Life in the countryside: How human behaviour shapes fear in eastern grey kangaroos

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CERTIFICATE OF ORIGINAL AUTHORSHIP

I, Caitlin Maree Austin declare that this thesis, is submitted in fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Life Sciences, Science 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 only academic institution.

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This thesis is a compilation of chapters and three published/publishable manuscripts. Chapters 3 - 5 use the language required for destination journals. This explains the disparity in the use of American English in Chapter 5. However, referencing styles were standardised throughout the thesis in accordance with the referencing style for the journal *Ecology*.

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THESIS ABSTRACT

The expanding human population has reduced the space for wildlife to exist without the influence of humans. Human disturbances can elicit fear responses in wildlife, often leading to avoidance and adjustments to antipredator behaviour. These responses can be justified when human activities are harmful but can be misplaced if human actions pose little threat. The ability of wildlife to accurately interpret risk associated with anthropogenic activities can be instrumental in facilitating persistence in landscapes shared with humans. In rural or countryside environments, landscapes comprise a mosaic of tourist locations, wildlife-friendly farms, or farms where acceptance and tolerance of wildlife can vary greatly.

This study aimed to determine whether eastern grey kangaroos (Macropus giganteus) were capable of assessing different kinds of behaviours engaged in by humans towards them in these shared landscapes and explore the behavioural adaptions they might utilise to persist in complex countryside landscapes. I studied a population of free-ranging kangaroos in a contiguous landscape of national parks and private properties where they encounter human disturbances that vary in intent (benign or harmful) and frequency (low or high).

I found strong evidence that eastern grey kangaroos respond to the intent and frequency of human disturbances and appear to be habituated to human disturbances in areas where interactions with humans are frequent and of benign intent. Desensitisation to benign disturbances was readily developed, as animals experiencing low encounter frequencies with humans displayed flight responses similar to those that encountered them at higher frequencies. Through the analysis of behavioural activity patterns and transitions, I found no indication that individuals experiencing benign disturbances were likely to incur fitness costs as a result of benign human disturbance. In comparison, when kangaroos experience hunting or harassment, typical antipredator behaviours, like forming larger groups when further from cover, was not observed. However, they were fearful of humans and spent less time grazing, which may negatively impact on their energy intake and associated fitness.

Furthermore, pouch young at these sites were restricted to the pouch more often than at sites of benign disturbance, reducing the amount of time young interacted with the environment and conspecifics, potentially impacting juvenile development and survival.

In this thesis, I have been able to show that behavioural plasticity in kangaroos to human behaviour is contributing to their persistence in the complex countryside landscapes shared with humans. Learning from previous interactions with humans informed the expression of behaviours and fostered coexistence. However, coexistence comes at a cost, and the harmful effects of hunting extended well beyond the lethal consequences of being shot, as living in fear can reduce individual fitness and juvenile survival.

CHAPTER 1:

GENERAL INTRODUCTION

Space for wildlife to exist without the influence of humans is rapidly declining, driven by an expanding human population and associated habitat loss through landscape conversion for agriculture and urbanisation. Some species have adapted to modified landscapes and even thrive in urban areas while others avoid anthropogenic disturbances and retreat to pockets of wilderness. However, responses to human disturbance are not always linear; species distributions appear to be shaped by more than habitat availability or the presence or intensity of human disturbance. The human activities affecting wildlife are complex and so are wildlife responses. For example, it is becoming clear that some species are responding to the intent of human activities, habituating to disturbances of benign intent or incorporating harmful human disturbances into their risk assessments. However, few studies have been designed to identify species that are capable of developing responses to both the intensity and purpose behind human behaviour. In many countryside landscapes, wildlife experience both these disturbances within their home range. Correctly interpreting the risk associated with these novel and nuanced disturbances at fine scales can provide wildlife with access to resources and safety, understanding of which may assist in policies directed towards facilitating coexistence in shared landscapes.

In Australia, eastern grey kangaroos (*Macropus giganteus*) share the majority of their range with human settlements and land use, commonly occurring in countryside landscapes where the modification of wilderness for agriculture and production dominates, but where some remnant habitat remains. As wild free-ranging herbivores, kangaroos appear to be persisting in these landscapes by exploiting remnant bushland and foraging in cleared pastures. Although coarse-scale surveys of kangaroo populations suggest that persistence of the species as a whole is not threatened with extinction, surprisingly little is known about local scale persistence and coexistence with people in these fragmented, and often threatening, countryside landscapes. Intriguingly, most research has focused on investigating the behavioural responses of kangaroos to gradients of human density, overlooking the complexity of human-kangaroo interactions in these landscapes. For example, kangaroos are often welcomed and encouraged in tourist locations, like campgrounds in national parks, by wildlife carers providing shelter, and on wildlife-friendly farming properties. Unfortunately, these examples represent only a very small fraction of the range of eastern grey kangaroos. By far the most common perception of kangaroos is one of them as an overabundant pest, with people unwilling to share space with these wild animals, leading to the widespread activity of legal (and illegal) hunting, either for recreation or damage mitigation; a past-time that is pervasive, tolerated, and often unnoticed in countryside landscapes. While these activities have obvious and direct consumptive effects on kangaroos, there is a myriad of non-consumptive effects that manifest from these actions.

This study is the first to explore the adaptability of eastern grey kangaroos to this complex mix of human behaviour, varying in both intent and frequency. The objective is to address the broad question of how eastern grey kangaroos persist in countryside landscapes shared with humans, exploring the role of learning in the development of adaptive responses to disturbances at fine scales, and examining the implications on the costs and benefits to fitness.

Chapter 2 is a literature review which provides background context sufficient to understand the framing of the thesis and leads into the experimental chapters which are presented as papers at various stages of publication. The first experimental chapter, **Chapter 3**, is an observational study that aimed to detect kangaroos' fear or attraction to different human disturbances by investigating differences in spatial arrangement and grouping across disturbance types. This chapter was published in the peer-reviewed journal *Animals,* 9 (5) 2019. The differences detected between disturbance types directed the following experimental chapters, which tested and explored the responses of kangaroos to human disturbances. **Chapter 4** tested the flight responses of kangaroos to determine if previous encounters with humans affected fear and risk perception as hypothesised in Chapter 3. This chapter has been accepted by *Ecology and Evolution.* **Chapter 5** is an observational study that investigated differences in behaviour across disturbance types to determine whether individuals were incurring fitness costs as a result of harmful or benign disturbances.

This paper also investigated the behaviour of pouch young to highlight any potential impacts of disturbance on juvenile mortality. To conclude, **Chapter 6** provides a general discussion, summarising the key findings of the project and highlights the contributions this thesis has made to the overall understanding of how kangaroos respond to the challenges of sharing landscapes with humans. In addition, this chapter discusses the possibilities of applying this framework to other wildlife species to understand adaptation to novel disturbances in the Anthropocene.

CHAPTER 2:

LITERATURE REVIEW

2.1. HUMANS AND WILDLIFE

The distribution of species is shaped by resources, biology, niche availability and complex interactions between species in the form of competition or predation. The effects of predation can be direct, resulting in death, or indirect, causing changes in behaviour (Laundre 2010, Laundre et al. 2014) and movement (White and Berger 2001, Bonnot et al. 2013). The indirect or non-consumptive effects of predation have been shown to have a significant effect on prey populations and the greater ecosystem (Fortin et al. 2004, Say-Sallaz et al. 2019). The reestablishment of wolves as apex predators at Yellowstone National Park altered the behaviour and movements of bison and elk, which in turn affected the surrounding plant community structure and the greater ecosystem (Laundre et al. 2001, Hernandez and Laundre 2005). These changes were not due to the effects of direct predation, but the variations in fear prey experienced throughout the landscape. The term ‘landscape of fear’ is used to explain how different levels of predation risk, and consequent fear, can be conceptualised as a spatial layer, similar to habitat type. Understanding the role of fear in shaping species presence and behaviour leads to a deeper understanding of species distribution, beyond resource and niche availability. Species mitigate the risk of predation from natural predators by modifying vigilance (Baskin and Hjalten 2001, Laundre et al. 2001), spatial grouping (Creel et al. 2005), foraging behaviour (Brown and Kotler 2004, Bonnot et al. 2013, McArthur et al. 2014), and movements (Berger 2007, Leighton et al. 2010, Atickem et al. 2014). However, as primary shapers of the landscape, the contribution humans make to a species’ landscape of fear needs to be considered when evaluating species distribution.

Human disturbance spans the majority of terrestrial environments, community dynamics have shifted to accommodate humans as ‘super predators’ (Darimont et al. 2015) which are often perceived by species as more threatening than natural predators (Ciuti et al. 2012, Clinchy et al. 2016, Stillfried et al. 2017). This effect is most pronounced for species which experience consumptive effects of human activities such as hunting. The novel threat of human hunting requires species to learn or evolve or else risk local extinction (Thurfjell et al. 2017). Even species that have been historically hunted by humans must continue to adapt to this threat. Modern developments to the performance of hunting weapons have allowed a precise lethal shot to be taken from a greater distance (Knight and Cole 1995), changing the behaviour of human hunters. Innate behaviours and personality traits attributed to genetics can provide individuals with the necessary behavioural repertoire to respond effectively to novel disturbances (Lowry et al. 2013). The selection of individuals with beneficial attributes which facilitate survival can lead to evolutionary adaptation within a population (Lowry et al. 2013, Snell-Rood 2013, Sol et al. 2013). This form of adaption is slow and local extinctions can occur before a viable portion of the population possesses the favourable innate traits. On the other hand, the flexibility of learning enables the rapid development of responses to harmful stimuli (Lima and Bednekoff 1999). The development of fine-tuned behavioural responses to avoid predation requires a high degree of behavioural plasticity (Sol et al. 2013) and cognitive function (Lowry et al. 2013, Thurfjell et al. 2017). Learning requires that an individual experiences a predation attempt and uses information from this encounter to inform antipredator behaviours. However, learning is not only restricted to the experiences of the individual but can be transferred to conspecifics via social learning (Crane and Ferrari 2013).

In rural and countryside landscapes human activities vary in intent and the degree of the disturbance they cause to wildlife. For species which are suffering a restriction of habitat, rural or countryside landscapes can provide a substitute habitat as many ecosystem structures are preserved (Daily et al. 2003). To access direct benefits in these landscapes, species are required to accurately assess the predatory threat of humans. Human-wildlife conflicts are common in these environments, particularly when land sparing approaches to agriculture seek to lethally exclude wildlife from productive land, rather than integrate conservation with production (Fischer et al. 2008, Dickman 2010). Moreover, lower levels of human presence in rural landscapes disinhibit negative human behaviour (Thibaut 2017) meaning, harmful actions towards wildlife can occur infrequently. The inconsistency of harmful disturbances can make it difficult for wildlife to recognise humans as threatening, impairing the development of appropriate responses. Species living in these landscapes need to develop risk assessments which can differentiate between a human that causes harm and one that do not.

Behavioural adjustments are crucial for species to persist in landscapes shared with humans (Dall et al. 2004, Sol et al. 2013). There is growing evidence that persecuted large mammals are developing adaptive responses to hunting (Berger 2007, Wheat and Wilmers 2016, Thurfjell et al. 2017), driven by both learning and selection processes (Snell-Rood 2013, Sol et al. 2013). Those who are learning from previous encounters with humans are incorporating humans into their landscape of fear, avoiding areas of high risk or increasing risk-aversive behaviours to decrease the propensity of risk (Tigas et al. 2002, Rode et al. 2006, Gaynor et al. 2018). These responses have been observed in a variety of ungulate species where hunting alters habitat use (Saïd et al. 2012, Bonnot et al. 2013) and behavioural patterns (Manor and Saltz 2003). Female elk modify behavioural patterns to avoid human hunters as they age, adjusting their movement rates to reduce the likelihood of encounters with humans and increasing their use of steep terrain which offers a safe refuge (Thurfjell et al. 2017). Furthermore, there is evidence to suggest the behavioural strategies of elk are sufficiently plastic and sensitive to select for appropriate behaviours in response to the mode of hunting, either with a bow or a rifle (Thurfjell et al. 2017). If adaptive behaviours can be learnt, wildlife with high behavioural plasticity will develop antipredator strategies in response to human activities that significantly contribute to mortality.

2.2. TOURISM AND HABITUATION

The vast majority of research examines the effects of tourism on wildlife examine the disruptive nature of recreational activities, finding that even well intention human activities disrupt behaviours of wildlife (Duchesne et al. 2000, Schummer and Eddleman 2003, Dyck and Baydack 2004, Blanc et al. 2006, Williams et al. 2006) and increase levels of stress hormones (Wingfield et al. 1997, Ellenberg et al. 2007), which can have further implications for reproductive success and survival (Sapolsky and Sapolsky 1992, Sapolsky et al. 2000, Kleist et al. 2018). This research is heavily biased towards avian species with a small proportion of investigations focusing on large mammals for which wildlife observations are popular: namely marine mammals, primates, and bears (Duchesne et al. 2000, Dyck and Baydack 2004, Maréchal et al. 2016). These studies found that the presence of observers with benign intent had a negative impact on the study species, reducing the time spent feeding (Duchesne et al. 2000) and increasing antipredator behaviours (Manor and Saltz 2003, Dyck and Baydack 2004, Reimers et al. 2011). The movement of individuals is also impacted by tourism, species avoid areas of tourist activity as the disturbance is synonymous with threatening activity (Karp and Guevara 2011, Gaynor et al. 2018). These disturbances do not intend to cause harm but can have a considerable effect on wildlife, reducing population growth (Blanc et al. 2006). This has been seen for several species of ground-dwelling birds which abandon their nests or hatch smaller clutches when disturbed by tourist activity (Ellison and Cleary 1978, Green and Giese 2004, Hutfluss and Dingemanse 2019), or whales which reduce time spent feeding when tourist boats are present (Williams et al. 2006).

However, there is also evidence of species developing a tolerance to disturbances of benign intent (Samia et al. 2015). The time mother seals spent nursing young and the mass of pups when weaned was not affected by the number of tourists present (Engelhard et al. 2002), and feeding rates in brown bears were not affected by the presence of observers (Rode et al. 2006). Tolerance develops as individuals associate human disturbance with the absence of negative consequence (Shackley 1995, Higginbottom 2004, Newsome et al. 2005). This desensitisation can facilitate persistence in urban zones (Stankowich 2008, Sih et al. 2011) and in turn permit access to favourable conditions (Sih et al. 2011). Tourism and recreational activities can provide benefits for many species, offering supplementary resources (Wheat and Wilmers 2016) and protection (Berger 2007, Leighton et al. 2010, Atickem et al. 2014). Non-lethal human activities can create protective areas for prey species by excluding their predators which are described as the ‘human shield effect’ (Berger 2007, Atickem et al. 2014). This mechanism sees prey species seeking close proximity to human settlements because their predators are fearful of humans and avoid those regions (Berger 2007, Atickem et al. 2014). The 'human shield effect' has been observed in mountain nyala (*Tragelaphus buxtoni*) which relocate to nearby human settlements to exploit lower densities of spotted hyenas (*Crocuta crocuta*) (Atickem et al. 2014). This has also been seen in pregnant moose (*Alces alces*) which select birthing sites nearer to roads to shield vulnerable mothers and young from brown bears (*Ursus arctos*) (Berger 2007). Female brown bears with cubs exploit the protection of tourists and spend longer feeding when tourists are present as human disturbance discourages aggressive males (Nevin and Gilbert 2005). The complexity of human activities and the interactions between species means that these situations are not always binary. Responding to one threat can expose populations and species to other stressors (Sih 2013). Roe deer (*Capreolus capreolus*) encounter these challenges as they seek human settlements as a shield against natural predators, but must trade-off the increased risk of poaching encountered in suburban zones (Bonnot et al. 2013, Lone et al. 2014, Norum et al. 2015). Animals seeking protection near human settlements are also vulnerable to unintended harmful risks such as vehicle collisions (Wolfe 2008) and disease (Friend 2006).

Habituating to benign disturbances is complicated for species that also experience lethal human disturbances, such as hunting, as the outcome of interactions with humans is imprecise and varied. However, habituation may still be possible given the species possess a high degree of behavioural plasticity which allows them to fine-tune behaviours in response to complex situations (Sih 2013). Species can use spatial and temporal cues, such as the location of humans in the landscape, as an indication of risk. One such species is red deer (*Cervus elaphus*) which can distinguish between hunters and recreationists based on where they encounter humans in the landscape, along cleared trails or amongst the vegetation. Humans on marked trails are most likely recreational and are perceived by deer as less threatening than those off the track. The ability to make this distinction at fine scales has been attributed to the species' high level of behavioural plasticity (Jayakody et al. 2008). African elephants (*Loxodonta*) rely on scent, visual, or audio cues to determine the potential threat of humans. They exhibit stronger fear behaviours when presented with stimuli from a threatening subgroup of people compared to that of an agricultural subgroup which poses little threat (Bates et al. 2007, McComb et al. 2014). The ability to distinguish between humans that mean harm and those which do not permits risk avoidance behaviours but does not inhibit cohabitation with humans.

2.3. MEASURING FEAR

There are many approaches to quantifying an individual's perception of risk or the degree of fear they experience in response to a given stimulus. Physiological or behavioural metrics can be recorded through direct observations or manipulative experiments of presenting individuals with a stimulus and recording their response (Fernández-Juricic et al. 2002, De Boer et al. 2004, Stankowich 2008). Physiological measurements of glucocorticoid concentration, endocrine activity, immunocompetence or cardiac response can be useful indicators of stress but require direct examination of the animal which can cause further distress (Tarlow and Blumstein 2007). These measurements are particularly difficult to obtain for wildlife species where the capture of individuals can be difficult; instead, analysis of hormone levels in faecal and hair samples can be conducted without interfering with the animal. Analysis of the hormone levels in hair samples from wolves determined that individuals that were hunted were under greater physiological stress than their unhunted counterparts (Bryan et al. 2013a). Physiological measures can determine whether an individual is experiencing chronic stress, but it is often difficult to determine which situations and circumstances are contributing to this response. Physiological stress can be caused by disease, poor nutrition, or reproductive state which do not reflect the degree of fear an animal is experiencing.

Flight initiation experiments, however, allow the quantification of fear in response to a particular stimulus (Tarlow and Blumstein 2007). Flight initiation distance (FID), the distance at which an animal flees from an approaching stimulus, is highly correlated with alert distance (AD), the distance at which prey become aware of the stimulus, and the distance from which the stimulus approach commenced (Dumont et al. 2012). There are concerns regarding the experimental artefacts of flight initiation distance, as conclusions can be confounded due to the correlation between FID, starting distance, and alert distance (Dumont et al. 2012). However, with correct analysis and experimental design, these challenges can be overcome. Alert distance allows for the more insightful measure, assessment distance to be recorded, which is the distance a stimulus can move towards an animal after it has been detected until flight is taken (Stankowich and Coss 2005). This measure directly relates to perceived predation risk as it reflects the period where threat level changes from low to high risk (Ydenberg and Dill 1986, Frid and Dill 2002, Stankowich and Blumstein 2005). Flight initiation experiments allow for the investigation of the effects of numerous variables relating to predators (Cárdenas et al. 2005, Stankowich and Coss 2005), the environment (Engelhard et al. 2002, Fernández-Juricic et al. 2002), and prey (Fernández-Juricic et al. 2002).

Flight initiation experiments have been used to determine the set-back distance or buffer zones to reduce the disturbance of recreationists observing animals in the wild and zoos (Holmes et al. 1993, Rodgers Jr and Smith 1995, Giese 1998). However, an animal can be suffering harmful effects of disturbance before taking flight. Behavioural studies are adept at detecting the effects of disturbance as well as the animals' response allowing studies to draw conclusions as to the effect of disturbance on the animals' wellbeing. Antipredator behaviours such as vigilance are often the focus of behavioural studies which aim to determine if animals have a fearful response to a particular disturbance (Christiansen et al. 2013). An increased occurrence of antipredator vigilance has been observed as a response to consumptive and non-consumptive human disturbances (Duchesne et al. 2000, Tigas et al. 2002,Schummer and Eddleman 2003, Dyck and Baydack 2004, Rode et al. 2006, Berger 2007, Wolf and Croft 2010, Gaynor et al. 2018). Vigilant behaviour is in conflict with other fitness-enhancing activities such as feeding (Quenette 1990, Benhaiem et al. 2008), grooming (Hart et al. 1992, Blumstein et al. 1999), resting (Casas et al. 2009), and mating (Say-Sallaz et al. 2019) which can increase the production of stress hormones which inhibit biological mechanisms resulting in reduced fitness (Wingfield et al. 1997, Bryan et al. 2013b). Utilising behavioural studies to conduct bioenergetic analysis can further estimate potential fitness implications of decreased foraging efficiency or increased movement as a result of disturbance (Christiansen et al. 2013).

