and, when exiting water continues to reduce temperature via evaporative cooling (Costa et al., 2013). However, water sources, particularly at high temperatures can also attract more predators to the area (Sutherland et al., 2018), therefore, potentially making cooling via immersion in water only a short-term option. Sheltering in the shade under vegetation, however, offers a safer and long-term option where prey species can rest while hiding from predators (Ferrari, 2009). Shade can also help prey detect predators more easily; brown-headed cowbirds (*Molothrus ater*), for example, were found to take longer to detect the presence of and flee from a predator when in sunlit patches with high light intensity than when in the shade (Fernández-Juricic et al., 2012).

That eastern grey kangaroos are considered a mesic species while red kangaroos arid-adapted (Dawson, 2012) may explain the different activity rates at waterpoints we observed between the two species, with eastern grey kangaroos increasing their activity rates at temperatures lower than for red kangaroos. Furthermore, both species seemed to show a preference for dammed watercourses over the artificiality of tanks. Modified natural waterpoints such as dammed watercourses offer more preferable conditions and opportunities for wildlife. They are riparian in nature and typically hold good topsoil from which dam waters flood and then leave exposed, stimulating vegetation growth. They also typically possess better microclimates and more extensive vegetation cover than tanks, providing cooling opportunities and protection from predators as well as the opportunity to forage (Alikhanova & 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 semi-arid and arid rangelands are designed to provide water to livestock, are made of dug-up clay soils and generally do not promote vegetation growth on their often steep sides (Croft et al., 2007). With this in mind, such waterpoints rarely offer suitable conditions for vegetation cover and forage on the edges of the water, creating muddy or silted dams sometimes trapping and killing animals, including livestock (Wallach et al., 2017).

While the Mourachan property was converted to a conservation property more than 20 years ago (Australia Zoo, nd), most of the tanks present today were established prior to that, yet still lack the vegetation and shade that make natural waterpoints more suitable to wildlife. That eastern grey kangaroos appear to strongly favour dammed watercourses as maximum daily temperatures increase rather than residing in open grasslands or under tree canopies suggests that these habitats offer better thermoregulatory opportunities. Daily water and energy requirements may be being met by foraging on vegetation growing on the surrounds and tailings of these more natural watercourses. They also offer safer opportunities for cooling down, either by submersion or drinking as temperatures become hotter. That both species of kangaroos disfavour using tanks may imply they only do so out of necessity, rather than choice, accessing them only when temperatures become too extreme to ignore such water sources. Evidence that dingoes frequently use tanks to predate on kangaroos, and the propensity for kangaroos to drown in them (because of the muddy and steep sides, exacerbated by predation attempts), suggests that the thermoregulatory benefit of tanks may only be sought when necessary. Because we can only infer motivations for actions we can only speculate about these findings. Although artificial water points have been shown to not alter the density and abundance of kangaroos in semi-arid rangelands (Croft et al., 2007; Montague-Drake & Croft, 2004), our findings nevertheless show that modified natural waterpoints may yet play a role in helping kangaroos thermoregulate during high temperatures. Our findings suggests that 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.

Figure 11. Eastern grey kangaroo in an ephemeral waterpoint of the MCP (*photo credits: CfCC*).

The rate at which the climate is currently changing, particularly in drylands around the world, brings major physiological challenges to species affected (Acevedo-Whitehouse & 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 & Witte, 2021; Robertson, 1986). On hot days, the ability of wildlife like kangaroos to avoid direct solar radiation by seeking shelter under tree canopies or else along riparian corridors may become increasingly important for their persistence. During intense droughts and heatwaves, wildlife often need to spend a considerable amount of their energy thermoregulating, even species with adaptive traits amenable to arid conditions (Veldhuis et al., 2019). Access to adequate conditions to thermoregulate is vital, particularly in ecosystems with a naturally hot climate like Australia's semi-arid and arid rangelands (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 all too common (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 with no legal repercussions to the landowners (State of Queensland, 2019). Fencing off waterpoints has been recommended as a method to reduce the local population density of kangaroos (NSW Biodiversity Conservation Trust, 2020), despite no evidence that presence of water influences population density or abundance (Croft & Witte, 2021; Lavery et al., 2018; Montague-Drake & Croft, 2004). One of the most significant impacts that blocking access to water does have is on the welfare of kangaroos (McLeod & Sharp, 2020), potentially pushing their vulnerability to extreme weather events such as heatwaves to limits incompatible with life. In an increasingly warm world, such common practices are a sure way to be putting wild animals in more peril as they attempt to navigate the impacts of climate change.

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CHAPTER 5: EXTREME TEMPERATURES CAN INTENSIFY PREDATOR PREY INTERACTIONS

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Chapter 5 preamble

In chapter 4 I showed that eastern grey kangaroos increased their activity rate at waterpoints during high temperatures.. In chapter 5 I show that such an increase in activity rate is not without risk as dingoes also use the waterpoints. By analysing co-occurrence data of kangaroos and dingoes, and using heat anomaly data calculated from temperature sensors deployed at Mourachan I show that kangaroos were unable to avoid interacting with dingoes at waterpoints during extreme temperatures, instead significantly aggregating with them.

ABSTRACT

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 examine how extreme conditions may intensify interactions between predators and prey. In particular, we explore whether predators can exploit the thermoregulatory requirements of prey as they increasingly require access to water. We present evidence from the use of artificial waterpoints by dingoes (*Canis dingo*) and eastern grey kangaroos (*Macropus giganteus*) on a wildlife property in Australia's semi-arid rangelands, 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 temperatures became extreme and resulted in heatwaves. Not only did waterpoints become increasingly important for both species during heatwaves, dingo hunting attempts on kangaroos at these times were significantly higher than expected based on the number of days when heat anomalies occurred. Additionally, the predisposition of dingoes to hunt kangaroos in poor body condition was relaxed such that hunting of kangaroos was opportunistic at these times. Our results highlight the capacity of climate change to intensify predator-prey interactions in ways that may impact on persistence if prey are unable to adapt to predators exploiting their thermoregulatory requirements.

Keywords: *Canis dingo*, climate change, heatwaves, *Macropus giganteus,* predator-prey interactions, semi-arid rangelands, waterpoints

5.1. INTRODUCTION

Anthropogenic climate change is recognised as one of the major threats to global biodiversity (IPCC, 2022). It can exacerbate existing threats such as habitat loss and fragmentation, over-exploitation, 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 pre-industrial levels due to 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 functioning of ecosystems (Bascompte, 2009). Mutualistic relationships can help sustain ecosystem productivity and biodiversity

(Dehling et al., 2022), while competitive interactions can push species to adapt and occupy narrower ecological niches, driving specialisation (Armbruster, 2017). Likewise, parasitic relationships are key structural components of ecosystems through their influence on 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 non-consumptive 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 spatio-temporal 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, predators may be able to exploit prey employing 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. Deviations can lead to biotic decoupling, where co-occurrence and resultant dependencies are disfavoured by phenological shifts in seasonality (Sentis et al., 2012). 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 spatio-temporal 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, access to water by wildlife 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 system, 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 potentially needing to rely on water sources more often than they usually would for thermoregulatory purposes (Fuller et al., 2021). Thus, savvy predators may utilise waterpoints to actively predate upon weaker prey. This is particularly the case for interactions between predators and prey in arid and semi-arid drylands, where water is a sparse yet vital resource.

Globally, rangelands make up about 54% of all land cover, and are found on most continents, with arid and semi-arid ecosystems making up 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 semi-arid 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 of 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; Davidson et al., 2013; Harris et al., 2015).

Here we hypothesize that high temperatures and heatwaves can intensify predator-prey interactions at waterpoints in Australia’s semi-arid rangelands, a biodiversity hotspot vulnerable to climate change (Urban, 2015). To do so 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), employing 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 visitations 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 (Clements et al., 2016; Genovart et al., 2010), to being more opportunistic during high heat anomalies.

5.2. METHODS

5.2.1. Study Site

This research was conducted on the 480 km^2 Mourachan Conservation Property (MCP) in south-western Queensland, near the township of St George. 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, 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 due to a major El Niño event (BOM, 2020).

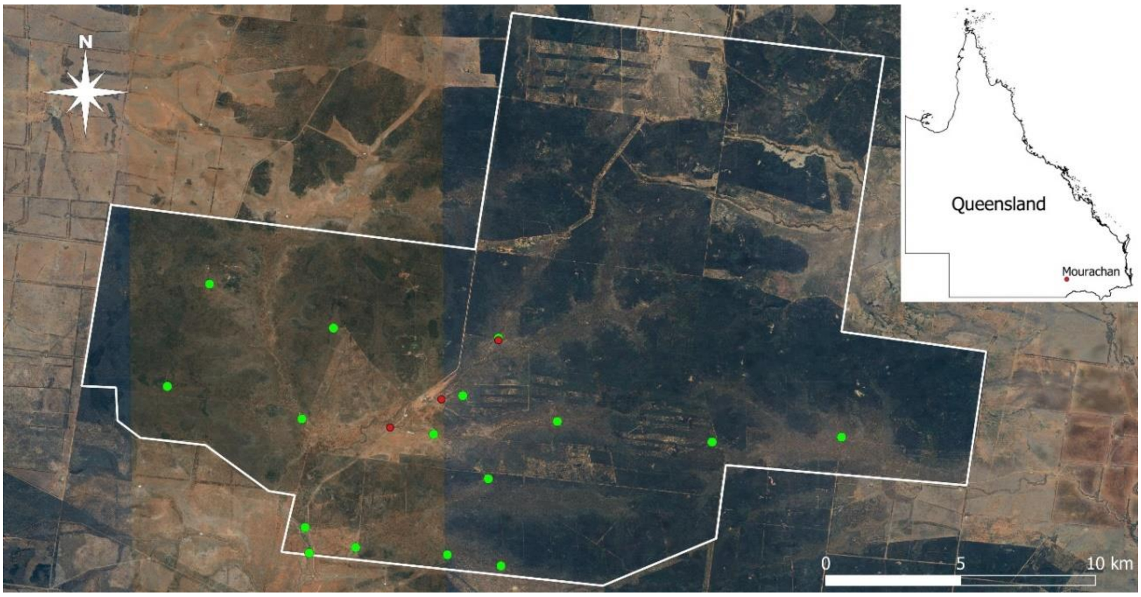

Figure 1. Map of the 480 km^2 Mourachan Conservation Property and location within Queensland, Australia. Locations of waterpoints (green dots) and iButton temperature sensors (red dots) are highlighted on the property.

5.2.2. 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 (Figure 1). We selected the waterpoints as they were the only available sources of water on the property when setting up the cameras in November 2019. We deployed 2 cameras per waterpoint for 13 of the waterpoints due to their smaller size, however, the remaining 3 waterpoints required 3 cameras each to cover their area. We setup the cameras so that they would cover much of the ground near the water while also having part of the water visible on frame (Figure 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.

5.2.3. Kangaroo and dingo activity rate

We measured the activity rate of kangaroos and dingoes to analyse how often they accessed waterpoints. To do so we recorded the total number of kangaroo and dingo events per day per waterpoint, defining events as a series of camera trap images captured within 5 minutes of the previous image. Hunting attempts were identified as every event where kangaroos and dingoes were seen interacting agonistically, e.g., kangaroos chased by dingoes, physical contact such as dingoes biting a kangaroo, or kangaroos using defensive behaviours against dingoes (Figure 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 (Figure 2 top), hops in the direction of the dingo while remaining in an upright posture, actively kicking at the predator, and flight behaviours such as fleeing away from the waterpoints, and fleeing towards water (Figure 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. To measure whether dingo activity at waterpoints was influenced by temperature alone or if kangaroo presence had an effect, we further tested the relationship between maximum daily temperature and dingo visits at waterpoints when kangaroos were absent and present using negative binomial regressions.

Figure 2. Example of predation events observed at the waterpoints of the Mourachan property. Both events were part of the 60 predation events recorded during the study period. (Top)

22.11.2019, maximum temperature: 43.39°C, mean daily temperature: 32.84°C. (Bottom) 11.01.2020, maximum temperature: 44.05°C, mean daily temperature: 35.98°C.

5.2.4. Temperature of the Mourachan Conservation Property

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, USA) 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 air flow (Ashcroft et al., 2012), which we then attached to star pickets. The iButtons were placed 50cm above ground to better represent the average height of kangaroos and dingoes. 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. 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 temperature half-hourly from January 24th 2023 to October 21st 2023. IButton deployment (January – October 2023) did not match the camera trap deployment (November 2019 – April 2021) as the original idea of this chapter was to use BOM temperature data when data analysis started in 2021. However, the deployment of the iButtons for a later project (Chapter 4) meant that a more accurate way of measuring on-site temperature and historical trends for the MCP was now available. We, therefore, decided to switch from using BOM temperature data to using on-site iButton data. However, this meant that we now needed to obtain site-calibrated temperatures for the camera trap deployment dates.

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

(BOM, 2023). We used a linear regression model to calibrate the BOM data using the iButton temperature data. Three BOM temperature variables were calibrated; daily minimum temperature, daily maximum temperature, and the mean temperature using the minimum and maximum temperatures. All statistical analyses were carried out in R v4.1.1 (R Core Team, 2023). We then applied the model to BOM daily maximum and minimum temperatures from 01.02.1913 to the end of the study period (18.04.2021). BOM station 043034 was used for temperatures from January 1913 to April 1997, and station 043109 from May 1997 to April 2021 (BOM, 2023).

5.2.5. 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 a MMM for the study site 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. Whilst 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 non-linearities into the model. Furthermore, due to the camera trap data used covering 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 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 via AIC (Aho et al., 2014). Furthermore, a

13 day window could explain changes in behaviour better than smaller windows as such changes can sometimes take multiple days to appear in a population. We then used a generalized linear model (GLM) 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 visualised 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 thermal neutral zone 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 as heat stress depending on the individual animal, even within species (Hoffmann & Sgrò, 2011). For example, an eastern grey kangaroo living in the semi-arid rangelands 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 thermal neutral zone. Hence, the use of a local MMM instead of a single threshold as a single threshold may not be semi-arid rangeland specific, or accurately represent relationships between kangaroos in semi-arid rangelands 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 1971-2000. 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.

5.2.6. Kangaroo demography and body condition

We classified the kangaroos captured by the camera traps by demography classes: large adult, medium adult, small adult, sub adult, young-at-foot, and pouch young (Austin & Ramp, 2019). A single researcher (LQJ) gave a body condition score to each individual using the chart described in chapter 3. The choice of a single researcher giving body condition scores was made to avoid potential confusion between BCS given by multiple people due 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 body condition of 5 was observed throughout the period of the study, therefore, only scores 1 to 4 appear in our results.

5.2.7. 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 explored the degree to which they overlap using the Δ_4 overlap statistic, considered reliable for estimating the overlap of activity patterns when sample sizes are >75 detections (Ridout & Linkie, 2009). To calculate the Δ_4 overlap statistic and 95% confidence intervals, we generated 10,000 bootstrapped detections for both kangaroo and dingo (Wooster et al., 2021). The 2.5% and 97.5% percentiles were adjusted using the “Basic0” approach to account for bootstrap bias. As our goal was to estimate how the overlap between kangaroos and dingoes changed relative to maximum daily temperature, we grouped detections into heat anomaly and non-heat anomaly bins, with heat anomaly representing days where the temperature exceeded the MMM threshold, and non-heat anomaly representing days with a temperature below the MMM. We measured the Δ_4 overlap statistic for both temperature groups (heat anomaly and non-heat anomaly) and inferred significance from the overlap of 95% confidence intervals.

5.2.8. Dingo prey selectivity

We explored the difference in hunting attempts between heat anomaly days (where temperature exceeded the MMM) and days of non-heat anomalies (where temperature was below the MMM) by calculating the number of events per days 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 non-heat 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 body condition score where interactions occurred with dingoes during periods of heat anomaly and periods of non-heat 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.

5.3. RESULTS

5.3.1. Mourachan Conservation Property temperature and heatwave metrics

5.3.1.1. 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 located 52km away (St George Airport, QLD). While the maximum temperature recorded by BOM reached 40.1°C, that of the MCP reached 50.69°C (Figure 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 (Figure 3b).

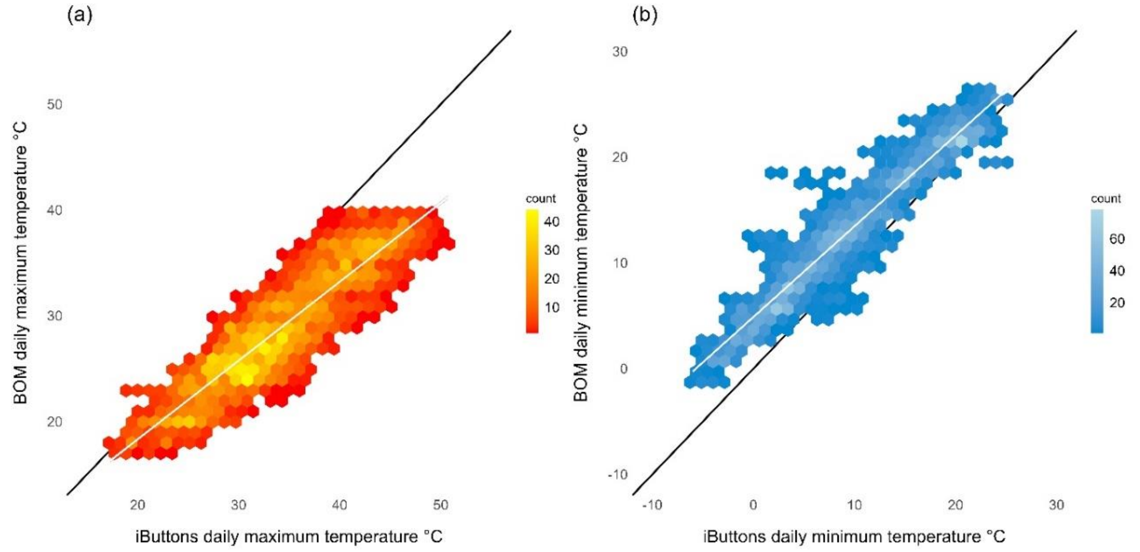

Figure 3. Temperature recorded by iButton sensors deployed at the MCP compared to BOM temperature recorded for the town of St George. **(a)** maximum temperature, **(b)** minimum temperature. The white line in both graphs represents a linear trend.

5.3.1.2. Heatwave metrics

Based on the average annual heat anomaly of a benchmark period from 1971-2000 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 (Figure 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 (Figure 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 1971-2000 was 7.39. The MCP experienced 48 days above the MMM in 2019 and 41 days in 2020 (Figure 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 (Figure 4b).

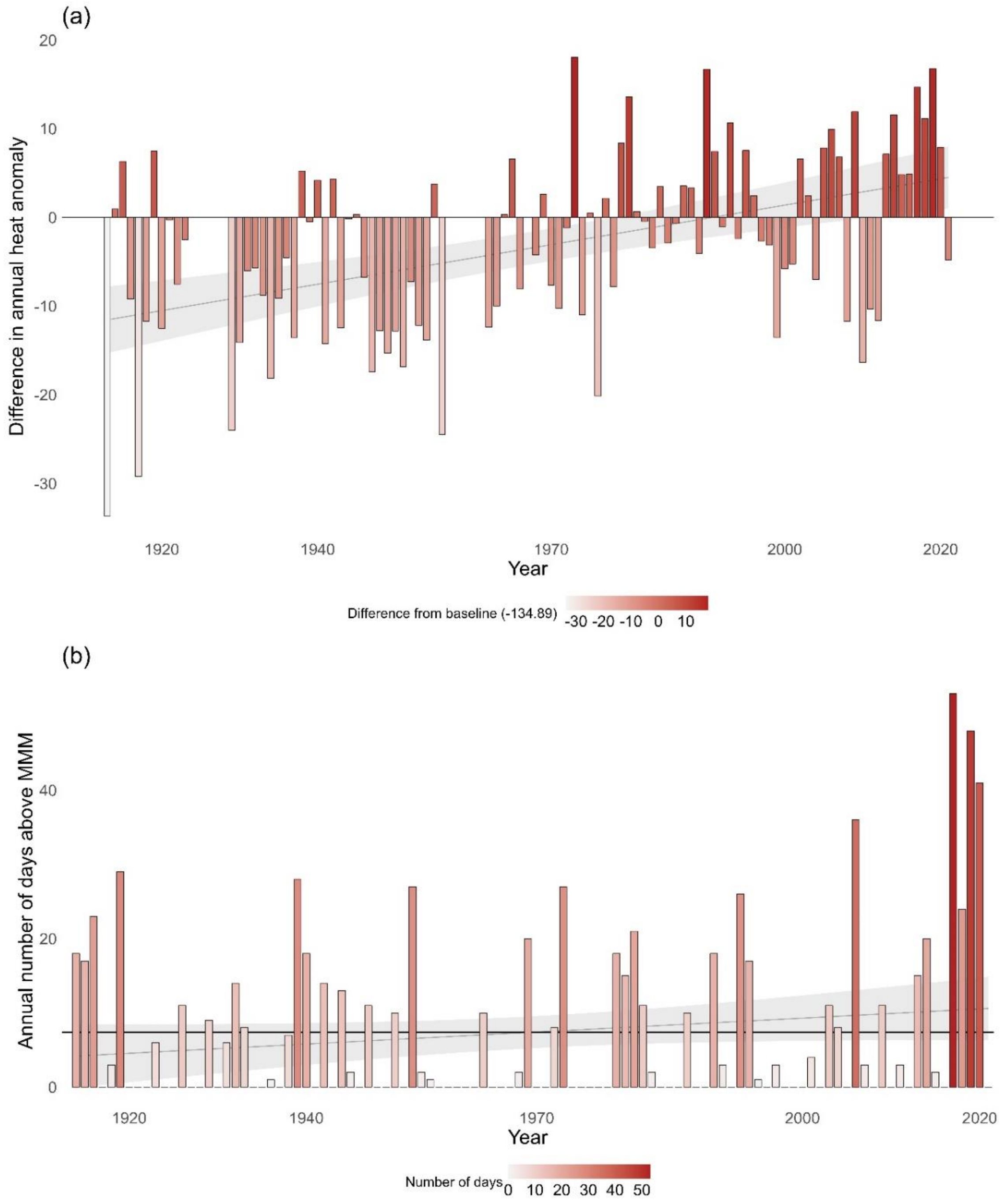

Figure 4. (a) Heatwaves at the MCP have been intensifying over time. The figure shows the difference in average annual heat anomalies at the MCP from 1913-2021 from the average annual heat anomaly for a benchmark period from 1971-2000 (-134.89). The trend line represents an increase in heatwave intensity over time using a linear regression. The grey confidence intervals on the trend line represent a 95% confidence interval. **(b) The annual number of days exceeding the MMM is increasing over time.** 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 1971-2000 (7.39). Years with no column had no days above the MMM. The trend line represents an increase in number of days over time using a linear regression. The grey confidence intervals on the trend line represent a 95% confidence interval.

5.3.2. 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=<0.001; Figure 5a). The same pattern was found for dingoes, with activity rate increasing significantly as temperatures rose (R^2=0.204, z=17.92, p=<0.001; Figure 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 = <0.001; kangaroos present: $R^2 = 0.172$, z = 12.850, p = <0.001; Figure S1 and S2).

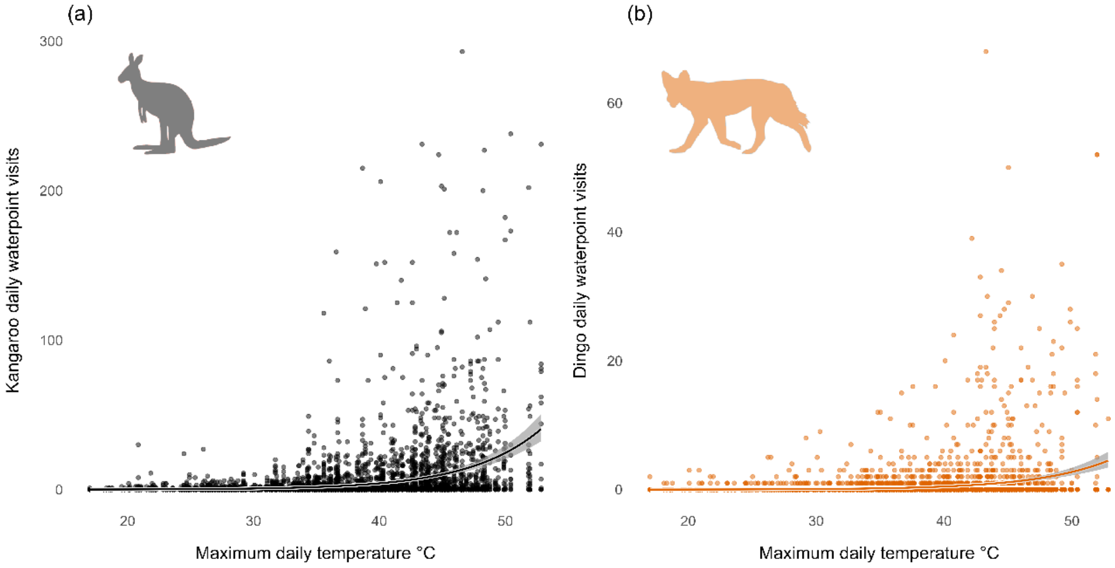

Figure 5. Total daily number of **(a)** eastern grey kangaroo and **(b)** dingo visits at waterpoints on the MCP by daily maximum temperature (°C). Each point represents a day. The lines represent the relationship between maximum temperature and number of events obtained from a logged negative binomial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

While kangaroo activity rates significantly increased with increasing temperatures, rates also increased with both higher heat anomalies and higher dingo activity (kangaroo ~ heat anomaly*dingo: z=3.621 p=<0.001; Figure 6a). These results suggest that kangaroos are unable to avoid aggregating with dingoes when both heat anomalies and dingo activity rate are high, creating potentially dangerous situations for the kangaroos during heat anomalies.

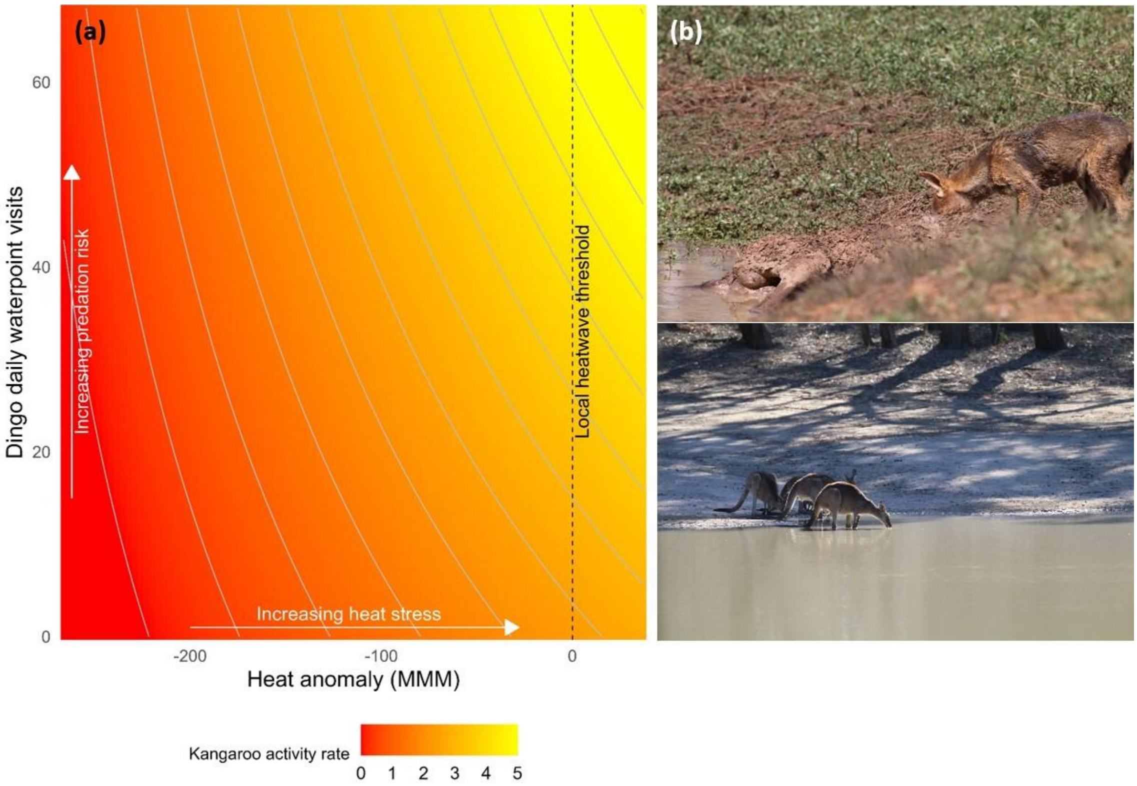

Figure 6. Kangaroos are unable to avoid aggregating with dingoes at waterpoints when heat anomalies increase. (a) Eastern grey kangaroo activity rate at waterpoints as a function of dingo activity and heat anomalies. The vertical line represents the local heatwave threshold for the MCP based on the MMM of 32.1°C, x axis values greater than the threshold represent heat anomalies while values lower represent cooler periods. **(b)** Juvenile dingo feeding on an eastern grey kangaroo carcass at a waterpoint (top) (*photo credits: Lisa M. Ashby*), and eastern grey kangaroos drinking at a waterpoint (bottom) (*photo credits: Taylor J. McEvoy*).

5.3.3. 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 (Figure 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 (non-heat anomaly $\Delta^4 = 0.791 \pm 0.742 - 0.821$, Figure 7a; heat anomaly: $\Delta^4 = 0.853 \pm 0.826 - 0.861$, Figure 7b). Days experiencing heat anomalies represented only 10.68% ($n = 55$) of the total number of days in our 18-month study period. While 74.63% ($n = 50$) of 67 documented hunting attempts at waterpoints occurred during those days and while overlap between the two species increased during periods of heat anomalies, we observed that 73.9% of interactions between kangaroos and dingoes led to 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 heat anomalies (Heat anomaly: $Wi = 6.99 \pm 2.06$; Non-heat anomaly: $Wi = 0.28 \pm 0.05$; Figure S3).

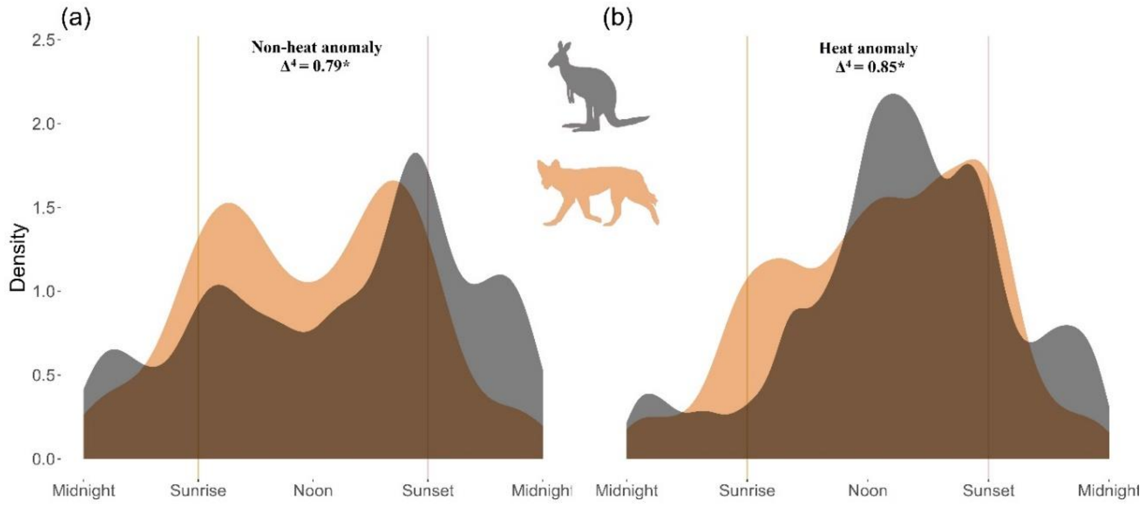

Figure 7. Heat anomalies drove a 7.8% increase in temporal overlap between dingoes and kangaroos and led to predation occurring significantly more than expected based on the number of days available. Overlap in the temporal activity density of kangaroos and dingoes for **(a)** non-heat anomaly and **(b)** heat anomaly periods. Asterisks indicate significance inferred by the non-overlapping of bootstrapped 95% Confidence Intervals.

By quantifying the body condition score of all individuals documented in the study, we found that on days with temperatures below MMM, dingoes favoured hunting of kangaroos with low body condition scores (BCS 1: Wi = 12.64 ± 7.51; BCS 2: Wi = 1.55 ± 0.331; Figure 8b; Table S1). However, dingoes abandoned these preferences during heat anomalies, instead hunting all kangaroos relative to their prevalence at waterpoints on those days (Figure 8a; Table S1).