2.4. PLAY BEHAVIOUR

Play behaviour has been recognized as a sensitive and informative tool for assessing animal welfare; in most cases, it requires good physical and psychological wellbeing (Boissy et al. 2007, Oliveira et al. 2010, Held and Špinka 2011). The suite of play behaviours conducted by an animal is species-specific and generally satisfies the following five criteria; (1) play behaviour is not fully functional, (2) it is spontaneous, voluntary, pleasurable or autoletic (3) it differs from serious performance of ethotypic behaviour structurally or temporally (4) behaviour is repeated but not stereotyped and (5) the behaviour occurs when the animal is relaxed (Burghardt 2005). Play behaviour is broadly viewed as a process for developing motor skills and adaptive responses that are relevant for survival such as anti-predatory behaviour (Oliveira et al. 2010, Held and Špinka 2011). Locomotive play involves running or jumping and can be solitary, directed towards an inanimate object (object play) or social, being directed towards another individual (Oliveira et al. 2010). The most frequent type of social play is play-fighting (Byers 1998). It is identified as a novice form of aggressive interaction between individuals, with the exception that injuries are rare (Oliveira et al. 2010). Social play can aid in the development of social structures within the community (Oliveira et al. 2010). The act of play stimulates pleasure centres in the brain and can also be contagious throughout a community making it effective at reducing social tension (Held and Špinka 2011).

Studying play behaviour can detect situations of poor welfare but it can also highlight positive welfare. A thorough assessment of animal welfare requires the assessment of the experience of pleasure for the animal. Experiences and emotions are difficult to assess but it is believed that play behaviour can provide considerable insight (Oliveira et al. 2010). The self-rewarding nature of play results in the animal achieving satisfaction and pleasure from the act of playing, which is as rewarding as the most highly valued food in chimpanzees (*Pan troglodytes*) (Mason et al. 1963) and rats (*Rattus norvegicus*) (Humphreys and Einon 1981). Play is not only instantly gratifying but in the instance of play fighting it can also improve physical fitness in the long term leading to improved reproductive success and survival (Spinka et al. 2001, Oliveira et al. 2010). Additionally, the occurrence of play is dependent on ideal environmental conditions. The frequency of play decreases when conditions deteriorate, for example when individuals are suffering from an injury, overcrowding or limited resources (Held and Špinka 2011).

There are situations in which high or an increased frequency of play does not indicate positive welfare. Play can occur at higher frequencies when there is a lack of maternal care (Bateson et al. 1990, Held and Špinka 2011). In these situations, it is believed that the purpose of play shifts from that of pleasure to adaptive development whereby young utilize play to develop survival skills in preparation for an environment where maternal care is limited (Bateson et al. 1990, Held and Špinka 2011). When animals are experiencing poor welfare as a result of limited environmental stimulus or social isolation, an increase in play behaviour has been observed when animals are offered a slightly better condition (Jensen 1999, Boissy et al. 2007). This is thought to occur as the animal views the change in conditions as a new opportunity to play (Held and Špinka 2011). It is unlikely for these situations to occur in wild populations as they generally arise from experimental restrictions to the animals in question.

For many species, play is most strongly affected by age with higher play frequencies occurring in infants and juveniles (Watson and Dawson 1993, Byers and Walker 1995). Unless adult play is common in the study species it is recommended that the presence or absence of play in adults should not be used to draw welfare conclusions (Held and Špinka 2011). The frequency of play also varies with sex, with males generally playing more often than females (Watson and Croft 1996, Watson 1998, Pellis et al. 2010). In social play, the sex of the other individual also affects the frequency of play with play occurring more often between individuals of the same sex (Watson and Dawson 1993, Watson and Croft 1996).

2.5. EASTERN GREY KANGAROOS

Eastern grey kangaroos (*Macropus giganteus*) are a large free-ranging mammal native to Australia. They are a gregarious woodland species (Caughley 1964b, Kaufmann 1975, Coulson 2009) that form open-membership fission-fusion groups (Jarman 1987, Clarke et al. 1995) forming large mobs when grazing (Kaufmann 1975, Southwell 1984) and dividing into smaller groups throughout the day. The composition of groups is not entirely random, as individuals show a preference for particular companions (Best et al. 2013) and form social connections with close kin (Best et al. 2014). Investigation into group dynamics found individuals benefit from spending time with preferred companions, grazing for longer when in the company of familiar individuals (Carter et al. 2009a). Associations between individuals are also determined by space use and overlapping home ranges of individuals (Best et al. 2014). The social structures of eastern grey kangaroo groups, mobs and populations are fragile; a loss of key members of the communities has been shown to alter grazing behaviour (Carter et al. 2009a). Disrupting these complex structures and fracturing cultural groups through hunting and fragmentation of the landscape by fences or roads may have a significant effect on the stress and wellbeing of the community and individuals.

There is discussion in the literature regarding group size at a landscape scale. Several studies investigated standard group size reaching different conclusions, with mean group size varying from 2 to 12 (Caughley 1964a, Kirkpatrick and McEvoy 1966, Kaufmann 1975). It has been suggested that these differences arose from variation in habitat or the level of disturbance between study sites (Kaufmann 1975). Increasing group size in eastern grey kangaroos has been shown to be an antipredator response, implemented when foraging in open areas to reduce the risk of predation (Heathcote 1987, Jarman and Coulson 1989a, Banks 2001) by foxes (primarily juveniles) (Banks and Dickman 2007) and dingoes (Wallach et al. 2010, Letnic and Crowther 2013). Forming larger groups enables prey species to detect threats sooner through the many-eyes hypothesis (Ale and Brown 2007, Beauchamp 2013) and benefit from the dilution effect where the probability of attack decreased as group size increased (Jarman 1987, Bednekoff and Lima 1998, Banks 2001, Carter et al. 2009b). It has been reported that group sizes also vary with the availability of resources (Favreau et al. 2018), distance from safety (Heathcote 1987, Jarman and Coulson 1989b), and predation risk (Heathcote 1987, Banks 2001). However, large groups are not always preferred; females with young at foot exhibit a preference for small groups, only joining large groups when predation risk is high (Banks 2001). This suggests that females might trade off the risk of foraging alone against the costs of foraging in a group; such as harassment by males, contaminated pasture and resulting parasite risk, or reduced resources (Garnick et al. 2010).

Eastern grey kangaroos have a naturally slow reproductive rate, similar to other macropods, with males and females reaching maturity at 18 and 48 months respectively (Dawson 1995). Following a gestation period of 36 days, young are born and develop in the pouch until they reach 20% of the mother’s body weight. Juveniles first emerge from the pouch after approximately 283 days and are weaned by 540 days (Dawson 1995). Although possible, embryonic diapause is rare in eastern grey kangaroos (Dawson 1995). Due to high juvenile mortality rates and the slow breeding nature of eastern grey kangaroos, females will raise 2-3 offspring throughout their lifetime, similar to western grey kangaroos (Bilton and Croft, 2004, Dawson 2012).

Kangaroos are among the largest of Australia’s herbivores, regulated by both bottom-up and top-down forces; their population growth is governed by the availability of resources and the presence of predators (Caughley and Gunn 1993, Banks et al. 2000, Letnic and Crowther 2013). In the absence of predators, rainfall limits the population growth of eastern grey kangaroos (Letnic and Crowther 2013). However, there is some evidence that artificial water points created by humans do not increase kangaroo populations: growth rates appear unchanged when kangaroos are excluded from these water points, even during drought (Fukuda et al. 2009). Furthermore, recent studies have found that a high density of artificial water points does not result in a greater abundance of kangaroos (Letnic and Crowther 2013, Letnic et al. 2015). In temperate regions, the predation of juveniles by foxes (Banks et al. 2000) and dingoes (Letnic and Crowther 2013) appears to have a limiting effect on population growth (Newsome et al. 1983). Dingo predation plays a significant role in limiting population growth when kangaroo abundance is low (Caughley et al. 1980, Letnic and Crowther 2013) and can drive local extinctions (Robertshaw and Harden 1986). In south-eastern New South Wales, the effect of predation by foxes was strong, with up to 40% more juveniles surviving mortality when foxes were controlled using 1080 baits (Banks et al. 2000). Human activities apply another layer of complexity to understanding population dynamics of wild populations, by controlling or removing top predators and modifying habitat.

Behavioural studies on eastern grey kangaroos frequently focus on vigilant behaviour, an alert posture which allows individuals to survey the surrounding area for threats or monitor conspecifics. Individual vigilance remains consistent with group size but there is a shift from anti-predator vigilance to social vigilance as group size increases (Favreau et al. 2010). Vigilance is highly variable between individuals and can be influenced by their position in the group (Carter et al. 2009b), sex (Pays and Jarman 2008, Rieucau et al. 2012), reproductive status (Colagross and Cockburn 1993), and personality (Dannock et al. 2013, Edwards et al. 2013). Play behaviour has been observed in eastern grey kangaroos with the most frequent display of play behaviour being solitary play, as joeys bound back and forth to their mothers (Kaufmann 1975, Coulson 1997), a behaviour which has also been categorized as 'exploratory dashes' (Watson 1998). Play behaviour also occurs between a mother and her joey and involves the joey pawing, cuffing and kicking at its mother (Jaremovic and Croft 1991, Coulson 1997) and generally follows suckling (Johnson 1987) This interaction between mother and offspring may continue even when offspring are permanently out of the pouch (Kaufmann 1975). Pouch young spend 5-10% of their day play fighting and was found to be more common in female juveniles than males (Stuart-Dick 1987). Studies on red neck wallabies have investigated the choice of partner for play fighting (Watson and Dawson 1993) and the effect of age on play behaviours (Watson and Croft 1996).

2.6. KANGAROOS AND HUMANS

Humans have a complex history with kangaroos: humans persecute kangaroos and remove their habitat for the development of urban regions and agriculture (Boom et al. 2012), but also control non-human predators, foxes and dingoes (Wallach et al. 2010). As landscapes become increasingly fragmented and agriculture is intensified, space for kangaroos to persist is declining. Humans directly influence top-down and bottom-up processes by altering the land through farming and agriculture, as well as lethally excluding wildlife from production lands. Agricultural development opens up pastures for agricultural grazing while fragmenting or destroying the woodland vegetation kangaroos rely on for shelter (Arnold et al. 1989, De Munk 1999). Furthermore, roads and fences fragment populations by isolating resources and prevent movements between populations (Ben-Ami and Ramp 2005, Ramp 2010, Taylor and Goldingay 2010, Bond and Jones 2014), jeopardizing social connections between individuals (Carter et al. 2009a). In rural landscapes, fences create hazardous barriers for dispersing males, as they can become entangled and injured attempting to clear fences (Coulson et al. 2014). Some fence designs can be easily traversed by kangaroos as they can pass underneath it.

The hunting of kangaroos dates back tens of thousands of years as Indigenous Australians engaged in sporadic hunting of macropod species (Gammage 2012). Since European occupation, kangaroos have been shot for food (for human and pets, commercially and for subsistence), recreation, or bounties (Boom et al. 2012). The commercial kangaroo industry legally harvests four species of kangaroo (red, eastern grey, western grey and wallaroo) in New South Wales for meat and hide. The industry is regulated by sustainable harvest practices to manage kangaroo populations and prevent species decline. Different management zones are monitored to set harvest quotas for each zone. Quotas for grey kangaroos are set at or below 15% of the estimated population and 20% for red kangaroos (NRMMC 2008a). The methods of estimating population sizes and calculating quotas are much debated (Ramp 2013, Ramp et al. 2013). As with any animal harvesting, the welfare of animals being killed is of high concern (Ramp 2013, Ben-Ami et al. 2014), with questions around the regulation and enforcement of the code of conduct frequently raised. Much focus has been on the welfare of young dependant on shot females, as pouch young and young-at-foot kangaroos are often left to die of exposure, dehydration or predation, although the Code of Practice stipulates that they must either be shot or bludgeoned. Research seeking to improve the methods of killing kangaroo young has been conducted but to date has been unable to find better alternatives (Sharp et al. 2015). The research guiding the commercial industry focuses only on the direct impacts of harvesting on populations and overlooks the potential for indirect impacts on hunted populations. The effect of lethal control on surviving individuals has not been considered and could have negative impacts as the wellbeing of surviving kangaroos has been overlooked.

Kangaroos are also killed illegally for sport and legally as pests to agriculture and biodiversity (NRMMC 2008b), a situation that is tolerated by government regulators

(Boom and Ben-Ami 2013, Ramp 2013, Descovich et al. 2015). Eastern grey kangaroos prefer to graze in grasslands adjacent to woodland that have been cleared for raising cattle and sheep. When they intrude into occupied landscapes they are unwelcome, resulting in killing and exclusion programs (Coulson 2001, Hercock and Tonts 2004, Boom et al. 2012). Early settlers viewed kangaroos as competing with their livestock, and in 1880, kangaroos and wallabies were legally declared vermin and monetary bounties offered (Boom et al. 2012). The notion of kangaroos as a pest is still present today, with licenses available to shoot kangaroos to mitigate their impact on production and agricultural land (NRMMC 2008b). Kangaroos in New South Wales are protected by National Parks and Wildlife Act 1974, and as such, the harming of a native species requires the issuing of a license. Licensees are encouraged to exhaust all non-lethal methods of protecting crops or pastures but it is not compulsory (NRMMC 2008b). The predatory behaviour of humans towards kangaroos has not been comprehensively studied and there are no studies that have examined whether kangaroos modify their behaviour in response to human hunting.

Interactions between humans and kangaroos are not always negative, as kangaroos can find safety and resources at national parks, golf courses, sporting ovals, and wildlife-friendly farms (King et al. 2011). Kangaroos may be exploiting these locations as the high frequency of humans showing kindness or benign interest typically excludes human hunters and natural predators (Muhly et al. 2011). They may be trading off less lethal forms of disturbance, such as noise and traffic, for the protection human activities offer from lethal disturbances.

2.7. REFERENCES

Ale, S. B., and J. S. Brown. 2007. The contingencies of group size and vigilance. Evolutionary Ecology Research **9**:1263-1276.

Arnold, G., D. Steven, and J. Weeldenburg. 1989. The Use of Surrounding Farmland by Western Gray Kangaroos Living in a Remnant of Wandoo Woodland and Their Impact on Crop Production. Wildlife Research **16**:85-93.

Atickem, A., L. E. Loe, and N. C. Stenseth. 2014. Individual Heterogeneity in Use of Human Shields by Mountain Nyala. Ethology **120**:715-725.

Banks, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. Animal Behaviour **61**:1013-1021.

Banks, P. B., and C. R. Dickman. 2007. Alien predation and the effects of multiple levels of prey naiveté. Trends in ecology & evolution **22**:229-230.

Banks, P. B., A. E. Newsome, and C. R. Dickman. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. Austral Ecology **25**:283-291.

Baskin, L. M., and J. Hjalten. 2001. Fright and flight behavior of reindeer. Alces **37**:435-445.

Bates, L. A., K. N. Sayialel, N. W. Njiraini, J. H. Poole, C. J. Moss, and R. W. Byrne. 2007. African elephants have expectations about the locations of out-of-sight family members. Biology Letters **4**:34-36.

Bateson, P., M. Mendl, and J. Feaver. 1990. Play in the domestic cat is enhanced by rationing of the mother during lactation. Animal Behaviour **40**:514-525.

Beauchamp, G. 2013. Social predation: how group living benefits predators and prey. Elsevier.

Bednekoff, P. A., and S. L. Lima. 1998. Re–examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. Proceedings of the Royal Society of London B: Biological Sciences **265**:2021-2026.

Ben-Ami, D., K. Boom, L. Boronyak, C. Townend, D. Ramp, D. Croft, and M. Bekoff. 2014. The welfare ethics of the commercial killing of free-ranging kangaroos: an evaluation of the benefits and costs of the industry. Animal Welfare **23**:1-10.

Ben-Ami, D., and D. Ramp. 2005. Modeling the effect of roads and other disturbances on wildlife populations in the peri-urban environment to facilitate long-term viability. Road Ecology Center.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour **76**:611-618.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters **3**:620-623.

Best, E. C., R. G. Dwyer, J. M. Seddon, and A. W. Goldizen. 2014. Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos. Animal Behaviour **89**:1-10.

Best, E. C., J. M. Seddon, R. G. Dwyer, and A. W. Goldizen. 2013. Social preference influences female community structure in a population of wild eastern grey kangaroos. Animal Behaviour **86**:1031-1040.

Bilton, A. D., & Croft, D. B. 2004. Lifetime reproductive success in a population of female red kangaroos *Macropus rufus* in the sheep rangelands of western New South Wales: Environmental effects and population dynamics. Australian Mammalogy, **26**:45-60.

Blanc, R., M. Guillemain, J.-B. Mouronval, D. Desmonts, and H. Fritz. 2006. Effects of non-consumptive leisure disturbance to wildlife. Revue d'écologie.

Blumstein, D. T., C. S. Evans, and J. C. Daniel. 1999. An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*. Animal Behaviour **58**:351-360.

Boissy, A., G. Manteuffel, M. B. Jensen, R. O. Moe, B. Spruijt, L. J. Keeling, C. Winckler, B. Forkman, I. Dimitrov, J. Langbein, M. Bakken, I. Veissier, and A. Aubert. 2007. Assessment of positive emotions in animals to improve their welfare. Physiology & Behavior **92**:375-397.

Bond, A. R., and D. N. Jones. 2014. Roads and macropods: interactions and implications. Australian Mammalogy **36**:1-14.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research **59**:185-193.

Boom, K., and D. Ben-Ami. 2013. Kangaroos at a crossroads: Environmental law and the kangaroo industry. Environmental and Planning Law Journal **30**:162-181.

Boom, K., D. Ben-Ami, D. B. Croft, N. Cushing, D. Ramp, and L. Boronyak. 2012. 'Pest' and Resource: A Legal History of Australia's Kangaroos. Animal Studies Journal **1**:17-40.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters **7**:999-1014.

Bryan, H. M., A. G. Adams, R. M. Invik, K. E. Wynne-Edwards, and J. E. G. Smits. 2013a. Hair as a Meaningful Measure of Baseline Cortisol Levels over Time in Dogs. Journal of the American Association for Laboratory Animal Science **52**:189-196.

Bryan, H. M., C. T. Darimont, P. C. Paquet, K. E. Wynne-Edwards, and J. E. G. Smits. 2013b. Stress and Reproductive Hormones in Grizzly Bears Reflect Nutritional Benefits and Social Consequences of a Salmon Foraging Niche. Plos One **8**.

Burghardt, G. M. 2005. The genesis of animal play: Testing the limits. Mit Press.

Byers, J. A. 1998. Animal play: Evolutionary, comparative and ecological perspectives. Cambridge University Press.

Byers, J. A., and C. Walker. 1995. Refining the motor training hypothesis for the evolution of play. American Naturalist:25-40.

Cárdenas, Y. L., B. Shen, L. Zung, and D. T. Blumstein. 2005. Evaluating temporal and spatial margins of safety in galahs. Animal Behaviour **70**:1395-1399.

Carter, A. J., S. L. Macdonald, V. A. Thomson, and A. W. Goldizen. 2009a. Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. Animal Behaviour **77**:839-846.

Carter, A. J., O. Pays, and A. W. Goldizen. 2009b. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behavioral Ecology and Sociobiology **64**:237-245.

Casas, F., F. Mougeot, J. Viñuela, and V. Bretagnolle. 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. Animal Conservation **12**:346-354.

Caughley, G. 1964a. Social Organization and Daily Activity of the Red Kangaroo and the Grey Kangaroo. Journal of Mammalogy **45**:429-436.

Caughley, G., G. Grigg, J. Caughley, and G. Hill. 1980. Does dingo predation control the densities of kangaroos and emus? Wildlife Research **7**:1-12.

Caughley, G., and A. Gunn. 1993. Dynamics of Large Herbivores in Deserts: Kangaroos and Caribou. Oikos **67**:47-55.

Caughley, G. J. 1964b. Density and dispersion of two species of kangaroo in relation to habitat. Australian Journal of Zoology **12**:238-249.

Christiansen, F., M. H. Rasmussen, and D. Lusseau. 2013. Inferring activity budgets in wild animals to estimate the consequences of disturbances. Behavioral Ecology **24**:1415-1425.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. Plos One **7**:e50611.

Clarke, J. L., M. E. Jones, and P. J. Jarman. 1995. Diurnal and nocturnal grouping and foraging behaviors of free-ranging eastern grey kangaroos. Australian Journal of Zoology **43**:519-529.