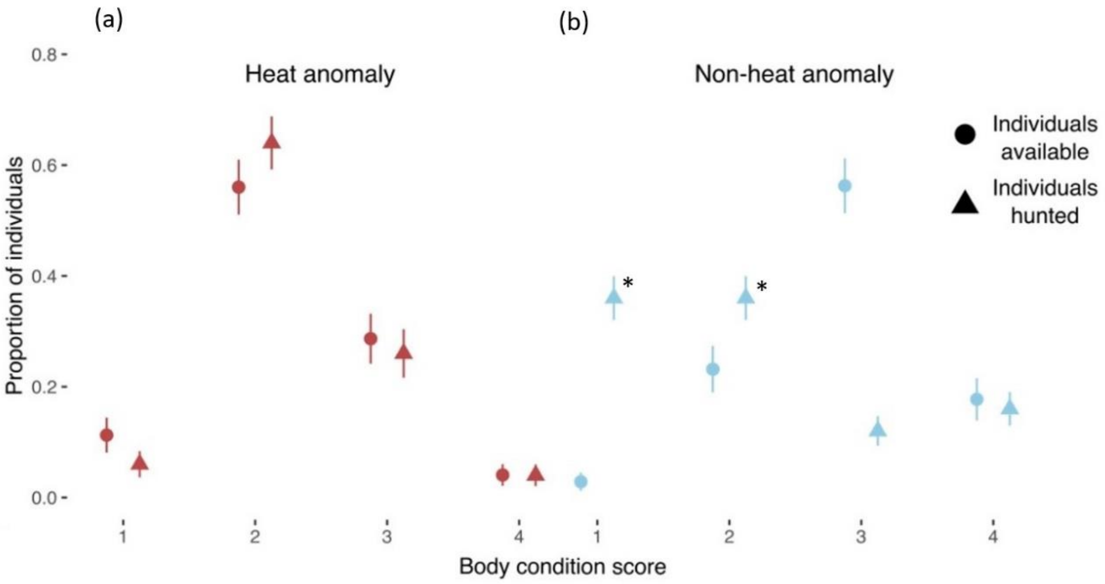

Figure 8. Heat anomalies alter the prey selection of dingoes. The proportion of individuals from each body condition score available in population and observed being hunted by dingoes during **(a)** heat anomaly and **(b)** non-heat anomaly periods, as calculated by the Manly selection measure. Asterisks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

5.4. 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 non-anomalous 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 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 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 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 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.

Furthermore, eastern grey kangaroos are a mesic species with some of their range extending into semi-arid and arid rangelands as is the case with our study site, leading to individuals in drier areas being exposed to conditions to which they are not fully adapted (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 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, due to dehydration and overheating (Acevedo-Whitehouse & Duffus, 2009; Costa et al., 2013; Norris & 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, through the increased need for thermoregulation (Acevedo-Whitehouse & Duffus, 2009). Our results suggest that under these conditions such intensified physiological requirements may create impossible trade-offs for prey; access water or avoid predation (Wallach & O’Neill, 2009; Wooster et al., 2022). This supports the concept of state-dependent risk-taking, where the physical state of the prey, such as hydration levels, influences their behaviour (Clark, 1994). Heat anomalies serve as a key stressor affecting physical condition, pushing prey species such as eastern grey kangaroos to make potentially dangerous decisions, prioritising physiological needs over predator avoidance. This then leads to the coupling effect of predator-prey interactions we observed, suggesting potentially troubling population trajectories for prey species who are water dependent and may already be experiencing decline (Fuller et al., 2021).

Herbivores in semi-arid and arid environments often aggregate around waterpoints, making such locations reliable sources of prey for predators (Valeix et al., 2010). With the availability of water in semi-arid rangelands being naturally low (Stokes et al., 2006) and likely to further decrease in a warming future where heatwaves and droughts are expected to intensify (Kiem et al., 2016; Kirono et al., 2020), the choice of waterpoints will become limited, further forcing prey species to congregate in larger numbers and access sites with higher predator activity rates (Sutherland et al., 2018; Western, 1975). Valeix, Fritz, et al. (2009), for example, explored how the risk of encountering lions influences African herbivore behaviour at waterpoints. They found that the times buffalo (*Syncerus caffer*) did not avoid risky waterpoints (high predator density) happened to be during a severe drought, suggesting their need to access water was greater than their instinct to avoid predators (Valeix, Fritz, et al., 2009). Additionally, Destefano et al. (2000) provided evidence that coyote (*Canis latrans*) activity at sites with water was seven times higher than at sites without water in southern Arizona, USA. 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 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 work shows that the intensification of heatwaves under climate change may be a key player in the coupling of predator-prey interactions in semi-arid rangelands 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 rangeland 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 waterpoints may become increasingly contested spaces, however, more work is needed to study how the shift in predator-prey interactions might play out in the rest of the landscape – do predator-prey interactions only increase at waterpoints but decrease at other locations, or do their rates increase throughout the landscape? Nonetheless, the increase in predator-prey interactions at waterpoints could be a more concerning matter for mesic species like eastern grey kangaroos, with ranges extending into drier regions, who may need to rely more on such locations (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 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.

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5.6. SUPPLEMENTARY MATERIAL

Table S1: Outputs from the Manly selective measure exploring how heat anomalies shape dingo predation

Body Condition Score	**Wi**	**Standard error**
	Heat anomaly	
1	0.553	0.259
2	1.142	0.133
3	0.907	0.207
4	0.986	0.680
	Non-heat anomaly	
1	12.64	7.52
2	1.55	0.331
3	0.213	0.51
4	0.903	0.259

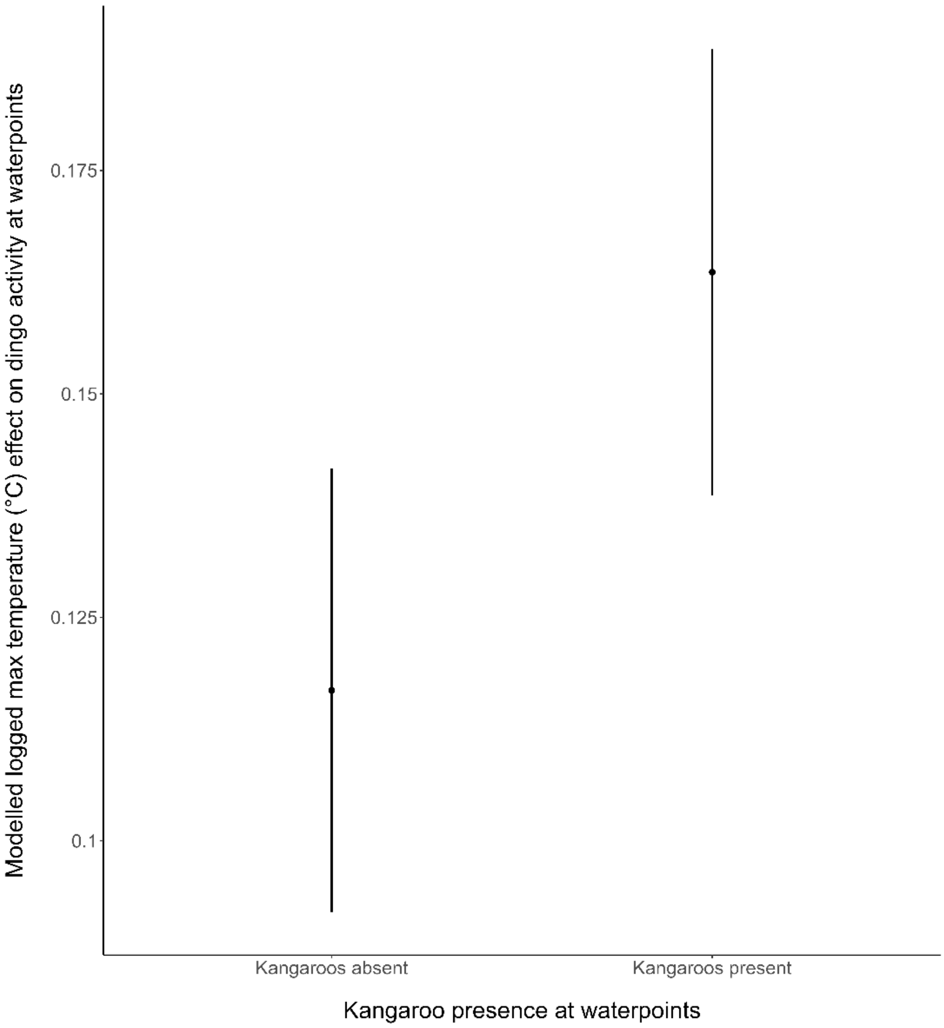

Figure S1. Effect of maximum daily temperature (°C) on dingo activity at waterpoints when kangaroos are present and absent, based on negative binomial regression models. The effect is logged, and error bars represent 95% confidence intervals.

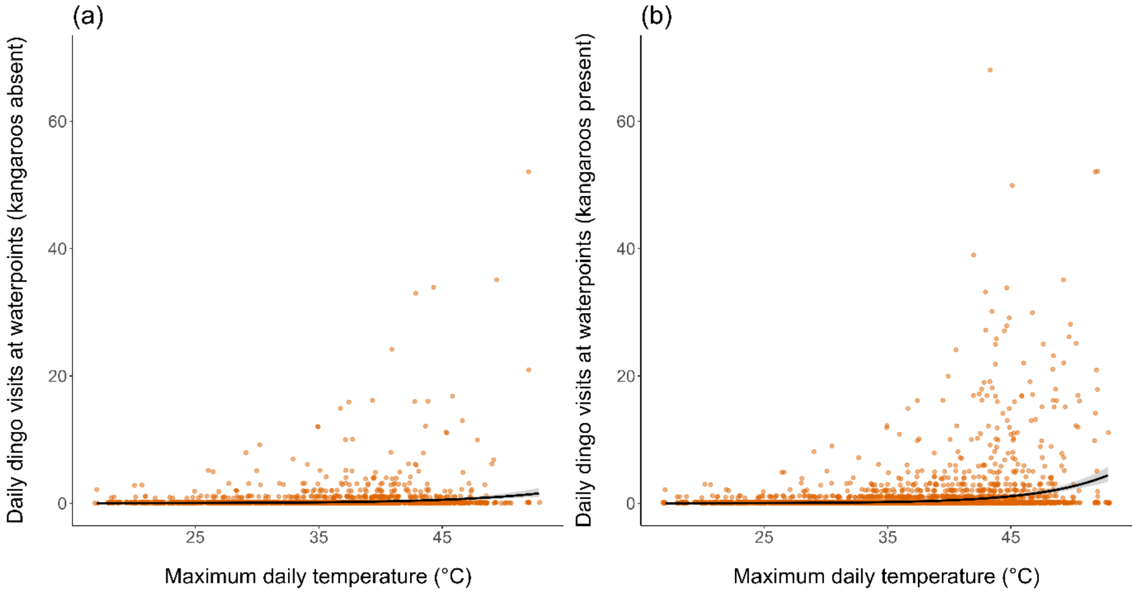

Figure S2. Number of daily dingo visits at waterpoints when kangaroos are (a) absent and (b) present. Each point represents a day. The lines represent the relationship between maximum temperature and number of events obtained from a negative binomial regression.

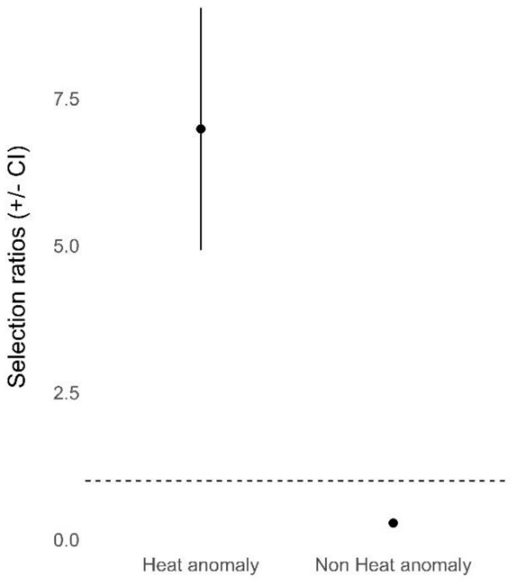

Figure S3. Predation rate was significantly higher during periods of heat anomaly. Selection ratios (Wi) of predation events during heat anomalies and non-heat anomalies, as calculated by the Manly selection measure. The horizontal line represents a selection ratio (Wi) of 1. Selection ratios greater than 1 imply predation events were significantly more likely to occur relative to the number of days available. Number of days available during heat anomalies was 55, number of days available during non-heat anomaly periods was 459.

Figure S4. Proportion of each kangaroo demographic category within the observed population for each month of the study period

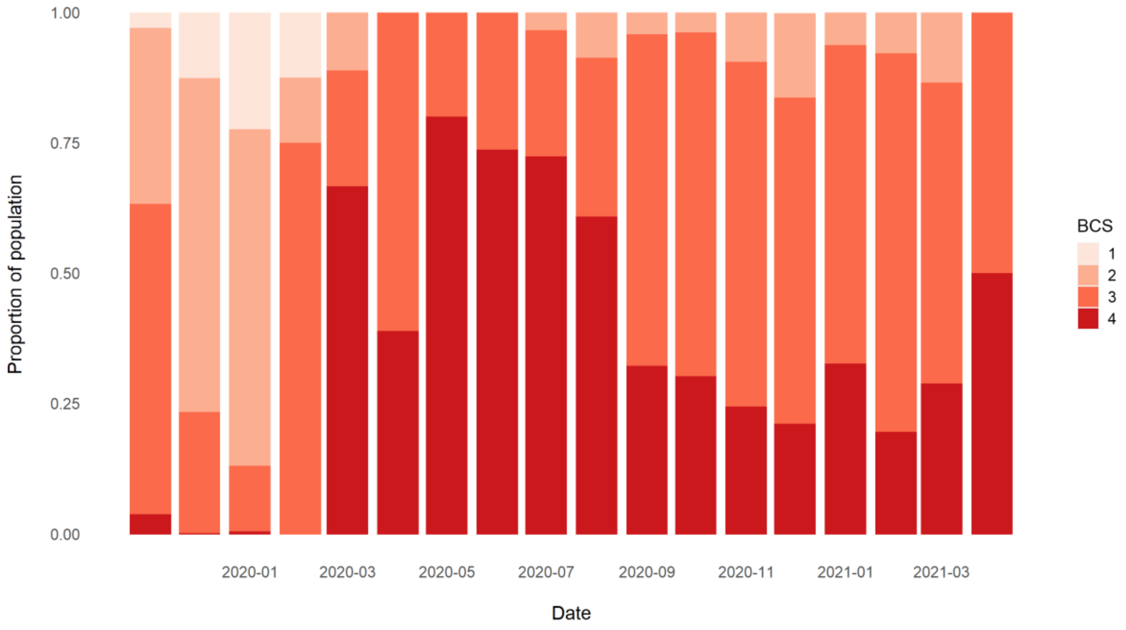

Figure S5. Proportion of each kangaroo Body Condition Score (BCS) within the observed population for each month of the study period

CHAPTER 6: THE USE OF REMOTE CAMERA TRAPS FOR INVESTIGATING POTENTIAL INDICATORS OF WELFARE CHALLENGES ASSOCIATED WITH THERMOREGULATORY BEHAVIOURS IN EASTERN GREY KANGAROOS