Clinchy, M., L. Y. Zanette, D. Roberts, J. P. Suraci, C. D. Buesching, C. Newman, and D. W. Macdonald. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behavioral Ecology **27**:1826-1832.

Colagross, A., and A. Cockburn. 1993. Vigilance and grouping in the eastern gray kangaroo, *Macropus giganteus*. Australian Journal of Zoology **41**:325-334.

Coulson, G. 1997. Repertoires of social behaviour in captive and free-ranging grey kangaroos, *Macropus giganteus* and *Macropus fuliginosus* (Marsupialia: Macropodidae). Journal of Zoology **242**:119-130.

Coulson, G. 2001. Overabundant kangaroo populations in southeastern Australia.*in* Proceedings of the second international wildlife management conference.

Coulson, G. 2009. Behavioural ecology of red and grey kangaroos: Caughley's insights into individuals, associations and dispersion. Wildlife research **36**:57-69.

Coulson, G., J. K. Cripps, and M. E. Wilson. 2014. Hopping down the main street: eastern grey kangaroos at home in an urban matrix. Animals **4**:272-291.

Crane, A. L., and M. C. Ferrari. 2013. Social learning of predation risk: a review and prospectus. Social learning theory: phylogenetic considerations across animal, plant, and microbial taxa:53-82.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387-3397.

Daily, G. C., G. Ceballos, J. Pacheco, G. Suzán, and A. SÁNchez-Azofeifa. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology **17**:1814-1826.

Dall, S. R., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters **7**:734-739.

Dannock, R. J., S. P. Blomberg, and A. W. Goldizen. 2013. Individual variation in vigilance in female eastern grey kangaroos. Australian Journal of Zoology **61**:312-319.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science **349**:858-860.

Dawson, T. J. 1995. Kangaroos : biology of the largest marsupials / Terence J. Dawson ; illustrated by Anne Musser and Jillian Hallam. UNSW Press, Sydney.

De Boer, H. Y., L. Van Breukelen, M. J. Hootsmans, and S. E. Van Wieren. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biology **10**:35-42.

De Munk, F. 1999. Resource use by the eastern grey kangaroo and the black wallaby in a managed remnant woodland community. Deakin University.

Descovich, K., I. McDonald, A. Tribe, and C. Phillips. 2015. A welfare assessment of methods used for harvesting, hunting and population control of kangaroos and wallabies. Animal Welfare **24**:255-265.

Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal Conservation **13**:458-466.

Duchesne, M., S. D. Côté, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation **96**:311-317.

Dumont, F., C. Pasquaretta, D. Réale, G. Bogliani, and A. von Hardenberg. 2012. Flight initiation distance and starting distance: biological effect or mathematical artefact? Ethology **118**:1051-1062.

Dyck, M. G., and R. K. Baydack. 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. Biological Conservation **116**:343-350.

Edwards, A. M., E. C. Best, S. P. Blomberg, and A. W. Goldizen. 2013. Individual traits influence vigilance in wild female eastern grey kangaroos. Australian Journal of Zoology **61**:332-341.

Ellenberg, U., A. N. Setiawan, A. Cree, D. M. Houston, and P. J. Seddon. 2007. Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. General and Comparative Endocrinology **152**:54-63.

Ellison, L. N., and L. Cleary. 1978. Effects of human disturbance on breeding of double-crested cormorants. The Auk **95**:510-517.

Engelhard, G. H., A. N. Baarspul, M. Broekman, J. C. Creuwels, and P. J. Reijnders. 2002. Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. Canadian Journal of Zoology **80**:1876-1886.

Favreau, F.-R., A. W. Goldizen, H. Fritz, and O. Pays. 2018. Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. Animal Behaviour **135**:165-176.

Favreau, F.-R., A. W. Goldizen, and O. Pays. 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proceedings of the Royal Society B-Biological Sciences **277**:2089-2095.

Fernández-Juricic, E., M. Jimenez, and E. Lucas. 2002. Factors affecting intra-and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. Canadian Journal of Zoology **80**:1212-1220.

Fischer, J., B. Brosi, G. C. Daily, P. R. Ehrlich, R. Goldman, J. Goldstein, D. B. Lindenmayer, A. D. Manning, H. A. Mooney, and L. Pejchar. 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment **6**:380-385.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos **107**:172-180.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**.

Friend, M. 2006. Disease emergence and resurgence: the wildlife-human connection.

Fukuda, Y., H. McCallum, G. Grigg, and A. Pople. 2009. Fencing artificial waterpoints failed to influence density and distribution of red kangaroos (*Macropus rufus*). Wildlife Research **36**:457-465.

Gammage, B. 2012. The biggest Estate on earth: How Aborigines made Australia. Allen & Unwin.

Garnick, S. W., M. A. Elgar, I. Beveridge, and G. Coulson. 2010. Foraging efficiency and parasite risk in eastern grey kangaroos (*Macropus giganteus*). Behavioral Ecology **21**:129-137.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Giese, M. 1998. Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis adeliae*). Polar Record **34**:287-292.

Green, R., and M. Giese. 2004. Negative effects of wildlife tourism on wildlife. Wildlife Tourism: Impacts, Management and Planning. CRC for Sustainable Tourism and Common Ground Publishing, Altona, Vic:81-97.

Hart, B. L., L. A. Hart, M. S. Mooring, and R. Olubayo. 1992. Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. Animal Behaviour **44**:615-631.

Heathcote, C. 1987. Grouping of Eastern Grey Kangaroos in Open Habitat. Wildlife Research **14**:343-348.

Held, S. D. E., and M. Špinka. 2011. Animal play and animal welfare. Animal Behaviour **81**:891-899.

Hercock, M., and M. Tonts. 2004. From the rangelands to the Ritz: Geographies of kangaroo management and trade. Geography:214-225.

Hernandez, L., and J. W. Laundre. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. Wildlife Biology **11**:215-220.

Higginbottom, K. 2004. Wildlife tourism : impacts, management and planning / edited by Karen Higginbottom. Common Ground Publishing [for] CRC for Sustainable Tourism, Altona, Vic.

Holmes, T. L., R. L. Knight, L. Stegall, and G. R. Craig. 1993. Responses of wintering grassland raptors to human disturbance. Wildlife Society Bulletin (1973-2006) **21**:461-468.

Humphreys, A. P., and D. F. Einon. 1981. Play as a reinforcer for maze-learning in juvenile rats. Animal Behaviour **29**:259-270.

Hutfluss, A., and N. Dingemanse. 2019. Human recreation reduces clutch size in great tits Parus major regardless of risk-taking personality. Behavioral Ecology.

Jaremovic, R., and D. Croft. 1991. Social organization of the eastern grey kangaroo (Macropodidae, Marsupialia) in southeastern New South Wales. I. Groups and group home ranges. Mammalia **55**:169-186.

Jarman, P., and G. Coulson. 1989a. Dynamics and adaptiveness of grouping in macropods. Kangaroos, Wallabies and Rat-kangaroos'.(Eds G. Grigg, P. Jarman and I. Hume.) pp:527-547.

Jarman, P. J. 1987. Group size and activity in eastern grey kangaroos. Animal Behaviour **35**:1044-1050.

Jarman, P. J., and G. Coulson. 1989b. Dynamics and adaptiveness of grouping in macropods. Kangaroos, Wallabies and Rat-kangaroos'.(Eds G. Grigg, P. Jarman and I. Hume.) pp:527-547.

Jayakody, S., A. M. Sibbald, I. J. Gordon, and X. Lambin. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology **14**:81-92.

Jensen, M. B. 1999. Effects of confinement on rebounds of locomotor behaviour of calves and heifers, and the spatial preferences of calves. Applied Animal Behaviour Science **62**:43-56.

Johnson, C. 1987. Macropod studies at Wallaby Creek. 4. Home range and movements of the red-necked wallaby. Wildlife Research **14**:125-132.

Karp, D. S., and R. Guevara. 2011. Conversational noise reduction as a win–win for ecotourists and rain forest birds in Peru. Biotropica **43**:122-130.

Kaufmann, J. H. 1975. Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. Animal Behaviour **23, Part 1**:214-221.

King, W., M. Wilson, T. Allen, M. Festa-Bianchet, and G. Coulson. 2011. A capture technique for free-ranging eastern grey kangaroos (*Macropus giganteus*) habituated to humans. Australian Mammalogy **33**:47-51.

Kirkpatrick, T., and J. McEvoy. 1966. Studies of Macropodidae in Queensland. 5. Effects of drought on reproduction in the grey kangaroo (*Macropus giganteus*). Queensland Journal of Agricultural and Animal Science **23**:439-442.

Kleist, N. J., R. P. Guralnick, A. Cruz, C. A. Lowry, and C. D. Francis. 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proceedings of the National Academy of Sciences **115**:E648-E657.

Knight, R. L., and D. N. Cole. 1995. Wildlife Responses to. Wildlife and recreationists: Coexistence through management and research:51.

Laundre, J. W. 2010. Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. Ecology **91**:2995-3007.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology-Revue Canadienne De Zoologie **79**:1401-1409.

Laundre, J. W., L. Hernandez, P. Lopez Medina, A. Campanella, J. Lopez-Portillo, A. Gonzalez-Romero, K. M. Grajales-Tam, A. M. Burke, P. Gronemeyer, and D. M. Browning. 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology **95**:1141-1152.

Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2010. Conservation and the scarecrow effect: Can human activity benefit threatened species by displacing predators? Biological Conservation **143**:2156-2163.

Letnic, M., and M. S. Crowther. 2013. Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. Oikos **122**:761-769.

Letnic, M., S. W. Laffan, A. C. Greenville, B. G. Russell, B. Mitchell, and P. J. S. Fleming. 2015. Artificial watering points are focal points for activity by an invasive herbivore but not native herbivores in conservation reserves in arid Australia. Biodiversity and Conservation **24**:1-16.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist **153**:649-659.

Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos **123**:641-651.

Lowry, H., A. Lill, and B. B. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological reviews **88**:537-549.

Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications **13**:1830-1834.

Maréchal, L., A. MacLarnon, B. Majolo, and S. Semple. 2016. Primates' behavioural responses to tourists: evidence for a trade-off between potential risks and benefits. Scientific reports **6**:32465.

Mason, W. A., S. V. Saxon, and L. G. Sharpe. 1963. Preferential responses of young chimpanzees to food and social rewards. The Psychological Record **13**:341.

McArthur, C., P. B. Banks, R. Boonstra, and J. S. Forbey. 2014. The dilemma of foraging herbivores: dealing with food and fear. Oecologia **176**:677-689.

McComb, K., G. Shannon, K. N. Sayialel, and C. Moss. 2014. Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proceedings of the National Academy of Sciences **111**:5433-5438.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. Plos One **6**:e17050.

Nevin, O. T., and B. K. Gilbert. 2005. Measuring the cost of risk avoidance in brown bears: further evidence of positive impacts of ecotourism. Biological Conservation **123**:453-460.

Newsome, A. E., P. C. Catling, and L. K. Corbett. 1983. The feeding ecology of the dingo II. Dietary and numerical relationships with fluctuating prey populations in south-eastern Australia. Australian Journal of Ecology **8**:345-366.

Newsome, D., R. K. Dowling, and S. A. Moore. 2005. Wildlife tourism. Channel View Publications.

Norum, J. K., K. Lone, J. D. Linnell, J. Odden, L. E. Loe, and A. Mysterud. 2015. Landscape of risk to roe deer imposed by lynx and different human hunting tactics. European Journal of Wildlife Research **61**:831-840.

NRMMC. 2008a. National Code of Practice for the Humane Shooting of Kangaroos and Wallabies for Commercial Purposes. Department of the Environment, Water, Heritage and the Arts. Canberra.

NRMMC. 2008b. National Code of Practice for the Humane Shooting of Kangaroos and Wallabies for Non-Commercial Purposes. Department of the Environment, Water, Heritage and the Arts. Canberra.

Oliveira, A. F. S., A. O. Rossi, L. F. R. Silva, M. C. Lau, and R. E. Barreto. 2010. Play behaviour in nonhuman animals and the animal welfare issue. Journal of Ethology **28**:1-5.

Pays, O., and P. J. Jarman. 2008. Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo? Behavioral Ecology and Sociobiology **62**:757-767.

Pellis, S. M., V. C. Pellis, and H. C. Bell. 2010. The function of play in the development of the social brain. American Journal of Play **2**:278-298.

Quenette, P. 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica **11**:801-818.

Ramp, D. 2010. Roads as drivers of change for macropodids. Pages 279-291 *in* G. Coulson and M. Eldridge, editors. Macropods: the Biology of Kangaroos, Wallabies and Rat-kangaroos. CSRIO Publishing, Melbourne.

Ramp, D. 2013. Bringing compassion to the ethical dilemma in killing kangaroos for conservation. Journal of bioethical inquiry **10**:267-272.

Ramp, D., D. Ben-Ami, K. Boom, and D. B. Croft. 2013. Compassionate conservation: A paradigm shift for wildlife management in Australasia. Ignoring nature no more: The case for compassionate conservation:295-315.

Reimers, E., S. Lund, and T. Ergon. 2011. Vigilance and fright behaviour in the insular Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Canadian Journal of Zoology **89**:753-764.

Rieucau, G., P. Blanchard, J. G. A. Martin, F.-R. Favreau, A. W. Goldizen, and O. Pays. 2012. Investigating Differences in Vigilance Tactic Use within and between the Sexes in Eastern Grey Kangaroos. Plos One **7**.

Robertshaw, J., and R. Harden. 1986. The Ecology of the Dingo in Northeastern New-South-Wales. 4. Prey Selection by Dingoes, and Its Effect on the Major Prey Species, the Swamp Wallaby, Wallabia-Bicolor (Desmarest). Wildlife Research **13**:141-163.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation **133**:70-80.

Rodgers Jr, J. A., and H. T. Smith. 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. Conservation Biology **9**:89-99.

Saïd, S., V. Tolon, S. Brandt, and E. Baubet. 2012. Sex effect on habitat selection in response to hunting disturbance: The study of wild boar. European Journal of Wildlife Research **58**:107-115.

Samia, D. S., S. Nakagawa, F. Nomura, T. F. Rangel, and D. T. Blumstein. 2015. Increased tolerance to humans among disturbed wildlife. Nature communications **6**:8877.

Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocrine reviews **21**:55-89.

Sapolsky, R. M., and R. M. Sapolsky. 1992. Stress, the aging brain, and the mechanisms of neuron death. MIT press Cambridge, MA.

Say-Sallaz, E., S. Chamaillé-Jammes, H. Fritz, and M. Valeix. 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. Biological Conservation **235**:36-52.

Schummer, M. L., and W. R. Eddleman. 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. The Journal of wildlife management:789-795.

Shackley, M. 1995. The future of gorilla tourism in Rwanda. Journal of Sustainable Tourism **3**:61-72.

Sharp, T., S. McLeod, K. Leggett, and T. J. Gibson. 2015. Evaluation of a spring-powered captive bolt gun for killing kangaroo pouch young. Wildlife Research **41**:623-632.

Sih, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Animal Behaviour **85**:1077-1088.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications **4**:367-387.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour **85**:1004-1011.

Sol, D., O. Lapiedra, and C. González-Lagos. 2013. Behavioural adjustments for a life in the city. Animal Behaviour **85**:1101-1112.

Southwell, C. 1984. Variability in grouping in the eastern grey kangaroo, *Macropus giganteus* II. Dynamics of group formation. Wildlife Research **11**:437-449.

Spinka, M., R. C. Newberry, and M. Bekoff. 2001. Mammalian play: training for the unexpected. Quarterly Review of Biology:141-168.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation **141**:2159-2173.

Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: A meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences **272**:2627-2634.

Stankowich, T., and R. G. Coss. 2005. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology **17**:246-254.

Stillfried, M., P. Gras, M. Busch, K. Börner, S. Kramer-Schadt, and S. Ortmann. 2017. Wild inside: Urban wild boar select natural, not anthropogenic food resources. Plos One **12**:e0175127.

Stuart-Dick, R. I. 1987. Parental investment and rearing schedules in the eastern grey kangaroo. University of New England.

Tarlow, E. M., and D. T. Blumstein. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. Applied Animal Behaviour Science **102**:429-451.

Taylor, B. D., and R. L. Goldingay. 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. Wildlife Research **37**:320-331.

Thibaut, J. W. 2017. The social psychology of groups. Routledge.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2017. Learning from the mistakes of others: How female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. Plos One **12**:e0178082.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation **108**:299-306.

Wallach, A. D., C. N. Johnson, E. G. Ritchie, and A. J. O'Neill. 2010. Predator control promotes invasive dominated ecological states. Ecology Letters **13**:1008-1018.

Watson, D., and T. Dawson. 1993. The effects of age, sex, reproductive status and temporal factors on the time-use of free-ranging red kangaroos. Wildlife Research **20**:785-801.

Watson, D. M. 1998. Animal play: Evolutionary, comparative and ecological perspectives. Cambridge University Press.

Watson, D. M., and D. B. Croft. 1996. Age-related Differences in Playfighting Strategies of Captive Male Red-necked Wallabies (*Macropus rufogriseus banksianus*). Ethology **102**:336-346.

Wheat, R. E., and C. C. Wilmers. 2016. Habituation reverses fear-based ecological effects in brown bears (*Ursus arctos*). Ecosphere **7**.

White, K. S., and J. Berger. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? Canadian Journal of Zoology-Revue Canadienne De Zoologie **79**:2055-2062.

Williams, R., D. Lusseau, and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation **133**:301-311.

Wingfield, J. C., K. Hunt, C. Breuner, K. Dunlap, G. S. Fowler, L. Freed, and J. Lepson. 1997. Environmental stress, field endocrinology, and conservation biology. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge:95-131.

Wolf, I. D., and D. B. Croft. 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. Applied Animal Behaviour Science **126**:75-84.

Wolfe, M. L. 2008. Avoiding the blame game in managing problem black bears. Human-Wildlife Conflicts **2**:12-14.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior **16**:229-249.

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CHAPTER 3:

BEHAVIOURAL PLASTICITY BY EASTERN GREY KANGAROOS IN RESPONSE TO HUMAN BEHAVIOUR

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SIMPLE SUMMARY

Many species of wildlife live in landscapes they share with people. Some exploit resources and protection provided by close proximity to people, while others learn to avoid people altogether. In this study, we sought to test whether individuals from a population of eastern grey kangaroos altered grouping and spacing behaviour in response to human presence, depending upon whether the intent and actions of those people were benign or harmful. Under harmful conditions, kangaroos failed to form larger groups when far from cover, however, this typical antipredator grouping behaviour persisted when human disturbances were benign. These differences in grouping and spacing behaviour suggest that kangaroos can exhibit bidirectional behavioural plasticity at fine scales, a trait that may confer adaptive advantages when sharing landscapes with humans.

3.1. ABSTRACT

Sharing landscapes with humans is an increasingly fraught challenge for wildlife across the globe. While some species benefit from humans by exploiting novel opportunities (e.g., provision of resources or removal of competitors or predators), many wildlife experience harmful effects, either directly through persecution or indirectly through loss of habitat. Consequently, some species are attracted to human presence while others avoid us. For any given population of a single species, though, the question of whether they can recognise and change their response to human presence depending on the type of human actions (i.e., either positive or negative) has received little attention to date. In this study, we chose to examine the behavioural plasticity within a single population of eastern grey kangaroos (*Macropus giganteus*) to both positive and negative human activity. Within a relatively small and contiguous landscape, we identified areas where kangaroos experience a combination of either low and high frequencies of benign and harmful human disturbances. From six sampling sessions over five months, we found that density and group sizes were higher where humans acted benignly towards them and that these groups had higher representations of sub-adults and juveniles than where humans had harmful intentions. Importantly, we found that the vital antipredator strategy of increasing group size with distance from cover was not detectable at sites with low and high levels of harm. Our findings suggest that these kangaroos are recognising and adjusting their behavioural response to humans at fine spatial scales, a plasticity trait that may be key to the survival of these species in human-dominated landscapes.