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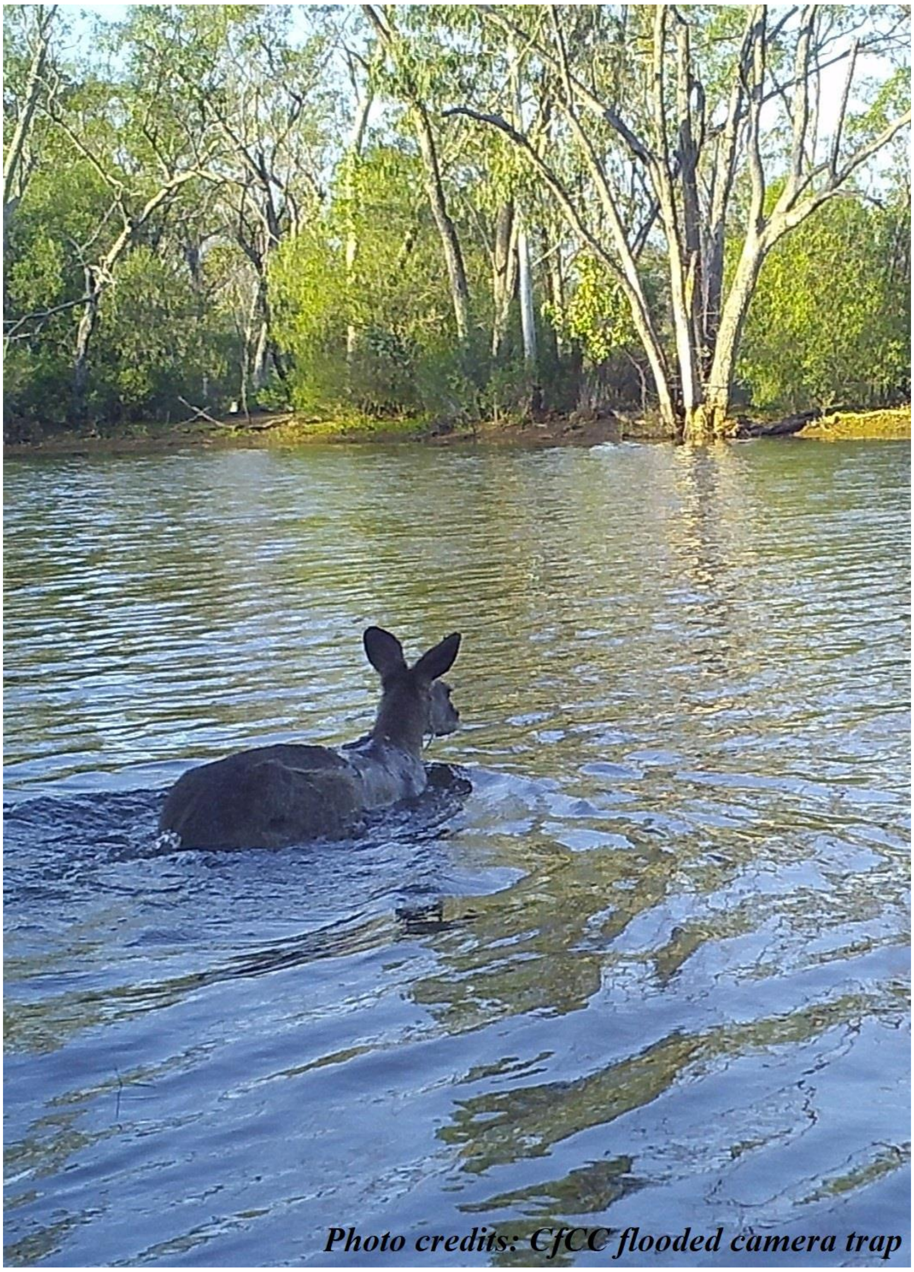

Photo credits: CfCC flooded camera trap

Chapter 6 preamble

Chapter 6 is the final data chapter of the thesis, where I use findings from chapters 3 – 5 to put together a list of behaviours and potential indicators of welfare challenges in eastern grey kangaroos related to thermoregulation, predation, as well as more general indicators and behaviours during heat anomalies. Through this chapter I also assess the use of camera traps to collect and measure data related to kangaroo welfare indicators. Finally, in this chapter I also assess the difference in the prevalence of the indicators and behaviours identified between tanks and dammed watercourses, also identifying some of the potential mental experiences related to those indicators.

ABSTRACT

Extreme weather events such as heatwaves are increasing in intensity, frequency, and duration as a consequence of climate change. While an extensive number of studies have focused on their impacts on wild animals, scientific assessments of wild animal welfare in the face of climate change have not been reported. Here I introduce the use of such assessments in a climate change context. I used camera traps at the waterpoints of a large conservation property in the semi-arid rangelands of south-western Queensland, Australia, to identify potential indicators of welfare challenges in eastern grey kangaroos related to thermoregulation and predation during heatwaves (e.g., water immersion, proximity to predators, physical contact with predators). In line with contemporary animal welfare science, I then cautiously interpret the indicators in terms of the subjective mental experiences that they are likely to reflect. Waterpoints of the property were split into excavated earth tanks (also called farm dams) and dammed watercourses (natural waterways dammed to contain water) to identify potential differences in the types of indicators and behaviours observed at both types of waterpoint. This work showed that identifying and analysing potential indicators of welfare challenges in eastern grey kangaroos is feasible using camera traps. I observed an increased prevalence of thermoregulatory behaviours including kangaroos standing in water and drinking during periods of heat anomaly when compared to non-heat anomaly

periods. Predation-related behaviours/indicators, including proximity to predators and flight responses, were more frequent at tanks and during heat anomalies, which were characterized by smaller areas and less vegetation cover, increasing predation risk. Dammed watercourses offered conditions better suited to behaviours like foraging and lying down to rest. Indicators inferring mental experiences such as fear and anxiety were higher at tanks due to increased predator presence, while indicators inferring mental experiences of heat discomfort and thirst were more prevalent during heat anomalies.

6.1. INTRODUCTION

Climate change is increasing the frequency and intensity of extreme weather events such as heatwaves and droughts in many parts of the world (Dosio et al., 2018; Kirono et al., 2020; Trancoso et al., 2020; Vicente-Serrano et al., 2019). These events are likely to be associated with an increase in specific welfare challenges. To date, studies exploring the impacts of extreme weather events on wild animals have focused on parameters such as species distribution (Hale et al., 2016; Seabrook et al., 2011), health (Chandranaik et al., 2022; Trondrud et al., 2023), behaviour (Abernathy et al., 2019; Buchholz et al., 2019), or biotic interactions such as predator-prey interactions (Brivio et al., 2024; Gauzens et al., 2024; Rafiq et al., 2023; Romero et al., 2018). However, despite the direct link between animal welfare and the survival of individuals (Beausoleil et al., 2018; Boys et al., 2022; Paquet & Darimont, 2010), scientific assessments of wild animal welfare in the face of climate change have not been reported (Simmonds, 2017). Detailed knowledge of how the welfare of wild animals is being impacted is of urgent concern and may assist in making appropriate conservation decisions (Harvey et al., 2021).

Wild animal welfare through a conservation lens is receiving an increasing amount of attention (Beausoleil et al., 2018; Boys et al., 2022; Dubois et al., 2017; Paquet & Darimont, 2010). Recent work has described frameworks to enable the scientific assessment of wild animal welfare, but these have yet to be widely applied (Harvey et al., 2020, 2023; Harvey et al., 2021; Harvey et al., 2022). Animal welfare is characterised mainly in terms of an animal's mental experiences, in other words, how the animal may be experiencing its own life (Beausoleil et al., 2018; Green & Mellor, 2011; Harvey et al., 2020; Mellor, 2016; Mellor et al., 2015; Stafford, 2013). Contemporary animal welfare science aims to interpret indicators of biological function and behaviour in terms of the mental experiences that those indicators are likely to reflect (Harvey et al., 2020). Mental experiences, or affective states, are subjective and cannot be measured directly, but indirect indices can be used to cautiously infer affective experiences. Previous work has described how such indicators of a range of mental experiences may be detected and validated in wild animals (Harvey, 2022; Harvey et al., 2023; Harvey et al., 2021).

Indicators of mental experiences have not been described and validated in any marsupial species to date. In the context of climate change, better understanding the welfare impacts on wild animals may assist in conservation efforts. This may be particularly useful for species found outside the climatic range that they are adapted to survive in. An example of this are mesic species with ranges extending into drier regions, such as eastern grey kangaroos (*Macropus giganteus*) (Dawson et al., 2006), due to such species being less adapted to drier and hotter conditions compared to their dryland conspecifics (e.g., red kangaroos – *Osphranter rufus*). Furthermore, with rates of aridification increasing due to land clearing as well as being exacerbated by climate change, the total area of land covered by semi-arid and arid rangelands in Australia is predicted to increase (Larkin et al., 2020). Assessing the impacts of heatwaves on eastern grey kangaroos currently living in semi-arid rangelands may, therefore, also give us a glimpse into the future of eastern grey kangaroos found in temperate zones should aridity reach those populations.

In previous chapters I have shown that at more extreme temperatures eastern grey kangaroos seek out waterpoints in preference to shade (Chapter 4), that increased temperatures result in increased interactions between dingoes and eastern grey kangaroos at waterpoints (Chapter 5), more predation events occur during heatwaves (Chapter 5), and that heatwaves disrupt dingo preference for eastern grey kangaroos in poor body condition with predation instead focusing on individuals of all body conditions (Chapter 5). These findings suggest that eastern grey kangaroos are using water for thermoregulation during extreme heat events, and therefore camera traps placed at water points are likely to detect thermoregulatory behaviours. A requirement to use water for thermoregulation may also give rise to specific welfare challenges. Firstly, heat events are likely to be associated with increased heat discomfort and dehydration, particularly if effective thermoregulation cannot be promptly achieved. Heat discomfort and dehydration would be expected to increase if access to water was obstructed such as through effects of predators, or inability to access water due to injury, weakness, physical obstruction e.g. mud. Secondly, the increased interaction with predators would be anticipated to give rise to additional welfare challenges of anxiety/fear associated with proximity to predators, and impacts of direct predation events which may include physical injuries resulting in pain and debilitation, submersion in water which may result in water aspiration, leading to breathlessness, where both may ultimately result in death through fatal injuries, through dehydration where non-fatal injuries prevent access to water, and from drowning.

Camera trapping has been used as a method to collect data for a wide variety of wild animal studies, for example to measure activity overlap between species (Ridout & Linkie, 2009), measure the body condition of wild animals (Pérez-Flores et al., 2016), analyse animal behaviour (Wooster et al., 2021), or to monitor and estimate population densities (Trolliet et al., 2014) among others, and more recently to assess welfare indicators in wild animals (Harvey et al., 2021).

The aim of this study was to 1) investigate the use of camera traps at waterpoints to evaluate what potential welfare indicators of specific mental experiences (heat discomfort, dehydration, anxiety/fear, pain) were feasible to detect with remote camera traps, 2) to evaluate the prevalence of these potential indicators during extreme heat events, 3) to document potential thermoregulatory behaviours and their prevalence during extreme heat events, 4) to document behaviours related to predator presence and their prevalence during extreme heat events, and 5) to identify potential differences in behaviours and indicators observed at tanks and dammed watercourses.

6.2. METHODS

6.2.1. *Study overview*

I made camera trap observations of eastern grey kangaroos at waterpoints of a large conservation property in the semi-arid rangelands of south-western Queensland, Australia, to identify potential indicators of welfare challenges associated with thermoregulation and predation during heatwaves.

6.2.2. *Study site*

This study was undertaken on the Mourachan Conservation Property (MCP), a conservation property located in the semi-arid rangelands of south-western Queensland, Australia. The MCP, owned by Australia Zoo, includes five macropod species; eastern grey kangaroos (herein kangaroos), red kangaroos (*Osphranter rufus*), black wallabies (*Wallabia bicolor*), red-necked wallabies (*Macropus rufogriseus*), and black-striped wallabies (*Notamacropus dorsalis*). Waterpoints present at Mourachan include excavated tanks (herein 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 earthen 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). All tanks present on the property had been established prior to Mourachan being converted to a conservation property in the early 2000s. While a small number of livestock lives on the property they do not have access to the waterpoints used in this study, therefore impacts related to livestock such as water quality or interactions with kangaroos, for example, were not considered. In contrast to tanks, here I 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 (Malerba et al., 2023), with the first dam wall of the property built in 1949 on the WTH watercourse (Figure 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). All tanks and dammed watercourses available on the property were used for the purpose of this study, totalling 14 tanks and 3 dammed watercourses (Figure 1).

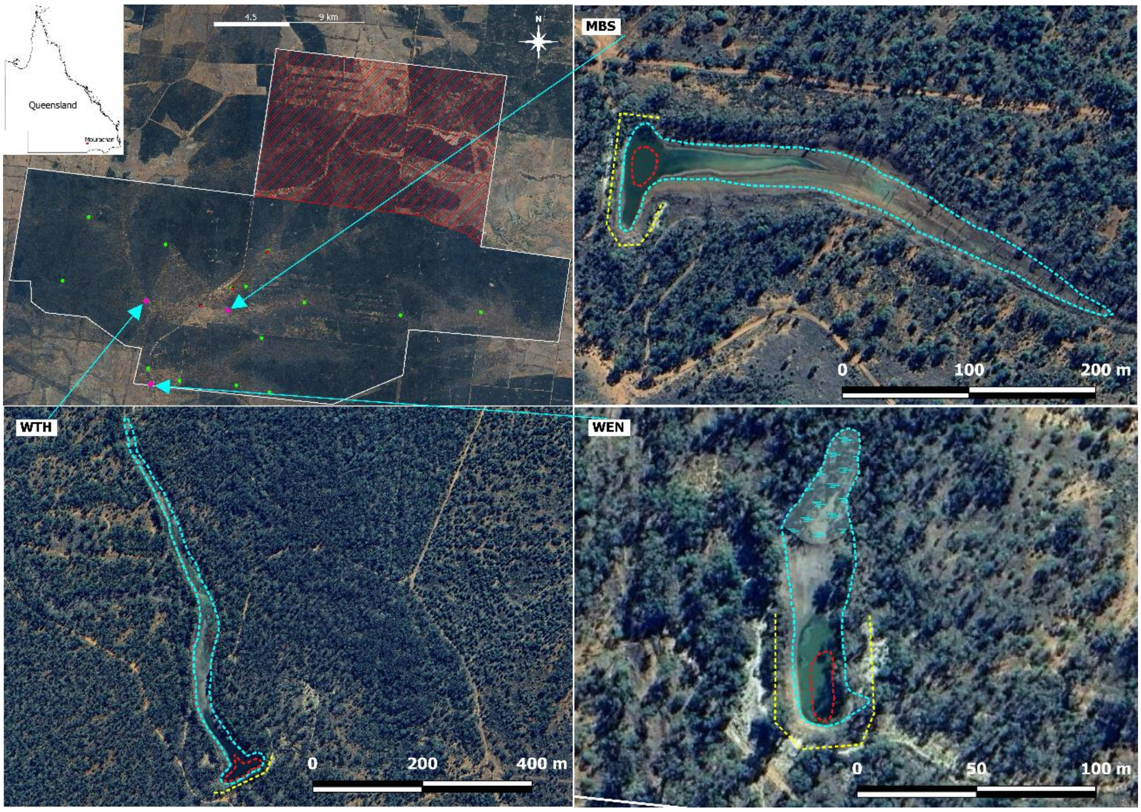

Figure 1. Map of the Mourachan property showing the location of all waterpoints where camera traps were deployed. The red section on the property map represents a zone of the property I did not have access to for this study, however, it was still included on the map so as to not cut the property boundaries. Tanks (n=14) are represented by green dots while dammed watercourses (n=3) are represented by pink diamonds and pointed at by blue arrows. Zoomed-in satellite imagery of the three dammed watercourses (WTH, MBS, WEN) are also shown with dam walls represented by yellow dotted lines, water volume at its highest during the study period represented

by blue dotted lines, and at its lowest by red dotted lines. The back section (non-dammed) of the WEN watercourse, represented by the swamp topography layer, is not made of open water but rather shallow (approximately 20cm deep) swamp conditions, with the ground then gradually transitioning into the deeper open water part.

Figure 2. Image of the back section of the WEN dammed watercourse showing the swamp like conditions along with trees standing in the water, water depth of the back section is no deeper than 20cm offering wild animals the opportunity to both drink and walk across the water (*photo credits: L.Q. Juillard*).

6.2.3. Camera trap placement and settings

I deployed camera traps (n=34) (Browning Strike Force HD Pro X) at the tanks (n=14) and dammed watercourses (n=3) of the MCP from November 2019 to October 2023 with two cameras per waterpoint (Figure 1). The 47-month study period included the most severe drought and heatwave (Chapters 3 and 5) on record for the field site, allowing the observation of thermoregulatory behaviours and potential indicators of welfare challenge during extreme weather events. I set-up the cameras so that footage would include both the ground and enough of the water to observe indicators related to water use (for example water immersion). Cameras were set to take a photo every second maximum once triggered. While the dammed watercourses cover a larger area than the tanks, I decided to only deploy 2 camera traps to those waterpoints as well. This decision was made following observation of the water level fluctuation throughout seasons with the "head" of the dammed watercourses (location of the dam wall) offering a constant supply of water as opposed to the tail, which was often dried up, as shown by the satellite imagery for MBS, WTH, and WEN on Figure 1. I, therefore, deployed the cameras near the head of the dammed watercourses to ensure that water be visible throughout the monitoring period. The head would likely also be where wildlife focused much of their activity due to the higher likelihood of water presence.

6.2.4. Assessment of kangaroo events

Using the camera trap footage collected, images were grouped by events, where an event represents a group of consecutive images taken by the same camera within 5 minutes of the previous image. Events were further separated by individual kangaroos, for example, where an event showed three individual kangaroos, it was split into three different events, one per kangaroo. To recognise kangaroo events coming from the same images the same ID name was given, and an extra identifying digit at the end of the event name was added, e.g., event_021098_1, event_021098_2. Due to the difficulty in identifying individual kangaroos, in order to recognise individuals, all events with multiple kangaroos were analysed from the left to the right of the images, with the individual further to the left given identifier "_1", and so on. For events with multiple images where kangaroos moved through the frame, the left to right analysis was based on the first image, with each individual then followed as they moved across the frame throughout the duration of the event. All images within an event were used to assess behaviours and indicators, with the camera setting of 1 image taken per second allowing for finer details to be observed than when only analysing single images.