Keywords: adaptation; behavioural plasticity; eastern grey kangaroos; grouping behaviour; human behaviour; human shield; hunting

3.2. INTRODUCTION

The global decline of mammals has been driven by a combination of increasing modification and urbanisation of landscapes (Ripple et al. 2016) and the exploitation and forcible exclusion of free-roaming animals (Ripple et al. 2019). This is particularly apparent for large mammals, many of which have declined, are considered threatened, or have gone extinct (Cardillo and Bromham 2001, Craigie et al. 2010). Of the remaining species, some are maintaining populations despite pressure from habitat loss, increasing fragmentation, and climate change, albeit at lower densities than in recent history (Driscoll et al. 2013). However, the persistence of populations at regional scales masks the complexity of challenges these species face when adjusting to local processes. The ability to make the most of novel opportunities at local scales may be as valuable as the ability to avoid or survive threats. Cognitive learning through individual and collective experiences of extrinsic processes is a key survival mechanism, facilitating both the acquisition of temporally and spatially variable resources and the ability to reduce uncertainty in risk assessment of threat signals. Similarly, differences in risk-taking can also be shaped by personality traits held by individuals, conditioned by innate temperaments (Favreau et al. 2014). There is growing evidence that persecuted species of large mammals show adaptive responses to hunting (Berger 2007, Leighton et al. 2010, Atickem et al. 2014, Wheat and Wilmers 2016, Thurfjell et al. 2017), driven by learning and selection processes (Snell-Rood 2013, Sol et al. 2013). While animals have been shown to distinguish and adjust behaviourally to different levels of threats posed by hunters (Ciuti et al. 2012a, Thurfjell et al. 2017), evidence for plasticity in response to both positive and negative behaviour by humans, which may be key to long term persistence, has so far received little focus.

Many species exhibit fear responses towards humans, often eliciting antipredator responses greater than those exhibited towards their natural predators (Ciuti et al. 2012b, Clinchy et al. 2016, Stillfried et al. 2017). With a rapidly expanding human population, community dynamics have shifted to accommodate humans as ‘super predators’ (Darimont et al. 2015). This effect has been particularly clear for hunted species like deer (*Cervus elaphus*), giraffes *(Giraffa Camelopardalis tippelskirchi*), and wild boars (*Sus scrofa*), where hunting alters sex ratios (Marealle et al. 2010, Saïd et al. 2012), demography (Langvatn and Loison 1999, Milner et al. 2007), habitat use (Saïd et al. 2012, Bonnot et al. 2013), and behavioural patterns (Manor and Saltz 2003). However, humans can also provide benefits for many species, offering protection (Berger 2007, Leighton et al. 2010, Atickem et al. 2014) and foraging opportunities (Wheat and Wilmers 2016). This effect can be direct, whereby species are attracted to urban zones to exploit novel resources and habitats (Sih et al. 2011), or else indirect by exploiting fear in others (e.g., the use of humans as a shield against predators) (Berger 2007, Atickem et al. 2014). Mountain nyala (*Tragelaphus buxtoni*) have been shown to relocate to nearby human settlements to exploit lower densities of spotted hyenas (*Crocuta crocuta*) (Atickem et al. 2014), while pregnant moose (*Alces alces*) select birthing sites nearer to roads to shield mothers and young from brown bears (*Ursus arctos*) (Berger 2007). These situations are not always binary: responding to one threatening process can expose populations/species to other stressors (Sih et al. 2011). For example, roe deer (*Capreolus capreolus*) seek human settlements as a shield against predators but must trade-off the increased risk of poaching encountered in urban zones (Bonnot et al. 2013, Lone et al. 2014, Norum et al. 2015). These examples show that animals can differentiate between different levels of threat and modify their behaviour accordingly. Furthermore, recent evidence suggests that some species can adjust their response to the presence of the same predator in opposing directions. Coyotes (*Canis latrans*) have been shown to alter their response to human disturbance, limiting exploratory behaviour in rural landscapes where they are regularly persecuted, while becoming bolder in urban settings where humans pose little threat and provide anthropogenic foods (Breck et al. 2019).

In Australia, eastern grey kangaroos (*Macropus giganteus*) are a large free-ranging mammal hunted by humans that also experience high levels of human presence with benign intent, making this species ideal for modelling how free-living mammals respond to contrasting levels of human interaction. Eastern grey kangaroos are a gregarious woodland species (Caughley 1964, Kaufmann 1975, Coulson 2009) that form open-membership fission-fusion groups (Jarman 1987, Clarke et al. 1995). Group composition changes as they move through the landscape, forming larger groups in the morning and afternoon while foraging in open areas and breaking down into smaller groups during rest times in the middle of the day (Southwell 1984). Increasing group size in eastern grey kangaroos has been shown to be an antipredator response, implemented when foraging in open areas to reduce the risk of predation (Heathcote 1987, Jarman and Coulson 1989, Banks 2001). Forming larger groups enables prey species to detect threats sooner through the many-eyes hypothesis (Ale and Brown 2007, Beauchamp 2013) and benefit from the dilution effect where the probability of attack decreased as group size increases (Jarman 1987, Bednekoff and Lima 1998, Banks 2001, Carter et al. 2009). Eastern grey kangaroos are prey for foxes (primarily juvenile kangaroos) (Banks 2001) and dingoes (Letnic and Crowther 2013), which are capable of limiting population growth (Caughley et al. 1980, Letnic and Crowther 2013). It has been reported that group sizes vary with the availability of resources (Favreau et al. 2018), distance from safety (Heathcote 1987, Jarman and Coulson 1989), and predation risk (Heathcote 1987, Banks 2001), but there is little knowledge of the effect of human disturbance on group size.

Eastern grey kangaroos are legally hunted throughout the majority of their range in eastern Australia, either for commercial harvest (NRMMC 2008a) or under licenses for damage mitigation (NRMMC 2008b). However, illegal hunting is common, with shooting taking place on private properties either by landholders or trespassers hunting for sport. Interactions between humans and kangaroos are not always negative, as kangaroos can find safety and resources at highly frequented tourist locations, such as campsites and picnic areas in national parks, as well as reserves, golf courses, and sporting ovals (King et al. 2011). Kangaroos may be exploiting these locations as the high frequency of humans showing kindness or benign interest typically excludes human hunters and natural predators (Muhly et al. 2011). The behaviour of humans towards kangaroos has not been comprehensively studied and no study has examined whether kangaroos modify their behaviour in response to human hunting or benign disturbances.

We suggest that differences in response to human presence maybe being driven by both the frequency of interactions (high or low) and the intent of those interactions (positive or negative). This study aimed to collect empirical evidence of behavioural plasticity of kangaroos to human presence when varying in both of these aspects, frequency and intent. In particular, the study was designed to test whether these patterns suggest kangaroos can adjust responses at fine scales, which would infer learning capacity. The study was not designed to explicitly differentiate between learning and selection (sometimes referred to as sorting), nor was it manipulative to identify plasticity among specific individuals. Rather, our goal was to quantify bi-directional (fear and attraction) behavioural plasticity in responses to human presence in a large mammal at fine scales. To achieve this, we recorded grouping and spacing behaviour in a population of eastern grey kangaroos that experiences different combinations of low and high frequencies of positive (or benign) and harmful human disturbances.

3.3 MATERIALS AND METHODS

3.3.1. Study Area

We located a free-ranging population of eastern grey kangaroos residing in the surrounds of Wombeyan Karst Conservation Reserve in the Southern Highlands of New South Wales (NSW), adjacent to Kanangra-Boyd National Park (Figure 1). The reserve and national park are surrounded by private properties with a mix of cleared land and forest. Once we located the general region of study, we informally interviewed landholders and national park staff on the patterns of human movement and whether they were wildlife-friendly or allowed hunting. We use the term hunting here to refer to any legal or illegal activities that result in kangaroos being shot, to ensure direct comparison with similar studies elsewhere where hunting is also done as a sport. Contiguous private properties and the reserve were chosen because they were similar in habitat and were frequently used by eastern grey kangaroos which could move freely across the entire area. The total area of the study area encompassed approximately 850 hectares, presenting a unique opportunity to quantify responses of kangaroos to high or low frequencies of human interactions that were either well-intentioned and benign or else harmful.

Quantitative evidence of the manner of disturbance (either positive or negative) was not obtainable due to safety concerns in areas of frequent hunting (hunters were not receptive to participating in data collection). However, we obtained permission to deploy motion-sensing camera traps for two months to confirm the disturbance activities taking place on each property, allowing us to describe properties as either high (greater than one interaction per week) or low frequency of human interaction (less than one interaction per week). The reserve was chosen as tourists and park staff frequently interacted with kangaroos at the Wombeyan Caves campground, an open expanse of cleared land covering 17.1 hectares, where human activity either ignored the kangaroos (benign) or else was well-intentioned (e.g., photography). We classified this location as High Benign. Some privately managed areas within the study area were wildlife-friendly, a total of 232.4 hectares of cleared land. These areas discouraged trespassers, especially hunters, kangaroos were left alone, and the frequency of interactions was low. We considered these locations as Low Benign. In contrast, there were privately managed areas where kangaroos experienced harmful disturbances, either through hunting or chasing, where the intent was to cause harm. The frequency of these interactions was either less than weekly, Low Harm (104 hectares), or greater than once per week (High Harm). High Harm areas typically saw regular shooting and covered 139 hectares of cleared land surrounded by forest.

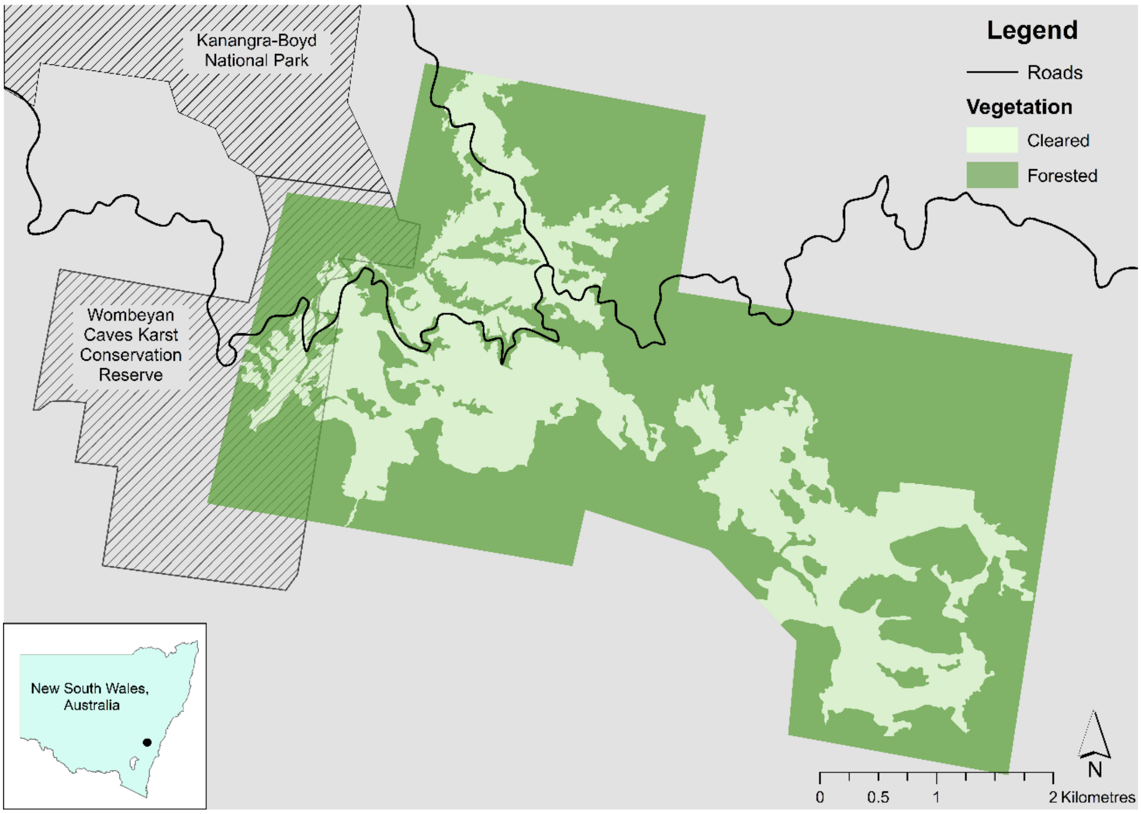

Figure 1. Location of the study area within New South Wales, Australia, showing roads and forested and cleared areas within the study area. Property boundaries and human disturbance were omitted to ensure anonymity.

3.3.2. Kangaroo Surveys

On-foot surveys were conducted between October 2016 and February 2017. Cleared areas across the entire area were surveyed six times on fair-weather days with low wind. As eastern grey kangaroos are crepuscular (Clarke et al. 1995), surveys were conducted either between 0600–0830 or 1630–1900, when kangaroos were most likely to be grazing in the open. Surveys consisted of systematically and covertly traversing all cleared areas on foot, hugging the tree line to avoid detection. Upon sighting an eastern grey kangaroo, video and photographs were recorded using a digital camera (Canon EOS 70D Digital SLR with Canon EF100-400 mm lens). Spatial coordinates of the observation location were recorded using a GPS (± 5 m) and the bearing and distance to the individual were recorded using a Bushnell rangefinder (± 0.9 m). Spatial coordinates for each individual were derived from these measurements and were imported into ArcGIS (v10, 2016 Esri). Surveying was conducted in a manner to ensure individuals were not recorded twice in a session, however, individuals were not identifiable between sessions.

Grazing density was defined as the total number of kangaroos surveyed within a given session per square kilometre of cleared habitat. Group membership is typically ascertained by applying nearest neighbour distance rules, with a variety of distances applied under different circumstances, herein described as the 'chain-rule'. Using ArcGIS, individuals were assigned to a group using three different distances frequently reported in the literature for eastern grey kangaroos: 15 m (Jarman 1987, Carter et al. 2009, Pays et al. 2013, Best et al. 2014), 30 m (Jarman and Coulson 1989, Colagross and Cockburn 1993, Banks 2001, Pays et al. 2007), and 50 m (Southwell 1984). Pouch young were not included in the total count of group size (Southwell 1984) unless they were out of the pouch.

3.3.3. Group Size, Clustering and Demography

Eastern grey kangaroos are known to exhibit antipredator responses that result in strong correlations between group size and distance to cover (Heathcote 1987, Jarman and Coulson 1989, Banks 2001). If humans are viewed as threats, we predicted that group size should increase with increasing distance from cover. Increasing group size with threat level (i.e., further from cover), would be expected under the 'many-eyes hypothesis' and conforms to the landscape of fear theory. We predicted that kangaroos would avoid areas with frequent harmful interactions with humans, resulting in lower densities than those experiencing less disturbance. We would also expect to see groups more tightly clustered where the human threat is higher. Conversely, attraction to the safety that positive human intentions create by shielding individuals from hunters or other predators conforms to the 'human shield hypothesis' (Berger 2007). If humans can also be viewed as providing a shield from other predators (including hunters), then we predicted that there would be higher densities and larger group sizes of kangaroos where human presence is higher (attraction), with the distance from cover relationship continuing to hold and looser group clustering.

To obtain a quantitative measure of clustering within each group we calculated the nearest neighbour distance for all individuals from groups with a group size >1. Geodesic distances between each individual and its nearest neighbour were measured in ArcGIS (v10.4, 2016 Esri) using the 'near table' tool. We used the average nearest neighbour distance for each group as a metric of group clusteredness. These measurements were conducted on groups determined using all three measures of chain-rule: 15 m, 30 m and 50 m.

To test for demographic differences across disturbance types, individuals were assigned to size/maturity categories using photographs; large adult, medium adult, small adult, sub-adult, young-at-foot, and pouch young (Figure 2). A random subset of 100 photographs was validated by an independent assessor familiar with eastern grey kangaroos; consensus was reached for all 100 individuals. The demographic composition of each group was calculated as a proportion of the total group size including joeys in the pouch. The proportions of each demographic category were averaged across groups and sampling sessions for each disturbance type at three definitions of chain-rule (15 m, 30 m, and 50 m).

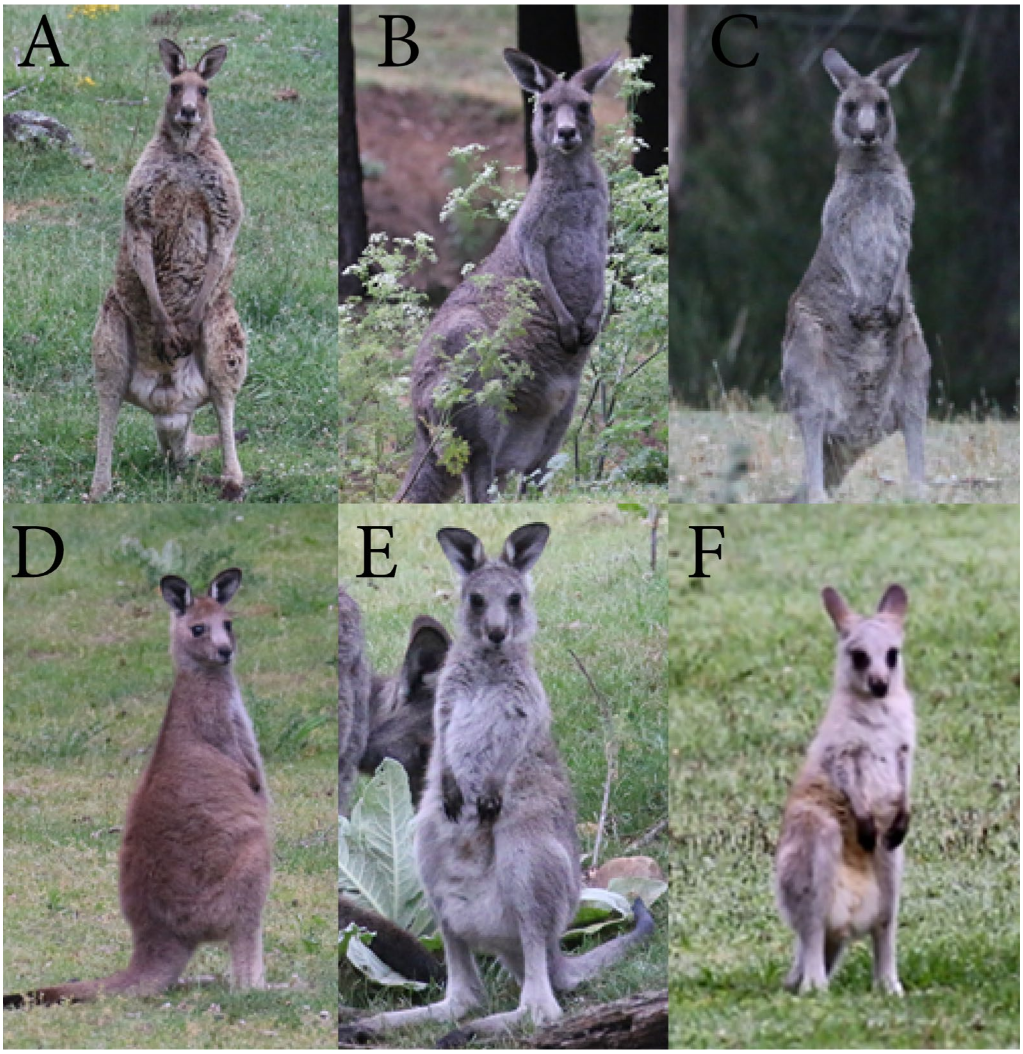

Figure 2. Demography classification reference images of (A) large adult, (B) medium adult, (C) small adult, (D) sub-adult, (E) young-at-foot, and (F) pouch young.

Using the 15 m chain-rule we determined the position of mothers, young-at-foot, and pouch young (vulnerable individuals) within the group with respect to forested cover. Position was classified as either in front or behind and was determined by measuring the distance between both the individual (IDC) and the group centre (GDC) from forested cover. The geometric centre for each group was calculated in the statistical package 'rgeos' (Bivand et al. 2019), R v3.5.1 (R Core Team, 2018). Distances were measured in ArcGIS using the 'near table' tool and applying the geodesic method parameter. Subtracting IDC from GDC yielded a positive or a negative value, where positive values reflected vulnerable individuals positioning themselves closer to the forest edge than the group centre, and negative values further away.

3.3.4. Landscape Characteristics

Eastern grey kangaroos use forested habitat as a refuge and forage closer to cover when predation risk is high (Heathcote 1987, Jarman and Coulson 1989, Banks 2001). The position of a group from forested cover was calculated in ArcGIS from the geometric centre of the group for all chain-rules. Foraging and patch choice by eastern grey kangaroos is strongly associated with resource quality (Ramp and Coulson 2002, 2004, Maguire et al. 2006). Kangaroos typically prefer green grass (Bell 1973, Clarke et al. 1989, Favreau et al. 2018) owing to its higher energetic value (Bradbury et al. 1996). Grass quality at the centre of each group of kangaroos was quantified by determining the relative green channel brightness (greenness) of vegetation from digital photographs. Due to the high correlation between greenness and biomass (Inoue et al. 2015), resource quality was inferred by the greenness of resources for each group of kangaroos. Following Richardson et al. (2007), colour channel information (digital number) for red, green, and blue channels were extracted for each pixel in the region of interest using the 'raster' package (Hijmans et al. 2015) in the program R. Total brightness was calculated as the sum of the three colour channels for all pixels which were in turn used to calculate the relative green channel brightness (greenness).