6.2.5. Selection of behaviours/indicators

Behaviours, potential indicators of welfare challenges, and other parameters that were recorded were divided into thermoregulatory behaviours/indicators, predation related behaviours/indicators, mortality, additional behaviours/indicators, and demographic parameters. These are detailed in Table 1 together with the possible mental experiences that can be cautiously inferred from these behaviours/indicators.

Table 1. Behaviour/indicators and demographic parameters that were recorded from camera trap images, and the possible mental experiences they reflect.

	Behaviour/indicator	**Possible mental experiences**
Thermoregulatory behaviours/indicators	Water immersion Standing in water Walking through mud Licking forelimbs Wet fur Drinking Splashing themselves	Thirst, pleasure of quenching thirst Heat discomfort, pleasurable feeling of cooling water
Specific predation related behaviours/indicators	Proximity to predators Physical contact with predators Upright stance On ground flight from predators Swimming to escape predator	Varying degrees of anxiety/fear Vitality of fitness Progressive exhaustion
	Injuries from predator attack Altered body posture/gait associated with injury	Pain, anxiety/fear, increased risk of dehydration, heat discomfort
Mortality	Died in water	Fear, weakness, exhaustion, breathlessness
	Died following predation	Fear, exhaustion, pain
	Died stuck in mud	Fear, frustration, weakness, exhaustion
	Died on dry ground, reason unknown	
Additional behaviours/indicators	BCS ≤ 2 (very thin to emaciated)	Hunger
	Weakness	Weakness, malaise
	Vigilance	Anxiety/fear, curiosity
	Proximity to other macropod species	Sociable, safe, content
	*Agonistic behaviour with other kangaroos	N/A
	*Lying down resting	N/A
	*Grooming	N/A
	*Foraging/grazing	N/A
Social structures and demographic parameters	Proximity to other kangaroos Age class Sex	N/A

*Time budget behaviours, mental experiences not applicable

6.2.5.1. Thermoregulatory behaviours/indicators

The range of thermoregulatory behaviours and indicators recorded from images are shown in Figure 3. ‘Water immersion’ was recorded when most of the kangaroo’s body was submerged in water, as opposed to ‘standing in water’ which was recorded when only the legs of the kangaroos were submerged. Kangaroos walking through mud to reach water was recorded since the edges of some of the waterpoints consisted of deep sticky mud which kangaroos were also observed to get stuck in. Licking of forearms has been well described as a thermoregulatory behaviour in kangaroos, resulting in evaporative cooling (Croft, 1980; Dawson et al., 2000), but is context specific as can also occur as a result of anxiety (Dawson, 2012). Presence of wet fur was recorded when a kangaroo could be observed as having wet fur but was not captured on camera to be entering the water. Water requirements increase during higher temperature and an increase in drinking replaces lost metabolic water preventing dehydration.

Figure 3. Camera trap images illustrating a range of thermoregulatory behaviours/indicators on days where maximum ambient temperatures ranged from 38.9 - 46°C. These kangaroos would have likely been experiencing varying degrees of heat discomfort, motivating them to perform these behaviours to cool down, and/or varying degrees of thirst, motivating them to seek water to drink **(a) Water immersion. (b) Standing in water. (c) Walking through mud.** While the same series of images is used in Figure 5e-f to describe kangaroos dying in the mud, the image here shows two kangaroos, one kangaroo eventually makes it out of the mud while the other one dies (Figure 5e-f). The surviving kangaroo is therefore used as the walking through mud example. **(d) Licking forelimbs. (e) Wet fur. (f) Drinking.**

6.2.5.2. Predation related behaviours/indicators

In chapter 5 I described how predation rate and pressure from dingoes increased significantly at waterpoints during periods of heat anomalies. Consequently, it was anticipated that welfare challenges related to predation may be increased. The range of predation related behaviours and indicators recorded from images are shown in Figure 4. Proximity to predators was identified as kangaroos and dingoes occurring on the same camera trap event regardless of their activity (e.g., both species drinking, hunting event etc.). Physical contact with predators relates directly to hunting events where physical contact between kangaroos and dingoes was observed on camera trap events. Other defensive behaviours described in the literature used by kangaroos during hunting events were included such as standing upright, fleeing, and entering waterpoints (Jarman & Wright, 1993; Purcell, 2010; Wright, 1993). The upright stance used in this work corresponds to vigilance class V3, described by Colagross and Cockburn (1993) as the highest level of vigilance, normally seen in kangaroos faced by a threat, in this work dingoes.

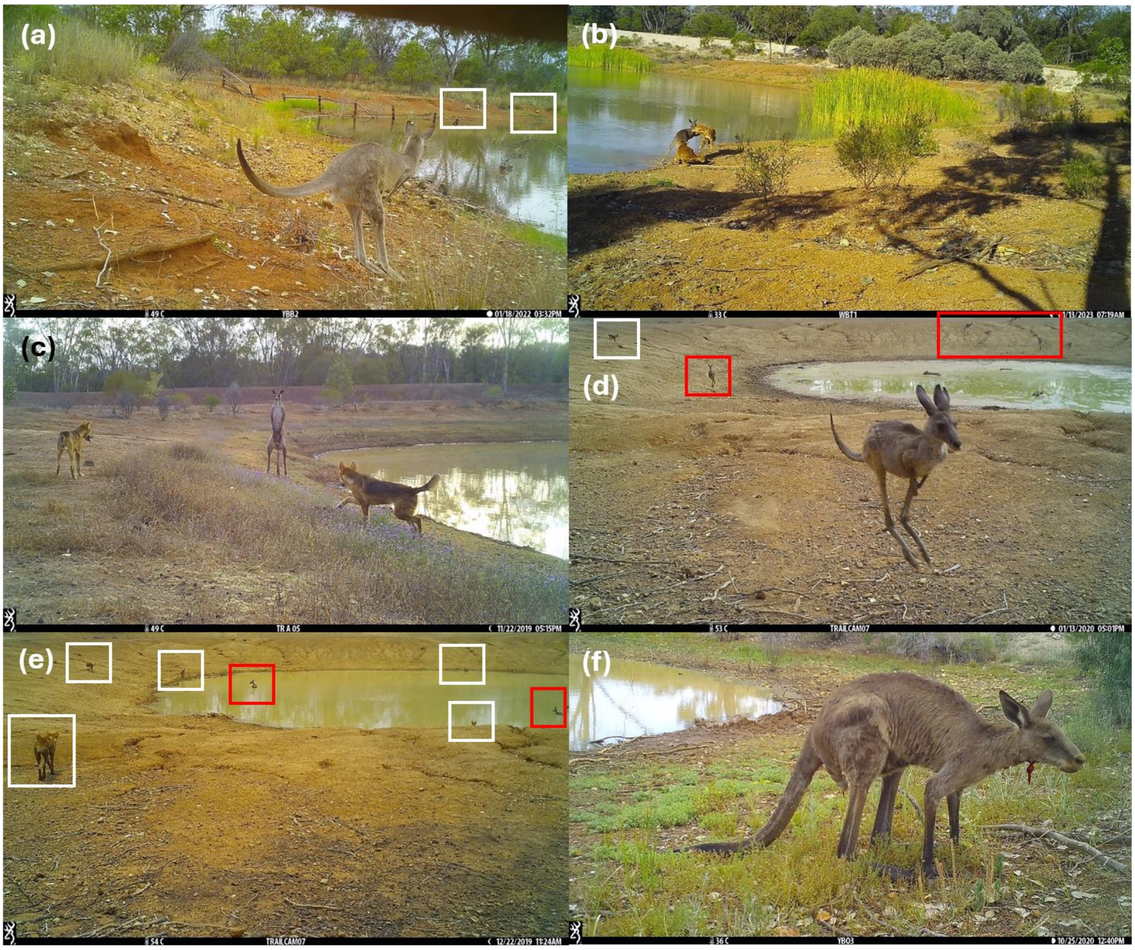

Figure 4. Camera trap images illustrating a range of predation related behaviours/indicators on days where maximum ambient temperatures ranged from 28.4 – 52.8°C. **(a) Proximity to**

predators. Kangaroo at a waterpoint where two dingoes (white squares) are already present and can be seen lying down on the opposite side of the water. **(b) Physical contact with predators.** Two dingoes are seen attacking a kangaroo accessing a waterpoint to drink. This kangaroo would likely have experienced extreme fear, and pain during the attack. The event ends with the death of the kangaroo (Figure 5). **(c) Upright stance.** Kangaroo standing upright in an attempt to intimidate two dingoes. **(d) On-ground flight from predators.** Six kangaroos (red squares) fleeing a waterpoint due to the arrival of a dingo (white square). **(e) Swimming to escape predators.** Two kangaroos (red squares) try to escape five dingoes (white squares) by going in a waterpoint, causing the dingoes to surround the waterpoint. **(f) Injuries from predator attack.** A kangaroo with an open wound on the ventral neck, most likely the result of a dingo attack. This kangaroo would have experienced extreme fear, and pain during the dingo attack, and depending on the duration of the attack, may have experienced increasing heat discomfort, +/- dehydration, +/- exhaustion. Ongoing pain will be present from the resultant wound, which depending on severity may impact on ongoing ability to carry out usual behaviours.

6.2.5.3. Mortality

I recorded mortality events every time a kangaroo was seen alive at the start of the event and deceased at the end of the event with death occurring on frame, enabling identification of the potential cause of death. I split mortalities into groups representing the various causes of death observed (Table 1), which are illustrated in Figure 5. The death of the kangaroos was confirmed using camera trap footage; for kangaroos dying in the water the deceased individual would often be floating face down and motionless (motionless being confirmed with series of images where the kangaroo remains in the same position from one image to the next). In the case of the kangaroo dying from predation dingoes can be seen feeding on the individual, and for kangaroos dying in the mud or on dry ground scavengers can be seen feeding on the dead individuals (Figure 5).

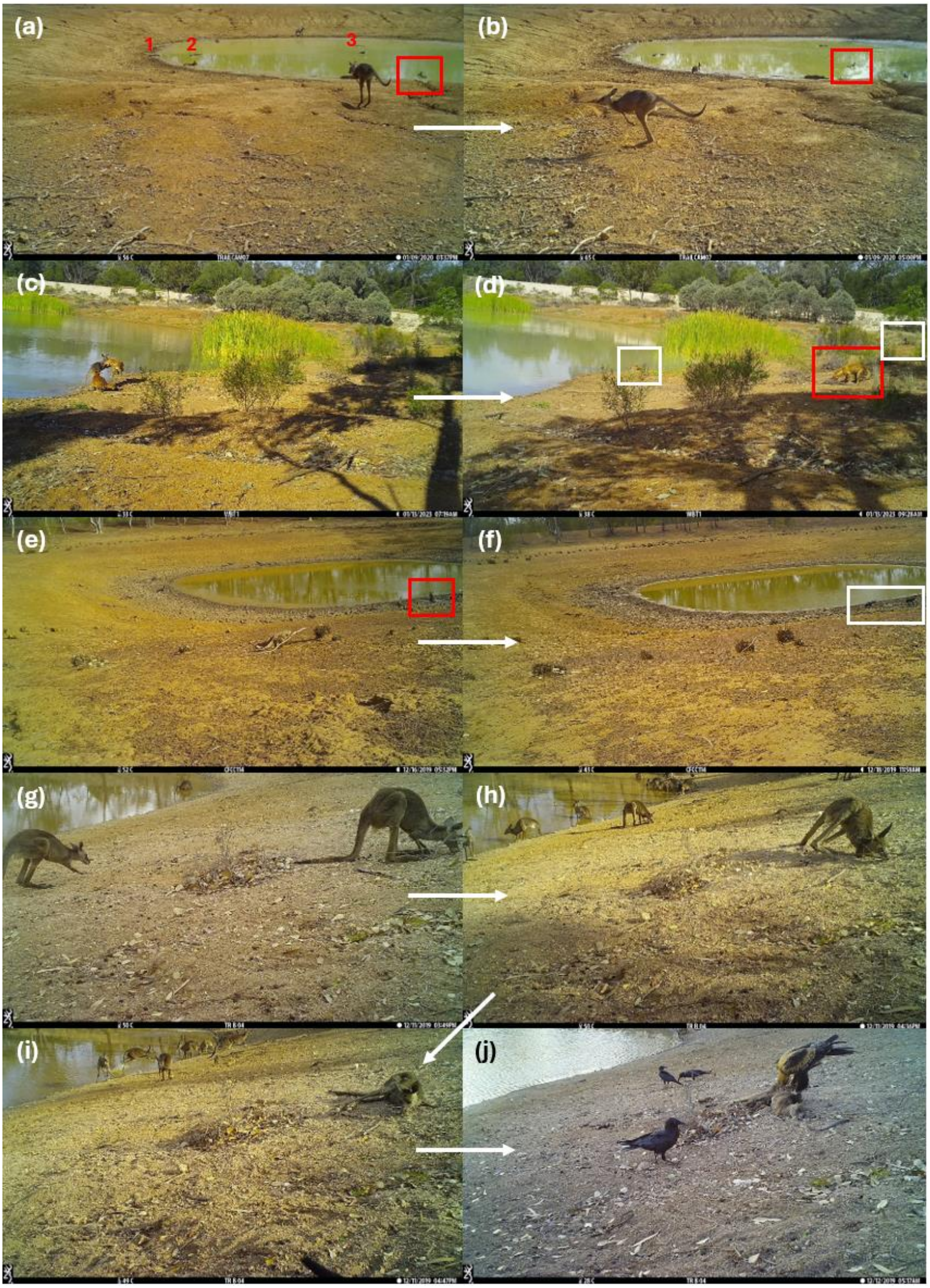

Figure 5. Camera trap images illustrating observed mortalities on days where maximum ambient temperatures ranged from 40.3°C - 49.9°C. **(a-b) Died in water. (a)** A kangaroo is observed swimming in a waterpoint at 1:37pm on the 9th of January 2020 (red square) **(b)** but is unable to

leave the water and can be seen apparently deceased, floating in the water at 5pm on the same day. Note numbers 1 to 3 show other kangaroos who previously died in the water. The precise cause of dying in the water is unknown but may be a result of getting stuck in the mud and being unable to leave the water, remaining in the water due to dingo presence, or unable to leave the water due to weakness and exhaustion. These kangaroos are likely to have experienced varying degrees of heat discomfort, weakness, exhaustion, anxiety, and breathlessness following water inhalation, prior to death. **(c-d) Died following predation. (c)** Dingoes hunting and killing a kangaroo. This kangaroo may have already been experiencing heat discomfort, dehydration and weakness. During the dingo attack they will be experiencing extreme fear and pain. **(d)** The pack can then be observed feeding on the dead kangaroo. **(e-f) Died in mud**. Kangaroo stuck in the mud trying to access water. The kangaroo is first seen stuck at 08:47am on the 16th of December 2019, while the last image with confirmed movement of the kangaroo (alive) was taken at 04:39pm on the following day (17.12.2019), 31hrs 52mins later. Lace monitors and ravens can then be seen scavenging on the dead kangaroo. This kangaroo would have experienced increasing degrees of anxiety, frustration, thirst, dehydration, heat discomfort, hunger, exhaustion, and weakness. **(g-j) Died on ground, reason unknown.** An emaciated kangaroo during the peak of the 2019-2020 drought/heatwave can be seen on the right side of the images (11th December 2019). **(g)** The kangaroo stood in this position for 20 minutes, **(h)** and **(i)** before collapsing to the ground. **(j)** On the morning of the following day birds including a wedge-tailed eagle can be observed scavenging on the now dead kangaroo. This kangaroo would likely have been experiencing extreme hunger, weakness, exhaustion, heat discomfort and dehydration. Likely causes of death may have been starvation, dehydration or heat stroke. If the animal was still alive at the point of the eagle scavenging on it, there would have been additional fear and pain experienced prior to death.

6.2.5.4. Additional behaviours/indicators

The range of additional behaviours and indicators recorded from images are shown in Figure 6. I previously described the impacts of drought on the body condition score (BCS) of eastern grey kangaroos, with poorer BCS observed during more severe drought conditions (Juillard & Ramp, 2022). In this work, the vigilance indicator represents both vigilance class V1 and class V2, described by Colagross and Cockburn (1993) as low-level vigilance where kangaroos can be seen scanning their surroundings – for example while foraging – before going back to their original activity.

Figure 6. Camera trap images illustrating additional behaviours/indicators recorded on days where maximum ambient temperatures ranged from 38.9°C - 48.6°C. **(a) BCS**. An emaciated kangaroo approaching the water during an extremely hot afternoon. It would be anticipated that this kangaroo would be experiencing hunger, heat discomfort and thirst. Being emaciated, in combination with the crouched body posture and low head posture suggests the kangaroo may also be weak which may exacerbate heat discomfort and thirst if weakness increases the duration of time taken to reach water. This in turn may additionally lead to malaise and exhaustion. If the kangaroo is aware of increased predator presence in the vicinity, they may also be experiencing

anxiety or fear on approaching the water since this puts them in a vulnerable position to predation. **(b) Weakness.** The kangaroo shown here (right side of image) visibly struggles to stand, with the head resting on the ground without moving across a series of images taken over 20 minutes, a clear indication of physical/physiological weakness. The outcome of the event (death) is described in Figure 5g-j. **(c) Proximity to other kangaroos. (d) Proximity to other macropod species. (e) Vigilance**. Kangaroos showing signs of being vigilant while foraging. **(f) Agonistic behaviour with other kangaroos**. **(g) Lying down resting and foraging. (h) Grooming.**

6.2.5.5. Demographic parameters

Demographic parameters such as sex and age class were also recorded since differences in resistance to extreme weather events, including droughts, between sexes and age classes have been highlighted (Juillard & Ramp, 2022; Norbury et al., 1988; Robertson, 1986). Age classes were identified using the definitions from Austin and Ramp (2019) who classifies them as: large adults, medium adults, small adults, sub adults, young at foot, and pouch young.

6.2.6. Data analysis

6.2.6.1. Feasibility of behaviour/indicator assessment using camera traps

Once all events were analysed the percentage of events for each indicator where the indicator was possible to assess, was calculated. When indicators were not assessable the reason the inability to assess occurred was identified. The percentage of events where each reason occurred was then calculated.

6.2.6.2. Rate of observation of behaviours/indicators

The rate of observation of each indicator was then measured under non-heat *vs* heat anomaly and waterpoint settings. The settings being: tank during heat anomaly, tank during non-heat anomaly, dammed watercourse during heat anomaly, and dammed watercourse during non-heat anomaly. For each indicator, the number of events during which they are observed in each of the four settings was calculated. Events analysed were randomly selected from the total number of events present in each of the four settings described. The number of events during heat anomaly is 1136 events which led to 4722 images, while the number of events during non-heat anomaly is 500 with 4600 images. The number of events at tanks is 1033 with 5539 images, while the number of events at dammed watercourses is 603 with 3783 images. The rate of occurrence of indicators was then calculated as 1/X, where X represents the number of events needed to observe an indicator once. The rate of occurrence was found by dividing the total number of events in a setting by the number of events for a specific indicator. For example, to find the rate of occurrence of water immersions at tanks during heat anomalies, the total number of events for that setting (n=755) was divided by the number of water immersions observed for the same setting (n=17). This gives us a rate of occurrence of 1/44, meaning water immersion was observed every 44 events. Chi-square tests were then performed to compare observation rates at tanks and dammed watercourses, and to compare observations during periods of heat anomaly and periods of non-heat anomaly. Indicators with observation rates higher than what would be expected according to the Chi-square tests were identified. Additionally, correlation between the prevalence of thermoregulatory indicators and kangaroos dying stuck in the mud or in the water, as well as correlation between prevalence of predation related behaviours and potential indicators of anxiety/fear, and pain were also calculated.

6.2.6.3. Prevalence of likely mental experiences

Using the mental experiences inferred by the range of physical indicators assessed, as described in Table 1, the percentage of events where different mental experiences are expected to have occurred under the different anomaly and waterpoint settings was also calculated. Chi-square tests were also performed to compare likely mental experiences at tanks and dammed watercourses, and mental experiences during heat anomalies and non-heat anomalies. All statistical analyses were carried out in R v4.1.1 (R Core Team, 2023).

6.2.7. Heat anomaly metrics of the Mourachan property

Heat metrics were calculated as described in Chapter 5 using locally corrected temperatures to calculate heat anomalies which were then used to identify the maximum monthly mean (MMM) for a long-term reference period (1971-2000) of 32.1°C. In this Chapter (Chapter 6), I split heat anomalies in two groups: heat anomaly (positive heat anomaly values, for days with a mean temperature above the MMM), and non-heat anomaly (negative heat anomaly values, for days with a mean temperature below the MMM). I then compare the prevalence of each indicator/behaviour between the two anomaly groups as described in section 6.2.6.

6.3. RESULTS

6.3.1. General statistics

Over the 47-month study period a total of nearly 1.8 million images and 46,785 videos (including false triggers) were collected. These included 75,690 images of eastern grey kangaroos. Of these, 1634 events were used for this study, with an average of 5.7 images per event (9322 images).

6.3.2. Feasibility of indicator assessments using camera traps

Indicators that were most often assessable were indicators where a clear view of the kangaroo's body was not needed, for example physical contact with predators (98.65% ± 0.56), swimming to escape predators (98.65% ± 0.56), proximity to other macropod species (98.65% ± 0.56), and upright stance (98.29% ± 0.63) (Table 2). The presence of injuries caused by predators (29.56% ± 2.21) and BCS (36.41 ± 2.33) were the least assessable indicators, likely due to requiring a clear close up view of the body to detect any injuries such as cuts or bite marks, and to confidently assess body condition.

Table 2. Percentage of events where potential indicators/behaviours were assessable out of a total of 1634 events, showing a 95% confidence interval.

Behaviours/indicators		Percentage (%) of events assessable (1634 total)	CI (95%)
Thermoregulatory behaviours/indicators	Water immersion	98.04	97.37 – 98.71
	Standing in water	94.98	93.92 – 96.04
	Walking through mud	98.23	97.59 – 98.87
	Licking forelimbs	93.15	91.92 – 94.37
	Wet fur	51.84	49.41 – 54.26
	Drinking	96.08	95.14 – 97.02
	Splashing	94.49	93.39 – 95.60
Predation related behaviours/indicators	Proximity to predators	98.16	97.51 – 98.81
	Physical contact with predators	98.65	98.09 – 99.21
	Upright stance	98.29	97.66 – 98.92
	On ground flight from predators	97.55	96.80 – 98.30
	Swimming to escape predators	98.65	98.09 – 99.21
	Injuries from predators	29.56	27.35 – 31.77
	Altered body posture/gait associated with injury	42.47	40.08 – 44.87
Mortality	Died in water	99.27	98.85 – 99.68
	Died following predation	99.33	98.93 – 99.72
	Died stuck in mud	98.23	97.59 – 98.87
	Died on dry ground, reason unknown	NA	NA
Additional behaviours/indicators	BCS	36.41	34.08 – 38.75
	Weakness	NA	NA
	Vigilance	94.86	93.79 – 95.93
	Proximity to other macropod species	98.65	98.09 – 99.21
	Agonistic behaviour with other kangaroos	93.21	91.99 – 94.43
	Lying down resting	93.15	91.92 – 94.37
	Grooming	97.18	96.38 – 97.99
	Foraging/grazing	93.15	91.92 – 94.37
Social structures and demographic parameters	Proximity to other kangaroos	65.06	62.74 – 67.37
	Sex	39.47	37.10 – 41.84
	Age class	76.62	74.57 – 78.67

The two main reasons for not being able to assess indicators were kangaroos being too far from the camera (38.84% of events), and the image being too dark (15.1%) (Table 3). Images being too dark to assess indicators only occurred at night. Other reasons indicators were not assessable included motion blur at night often caused by kangaroos moving too fast in front of the infrared flash (10.96%), kangaroos mostly out of frame (4.11%), fleeing trigger off screen if fleeing was observed (3.01%), and kangaroos hidden by landscape features (e.g., tree, high grass, rock) (3.01%).

Table 3. Main reasons why indicators could not be assessed, with the percentage of events where each reason was identified.

Reasons for not being able to assess indicators	**Percentage (%) of events (1634 total)**
Kangaroo too far from camera	38.84
Image too dark (at night)	15.1
Motion blur at night (often due to kangaroos moving too fast for the camera trap)	10.96
Kangaroo mostly out of frame (e.g., only tail visible)	4.11
Fleeing trigger off-screen (specific to fleeing indicator)	3.01
Kangaroo hidden by landscape feature (e.g., tree)	3.01
Kangaroo body at an unsuitable angle	2.33
Kangaroo submerged in water	1.78
Kangaroo hidden by other kangaroos	0.92
Image too blurry	0.5

6.3.3. Rate of observation of behaviours/indicators

The thermoregulatory behaviour of kangaroos standing in water was observed significantly more during heat anomalies (X^2=14.2, p=<0.001; Table 4) and at dammed watercourses (X^2=61.89, p=<0.001; Table 4). Kangaroos with wet fur were observed significantly more at tanks (X^2=7.55, p=0.01; Table 4), however, there was no evidence of a significant difference between heat and non-heat anomaly. Kangaroos were also found to be drinking significantly more during periods of heat anomaly (X^2=10.49, p-value=<0.001; Table 4). All predator related behaviours/indicators where a significant difference was identified had a higher observation rate during periods of heat anomaly and at tanks, those included proximity to predators (anomaly type: X^2=27.9, p=<0.001;

waterpoint type: X^2=44.85, p=<0.001; Table 4), upright stance (anomaly type: X^2=5.27, p=0.02; waterpoint type: X^2=16.29, p=<0.001; Table 4), and on ground flight from predators (anomaly type: X^2=22.23, p=<0.001; waterpoint type: X^2=13.77, p=<0.001; Table 4). Swimming to escape predators was only significantly higher at tanks (X^2=6.72, p=0.01; Table 4), no evidence was found for a difference with heat anomaly. Behaviours and indicators that were rarely observed or only observed in one specific setting (e.g., tanks during heat-anomalies) made it impossible to find any statistically significant difference between groups due to their low sample sizes (Table 4). Such behaviours/indicators included walking through mud, physical contact with predators, injuries from predators, altered body posture/gait associated with injury, all mortality types identified, weakness, and agonistic behaviour with other kangaroos (Table 4).

The correlation coefficient between prevalence of thermoregulatory behaviours/indicators and kangaroos dying stuck in the mud was found to be R=0.77, while that of thermoregulatory behaviours/indicators and kangaroos dying in the water was R=0.87. The correlation between prevalence of predation related behaviours and potential indicators of anxiety/fear, and pain showed that the prevalence of predation related behaviours/indicators and anxiety/fear had a perfect relationship with R=1, while the correlation between predation related behaviours/indicators and pain was also positive but lower with R = 0.22.

Table 4. Rate of observation of each indicator at both waterpoint types during and outside periods of heat anomalies. The fraction (1/X) represents the number of events needed to observe each indicator once, while the number in bracket is the number of events where indicators were observed within each group. Outputs from Chi-square tests for the difference between anomaly type (heat and non-heat anomaly) and between waterpoint type (tank and dammed watercourse) along with their p-values is also shown in the table for each behaviour/indicator. Significant outputs are shown in bold and underlined. When an output is significant in the anomaly type column the symbol * shows heat anomaly as being significantly higher than expected and ^ shows non-heat anomaly as being significantly higher than expected. The same symbols are used for the waterpoint type column with * = tank, and ^ = dammed watercourse.

		Heat anomaly		**Non heat anomaly**		**Anomaly type (*heat ^non-heat)**		**Waterpoint type (*tank ^dammed watercourse)**	
Behaviours/indicators		**Tanks - Observation rate (event count/755)**	**Dammed watercourses - Observation rate (event count/380)**	**Tanks - Observation rate (event count/277)**	**Dammed watercourse - Observation rate (event count/222)**	X^2	**p-value**	X^2	**p-value**
Thermoregulatory behaviours/indicators	Water immersion	1/44 (17)	1/190 (2)	1/277 (1)	1/222 (1)	3.48	0.06	3.72	0.05
	Standing in water	1/16 (47)	1/4 (90)	1/25 (11)	1/12 (18)	14.20	**<0.001***	61.89	**<0.001^**
	Walking through mud	1/94 (8)	1/380 (1)	NA	NA	2.66	0.10	1.58	0.21
	Licking forelimbs	1/84 (9)	1/76 (5)	1/138 (2)	1/32 (7)	0.45	0.50	1.74	0.19
	Wet fur	1/11 (71)	1/19 (20)	1/13 (22)	1/22 (10)	1.19	0.28	7.55	**0.01***
	Drinking	1/3 (225)	1/2 (174)	1/3 (100)	1/7 (34)	10.49	**<0.001***	1.48	0.22
	Splashing	NA	NA	NA	NA	NA	NA	NA	NA
Predation related behaviours/indicators	Proximity to predators	1/10 (74)	NA	1/138 (2)	NA	27.90	**<0.001***	44.85	**<0.001***
	Physical contact with predators	1/755 (1)	NA	1/277 (1)	NA	0.00	1.00	0.12	0.73
	Upright stance	1/24 (31)	NA	1/92 (3)	1/222 (1)	5.27	**0.02***	16.29	**<0.001***

	On ground flight from predators	1/10 (75)	1/24 (16)	1/46 (6)	1/74 (3)	22.23	**<0.001***	13.77	**<0.001***
	Swimming to escape predators	1/58 (13)	NA	1/277 (1)	NA	2.62	0.11	6.72	**0.01***
	Injuries from predator attack	1/755 (1)	1/127 (3)	NA	NA	0.62	0.43	1.13	0.29
	Altered body posture/gait associated with injury	1/755 (1)	NA	1/277 (1)	1/222 (1)	0.54	0.46	0.00	1.00
Mortality	Died in water	1/108 (7)	1/380 (1)	NA	NA	2.24	0.13	1.13	0.29
	Died following predation	1/755 (1)	1/380 (1)	NA	NA	0.03	0.86	0.00	1.00
	Died stuck in mud	1/126 (6)	NA	NA	NA	1.40	0.24	2.10	0.15
	Died on dry ground, reason unknown	NA	NA	NA	1/222 (1)	0.18	0.67	0.07	0.78
Additional behaviours/indicators	BCS ≤ 2 (very thin to emaciated)	1/7 (105)	1/8 (48)	1/46 (6)	1/11 (21)	22.21	**<0.001***	0.13	0.72
	Weakness	NA	NA	NA	1/222 (1)	0.18	0.67	0.07	0.78
	Vigilance	1/5 (157)	1/3 (121)	1/3 (97)	1/4 (58)	7.35	**0.01^**	4.86	**0.03^**
	Proximity to other macropod species	1/4 (177)	1/11 (35)	1/92 (3)	1/10 (22)	51.12	**<0.001***	18.86	**<0.001***
	Agonistic behaviour with other kangaroos	1/378 (2)	NA	1/69 (4)	NA	2.19	0.14	2.10	0.15
	Lying down resting	1/252 (3)	1/32 (12)	NA	1/12 (18)	8.03	**<0.001^**	39.97	**<0.001^**
	Grooming	1/252 (3)	1/54 (7)	NA	1/111 (2)	0.54	0.46	6.00	**0.01^**
	Foraging/grazing	NA	1/7 (55)	1/92 (3)	1/3 (69)	43.08	**<0.001^**	215.91	**<0.001^**
Social structures and demographic parameters	Proximity to other kangaroos	1/2 (545)	1/1 (328)	1/2 (147)	1/1 (206)	6.73	**0.01***	93.97	**<0.001^**
	Large adult	1/15 (52)	1/14 (28)	1/16 (17)	1/25 (9)	1.64	0.20	0.10	0.75
	Medium adult	1/2 (433)	1/2 (290)	1/2 (190)	1/2 (188)	22.36	**<0.001^**	61.81	**<0.001^**

	Small adult	NA	1/127 (3)	1/13 (22)	1/22 (10)	59.61	**<0.001^**	0.00	1.00
	Sub adult	1/755 (1)	1/380 (1)	1/55 (5)	1/222 (1)	5.53	**0.02^**	0.11	0.74
	Young at foot	1/755 (1)	1/380 (1)	1/92 (3)	1/74 (3)	5.53	**0.02^**	0.16	0.68
	Pouch young	1/40 (19)	1/17 (23)	1/9 (30)	1/12 (18)	22.21	**<0.001^**	2.72	0.10

Figure 7. (a) An eastern grey kangaroo foraging at a dammed watercourse of the MCP while three other kangaroos rest in the background. Dammed watercourses offer more foraging and resting opportunities through flatter surfaces and more vegetation growth. **(b)** Tanks offered harsher terrain with little to no vegetation and often steeper banks, making resting and foraging more difficult if not impossible.