3.3.5. Statistical Analysis

We conducted a one-way analysis of variance to test for differences in grazing density between disturbance types. Data were log-transformed to satisfy assumptions of normality and homoscedasticity. We conducted TukeyHSD to examine the differences between the four disturbance types: High Benign, Low Benign, Low Harm, and High Harm. To detect distributional skew or kurtosis in group size data from each disturbance type and chain-rule we ran D'Agostino tests of skewness and the Anscombe–Glynn tests of kurtosis from the statistical package 'moments' (Komsta and Novomestky 2015). Differences in mean group size determined by the three chain-rules were examined using linear mixed models from the statistical package 'lmer4' (Bates 2010). To test our hypotheses, we analysed the effect of disturbance type and chain-rule on logged group size, with sampling session as a random variable. To test for differences in group size across disturbance types within and between chain-rules we ran pairwise least-square means comparisons using the ‘lsmeans’ package (Lenth and Hervé 2015). Similarly, we used linear mixed models to test for differences in clustering across disturbance types using likelihood ratio tests and multiple comparisons of means with Tukey contrasts from statistical package ‘multcomp’ (Hothorn et al. 2008). The clustering metric (mean nearest neighbour distance) was log-transformed prior to analysis to satisfy assumptions of normality. Separate models were run for each chain-rule with sampling session and group size as random variables. To test for demographic differences across disturbance types we ran a series of linear mixed models for each demographic category with session and group size as random variables. These analyses were applied separately to data resulting from different measures of chain-rule: 15 m, 30 m, and 50 m. Inference was conducted with likelihood ratio tests and multiple comparisons of means with Tukey contrasts. To determine whether the positioning of vulnerable individuals varied among disturbance types, the proportion of individuals occurring either closer or further from forest edges was calculated for groups, classified into 20 m brackets of distance from cover. To determine if there was a significant difference between disturbance types we ran generalised additive models with disturbance as a fixed factor and distance to cover as a smoothing factor. A series of models were run with each disturbance type as the reference level (intercept).

Generalised linear mixed models were run to test predictions of the response of group size to distance from cover. Logged group sizes were regressed against logged distance from cover, nested within disturbance types, with sampling session as a random variable. Using a negative binomial function, we ran these models for three different chain-rules. Statistical inference was conducted by assessing 95% confidence intervals which were estimated using Laplace approximation (Bolker et al. 2009). Similarly, to test for differences in resource greenness across disturbance types we ran linear mixed models with disturbance type as a fixed factor and sampling session as a random variable. Inference was conducted using a likelihood ratio test and multiple comparisons of means to determine which disturbance types were statistically different from one another. Linear mixed models were also used to test the response variable of logged group size to resource greenness, nested within disturbance type and with sampling session as a random variable. Confidence intervals were estimated using Laplace approximation. All analyses were conducted in R v3.5.1.

3.4. RESULTS

3.4.1. Grazing Densities and Group Sizes

A total of 2228 kangaroos were recorded across the six sampling sessions; the mean number of individuals recorded each session was 368.2 (±14.2). Nineteen kangaroos were disturbed during data collection; these individuals were included in density analysis but were removed from all other analyses. Disturbance type had a significant effect on grazing density ($F_{3, 20} = 74.83$, $p < 0.001$) (Figure 3A). On average, there were 2 kangaroos more per square kilometre at High Benign (HB) sites than at Low Benign (LB) ($p < 0.001$) and Low Harm (LH) sites ($p < 0.001$), while there were around 3.5 fewer individuals per square kilometre at High Harm (HH) sites ($p < 0.001$). There was no significant difference in grazing density between LH and LB sites ($p = 0.714$). This trend was mirrored by group sizes, where more groups were consistently observed at both benign sites relative to harm sites (Figure 3B). Group size data for all disturbance types exhibited a positive skew (>1) (Table 1), which was stronger for benign disturbances as the presence of large groups sizes (>25 individuals) resulted in longer right-tailed distributions (Figure 3B). Distributions for all disturbances were leptokurtic, exhibiting a strong degree of “peakedness” resulting in high positive kurtosis estimates (>3) (Table 1). Both skewness and kurtosis decreased with increasing chain-rule as smaller groups became consolidated (Table 1), shifting the distribution to the right and reducing the peak (Figure 3B). However, this trend was not consistent for HH sites, where the merging of smaller groups using the 50 m chain-rule resulted in a stronger skew and kurtosis than observed when the 15 m or 30 m chain-rules were used (Table 1). Despite this, there was no significant difference in mean group sizes across disturbance types, except using 50 m chain-rule which resulted in significantly larger group sizes at HB than HH ($p = 0.003$).

Table 1. Results of statistical tests of skewness and kurtosis for the distribution of group size data from different disturbance types. Estimates and p-values are provided for each disturbance type expressed as an abbreviation; HB (High Benign), LB (Low Benign), LH (Low Harm), and HH (High Harm) across chain-rules (15 m, 30 m, and 50 m).

	Chain 15 m		**Chain 30 m**		**Chain 50 m**	
	Skew	*Kurtosis*	*Skew*	*Kurtosis*	*Skew*	*Kurtosis*
HB	3.72, p<0.001	20.57, p<0.001	3.59, p<0.001	20.06, p<0.001	2.63, p<0.001	10.58, p<0.001
LB	2.41, p<0.001	10.64, p<0.001	2.28, p<0.001	9.42, p<0.001	1.97, p<0.001	7.25, p<0.001
LH	2.72, p<0.001	14.08, p<0.001	1.76, p<0.001	6.24, p=0.001	1.35, p<0.001	4.10, p=0.046
HH	1.62, p<0.001	6.01, p=0.004	1.42, p<0.001	4.91, p=0.021	2.27, p<0.001	9.83, p<0.001

3.4.2. Clustering and Demography

We did not detect an effect of disturbance type or chain-rule on the average distance between individuals within a group (15 m: $p = 0.158$, 30 m: $p = 0.560$, 50 m: $p = 0.853$) (Figure 3C), although mean near neighbour distances were highest at high harm sites.

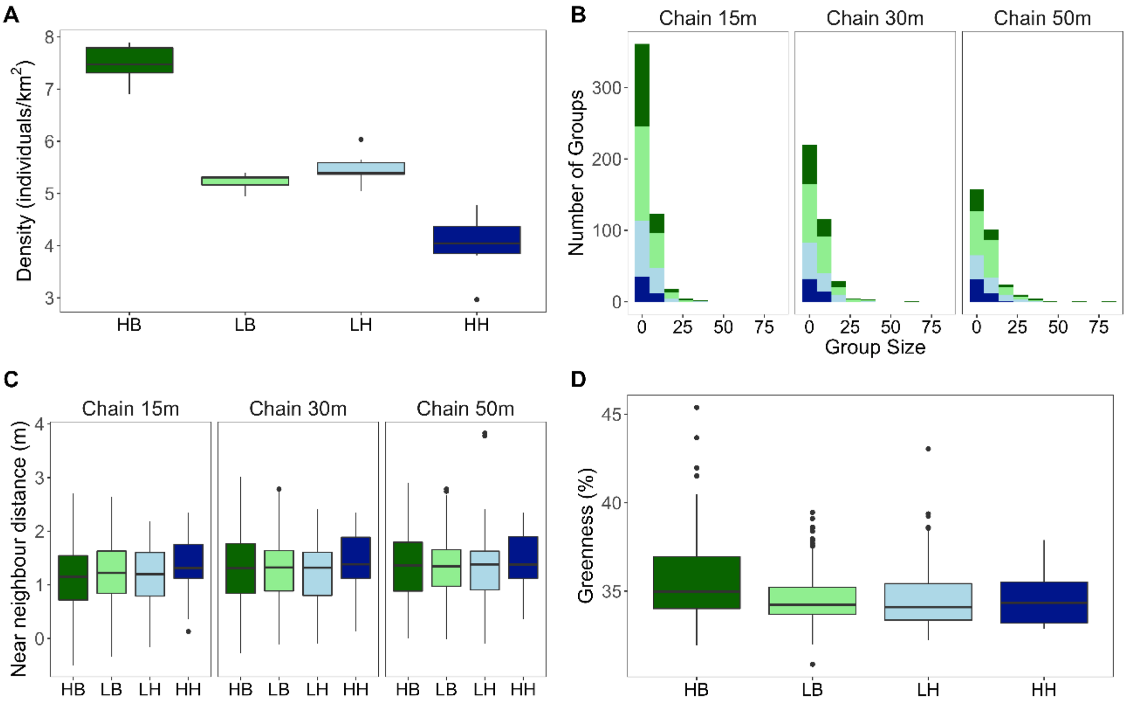

Figure 3. (A) Logged grazing density of eastern grey kangaroos in cleared habitat across different types of human disturbance. (B) Logged group size as a function of disturbance and different chain-rule (15 m, 30 m, and 50 m). (C) Logged nearest neighbour distance per group across disturbance types of human disturbance and at each chain-rule; 15 m, 30 m, and 50 m. (D) Resource greenness across disturbance types, error bars indicated standard error. Groups were determined using the 15 m chain-rule. For all plots human disturbance was expressed as an abbreviation; HB: High Benign (dark green), LB: Low Benign (light green), LH: Low Harm (light blue), HH: High Harm (dark blue).

Distance from cover influenced the positioning of individuals in groups, with the majority of vulnerable individuals positioned closer to the forest edge when nearer to cover (Figure 4). The proportion of vulnerable individuals closer to the forest edge decreased as the group moved further from cover. This general trend was consistent across all disturbance types, however, significantly fewer vulnerable individuals were positioned closer to cover at HB than other for disturbance types, regardless of the group's distance from cover (LB: $p < 0.001$, LH: $p = 0.019$, and HH: $p = 0.018$).

Groups of kangaroos at HB had significantly larger proportions of small adults than at LB, which was consistent for all chain-rules (15 m: $p = 0.005$, 30 m: $p = 0.017$, and 50m: $p = 0.012$) (Figure 5). The proportion of young-at-foot in each group was also significantly higher at HB than at all other disturbance types regardless of which chain-rule was implemented, 15 m (LB: $p < 0.001$, LH: $p < 0.001$, HH: $p = 0.002$), 30 m (LB: $p < 0.001$, LH: $p < 0.001$, HH: $p = 0.002$) and 50 m (LB: $p = 0.001$, LH: $p = 0.002$, HH: $p = 0.001$). Due to higher percentages of small adults and young at foot in groups at HB proportion of other demographic categories had to be reduced. This was evident at HB as medium adults contributed to a significantly lower proportion of the group than at all other disturbance types using the 15 m chain-rule (LB: $p < 0.001$, LH: $p = 0.012$, HH: $p = 0.001$). This trend was also observed using the 30 m and 50 m chain-rules, with significantly lower portions of medium adults at HB than at LB and HH (30 m: $p < 0.001$, $p = 0.001$; 50 m: $p < 0.001$, $p = 0.001$ respectively).

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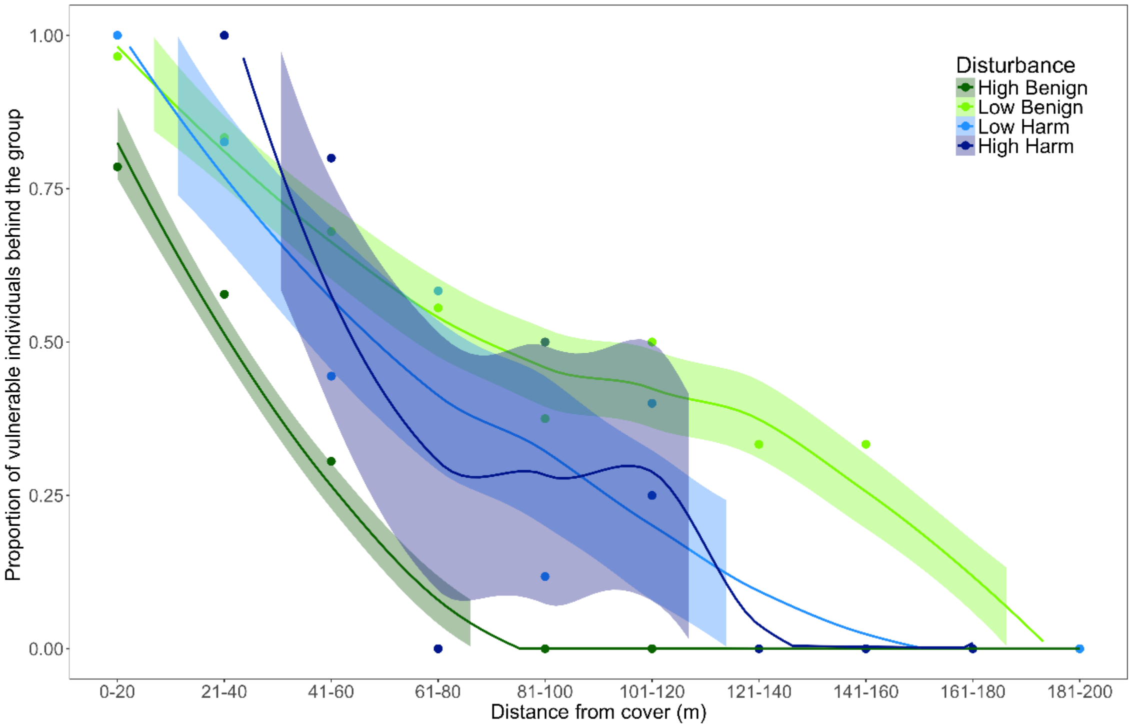

Figure 4. The relationship between the proportion of mothers, pouch young, and young-at-foot (vulnerable individuals) positioned closer to the forest edge and the group's distance from cover. The relationships are plotted for each disturbance type with shaded regions reflecting confidence intervals (95%).

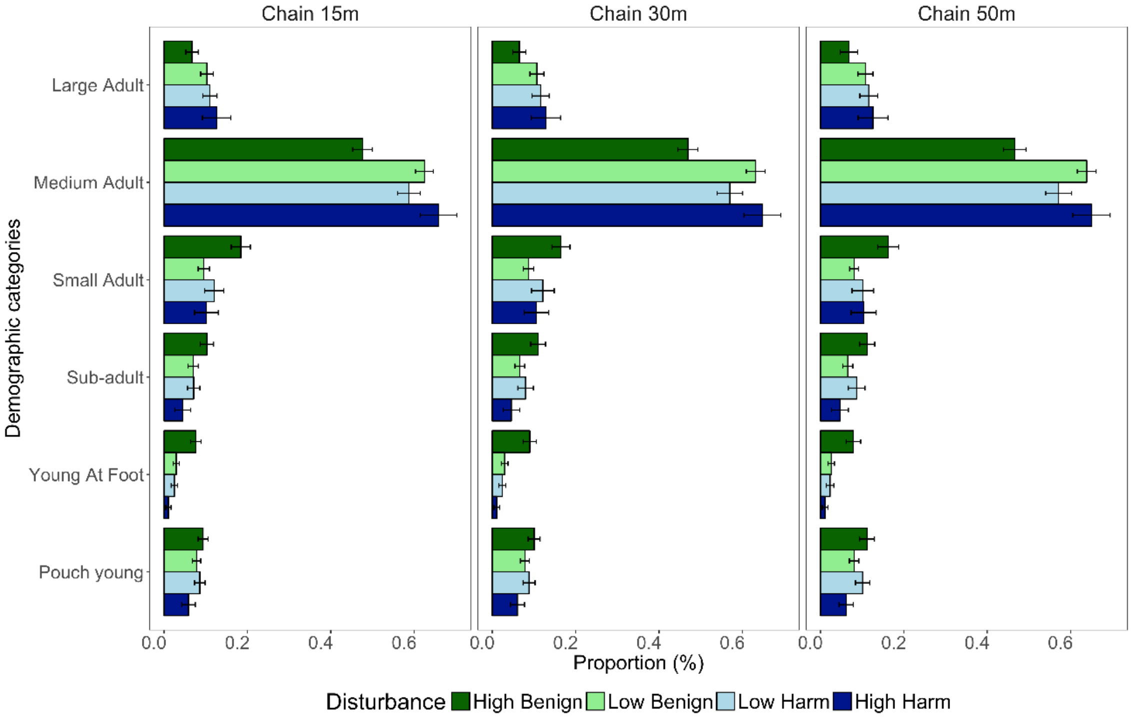

Figure 5. Demographic composition across different disturbance types using three measures of chain-rule to determine group membership; 15 m, 30 m, and 50 m. Demographic categories were large adult, medium adult, small adult, sub-adult, young-at-foot, and pouch young. Values are mean proportional contributions to groups, while error bars indicate standard errors.

3.4.3. Landscape Responses

Distance to cover and group size was positively correlated at HB and LB sites, with the relationship strengthening as the chain-rule increased at HB sites (Figure 6, Table 2). No significant correlation between group size and distance from cover was detected at LH and HH sites (Figure 6, Table 2), which was consistent across all chain-rules.

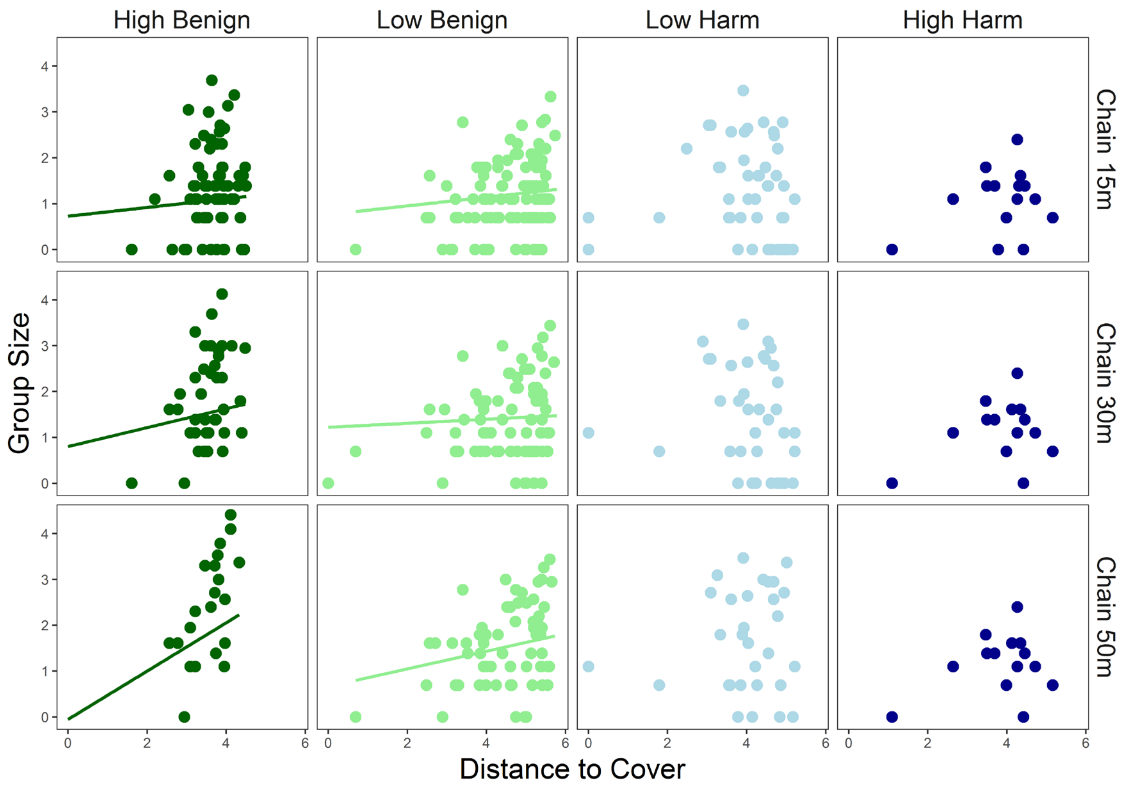

Figure 6. Relationship between logged distance to cover (m) on logged group size (n) as a function of human disturbance at each definition of chain rule (15 m, 30 m, and 50 m). Linear trend lines were plotted for significant relationships.

Table 2. Results of GLMMs testing for the effect of disturbance (High Benign, Low Benign, High Harm, High Harm) and logged distance to cover on log-transformed group size. Each model considers the data using a different chain-rule (15 m, 30 m, or 50 m) using negative binomial errors. Effects (β) are presented with 95% confidence intervals (method: Wald) which are highlighted in bold when intervals do not cover zero. Categorical fixed effects are relative to the reference level (High Benign).