6.3.4. Prevalence of likely mental experiences

Indicators of suspected thirst and heat discomfort occurred significantly more during heat anomalies and at dammed watercourses (Thirst: anomaly type: X^2=99.83, p=<0.001; waterpoint type: X^2=16.19, p=<0.001; Heat discomfort: anomaly type: X^2=99.83, p=<0.001; waterpoint type: X^2=16.19, p=<0.001; Table 5). For predation related indicators, indicators of anxiety/fear, vitality of fitness and exhaustion were significantly higher during heat anomalies and at tanks; anxiety/fear (anomaly type: X^2=63.48, p=<0.001; waterpoint type: X^2=81.63, p=<0.001; Table 5), vitality of fitness (anomaly type: X^2=64.77, p=<0.001; waterpoint type: X^2=87.63, p=<0.001; Table 5), and progressive exhaustion (anomaly type: X^2=64.77, p=<0.001; waterpoint type: X^2=87.63, p=<0.001; Table 5). Due to most mortality events observed occurring during heat anomalies (16 of 17), indicators of fear and exhaustion were significantly higher during periods of heat anomaly, however, no difference was found between waterpoint type (Fear: anomaly type: X^2=5.72, p=0.02; Exhaustion: anomaly type: X^2=5.72, p=0.02; Table 5). Indicators of weakness, related to kangaroos dying in water or when stuck in the mud was significantly higher during heat anomalies and at tanks (anomaly type: X^2=4.84, p=0.03; waterpoint type: X^2=4.14, p=0.04; Table 5).

Table 5. Percentage and number of events where mental experiences occurred for both waterpoint types during and outside periods of heat anomalies. Outputs from Chi-square tests for the difference between anomaly type (heat and non-heat anomaly) and between waterpoint type (tank and dammed watercourse) along with their p-values is also shown in the table for each behaviour/indicator. Significant outputs are shown in bold and underlined. When an output is significant in the anomaly type column the symbol * shows heat anomaly as being significantly higher than expected and ^ shows non-heat anomaly as being significantly higher than expected. The same symbols are used for the waterpoint type column with * = tank, and ^ = dammed watercourse.

Inferred mental experiences		**Heat anomaly**		**Non-heat anomaly**		**Anomaly type (*heat ^non-heat)**		**Waterpoint type (*tank ^dammed watercourse)**	
		Tanks % (count/755)	**Dammed watercourse % (count/380)**	**Tanks % (count/277)**	**Dammed watercourse % (count/222)**	X^2	**p-value**	X^2	**p-value**
Associated with thermoregulation indicators/behaviours	Thirst	49.93 (377)	76.84 (292)	49.09 (136)	31.53 (70)	99.83	**<0.001***	16.19	**<0.001^**
	Heat discomfort	49.93 (377)	76.84 (292)	49.09 (136)	31.53 (70)	99.83	**<0.001***	16.19	**<0.001^**
Associated with predation indicators/behaviours	Anxiety/fear	25.96 (196)	5 (19)	5.05 (14)	2.25 (5)	63.48	**<0.001***	81.63	**<0.001***
	Vitality of fitness	25.7 (194)	4.21 (16)	4.69 (13)	1.8 (4)	64.77	**<0.001***	87.63	**<0.001***
	Progressive exhaustion	25.7 (194)	4.21 (16)	4.69 (13)	1.8 (4)	64.77	**<0.001***	87.63	**<0.001***
	Pain	0.26 (2)	0.79 (3)	0.36 (1)	0.45 (1)	<0.001	1	0.52	0.47
	Increased risk of dehydration	0.26 (2)	0.79 (3)	0.36 (1)	0.45 (1)	<0.001	1	0.52	0.47
	Heat discomfort	0.26 (2)	0.79 (3)	0.36 (1)	0.45 (1)	<0.001	1	0.52	0.47
Associated with mortalities	Fear	1.85 (14)	0.53 (2)	0 (0)	0 (0)	5.72	**0.02***	3.13	0.08
	Weakness	1.72 (13)	0.26 (1)	0 (0)	0 (0)	4.84	**0.03***	4.14	**0.04***
	Exhaustion	1.85 (14)	0.53 (2)	0 (0)	0 (0)	5.72	**0.02***	3.13	0.08
	Breathlessness	0.93 (7)	0.26 (1)	0 (0)	0 (0)	2.24	0.13	1.13	0.29
	Pain	0.13 (1)	0.26 (1)	0 (0)	0 (0)	0.03	0.86	<0.001	1.00

6.4. DISCUSSION

I have demonstrated that by using remote camera traps at waterpoints it may be feasible to assess a range of potential welfare indicators and behaviours associated with thermoregulation and predation, in addition to time budget behaviours and documentation of mortality events. I have further shown that many thermoregulatory (standing in water, drinking) and predation (proximity to predators, upright anti-predator stance, on-ground fleeing from predators) indicators/behaviours were observed more frequently during extreme heat events. I also identified a difference in the prevalence of some of these indicators and behaviours between tanks and dammed water sources, for example standing in water being observed more commonly at dammed watercourses, and predation related indicators/behaviours including swimming to escape predators, being observed more commonly at tanks. Uncommonly observed behaviours or indicators included walking through mud, physical contact with predators, injuries from predators, altered body posture/gait associated with injury, mortality, weakness, and agonistic behaviour with other kangaroos and were only observed during heat anomalies and at tanks. There was also a high correlation between the presence of thermoregulatory behaviours/indicators and kangaroos dying stuck in the mud or dying in the water.

As previously described, based on species specific knowledge, I cautiously inferred the likely mental experiences associated with different indicators/behaviours (Harvey et al., 2023; Mellor, 2017; Mellor & Beausoleil, 2015; Mellor et al., 2020). Inferred mental experiences associated with thermoregulatory indicators/behaviours were predominantly thirst and heat discomfort, whilst those associated with predator related indicators/behaviours were predominantly varying degrees of anxiety/fear, exhaustion, and pain. Indicators of thirst and heat discomfort were observed more often during heat anomalies, providing supporting evidence that these are likely to be valid indicators of these mental experiences. They also occurred more often at dammed watercourses, perhaps suggesting that these are preferred waterpoints during extreme heat events.

Indicators of anxiety/fear and exhaustion associated with predation were higher during heat anomalies, and at tanks.

The use of remote camera trap images or videos to document a range of potential welfare indicators remains novel with only one previous report of remote camera traps being used in this way (Harvey et al., 2021). The current study showed similar findings in the most common reasons where indicators could not be assessed on camera trap images, being when animals were standing too far from the camera, and at nighttime. Indicators where the body of the kangaroo does not need to be observed in detail (e.g., physical contact with predators, swimming to escape predators, proximity to other macropod species) were the more easily assessable indicators using camera trap images, whereas indicators that rely on the full body being visible, such as BCS and presence of injuries caused by predators, were the indicators that were not able to be assessed as frequently.

The increased observation during heat anomalies of the thermoregulatory behaviours of standing in water and drinking suggests that kangaroos are seeking water sources for thermoregulation during extreme heat events, as utilizing other thermoregulatory behaviours such as shade use and licking forearms may no longer be enough on its own. Kangaroos are known to lick their forearms to allow evaporative cooling to occur (Croft, 1980; Dawson et al., 2006). However, we did not find evidence that the licking of forearms increased significantly during heat anomalies, which could suggest that use of external water may be a more effective thermoregulatory strategy. Increased drinking is to be expected during higher temperatures (Mella et al., 2019). When the thermal neutral zone (TNZ) of an animal is exceeded, metabolic rate increases to try and maintain a constant body temperature (T_B) (Norris & Kunz, 2012). The increased rate of metabolic water loss triggered by the fast metabolic rate leads to the affected individual needing to hydrate more to replace the lost metabolic water (Costa et al., 2013). Standing in water while drinking may also increase safety in the presence of predators. Standing in water was observed more frequently at dammed watercourses, whilst predator related indicators were observed more frequently at tanks. This could possibly represent a difference in the ability to stand in water, such as tanks potentially having more muddy bases and/or steeper gradients. This would also support the increased observation of kangaroos getting stuck in mud and dying in the water.

Whilst more work would be needed to confirm the correlation between the prevalence of thermoregulatory behaviours and kangaroos dying stuck in the mud or in the water, it suggests that at times of extreme heat kangaroos were more likely to engage in risky behaviour to access water, such as walking across the muddy edges of some tanks. While the concept of state-dependent-risk-taking usually suggests that the physical state of a prey can influence their behaviour and push them to take more risks in relation to predators (Clark, 1994), the physical state of the kangaroos here is likely what pushed them to venture through the mud and risk becoming stuck in an attempt to access water. The increased observation of kangaroos dying in the water at tanks is also likely to be associated with surrounding mud making it difficult for kangaroos to exit the water.

The increase in observation of predation related indicators/behaviours during extreme heat events is in line with my previous findings that predator interactions increase during heat anomalies and are higher at tanks (Chapter 5). Combined, these findings have important implications for kangaroo conservation and welfare as extreme heat events increase. Water sources are preferred for thermoregulation, but increased time spent at water sources comes at a risk of increased predation and mortality not just from predation but also from being stuck in mud surrounding water sources, and drowning. My study provides evidence suggesting that kangaroos have a preference for dammed waterpoints rather than tanks, with dammed waterpoints being safer than tanks with fewer predator events.

Artificial waterpoints in drylands, such as the tanks described in this thesis, can often act as hotspots of predator activity (Makin et al., 2017; Wallach & O’Neill, 2009; Wooster et al., 2021). Tanks are often characterized by smaller areas and less vegetation cover making prey detection and hunting easier, as opposed to the larger dammed watercourses. Furthermore, perhaps due to the lower risks of predation at dammed watercourses but also likely due to their configuration (e.g., more grass, flatter surfaces near the water), behaviours such as foraging and lying down to rest were more prevalent at dammed watercourses. These waterpoints can offer greater vegetation cover, providing both a source of food and protection from environmental conditions, encouraging foraging behaviour (James et al., 1999; Morton et al., 1995). The flatter, more stable terrain around dammed watercourses also makes it easier for kangaroos to rest, as they are less likely to encounter harsher surfaces such as the muddy terrain found near some of the tanks (Mpalo et al., 2024). Additionally, the presence of more established ecosystems around dammed watercourses, including increased biodiversity, likely contributes to the higher availability of forage and safer resting spots (James et al., 1999). This combination of foraging opportunities and safe resting areas may explain the preferred use of these waterpoints by kangaroos, particularly during non-heat anomaly periods, allowing kangaroos more opportunities to exhibit such behaviours. During higher temperatures, kangaroos may be under more pressure to use the alternative dammed water source, for example if it involves a shorter travel distance to water or due to competition for water sources. Kangaroos are known to rely on access to water for thermoregulation with cooling mechanisms relying on evaporative heat loss (Blaney et al., 2000; Dawson et al., 2000b; McCarron et al., 2001). At ambient temperature increasing from 26°C to 43.5°C eastern grey kangaroo body temperature will increase slightly from 36.3°C to 37.1°C (Dawson et al., 2000b). With water restriction during prolonged exposure to high ambient heat (45°C), their body temperature will rise to above 40°C (Dawson et al., 2007). With continued heat exposure and ineffective cooling mechanisms, kangaroos may show signs of hyperthermia including panting, sweating, raised pulse rate, elevated temperature and ultimately convulsions and death (Hume et al., 1989; Jackson, 2007).

One important limitation of this study is that it has only captured data on kangaroos that are at water sources. What is unknown is what proportion of kangaroos may not make it to water sources for whatever reason, for example due to weakness or injury, and therefore are unable to effectively thermoregulate and the welfare impacts of this; or what proportion manage to effectively thermoregulate via other mechanisms (e.g. shade use) and utilise water sources less frequently, and how the welfare impacts vary across kangaroos that may not have been captured by cameras at waterpoints.

More work needs to be done to scientifically validate the inferred mental experiences (Harvey et al., 2023). However this work suggests that during extreme heat events, kangaroos are more likely to experience thirst, heat discomfort, and anxiety/fear and pain related to predation. If effective thermoregulation is not promptly achieved, they are likely to experience progressive dehydration, hyperthermia and subsequent weakness. These experiences will be exacerbated if they are facing additional hurdles in attempts to access water, for example getting stuck in mud, or facing threats of predators, and in these cases progressive exhaustion may also occur. Overall the work suggests that eastern grey kangaroos are likely to experience increasing welfare impacts as climate change progresses and extreme heat events occur more frequently. This has significant implications for kangaroo conservation and welfare. Increased access to safe water sources may mitigate some of these impacts.

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CHAPTER 7: THESIS DISCUSSION

7.1. A RAPIDLY CHANGING CLIMATE

While the Earth's climate has always experienced variations, it has now entered a period of changing so rapidly that many living organisms stand little to no chance of adapting to such changes (IPCC, 2021). Indeed, across the world, climate change has already been the cause of extinctions (Pounds et al., 1999), with many currently extant species experiencing various levels of local extinctions as well (Román-Palacios & Wiens, 2020). It is now predicted that by the year 2070, a third of all wildlife and plant species globally could be lost due to climate change (Román-Palacios & Wiens, 2020). These climate changes are mainly due to anthropogenic activities over the past century (IOM, 2023; IPCC, 2021, 2022, 2023). For example, the rate of land clearing in Australia is significant on a global scale, with vast ecological consequences (Andrich & Imberger, 2013; Heagney et al., 2021; Reside et al., 2017). Land clearing has been directly linked to impaired terrestrial, freshwater, and marine ecosystem functioning, as well as being a key factor in anthropogenic climate change (Reside et al., 2017). As a consequence, extreme weather events such as heatwaves and droughts in many parts of the world are now lasting longer, increasing in frequency, and intensity (Dosio et al., 2018; Kirono et al., 2020; Trancoso et al., 2020; Vicente-Serrano et al., 2019). Indeed, global surface temperatures increased at a faster rate during the last 50-year period than any other 50-year period in the last 2000 years (IPCC, 2023).

Amidst these climatic challenges, successful conservation of wild animals and their habitats cannot be fully achieved without a better understanding of precisely how populations are being impacted. While knowledge of such impacts is already extensive for many species, in the case of kangaroos, research focusing on the impacts of extreme weather events including droughts and heatwaves remains relatively sparse and generally pre-dates current weather extremes (Caughley et al., 1985; Newsome et al., 1967; Robertson, 1986). Other work published to date focuses on the influence of rainfall patterns rather than drought itself, and were also published pre-2000 (Cairns & Grigg, 1993; Caughley et al., 1984). Articles mentioning events like drought published post-2000 often only mention droughts in the context of kangaroo population management (Pedler et al., 2021; Pople, 2003; Zanker, 2021). Furthermore, while the previously mentioned publications dating pre-2000 are valuable in showing us some of the impacts faced by kangaroos during extreme events, the rapid rate of climate change today likely means that current extreme events are more intense than they were in the 1980s and 1990s. These more intense events may be causing increased and more varied challenges for wildlife, but we currently have limited understanding of these.

Therefore, in this thesis, I aimed to bring attention to challenges faced by eastern grey kangaroos (*Macropus giganteus*) during droughts and heatwaves in today's climate. Eastern grey kangaroos were specifically chosen as they are a mesic species whose range partly extends into semi-arid and arid rangelands (Croft, 1980; Dawson et al., 2007). As a mesic species, eastern grey kangaroos lack some of the adaptive advantages of arid-adapted macropod species, such as the red kangaroo (*Osphranter rufus*). For example, red kangaroos are able to suspend embryonic development (embryonic diapause) when environmental conditions are poor (Moss & Croft, 1999), a trait that has evolved to promote survival under arid conditions (Dawson, 2012). Without this advantage, eastern grey kangaroos are less resilient to both droughts and heatwaves. While current evidence suggests otherwise, we are still unsure whether eastern grey kangaroos will be able to use such adaptations during extreme conditions. Furthermore, trends in aridification in Australia suggest that aridity is going to expand into the range of eastern grey kangaroos (Larkin et al., 2020), making it a matter of urgent concern for us to understand what is likely to happen to affected individuals in the future. Eastern grey kangaroo populations already living in semi-arid or arid rangelands can offer us a glimpse into the future of more populations should current trends in extreme weather intensification continue.

7.2. CLIMATE CHANGE AND KANGAROOS (GENERAL FINDINGS SUMMARY)

7.2.1. Drought

Throughout the various chapters of this thesis I showed that the body condition (BC) of eastern grey kangaroos was closely linked to environmental conditions. As the drought index I used in this thesis (SPEI) reached its lowest point during the 18-month study period for Chapter 3 (November 2019 – April 2021), in December 2019, so did the average BC of the kangaroos. Furthermore, the decrease in SPEI was followed by a drop in the amount of vegetation available, as shown by the Normalised Difference Vegetation Index (NDVI) in chapter 3. Lower vegetation availability along with drier and hotter conditions explain why an increase in the prevalence of poor BC was observed. Indices such as NDVI have been proven useful in explaining trends in wild animal life history traits, as well as abundance and distribution both spatially and temporally (Pettorelli et al., 2011). NDVI has already been shown as being a strong predictor of body mass for other species, for example roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) (Pettorelli et al., 2006; Pettorelli et al., 2011), while it was found to influence the body condition and reproductive timing of the African buffalo (*Syncerus caffer*) and African elephant (*Loxodonta africana*) (Ryan et al., 2012). Perhaps unsurprisingly due to the close link between BC and nutritional status (Harvey et al., 2020), poor BC is said to be one of the main causes of death during droughts (Knight, 1995). Poor body condition can trigger a range of physiological impairments impacting the immune and reproductive systems, as well as cognitive functions (Acevedo-Whitehouse & Duffus, 2009). With kangaroos often choosing the greener, more nutritious vegetation, when such resources become quickly unavailable during droughts, subsequent high mortality rates are likely (Moss & Croft, 1999). As body condition declines, animals are likely to become weaker (Harvey, 2022) and their ability to effectively thermoregulate, reach water sources to maintain hydration, whilst also avoiding predation is likely to decline. These factors may contribute to increased morbidity and more rapid mortality than death due to starvation alone.

7.2.2. Heatwaves

While drought conditions at Mourachan were broken at the end of January 2020, heatwaves occurred multiple times throughout the study period. This was found by calculating heatwave metrics appropriate to the Mourachan property (Chapter 5). As temperatures increased, I found that the likelihood of observing kangaroos (both eastern grey and red) using the shade provided by trees was significantly higher. Shade use is one of the most common methods used by terrestrial mammals to thermoregulate (Terrien et al., 2011), including kangaroos (Dawson et al., 2006). Being continuously exposed to solar radiations, particularly when temperatures are high, can push individuals outside of their thermoneutral zone (TNZ). Exceeding the TNZ leads to faster metabolic rates to keep an optimal body temperature, which triggers a more rapid evaporation of metabolic water (Norris & Kunz, 2012). However, simply sheltering from solar radiation can significantly reduce the risk of exceeding the TNZ and overheating (Norris & Kunz, 2012). Although I observed both kangaroo species in the shade significantly more at high temperatures, I found that red kangaroos had a higher probability of being in shade than eastern grey kangaroos. When looking at the number of kangaroos in the sun I also showed that red kangaroos seemed to be leaving the sun at temperatures lower than eastern grey kangaroos, with the probability of observing a red in the sun falling below 50% at only 17°C compared to 28°C for eastern greys. While the kangaroos presence in the shade or sun may be thermoregulation related, the methods I used do not allow for thermoregulation related conclusions to be made as I did not measure physiological data or T_B, so here I only cautiously speculate that thermoregulation may be playing a role in the observation probability. The difference between the two species could therefore also be related to other unknown circumstances.

Another shift that I observed during extreme temperature events was a significantly higher activity rate of kangaroos at waterpoints. Replacing metabolic water lost through evaporation during high temperature events is vital to an organism’s survival (Costa et al., 2013). Failure to do so can lead to impacts ranging from thirst to more pronounced heat stress, impairing cognitive abilities and systems like the reproductive and immune systems as well as causing organ failures (e.g., kidneys) (Acevedo-Whitehouse & Duffus, 2009), and ultimately leading to the death of the affected individual. While an increased activity rate of kangaroos at waterpoints may be to replace lost metabolic water, at extreme temperatures, immersing in water also works as a way to cool down. Using water to thermoregulate either through immersion or behaviours such as wallowing has been observed in many species (Parker & Robbins, 2018; Ruf et al., 2023). For example, black bears 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 et al., 2017).

7.2.3. Differences in activity at different waterpoints

Interestingly, while eastern grey kangaroos increased their activity rate at all waterpoints of the property with increasing temperatures, they did not do so equally. Their activity rate started to increase significantly at dammed natural watercourses when maximum daily temperatures exceeded only 27.6°C, while it only increased significantly at tanks when temperatures exceeded 36.8°C, a 9.2°C difference. Furthermore, in Chapter 6 I showed that some indicators were significantly more prevalent at dammed watercourses than at tanks, for example: standing in water, lying down resting, proximity to other kangaroos, grooming, and foraging/grazing. While the dammed watercourses here have been modified by human-made structures (dam walls) they still retain some of the characteristics that make natural watercourses more beneficial to biodiversity than tanks, or other artificial waterpoints. Natural waterpoints, such as creeks, support a large aquatic and terrestrial biodiversity, including through higher water quality and vegetation diversity as well as abundance than artificial waterpoints (Malerba et al., 2023). Furthermore, artificial waterpoints, particularly those with mud or silt on the edges can trap and kill animals, including livestock (Wallach et al., 2017). The differences between the dammed watercourses and tanks of the property highlighted here may explain why the eastern grey kangaroos showed a preference for the former, as dammed watercourses may offer not only a safer environment but also more opportunities to undertake activities such as foraging, standing in water to cool down, or resting for example.

7.2.4. Increased interactions with dingoes

The increase in the activity rate of kangaroos at waterpoints was accompanied by an increase in dingo activity rate at waterpoints. As a result, during heatwaves, kangaroos experienced a significantly higher rate of interactions with dingoes at waterpoints. Herbivores in semi-arid and arid environments often aggregate around waterpoints, making such locations reliable sources of prey for predators (Valeix et al., 2010). With the availability of water in semi-arid rangelands being naturally low (Stokes et al., 2006) and likely to further decrease in a warming future where heatwaves and droughts are expected to intensify (Kiem et al., 2016; Kirono et al., 2020), the choice of waterpoints will become limited, further forcing prey species to congregate in larger numbers and access sites with higher predator activity rates (Sutherland et al., 2018; Western, 1975). However, similar to other indicators of welfare and behaviours assessed in Chapter 6, the prevalence of predation related ones did not shift equally between waterpoint type. Proximity to predators, adopting an upright stance in an attempt to intimidate predators, on-ground flight, and swimming to escape predators were significantly more prevalent at tanks as opposed to dammed watercourses. The tanks of the property, and farm dams in general, are relatively small in comparison to natural waterways. When a kangaroo is present at a tank the dingoes can easily surround the waterpoint giving the kangaroo the option to either face the dingoes or try to escape by entering the water as I observed (Figure 1). The lower prevalence of predation related activities, and predation related indicators and behaviours, may further explain the preference of eastern grey kangaroos for dammed watercourses.

Figure 1. Tanks can offer easier hunting opportunities due to their smaller sizes and lack of shelter (e.g., vegetation), as well as sometimes steeper banks compared to larger dammed watercourses. Three eastern grey kangaroos in the water of a tank on the Mourachan property while dingoes surround the waterpoint. Dingoes are shown by red squares while kangaroos are shown by white squares.

7.2.5. Increase in thermoregulatory and predation related indicators and behaviours

After assessing the prevalence of thermoregulatory and predation related indicators and behaviours during heat anomalies, I showed that many were significantly more prevalent during times of extreme heat. Those included standing in water and drinking for thermoregulation, and proximity to predators, upright stance, and on-ground flight from predators for predation. During extreme heat eastern grey kangaroos, like many species including humans, lose metabolic water at higher rates due to increased metabolic rate attempting to keep T_B constant (Norris & Kunz, 2012), this alone explains why the prevalence of drinking increased. Standing in water while drinking may also allow the kangaroos to shorten the time spent at water sources by enabling drinking and cooling down to occur simultaneously, potentially lowering the risk of predation occurring. However, the increase in thermoregulatory behaviours/indicators also correlated with an increase in kangaroos dying in the water or stuck in the mud. The inferred mental experiences

I associated with thermoregulation – heat discomfort and thirst – could suggest that during extreme heat, should such inferred mental experiences become too overwhelming, kangaroos may be pushed to take more risks by, for example, attempting to access water from a source surrounded by deep sticky mud.

Predation related indicators and behaviours being more prevalent during heat anomalies fits with the findings shown in Chapter 5, where I observed an increase in interactions between kangaroos and dingoes during heat anomalies. Furthermore, those indicators and behaviours also occurred significantly more at the tanks of the property. Predation related indicators/behaviours were associated with mental experiences such as anxiety/fear, exhaustion, and pain, with anxiety/fear and exhaustion being more prevalent during heat anomalies and at tanks. The increase in predation indicators/behaviours and their associated mental experiences further suggest that kangaroos accessing tanks during heat anomalies may only do so out of necessity when they can no longer afford to avoid artificial waterpoints, even if it means exposing themselves to high risk situations.

7.3. INCREASING TEMPERATURES REQUIRE INCREASED WATER ACCESS

While the use of other landscape features including shade can be vital thermoregulatory requirements to wild animals in drylands, for many wild animal populations, the simple act of finding shade under trees is made more difficult by anthropogenic processes such as land clearing (Giroux et al., 2022). On a global scale it is estimated that 10 to 20% of drylands have been cleared with a rate of 12 million hectares per year (Yirdaw et al., 2017), with 5,896,300 hectares of tree cover cleared between 2000 and 2012 in Australia alone (Hansen et al., 2013).

Lack of shade along with higher temperatures may drive an increased requirement for water. Water availability in semi-arid and arid rangelands is naturally low and, therefore, already presents a challenge to mesic species such as eastern grey kangaroos, Australia is known to block access to waterpoints. Indeed, as part of kangaroo management efforts, fencing off water points has been recommended as a method to reduce the local population density of kangaroos (NSW Biodiversity Conservation Trust, 2020). Unlike originally believed however, there is no evidence that presence of water influences the population density or abundance of kangaroos (Croft & Witte, 2021; Lavery et al., 2018; Montague-Drake & Croft, 2004). With this in mind, providing access to waterpoints during droughts and heatwaves could help eastern grey kangaroos survive such extreme weather. Indeed, the findings I present here through chapters 3 to 6 suggest that increased water access is likely required to improve the welfare and survival of eastern grey kangaroos as the climate intensifies.

7.4. FUTURE RESEARCH DIRECTIONS

While in this thesis I researched some of the impacts eastern grey kangaroos face during droughts and heatwaves, and then used these findings to create a list of potential indicators and behaviours of welfare challenges related to thermoregulation and predation risk during extreme weather, I do not show a complete and detailed welfare assessment as the aim here was to focus solely on what happens at waterpoints.

To make a complete and detailed assessment of the influence of extreme weather on eastern grey kangaroo welfare, particularly with frameworks such as the Five Domains Model in mind, my work can be expanded in a number of ways. Firstly, here I focused on impacts occurring or observable at waterpoints. Including other locations important to kangaroos (e.g., foraging sites, resting sites) would allow for a wider variety of behaviours, interactions (whether with kangaroos or other species), and welfare indicators to be assessed. Secondly, focusing on the various age classes of kangaroos separately would have significant benefits, mortality rate of juveniles during extreme events for example is likely to be higher than that of adults (Robertson, 1986). Past research focusing on kangaroo mortality during drought has found that males were more likely to die than females, and that both young and old individuals had higher mortality rates compared to other age groups (Robertson, 1986). Additionally, future research should focus on new field sites and other eastern grey kangaroo populations. The conditions offered to kangaroos on Mourachan are also fairly uncommon compared to the rest of their range. The kangaroos I observed are fully protected and are not exposed to any of the additional impacts faced by kangaroos living on or around agricultural landscape, for example lethal management, interactions with livestock, waterpoints fenced off to block wildlife access (Lavery et al., 2018), or any effects related to proximity to urban areas (Brunton et al., 2018; Herbert et al., 2021). It is, therefore, likely that kangaroos in more common areas of their range would be subject to more pressure during extreme weather events, making knowledge of their welfare during such times a matter of more urgent concern.

Finally, as shown by Harvey et al. (2021) further welfare research would benefit from using videos from camera traps as opposed to only images. While I was able to observe and describe an extensive list of behaviours and indicators in chapter 6, videos allow for a wider range of indicators to be observed, for example more subtle indicators such as breathing rate, panting, shivering, or tremors. The addition of direct observations recorded using handheld cameras may also allow for higher quality footage to be recorded, as well as longer videos. Indeed, direct observations, when undertaken in a way that does not alert the animal to the presence of the researcher, allow the researcher to focus on specific individuals and follow them through the landscape when possible, as opposed to camera traps fixed to a specific location that may sometimes only record part of the body (e.g., tail, leg). However, camera traps should remain the main method of data collection as they do offer more benefits than direct observations, the more significant one being the absence of a person in the field who may alert and scare away the wild animals of interest. Direct observations should therefore simply be an addition to the research when possible.

7.5. IMPLICATIONS FOR KANGAROO AND WILDLIFE CONSERVATION

The research I present in this thesis shows that eastern grey kangaroos living in the more arid parts of their range may need to rely more on waterpoints to maintain a stable welfare level due to intensifying heatwave events and droughts. However, as previously mentioned, in much of the Australian agricultural landscape waterpoints are often fenced off to only allow access to livestock (Croft et al., 2007; Lavery et al., 2018). While kangaroo species such as the arid adapted red kangaroo may be able to withstand longer periods without access to water, temperate species such as eastern grey kangaroos are more vulnerable (Dawson et al., 2007). Therefore, protecting natural watercourses in drylands, including natural dammed watercourses, and improving access to water may benefit eastern grey kangaroos by ensuring they meet their physiological requirements during extreme temperature events, either by drinking or cooling down through immersion.

Additionally, as discussed in chapters 4-6 of my thesis, natural watercourses promote extensive vegetation cover, providing cooling opportunities, protection from predators, and the opportunity to forage, as well as supporting local biodiversity by harbouring various species, including macroinvertebrates and amphibians (Alikhanova & Bull, 2023; Maestas et al., 2023; Malerba et al., 2023; Westgate et al., 2021). Alternatively, where natural watercourses are no longer present, artificial waterpoints can be managed in ways that promote biodiversity by creating “enhanced dams” (Westgate et al., 2021). Westgate et al. (2021) called enhanced dams artificial waterpoints that either fully exclude livestock through the use of fences, or that contain a single entry point for livestock. Furthermore, the fences used at enhanced dams only exclude livestock while they allow wildlife species, including macropods, to access water freely (Westgate et al., 2021). Such artificial waterpoints also promote vegetation diversity through re-planting of vegetation, including shrubs and trees (Westgate et al., 2021). Finally, Westgate et al. (2021) also found that those dams had higher water quality when compared to non-managed artificial tanks. However, Westgate et al. (2021) concluded that natural waterpoints still promoted better conditions (e.g., biodiversity, water quality), hence conservation and protection of natural waterpoints where they are present should still be the priority, with enhanced dams then coming in as biodiverse artificial additions. With Australia containing at least 1.7 million artificial tanks (Malerba et al., 2021), the opportunity to promote biodiversity and wildlife welfare through better waterpoint management is highly significant and should be explored further as a solution to help wildlife become more climate resilient. While this could have a significant benefit for eastern grey kangaroos, other species, including threatened and endangered ones would also benefit from it.

Furthermore, waterpoint protection and provision does not only support better welfare outcomes for wildlife, it can also assist coexistence between different species by promoting niche-partitioning opportunities (Sandoval-Serés et al., 2025). For example, by providing prey species (e.g., eastern grey kangaroos) with better opportunities to avoid predators (e.g., dingoes) by selecting safer waterpoints with lower predator activity, or by lowering potential competition for resources with dominant conspecifics and other herbivore species, including domestic cattle. When it comes to coexisting with cattle, I showed in Chapter 4 that the kangaroos of the MCP preferred natural watercourses over artificial tanks. Protecting natural watercourses, particularly in proximity to cattle farms, might, therefore, have the potential to further lower the co-occurrence of kangaroos and cattle at the same water sources, if kangaroos select the natural watercourses over tanks (e.g., farm dams), however, more research is needed to test this theory.

7.6. CONCLUSION

While eastern grey kangaroos are a mesic species they are also found in semi-arid and arid rangelands, where they are likely to face conditions they are less adapted to, particularly compared to the arid adapted red kangaroo. Furthermore, extreme weather events such as droughts and heatwaves in the Australian drylands are now more intense, frequent, and are lasting longer. Here I showed an increase in indicators and behaviours of welfare challenges related to thermoregulation and predation during heat anomalies, with cautiously inferred mental experiences related to such indicators and behaviours – e.g., thirst, hunger, exhaustion, and fear/anxiety – being more prevalent during extreme weather events. With such welfare challenges in mind, extreme weather events intensified by climate change such as heatwaves and droughts should be viewed as a welfare concern for eastern grey kangaroos, particularly those already found in drylands. Impacts related to climate change and extreme weather events should also be considered when making conservation decisions appropriate to the eastern grey kangaroo. Protecting natural watercourses in drylands, including natural dammed watercourses, as well as improving waterpoint management through the implementation of enhanced dams and better access to water may assist eastern grey kangaroos, and other wildlife including threatened and endangered species, by improving their welfare and survival as they attempt to navigate the impacts of an increasingly warming world.

7.7. REFERENCES

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