Fixed effects	**Chain 15 m**	**Chain 30 m**	**Chain 50 m**
	β (CI)	β (CI)	β (CI)
Intercept (HB)	-0.88 (-2.02, 0.25)	-1.19 (-2.40, 0.01)	**-1.64 (-3.10, -0.18)**
LB	-0.04 (-1.58,1.50)	0.72 (-0.74, 2.17)	1.00 (-0.64, 2.65)
LH	1.19 (-0.21, 2.58)	**1.97 (0.48, 3.46)**	**1.88 (0.01, 3.75)**
HH	0.11 (-2.68, 2.91)	0.60 (-1.97, 3.17)	1.05 (-1.48, 3.59)
HB:Cover	**0.31 (0.01, 0.61)**	**0.50 (0.17, 0.83)**	**0.69 (0.29, 1.08)**
LB:Cover	**0.23 (0.01, 0.46)**	**0.18 (0.02, 0.38)**	**0.24 (0.02, 0.46)**
LH:Cover	-0.01 (-0.23, 0.21)	-0.10 (-0.33, 0.14)	0.07 (-0.22, 0.35)
HH:Cover	0.21 (-0.41, 0.83)	0.19 (-0.37, 0.75)	0.19 (-0.34,0.72)
Random effects	**σ (obs)**	**σ (obs)**	**σ (obs)**
Session	1.53 x 10-^{12} (234)	5.71 x 10^{-12} (166)	1.83 x 10^{-12} (130)

We found that forage greenness varied significantly across disturbance types ($p < 0.001$) (Figure 3D). Mean greenness at HB was 35.76%; significantly greener than all other disturbance types (all comparisons, $p < 0.001$) and 1.23% higher than the next greenest disturbance type, HH, which had a mean of 34.53%. However, no correlation between forage greenness and group size was detected at any disturbance type. This was evident for all chain-rules (Table 3).

Table 3. Results of LMMs testing for the effect of disturbance (High Benign, Low Benign, Low Harm, High Harm) and forage greenness on group size. Each model considered the data using a different chain rule (15 m, 30 m, or 50 m). Effects (β) are presented with 95% confidence intervals (method: Wald) which are highlighted a bold when intervals do not cover zero. Categorical fixed effects are relative to the reference level (High Benign).

Fixed effects	**Chain 15 m**	**Chain 30 m**	**Chain 50 m**
	β (CI)	β (CI)	β (CI)
Intercept (HB)	0.72 (-2.48, 3.93)	-2.06 (-6.93, 2.81)	-2.20 (-8.30, 3.90)
LB	0.00 (-5.31, 5.31)	3.21 (-4.06, 1.48)	2.18 (-6.63, 10.99)
LH	-3.29 (-8.38, 1.79)	-0.39 (-7.18, 6.39)	-5.54 (-14.23, 3.14)
HH	6.43 (-5.57, 18.44)	12.6 (-1.35, 26.55)	12.68 (-1.63, 26.98)
HB:Green	-0.02 (-0.07, 0.11)	0.11 (-0.03, 0.25)	0.13 (-0.04, 0.30)
LB:Green	-0.01 (-0.11, 0.14)	0.01 (-0.15, 0.16)	0.05 (0.14, 0.23)
LH:Green	0.11 (-0.01, 0.22)	0.11 (-0.02, 0.25)	0.27 (-0.01, 0.45)
HH:Green	-0.17 (-0.51, 0.16)	-0.27 (-0.64, 0.11)	-0.27 (-0.64, 0.11)
Random effects	**σ (obs)**	**σ (obs)**	**σ (obs)**
Session	0.00 (234)	1.73 x 10^{-14} (166)	0.131 (130)

3.5. DISCUSSION

We found that eastern grey kangaroos can respond behaviourally to both the frequency and intent of human disturbances. Although average group sizes varied little between human disturbance types, groups of larger sizes were consistently observed at benign sites relative to harmful sites and were also influenced by the frequency of the disturbance (higher with high benign but lower with high harm). Furthermore, these responses significantly altered the previously reported relationship between group size and distance from cover. At our study location, the typical antipredator response of forming larger groups when grazing further from the forest cover (Heathcote 1987, Jarman and Coulson 1989, Banks 2001) broke down when human interactions with kangaroos were of harmful intent. Counter to our predictions, we detected no significant relationship between group size and distance to cover for kangaroos at low and high harm sites. However, the antipredator response of forming larger groups when grazing further from cover was detected when groups were subject to benign human interactions (both at low and high frequencies). Forming larger groups when grazing in open habitat has been hypothesised to assist with detecting and evading predators such as dingoes or foxes (according to the many-eyes hypothesis (Ale and Brown 2007, Beauchamp 2013)), but leaves groups vulnerable to attack by human hunters whose success rate improves when clear site lines are obtained (Banks 2001). Hunters often go unnoticed by prey until the first shot is fired and are also able to fire shots in quick succession, allowing them to shoot several targets within the group, voiding the benefits of the dilution hypothesis (Bednekoff and Lima 1998).

One explanation of our findings is that kangaroos are modifying their antipredator behaviour in response to the novel threat posed by humans. Our results show that eastern grey kangaroos can maintain typical antipredator responses when humans are frequently present and their intent is benign, but that these responses are suppressed when humans act with aggression. Clearly, kangaroos did not favour foraging in the open at harmful sites, as foraging densities were lower than at benign sites (either by choice or by being killed), but our findings suggest that the changes in responses were not driven by differences in density alone. Nor were they being driven by differences in resource quality as we did not detect any significant response to grass greenness. It has been well established that resource quality and quantity is an important factor in the selection of foraging habitat by eastern grey kangaroos (Ramp and Coulson 2002, 2004, Maguire et al. 2006), especially where the grass is greener and therefore higher in energetic value (Bell 1973, Clarke et al. 1989, Favreau et al. 2018). Although resources at our high benign sites were significantly greener than at other sites, the difference was small (1.23%) and unlikely to greatly affect decision making at this magnitude. One recent study similarly reported no relationship between group size and distance to cover, possibly because resource availability was a positive driver of group size at their study site (Favreau et al. 2018). Although poisoning efforts targeting foxes and dingoes at our study location are frequent, low-level predation effects (direct and indirect) are likely to be present.

Several prey species have been shown to exploit humans directly or indirectly to avoid predation or secure resources (McKinney 2002, Gilroy and Sutherland 2007, Lesmerises et al. 2017). In line with our predictions, we found that eastern grey kangaroos within our study site were at higher densities in areas of frequent benign human activity. Although there may be unmeasured reasons why densities were higher at high benign sites, this finding implies that they can habituate to benign presence and may benefit from being shielded from persecution of harmful human activity (Berger 2007). In Australia, hunting native species without a permit is illegal, yet it is widely known that shooting is common in areas where encounters with other humans are rare, often on vacant land or private land where owners are not permanently living. However, in areas with high levels of human activity, hunting, both legally or illegally, is hazardous for recreationists and carries the risk of the shooter being reported to authorities. Additionally, it is possible that frequent human activity may suppress predation and provide sanctuary for kangaroos (Muhly et al. 2011), although we have no direct evidence of this. With high levels of benign disturbance potentially deterring both natural predators and human hunters, it is difficult to disentangle their complementary effects. For example, we found that small adults and young-at-foot comprised a significantly greater proportion of groups at high benign sites than at harm sites. This suggests that raising of young may be easier at high benign sites, either through protection from shooting or predation. Juvenile mortality rates in eastern grey kangaroos can be high as they are subject to disease, malnutrition, exposure, and predation (Arundel et al. 1977, Arundel et al. 1990, Banks et al. 2000). Where hunting is prevalent, juvenile mortality should increase due to increased stress and reduced parental care. Further research is required to track the causes of mortality across the disturbance types utilised in our study. Such information is lacking as previous work on juvenile mortality was conducted at locations with benign human disturbance (Cripps et al. 2014, Gélin et al. 2015).

We found that eastern grey kangaroos modified their grouping behaviour and spatial dispersion in response to the intent and frequency of human disturbances at our study site. The plasticity of these responses alludes to cognitive learning in both forms; kangaroos habituating to the absence of consequence from a stimulus (human presence) at sites with benign human disturbance and associating negative consequences from the same stimulus at neighbouring sites with harmful human disturbances. While our evidence for this is currently observational, further work will seek to clarify the causal effect of human presence on fear responses in these kangaroos. Behavioural plasticity may be instrumental to survival in rapidly changing environments, where human activities may offer both novel opportunities and significant risk. This study provides insight into how kangaroos are persisting in these complex landscapes and paves the way for long-term behavioural studies to investigate the mechanisms through which wildlife are persisting in landscapes shared with humans.

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3.6. REFERENCES

Ale, S. B., and J. S. Brown. 2007. The contingencies of group size and vigilance. Evolutionary Ecology Research **9**:1263-1276.

Arundel, J., I. Barker, and I. Beveridge. 1977. Diseases of marsupials. Pages 141-154 The biology of marsupials. Springer.

Arundel, J., K. Dempster, K. Harrigan, and R. Black. 1990. Epidemiological observations on the helminth parasites of *Macropus giganteus* Shaw in Victoria. Wildlife Research **17**:39-51.

Atickem, A., L. E. Loe, and N. C. Stenseth. 2014. Individual Heterogeneity in Use of Human Shields by Mountain Nyala. Ethology **120**:715-725.

Banks, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. Animal Behaviour **61**:1013-1021.

Banks, P. B., A. E. Newsome, and C. R. Dickman. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. Austral Ecology **25**:283-291.

Bates, D. M. 2010. lme4: Mixed-effects modeling with R. Berlin.

Beauchamp, G. 2013. Social predation: how group living benefits predators and prey. Elsevier.

Bednekoff, P. A., and S. L. Lima. 1998. Re–examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. Proceedings of the Royal Society of London. Series B: Biological Sciences **265**:2021-2026.

Bell, H. 1973. The ecology of three macropod marsupial species in an area of open forest and savannah woodland in north Queensland, Australia. Mammalia **37**:527-544.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters **3**:620-623.

Best, E. C., R. G. Dwyer, J. M. Seddon, and A. W. Goldizen. 2014. Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos. Animal Behaviour **89**:1-10.

Bivand, R., C. Rundel, E. Pebesma, R. Stuetz, K. O. Hufthammer, P. Giraudoux, M. Davis, S. Santilli, and M. R. Bivand. 2019. Package ‘rgeos’.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in ecology & evolution **24**:127-135.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research **59**:185-193.

Bradbury, J. W., S. L. Vehrencamp, K. E. Clifton, and L. M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. Ecology **77**:2237-2255.

Breck, S. W., S. A. Poessel, P. Mahoney, and J. K. Young. 2019. The intrepid urban coyote: A comparison of bold and exploratory behavior in coyotes from urban and rural environments. Scientific reports **9**:2104.

Cardillo, M., and L. Bromham. 2001. Body size and risk of extinction in Australian mammals. Conservation Biology **15**:1435-1440.

Carter, A. J., O. Pays, and A. W. Goldizen. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behavioral Ecology and Sociobiology **64**:237-245.

Caughley, G. 1964. Social Organization and Daily Activity of the Red Kangaroo and the Grey Kangaroo. Journal of Mammalogy **45**:429-436.

Caughley, G., G. Grigg, J. Caughley, and G. Hill. 1980. Does dingo predation control the densities of kangaroos and emus? Wildlife Research **7**:1-12.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012a. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society of London B: Biological Sciences:rspb20121483.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012b. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. Plos One **7**:e50611.

Clarke, J., M. Jones, and P. Jarman. 1989. A day in the life of a kangaroo: activities and movements of eastern grey kangaroos *Macropus giganteus* at Wallaby Creek. Kangaroos, Wallabies and Rat-kangaroos'.(Eds G. Grigg, P. Jarman and I. Hume.) pp:611-618.

Clarke, J. L., M. E. Jones, and P. J. Jarman. 1995. Diurnal and nocturnal grouping and foraging behaviors of free-ranging eastern grey kangaroos. Australian Journal of Zoology **43**:519-529.

Clinchy, M., L. Y. Zanette, D. Roberts, J. P. Suraci, C. D. Buesching, C. Newman, and D. W. Macdonald. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behavioral Ecology **27**:1826-1832.

Colagross, A., and A. Cockburn. 1993. Vigilance and grouping in the eastern gray kangaroo, *Macropus giganteus*. Australian Journal of Zoology **41**:325-334.

Coulson, G. 2009. Behavioural ecology of red and grey kangaroos: Caughley's insights into individuals, associations and dispersion. Wildlife Research **36**:57-69.

Craigie, I. D., J. E. Baillie, A. Balmford, C. Carbone, B. Collen, R. E. Green, and J. M. Hutton. 2010. Large mammal population declines in Africa's protected areas. Biological Conservation **143**:2221-2228.

Cripps, J., I. Beveridge, R. Ploeg, and G. Coulson. 2014. Experimental manipulation reveals few subclinical impacts of a parasite community in juvenile kangaroos. International Journal for Parasitology: Parasites and Wildlife **3**:88-94.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science **349**:858-860.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A. L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in ecology & evolution **28**:605-613.

Favreau, F.-R., A. W. Goldizen, H. Fritz, S. P. Blomberg, E. C. Best, and O. Pays. 2014. Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos. Animal Behaviour **92**:175-184.

Favreau, F.-R., A. W. Goldizen, H. Fritz, and O. Pays. 2018. Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. Animal Behaviour **135**:165-176.

Gélin, U., M. E. Wilson, G. Coulson, and M. Festa-Bianchet. 2015. Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. Journal of Animal Ecology **84**:239-248.

Gilroy, J. J., and W. J. Sutherland. 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends in ecology & evolution **22**:351-356.

Heathcote, C. 1987. Grouping of Eastern Grey Kangaroos in Open Habitat. Wildlife Research **14**:343-348.

Hijmans, R. J., J. van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, O. P. Lamigueiro, A. Bevan, E. B. Racine, and A. Shortridge. 2015. Package ‘raster’. R package.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal: Journal of Mathematical Methods in Biosciences **50**:346-363.

Inoue, T., S. Nagai, H. Kobayashi, and H. Koizumi. 2015. Utilization of ground-based digital photography for the evaluation of seasonal changes in the aboveground green biomass and foliage phenology in a grassland ecosystem. Ecological informatics **25**:1-9.

Jarman, P., and G. Coulson. 1989. Dynamics and adaptiveness of grouping in macropods. Kangaroos, Wallabies and Rat-kangaroos’.(Eds G. Grigg, P. Jarman and I. Hume.) pp:527-547.

Jarman, P. J. 1987. Group-size and activity in eastern grey kangaroos Animal Behaviour **35**:1044-1050.

Kaufmann, J. H. 1975. Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. Animal Behaviour **23, Part 1**:214-221.

King, W., M. Wilson, T. Allen, M. Festa-Bianchet, and G. Coulson. 2011. A capture technique for free-ranging eastern grey kangaroos (*Macropus giganteus*) habituated to humans. Australian Mammalogy **33**:47-51.

Komsta, L., and F. Novomestky. 2015. Moments, cumulants, skewness, kurtosis and related tests. R package version **14**.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer Cervus elaphus in central Norway. Wildlife Biology **5**:213-223.

Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2010. Conservation and the scarecrow effect: Can human activity benefit threatened species by displacing predators? Biological Conservation **143**:2156-2163.

Lenth, R. V., and M. Hervé. 2015. lsmeans: Least-squares means. R package version **2**.

Lesmerises, F., C. J. Johnson, and M. H. St-Laurent. 2017. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. Ecology and evolution **7**:845-854.

Letnic, M., and M. S. Crowther. 2013. Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. Oikos **122**:761-769.

Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos **123**:641-651.

Maguire, G., D. Ramp, and G. Coulson. 2006. Foraging behaviour and dispersion of eastern grey kangaroos (*Macropus giganteus*) in an ideal free framework. Journal of Zoology **268**:261-269.

Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications **13**:1830-1834.

Marealle, W. N., F. Fossøy, T. Holmern, B. G. Stokke, and E. Røskaft. 2010. Does illegal hunting skew Serengeti wildlife sex ratios? Wildlife Biology **16**:419-429.

McKinney, M. L. 2002. Urbanization, Biodiversity, and ConservationThe impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. BioScience **52**:883-890.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology **21**:36-47.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. Plos One **6**:e17050.

Norum, J. K., K. Lone, J. D. Linnell, J. Odden, L. E. Loe, and A. Mysterud. 2015. Landscape of risk to roe deer imposed by lynx and different human hunting tactics. European Journal of Wildlife Research **61**:831-840.

NRMMC. 2008a. National Code of Practice for the Humane Shooting of Kangaroos and Wallabies for Commercial Purposes. Department of the Environment, Water, Heritage and the Arts. Canberra.

NRMMC. 2008b. National Code of Practice for the Humane Shooting of Kangaroos and Wallabies for Non-Commercial Purposes. Department of the Environment, Water, Heritage and the Arts. Canberra.

Pays, O., G. Beauchamp, A. J. Carter, and A. W. Goldizen. 2013. Foraging in groups allows collective predator detection in a mammal species without alarm calls. Behavioral Ecology **24**:1229-1236.

Pays, O., P. J. Jarman, P. Loisel, and J.-F. Gerard. 2007. Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? Animal Behaviour **73**:595-604.

Ramp, D., and G. Coulson. 2002. Density dependence in foraging habitat preference of eastern grey kangaroos. Oikos **98**:393-402.

Ramp, D., and G. Coulson. 2004. Small-scale patch selection and consumer-resource dynamics of eastern grey kangaroos. Journal of Mammalogy **85**:1053-1059.

Richardson, A. D., J. P. Jenkins, B. H. Braswell, D. Y. Hollinger, S. V. Ollinger, and M.-L. Smith. 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. Oecologia **152**:323-334.

Ripple, W. J., G. Chapron, J. V. López-Bao, S. M. Durant, D. W. Macdonald, P. A. Lindsey, E. L. Bennett, R. L. Beschta, J. T. Bruskotter, and A. Campos-Arceiz. 2016. Saving the world's terrestrial megafauna. BioScience **66**:807-812.

Ripple, W. J., C. Wolf, T. M. Newsome, M. G. Betts, G. Ceballos, F. Courchamp, M. W. Hayward, B. Van Valkenburgh, A. D. Wallach, and B. Worm. 2019. Are we eating the world's megafauna to extinction? Conservation Letters:e12627.

Saïd, S., V. Tolon, S. Brandt, and E. Baubet. 2012. Sex effect on habitat selection in response to hunting disturbance: The study of wild boar. European Journal of Wildlife Research **58**:107-115.

Sih, A., M. C. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications **4**:367-387.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour **85**:1004-1011.

Sol, D., O. Lapiedra, and C. González-Lagos. 2013. Behavioural adjustments for a life in the city. Animal Behaviour **85**:1101-1112.

Southwell, C. 1984. Variability in grouping in the eastern grey kangaroo, *Macropus giganteus* II. Dynamics of group formation. Wildlife Research **11**:437-449.

Stillfried, M., P. Gras, M. Busch, K. Börner, S. Kramer-Schadt, and S. Ortmann. 2017. Wild inside: Urban wild boar select natural, not anthropogenic food resources. Plos One **12**:e0175127.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2017. Learning from the mistakes of others: How female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. Plos One **12**:e0178082.

Wheat, R. E., and C. C. Wilmers. 2016. Habituation reverses fear-based ecological effects in brown bears (Ursus arctos). Ecosphere **7**:e01408.

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CHAPTER 4:

FLIGHT RESPONSES OF EASTERN GREY KANGAROOS TO BENIGN OR HARMFUL HUMAN BEHAVIOUR

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4.1. ABSTRACT

Globally, wilderness is being converted for rural and agricultural land use. In countryside landscapes, many habitat structures remain intact, providing suitable habitat for wildlife species that can accurately assess novel risks and develop tolerance to benign disturbances. Associative learning that promotes avoidance and also facilitates desensitisation to benign disturbance is key to persisting in these landscapes. Conversely, learning to distinguish and avoid negative interactions with humans, like hunting, is vital. To determine if eastern grey kangaroos are capable of learning from previous interactions with humans, we tested the flight responses of wild kangaroos which have previously experienced either low or high frequencies of harmful and benign encounters with humans. We found evidence for eastern grey kangaroos rapidly habituated to benign disturbance as there was no significant difference in assessment distance between groups that previously experienced low or high frequencies of disturbance. The threat of harmful disturbances was not as quickly learnt, as groups that experienced low frequencies of harmful disturbance delayed flight longer than those experiencing frequent harm. We found that the influence of environmental and group parameters on a kangaroo's decision to flee depended on the intent and frequency of previous interactions with humans. Our study indicates that kangaroos are learning from previous encounters with humans, correctly assessing novel risks which may be contributing to their persistence in countryside landscapes.

Keywords: Flight initiation distance (FID); human behaviour; countryside landscapes; eastern grey kangaroos; *Macropus giganteus*; human-wildlife interactions; coexistence; shooting; hunting

4.2. INTRODUCTION

Humans present a complex mix of negative and beneficial circumstances for many wildlife species. On one hand, the actions of humans have catastrophic unintended consequences for wildlife as their homes are either modified or occupied by development and land use (Fraser and MacRae 2011). Wilderness, defined as areas that are mostly void of human presence, has declined by 9.6% in the last 20 years as the human population expands (Watson et al. 2016), while agriculture now utilises roughly 30% of the ice-free terrestrial land surface (FAO, 2012). However, where wild animals persist, they are increasingly challenged by having to accommodate humans in their daily routine (Soulsbury and White 2016). For some, this creates novel opportunities to gain resources like exploiting waste and refuse (Gabrey 1997, Ross 2004), opportunities to share homes (Russell et al. 2011), and many positive interactions like supplemental feeding (Orams 2002, Plummer et al. 2019). In contrast, many species find sharing space with humans makes life fraught and stressful (Ciuti et al. 2012). It stands to reason, that wildlife which adapt to, and persist within, anthropogenic landscapes, are able to balance the different benefits and costs associated with living with humans. Although a range of attributes and traits that promote the successful exploitation (or persistence) in these landscapes, the ability to accurately assess risk and respond accordingly is a key trait (Kretser et al. 2008, Lowry et al. 2013, Samia et al. 2015).

Evidence of wildlife responding to human-mediated fear in anthropogenic landscapes is strong. Some species avoid areas of high risk or else increase risk-aversive behaviours to decrease risk propensity (Tigas et al. 2002, Rode et al. 2006, Gaynor et al. 2018), while others habituate to benign disturbances so that they may exploit favourable conditions (Sih et al. 2011). Adaptation to urban environments by wildlife led to an appreciation of urban exploiters (Kark et al. 2007, Fischer et al. 2015, Soulsbury and White 2016, Ducatez et al. 2018), wildlife who benefit from novel human-dominated landscapes, requiring finely-tuned behavioural strategies that permit risk avoidance but which do not inhibit cohabitation. Things are less clear in countryside environments, where there may be a mix of extant habitat and land cleared for agriculture (Daily et al. 2003). Human-wildlife conflicts are common in countryside environments, particularly when land-sparing approaches to agriculture seek to exclude wildlife from productive land rather than integrating conservation with production (Fischer et al. 2008, Dickman 2010). Methods of exclusion are often harmful to wildlife, which contributes to their perception of humans as threatening in these landscapes. Moreover, lower frequencies of human presence present challenging conditions for wildlife habituation while simultaneously disinhibiting negative human behaviour (Thibaut 2017). As a consequence, although the countryside can offer favourable conditions for wildlife, greater variation in human behaviour excludes those species whose risk assessment is insufficiently sensitive and nuanced to accurately determine the risks humans pose in different circumstances.

For large mammals (>15kg), evidence suggests many are resilient to minor modification of habitat in the countryside but commonly exhibit behavioural changes to avoid direct interactions with humans (Daily et al. 2003, Lawrence 2008, Zhou et al. 2013). For these “avoiders”, encounters with humans are often perceived as threatening regardless of their intent or actions (Frid and Dill 2002). However, the associative learning that promotes avoidance can also facilitate desensitisation to benign disturbance (Stankowich 2008), even though habituating to benign interactions must be complicated for species that also experience lethal human disturbances such as hunting. Despite this, there is growing evidence that some species can differentiate between contextual circumstances of harm and benign intent. Red deer (*Cervus elaphus*) have succeeded in making this distinction, perceiving recreationists as less threatening than hunters (Jayakody et al. 2008). African elephants also exhibit stronger fear behaviours when presented with scent, visual, or audio stimuli from a threatening subgroup of people compared to that of an agricultural subgroup who poses little threat (Bates et al. 2007, McComb et al. 2014).

In Australia, eastern grey kangaroos (*Macropus giganteus*) are a large mammal faced with similar challenges: they are hunted by humans but also experience benign interactions with humans in recreational contexts. Eastern grey kangaroos are a gregarious woodland species (Caughley 1964, Kaufmann 1975, Coulson 2009) that form open-membership fission-fusion groups (Jarman 1987, Clarke et al. 1995). Changes in group size have been attributed to perceived levels of predation risk which vary spatially and temporally (Heathcote 1987, Jarman and Coulson 1989). Eastern grey kangaroos increase group size when foraging in cleared landscapes during the morning and afternoon (Banks 2001) then break into smaller groups during the middle of the day when the likelihood of predation decreases (Southwell 1984). Eastern grey kangaroos are prey for foxes (primarily juveniles) (Banks and Dickman 2007) and dingoes (Wallach et al. 2010, Letnic and Crowther 2013), but are also hunted by humans throughout their range. Indigenous people engaged in sporadic hunting of kangaroos for tens of thousands of years (Gammage 2012). Since European occupation, kangaroos have been shot for food (for human and pets, commercially and for subsistence), sport, or bounties (Boom et al. 2012). The notion of hunting for sport is common as kangaroos in rural regions are often hunted illegally, a situation that is tolerated by government regulators (Boom and Ben-Ami 2013, Ramp 2013, Descovich et al. 2015). However, interactions between humans and kangaroos are not always negative, as kangaroos can find safety and resources in national parks, golf courses, sporting ovals, and wildlife-friendly farms (King et al. 2011). It appears that kangaroos are tolerant of, and habituate to, human disturbances of benign intent, such as tourism and wildlife-friendly landholders (Austin and Ramp 2019). It is unclear if these responses are caused by the frequency or intent of previous interactions with humans.

In a previous study (Austin and Ramp 2019), we found that grouping behaviour of eastern grey kangaroos varied in response to the intent and frequency of human disturbances. Under benign conditions, kangaroos formed larger groups when far from cover, following the “Many Eyes Hypothesis” (Ale and Brown 2007, Beauchamp 2013), but this relationship was not detectable under harmful conditions as group size did not change with distance to cover. This response was hypothesized as a behavioural adaption to human hunting as individuals learnt that forming large groups far from cover may make them targets for hunters (Austin and Ramp 2019). Here our goal was to test how these same kangaroos responded to the presence of a human stimulus to determine whether the intent and frequency of previous human-kangaroo interactions directly shaped kangaroo’s fear of humans through associative learning. To test this, we conducted a flight response experiment on a population of free-living kangaroos experiencing low and high frequencies of benign and harmful human disturbances (Austin and Ramp 2019). If kangaroos learn from previous encounters with humans, we expected them to exhibit shorter assessment distances prior to flight when approached by a human when previous encounters were of harmful intent, relative to those who experienced encounters of benign intent. Incorrectly assessing risks posed by humans in countryside landscapes, like our study area, can have lethal consequences or result in lost foraging opportunities and increased energy expenditure. Additionally, we quantified the degree to which environmental and demographic parameters amplified risk perception by modelling the importance of distance to refuge, resource quality, group size, and demography on the group's decision to flee under each frequency and intent of human disturbance.

4.3. METHODS

4.3.1. Site Description

We studied a free-ranging population of eastern grey kangaroos in the surrounds of Wombeyan Karst Conservation Reserve in the Southern Highlands of NSW, adjacent to Kanangra-Boyd National Park, previously described by Austin and Ramp (2019) (Fig. 1). The area contains a mix of conservation reserve and private properties over 850 hectares, across which kangaroos are free to move. We previously established that the region included a mix of complex human presence, with areas of low (<1 kangaroo/human interaction per week) and high (>1 kangaroo/human interaction per week) frequency interaction, and a mix of benign (either ignored or well-intentioned, e.g. tourists taking photographs) and harmful (harassing or shooting) interactions (Austin and Ramp 2019). Consequently, we were able to classify regions by frequency and intent: High Benign (HB), Low Benign (LB), Low Harm (LH), and High Harm (HH). For the purposes of anonymity, we have not included map locations of each treatment. However, the study area was comprised of 4% HB, 47% LB, 21% LH, and 28% HH.

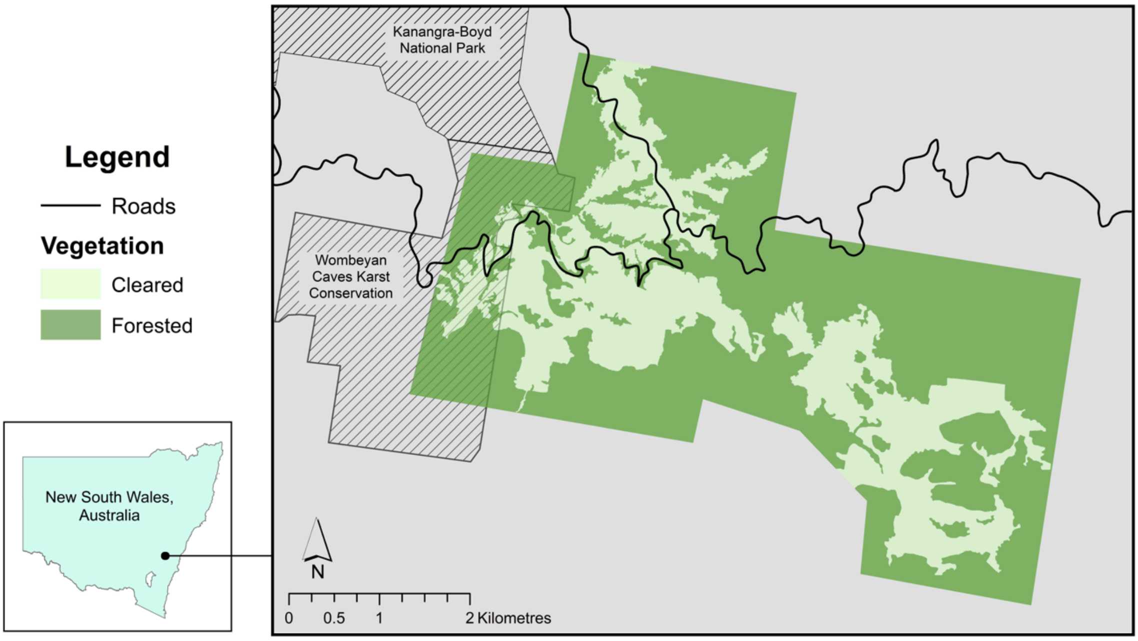

Figure 1: Location of the study area within New South Wales, Australia, showing roads and forested and cleared areas within the study area. Property boundaries and human disturbance were omitted to ensure anonymity.

4.3.2. Behavioural Responses

Measuring direct responses to fear can be inferred from observation of antipredator behaviours such as flight, vigilance, grouping, and crypsis, helping to identify and quantify stimuli that trigger fear responses. Flight response to a stimulus is frequently relied upon in wildlife studies and can be recorded in a variety of ways (Miller et al. 2006). Flight initiation distance (FID), the distance at which an animal flees from an approaching stimulus, is highly correlated with alert distance (AD), the distance at which prey become aware of the stimulus, and the distance from which the stimulus approach commenced (Dall et al. 2004) (Dumont et al. 2012). Alert behaviours can be difficult to identify in some species as there may be no clear indicators of stimulus detection. However, alert postures in kangaroos are clearly observable as they become upright, standing high on their hind legs, and focus their attention (eye and ear orientation) in the direction of the disturbance (Edwards et al. 2013). Alert distance allows for the more insightful assessment distance (Dall et al. 2004) to be measured, the distance a stimulus can move towards an animal after it has been detected until flight is taken. This measure directly relates to perceived predation risk as it reflects the period where threat level changes from low to high risk (Ydenberg and Dill 1986, Frid and Dill 2002, Stankowich and Blumstein 2005). This measure has previously been used to quantify perceived risk by Columbian black-tailed deer (*Odocoileus hemionus columbianus*) to different types of threats (speed of approach, directness, and presence of gun) (Stankowich and Coss 2005).

We, therefore, determined flight responses of 138 groups of eastern grey kangaroos by measuring assessment distance across the four types of human disturbance. We sampled flight responses from each disturbance type over six-fortnight windows, between October 2016 and February 2017, recording responses between 0600-0830 and 1630-1900 when kangaroos were grazing in open areas (Clarke et al. 1995). We covertly located groups of more than one individual, selecting groups for testing to ensure the same individuals were not recorded twice in the same sampling session (although individuals were not identifiable between sessions). Before testing flight responses, video of the group was recorded using a digital camera (Canon EOS 70D Digital SLR with Canon EF100-400mm lens) for three minutes to ensure they had not detected our presence. The GPS coordinates (± 5m) of the starting location were recorded along with the distance between the starting location and the most central individual in the group, using a laser rangefinder (Bushnell, ± 0.9m). The test commenced as the human stimulus (CMA) walked in a direct line towards the group, keeping the group in sight but avoiding eye contact. The approacher maintained a constant speed during the approach (0.7 ± 0.03 m/s) and always wore the same clothing. Following Stankowich and Coss (2005), a marker was dropped when one or more members of the group displayed a vertical vigilance stance towards the approacher (alert distance). The approacher continued without stopping until one or more individuals moved from their original position (flight initiation distance), concluding the test. We recorded the final location of the approacher and the dropped marker using a GPS. The exact position of the group was determined using the directional bearing, start location, and initial distance of the group.

4.3.3. Environmental and Group Parameters

Eastern grey kangaroos use forested habitat as a refuge and forage closer to cover when predation risk is high (Banks 2001). The group's distance from forested cover was calculated from the GPS position at the centre of the group in ArcGIS (v10, 2016 ESRI). We measured the resource quality at the centre of each group by determining the relative green channel brightness (greenness) of vegetation from digital photographs. Due to the high correlation between greenness and biomass (Inoue et al. 2015), resource quality was inferred by the mean greenness of resources for each group of kangaroos as per Austin and Ramp (2019). Using video footage collected prior to the approach, we assigned individuals to demographic categories: size/maturity (pouch young, young-at-foot, sub-adult, small adult, medium adult, and large adult (Austin and Ramp 2019). The presence of all pouch young was noted but they were only recorded as contributing to group size when they were out of their mother's pouch. An independent assessor familiar with eastern grey kangaroos was provided with a subset of 100 photographs to help validate our categorisation of demographic groups. Group size was determined using the 15 metre chain-rule, where individuals within 15 metres of another member of the group were included in the group (Jarman 1987, Carter et al. 2009, Pays et al. 2013, Best et al. 2014).

4.3.4. Statistical Analysis

We examined Assessment Distance (AsD) using a generalised linear mixed model to detect significant differences between our four disturbance types (High Benign, Low Benign, Low Harm, and High Harm), with inference determined using likelihood ratio tests. Sampling session was included as a random variable to control for possible dependence due to repeated sampling of sites. However, parametric bootstrapping found sampling session had no significant effect on AsD. Multiple comparisons of means with Tukey contrasts were conducted to test for statistical differences between disturbances. To determine if the presence of vulnerable individuals (mothers, pouch young, and young-at-foot) significantly affected AsD we ran a series of independent sample t-tests within each disturbance type. The response variable AsD was log-transformed to satisfy the assumption of homogeneity of variance. Linear regressions were conducted to determine if the distance at which kangaroos were alerted to the approach (AD) had a significant effect on AsD, nested within disturbance type. We conducted an analysis of covariance to identify significant interactions between disturbance type and AsD, controlling for AD. This analysis was repeated with each disturbance type set as the reference level.

The effect of environmental and group parameters on AsD were tested using multiple model inferencing. The global model for AsD included the following predictors: proportion of individuals from each demographic category, group size, distance to refuge, and resource greenness. All variables were standardised and scaled to remove bias (Grueber et al. 2011). For each disturbance type, a set of models were generated from all combinations of predictors using the R package '*MuMIn*' (Barton and Barton 2018). Models for each treatment were ranked according by AICc and all models within 2+AICc of the best model were averaged using the natural average method (Burnham and Anderson 2002). Coefficients and confidence intervals were generated from full averaged models.

4.4. RESULTS

Human disturbance type significantly influenced the assessment distance of eastern grey kangaroos ($p < 0.001$). The frequency of benign human interactions had no significant effect on assessment distance (HB: LB, $p = 0.638$), with average assessment distances of 16.17m (± 2.02) and 12.73m (± 1.55) respectively. However, assessment distances were significantly longer at both LB and HB than for groups at LH ($p=0.001$, $p < 0.001$) and HH ($p < 0.001$, $p < 0.001$) (Fig. 2A). The frequency of harmful interactions with humans significantly affected assessment distance, with mean assessment distances at HH of 2.21m (± 0.70), which were significantly shorter than those at LH by 3.76m (± 1.09) on average ($p=0.004$) (Fig. 2A). The proportion of groups with vulnerable individuals present (young-at-foot, and pouch young) varied across disturbance types; vulnerable individuals were present in 94% of the groups sampled at HB; 41% at LB; 33% at LH, and 29% at HH. At HH, the presence of vulnerable individuals in a group resulted in mean assessment distances that were 2.8 times longer than when vulnerable individuals were absent (4.13m to 1.48m, $t_{27} = -2.671$, p =

0.013). However, the presence of vulnerable individuals had no significant effect on assessment distance at all other treatments (HB: t_{33}= -0.671, p = 0.507; LB: t_{39} = 0.947, p = 0.3494; LH: t_{31} = -0.942, p = 0.353) (Fig. 2B).

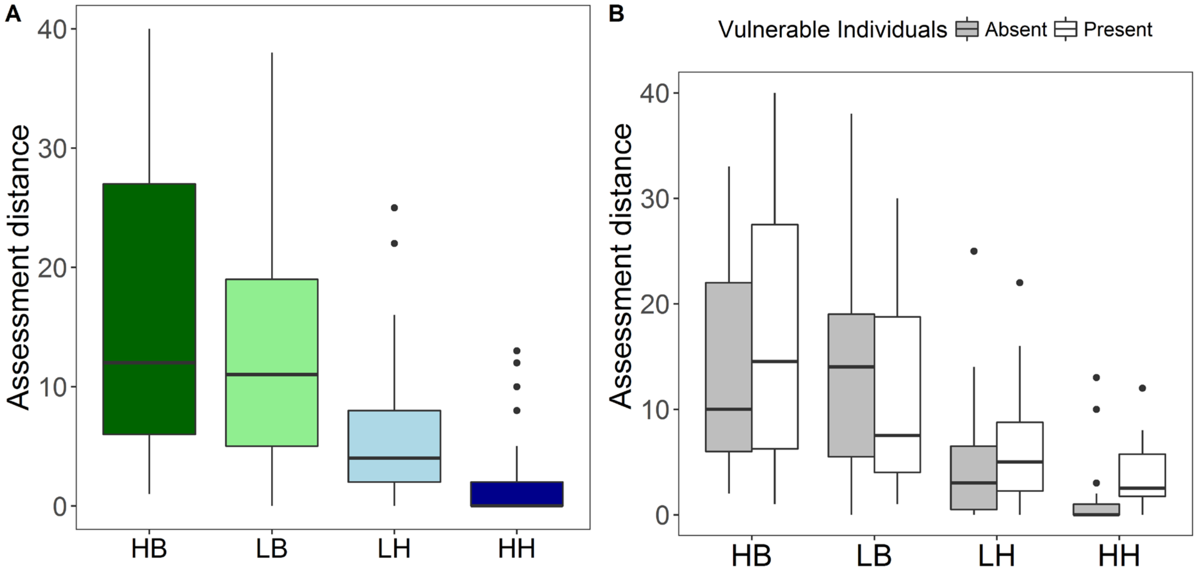

Figure 2: A) Mean assessment distances for groups of eastern grey kangaroos under different human disturbances, HB: High Benign, LB: Low Benign, LH: Low Harm, and HH: High Harm. B) Mean assessment distances for groups of eastern grey kangaroos as a function of human disturbance and the presence of vulnerable individuals (pouch young and young at foot). Widths of boxes are proportional to the square root of the sample sizes. Shaded boxes represent groups without vulnerable individual and hollow boxes groups containing vulnerable individuals.

Alert distance was positively correlated with assessment distance for kangaroos that have previously experienced benign disturbances (HB: f=13.48, p=0.001; LB: f=24.33, p<0.001), such that kangaroos could afford to spend longer assessing threat levels when the detected threat was further away (Fig. 3). This relationship was similar for both benign disturbance types, as the slopes for HB and LB were not significantly different (f=17.81, p=0.1). In contrast, no significant linear relationship between alert distance and assessment distance for groups that experience harmful disturbances was detected (LH: f=0.26, p=0.611; HH: f=0.11, p=0.741), suggesting that the decision to flee at harmful sites was independent of how far away the threat was (Fig. 3).

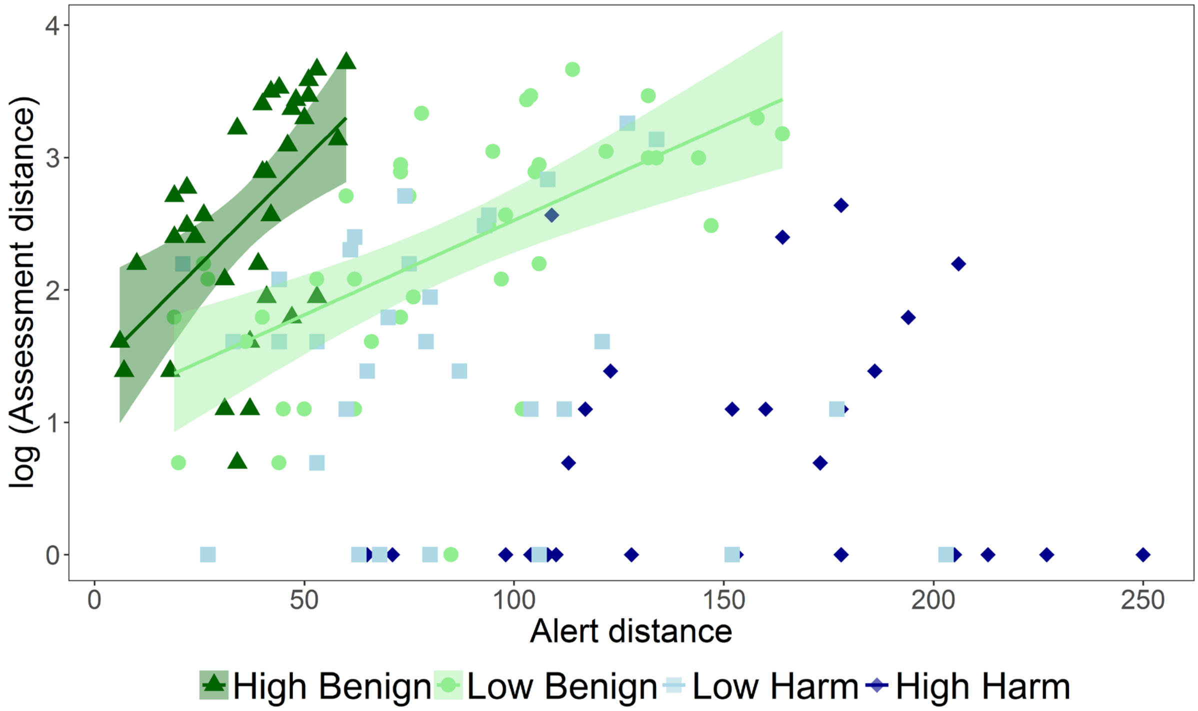

Figure 3: Relationship between logged assessment distance and alert distance under different human disturbances, HB: High Benign, LB: Low Benign, LH: Low Harm, and HH: High Harm. Linear trend lines were plotted for significant relationships with shaded regions reflecting confidence intervals (95%).

There was a considerable difference in the influence of environmental and grouping variables across disturbance types (Table 1, Fig. 4A). Distance to refuge was an important positive predictor of assessment distance at LH (β = 0.380, p = 0.003), with those further from refuge taking longer to assess the threat. There was also a weak trend at LH where the presence of large adults in the group also increased the length of assessment distance (β = 0.315, p = 0.016) (Fig. 4B). However, increasing group size led to shorter assessment distances at LH (β = -0.288, p = 0.022) (Fig. 4D). Conversely, increasing group size led to significantly longer assessment distances at HB sites (β = 0.349, p = 0.001) (Fig. 4E). At HH sites, kangaroos took longer to assess threats (i.e. were more reluctant to leave) when plant quality (i.e. resource greenness) was higher (β = 0.179, p = 0.015) (Fig. 4C).

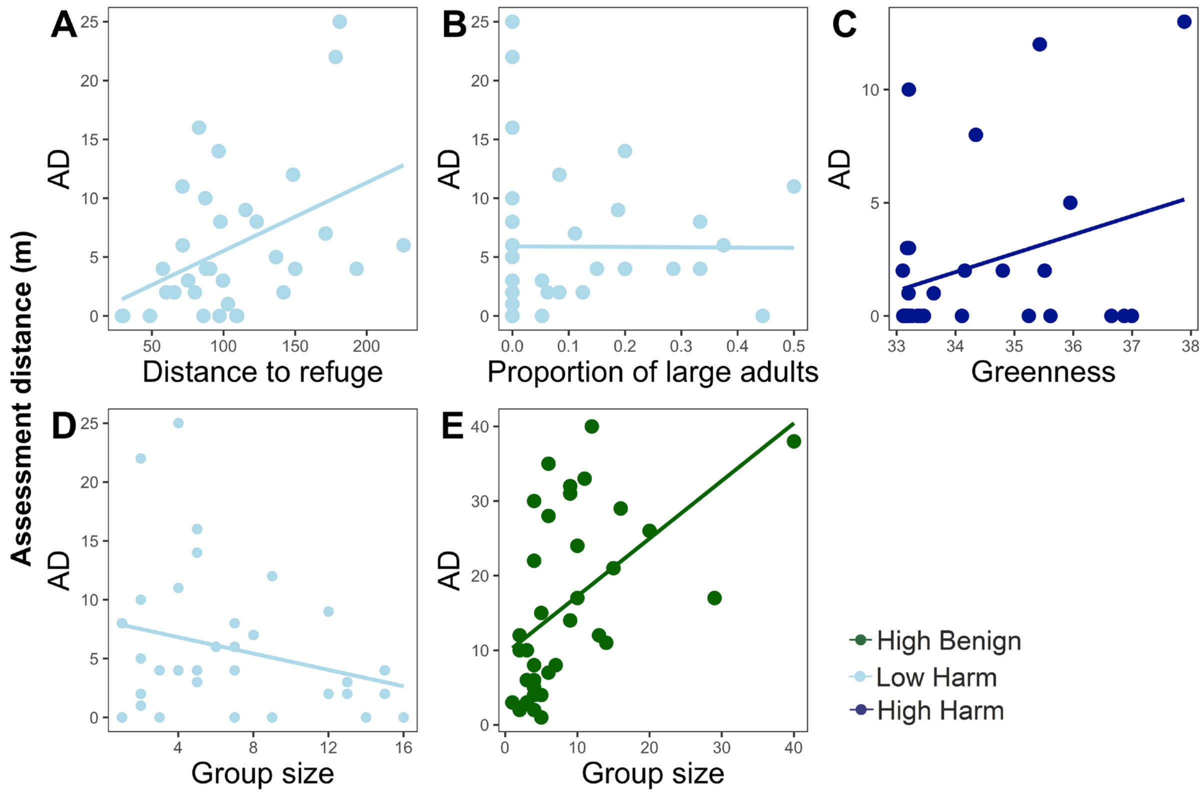

Figure 4: Significant responses of assessment distance to environmental and group parameters across disturbance types. Variables have been scaled to allow comparison across variables. Relationship between assessment distance and A) distance to refuge at LH, B) the proportion of large adults in the group at LH, C) resource greenness at HH, D) group size at LH, and E) group size at HB.

Table 1: Average model summaries of assessment distance across different human disturbances, High Benign, Low Benign, Low Harm, and High Harm. Statistically significant variables at 95% confidence level are shown in bold. A dash indicates that the variable was not present in the model.

Disturbance	*Parameter*	*Estimate**	*Adjusted SE*	*p value*	*Relative importance*
High Benign *n = 35*	Intercept	0.638	0.381	0.102	NA
	Large adult	-	-	-	-
	Medium adult	-	-	-	-
	Small adult	0.065	0.141	0.652	0.29
	Sub-adult	-0.025	0.090	0.784	0.14
	Young-at-foot	0.018	0.088	0.844	0.10
	Pouch young	-	-	-	-
	Group size	**0.394**	**0.118**	**0.001**	**1**

	Distance to refuge	0.200	0.387	0.612	0.32
	Resource greenness	-	-	-	-
Low Benign	Intercept	0.199	0.147	0.191	NA
n = 41	Large adult	-0.020	0.075	0.790	0.9
	Medium adult	0.319	0.179	0.082	0.91
	Small adult	0.024	0.089	0.793	0.16
	Sub-adult	-0.060	0.143	0.680	0.26
	Young-at-foot	-0.095	0.122	0.443	0.52
	Pouch young	0.012	0.064	0.858	0.8
	Group size	-	-	-	-
	Distance to refuge	0.016	0.070	0.823	0.14
	Resource greenness	-	-	-	-
Low Harm	Intercept	-0.494	0.108	<0.001	NA
n = 33	**Large adult**	**0.315**	**0.121**	**0.016**	**1**
	Medium adult	-	-	-	-
	Small adult	-	-	-	-
	Sub-adult	-	-	-	-
	Young-at-foot	0.023	0.064	0.729	0.26
	Pouch young	-	-	-	-
	Group size	**-0.288**	**0.121**	**0.022**	**1**
	Distance to refuge	**0.380**	**0.123**	**0.003**	**1**
	Resource greenness	-	-	-	-
High Harm	Intercept	-0.474	0.115	<0.001	NA
n = 29	Large adult	-0.126	0.107	0.244	0.68
	Medium adult	-0.183	0.143	0.205	0.68
	Small adult	0.052	0.084	0.545	0.32
	Sub-adult	0.034	0.102	0.742	0.14
	Young-at-foot	-0.116	0.275	0.680	0.21
	Pouch young	0.064	0.103	0.539	0.32
	Group size	0.173	0.118	0.153	0.84
	Distance to refuge	-	-	-	-
	Resource greenness	**0.179**	**0.115**	**0.015**	**1**

*effect sizes are standardized

4.5. DISCUSSION

We found that the nature and frequency of previous interactions with humans shaped risk perception in eastern grey kangaroos. Empirical results suggest that kangaroos whose primary experiences with humans are benign encounters, at both high and low frequencies, perceive an experimental human stimulus as less threatening than those who have experienced harmful interaction with humans. The frequency of benign interactions did not significantly alter assessment distance, which implies that tolerance of benign human disturbances is readily learnt, even when the disturbance is encountered infrequently. However, the frequency of past harmful experiences with humans significantly affected their perception of risk. Kangaroos that experienced disturbance at low frequencies spent longer assessing the potential threat than those who experienced higher frequencies of harmful disturbance, which fled almost immediately after the human stimulus was detected. When previous interactions are benign, our results align with the general notion that birds, mammals, and lizards learn that a non-threatening stimulus poses little to no threat after several encounters with the stimulus (Delacasa and Lubow 1995, Gonzalo et al. 2013, Samia et al. 2015). In our study, low levels of benign disturbance also resulted in tolerance. Previous research has shown that repeated presentation of a consistently benign stimulus leads to rapid habituation, for example in marmosets (Dacier et al. 2006) and bears (Elfström et al. 2014). Habituating to benign disturbance has economic benefits, enabling individuals to avoid the costs of fleeing non-threatening disturbances, namely the loss of resources and unnecessary expenditure of energy (Ydenberg and Dill 1986).

Flight behaviour and risk assessment in eastern grey kangaroos in response to people has received little academic focus. Previous studies of macropod flight behaviour have used flight initiation distance to detect changes in antipredator behaviour following the loss of predators on islands (Blumstein 2002, Blumstein and Daniel 2005) or to investigate the role of flight behaviour in vehicle collisions (Lee et al. 2010). Our study found that distance to refuge, resource quality, group size, and group demography all variously influenced assessment distance across disturbance types. Generally, prey are more fearful when safety is further away (Dill and Houtman 1989, Bonenfant and Kramer 1996). However, we found that kangaroos spent longer assessing the threat before fleeing when they were further from safety. We propose that this is likely due to the energy costs of fleeing further to reach safety. Monitoring the disturbance stimulus for longer allows kangaroos to make an accurate assessment of the potential risk before incurring energetic costs.

Group size is known to have a highly variable effect on assessment distance across species (Stankowich and Blumstein 2005), and, as our study showed, this effect can also be influenced by the nature of previous interactions with humans. For example, larger groups at Low Harm sites exhibited shorter assessment distances than those with fewer individuals, while the opposite was found at High Benign sites where there was a positive correlation between assessment distance and group size. The trend at sites with harmful interactions may be explained by the notion that some individuals in a group will have had negative experiences with humans, making them less inclined to delay fleeing one a threat has been noticed. On the other hand, at benign sites, increasing assessment distance with group size fits well with the notion that individuals perceive lower levels of risk when in a larger group, as the likelihood of a given individual falling prey to a predator is reduced when more individuals are present (Jarman 1987, Carter et al. 2009). This effect has been observed in similar-sized herbivore species such as deer (De Boer et al. 2004) and caribou (Aastrup 2000).

The demographic composition of groups also influenced flight response. Groups with large adult kangaroos typically spent longer assessing the stimulus, as animals may perceive a degree of increased safety when in the presence of larger animals (Norberg 2012). Likewise, groups containing vulnerable young also spent significantly longer assessing risk than those composed only of adults at sites of high harm, but not at benign sites. This finding is contrary to our initial expectations, where we expected that groups with vulnerable individuals would respond quicker to risk in threatening landscapes (Stankowich 2008, Blumstein 2010, Cooper and Blumstein 2013). The delay in flight could be due to the higher energetic needs of young and mothers (Cripps et al. 2011, Gélin et al. 2013), as these groups might not wish to abandon foraging opportunities until the threat is confirmed to be imminent (Ydenberg and Dill 1986, Cooper et al. 2003, Stankowich and Blumstein 2005). This explanation is supported by our finding that resource quality also influenced assessment distance at High Harm sites. When foraging in areas with high-quality resources, eastern grey kangaroos reduce the amount of time spent on antipredator behaviours such as vigilance

(Favreau et al. 2018). Similar reductions of antipredator behaviour have also been observed for impalas, which were less vigilant when patch quality was high (Pays et al. 2012). A second possibility is that in this threatening landscape, flight itself might increase risk, particularly for vulnerable individuals and their guardians.

Studies of flight responses of ungulates have found that many species spend more time assessing threats if they were alerted to the disturbance further away (Stankowich and Coss 2005). This gives prey the opportunity to process additional information about the risk to more accurately assess the level of threat posed, enabling appropriate antipredator behaviours to be selected (Cárdenas et al. 2005). Our findings supported this explanation under benign conditions, like at campgrounds, as kangaroos habituate to human presence, leading to groups expressing smaller spatial zones of risk. In these circumstances, kangaroos learn that monitoring potential threats and delaying flight incurs little increased risk. In contrast, this response broke down when past disturbances were harmful. Disturbances like shooting remain a risk from a greater distance, which could explain the lack of correlation between assessment distance and alert distance in landscapes where previous interactions with humans have involved shooting. The adaptation of wildlife to human hunting has been widely reported, where wildlife exhibit stronger fear responses towards humans in threatening scenarios, e.g. during hunting season (De Boer et al. 2004, Matson et al. 2005, Jayakody et al. 2008). Hunting has also had a marked effect on wildlife behaviour, which sees animals modifying activity patterns and their use of habitats (Manor and Saltz 2003, Saïd et al. 2012, Bonnot et al. 2013, Lone et al. 2015). Our findings suggest that kangaroos have learnt more than just when and where humans pose a significant threat but have also developed responses to mitigate these novel risks. Similar modification of antipredator behaviour was observed by Austin and Ramp (2019), where kangaroos modified their antipredator grouping in response to human hunting. Behavioural changes in hunted populations may be attributed to the selection of individuals which possess beneficial traits that facilitate survival (Ciuti et al. 2012, Sol et al. 2013). In order for the trends we detected to be attributed to selection, the entire population would have to experience widespread and sustained hunting to eliminate individuals with unfavourable characteristics. It is unlikely that human disturbances at our study site were sufficiently intensive to alter behaviours through selection.

Our study indicates that kangaroos are learning from their previous interactions with humans, rapidly habituating to benign human disturbances and identifying humans as a threat when previous interactions were harmful. The ability to modify antipredator behaviours and correctly assess the risk of humans in countryside landscapes can provide foraging opportunities and habitat in a time where wilderness is decreasing at an astonishing rate. Our exploration of how environmental and group parameters affected kangaroo's fear of humans will inform future studies in understanding the ways in which kangaroos are persisting in countryside habitats when faced with novel threats and opportunities.

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4.6. REFERENCES

Aastrup, P. 2000. Responses of West Greenland caribou to the approach of humans on foot. Polar Research **19**:83-90.

Ale, S. B., and J. S. Brown. 2007. The contingencies of group size and vigilance. Evolutionary Ecology Research **9**:1263-1276.

Austin, C. M., and D. Ramp. 2019. Behavioural plasticity by eastern grey kangaroos in response to human behaviour. Animals **9**:244.

Banks, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. Animal Behaviour **61**:1013-1021.

Banks, P. B., and C. R. Dickman. 2007. Alien predation and the effects of multiple levels of prey naiveté. Trends in ecology & evolution **22**:229-230.

Barton, K., and M. Barton. 2018. Package 'MuMIn'. R package version 3.1.

Bates, L. A., K. N. Sayialel, N. W. Njiraini, J. H. Poole, C. J. Moss, and R. W. Byrne. 2007. African elephants have expectations about the locations of out-of-sight family members. Biology Letters **4**:34-36.

Beauchamp, G. 2013. Social predation: how group living benefits predators and prey. Elsevier.

Best, E. C., R. G. Dwyer, J. M. Seddon, and A. W. Goldizen. 2014. Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos. Animal Behaviour **89**:1-10.

Blumstein, D. T. 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. Journal of Biogeography **29**:685-692.

Blumstein, D. T. 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behavioral Ecology **21**:440-442.

Blumstein, D. T., and J. C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B: Biological Sciences **272**:1663-1668.

Bonenfant, M., and D. L. Kramer. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. Behavioral Ecology **7**:299-303.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research **59**:185-193.

Boom, K., and D. Ben-Ami. 2013. Kangaroos at a crossroads: Environmental law and the kangaroo industry. Environmental and Planning Law Journal **30**:162-181.

Boom, K., D. Ben-Ami, D. B. Croft, N. Cushing, D. Ramp, and L. Boronyak. 2012. 'Pest'and resource: a legal history of Australia's kangaroos. Animal Studies Journal **1**:17-40.

Burnham, K. P., and D. R. Anderson. 2002. A practical information-theoretic approach. Model selection and multimodel inference, 2nd ed. Springer, New York.

Cárdenas, Y. L., B. Shen, L. Zung, and D. T. Blumstein. 2005. Evaluating temporal and spatial margins of safety in galahs. Animal Behaviour **70**:1395-1399.

Carter, A. J., O. Pays, and A. W. Goldizen. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behavioral Ecology and Sociobiology **64**:237-245.

Caughley, G. J. 1964. Density and dispersion of two species of kangaroo in relation to habitat. Australian Journal of Zoology **12**:238-249.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. Plos One **7**:e50611.

Clarke, J. L., M. E. Jones, and P. J. Jarman. 1995. Diurnal and nocturnal grouping and foraging behaviors of free-ranging eastern grey kangaroos. Australian Journal of Zoology **43**:519-529.

Cooper, W. E., and D. T. Blumstein. 2013. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. Behavioral Ecology **25**:44-52.

Cooper, W. E., V. Pérez-Mellado, T. Baird, T. A. Baird, J. P. Caldwell, and L. J. Vitt. 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. Behavioral Ecology **14**:288-293.

Coulson, G. 2009. Behavioural ecology of red and grey kangaroos: Caughley's insights into individuals, associations and dispersion. Wildlife research **36**:57-69.

Cripps, J. K., M. E. Wilson, M. A. Elgar, and G. Coulson. 2011. Experimental manipulation of fertility reveals potential lactation costs in a free-ranging marsupial. Biology Letters **7**:859-862.

Dacier, A., R. Maia, D. Agustinho, and M. Barros. 2006. Rapid habituation of scan behavior in captive marmosets following brief predator encounters. Behavioural Processes **71**:66-69.

Daily, G. C., G. Ceballos, J. Pacheco, G. Suzán, and A. SÁNchez-Azofeifa. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology **17**:1814-1826.

Dall, S. R., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters **7**:734-739.

De Boer, H. Y., L. Van Breukelen, M. J. Hootsmans, and S. E. Van Wieren. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biology **10**:35-42.

Delacasa, G., and R. Lubow. 1995. Latent inhibition in conditioned taste aversion: The roles of stimulus frequency and duration and the amount of fluid ingested during preexposure. Neurobiology of learning and memory **64**:125-132.

Descovich, K., I. McDonald, A. Tribe, and C. Phillips. 2015. A welfare assessment of methods used for harvesting, hunting and population control of kangaroos and wallabies. Animal Welfare **24**:255-265.

Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal Conservation **13**:458-466.

Dill, L. M., and R. Houtman. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology **67**:233-235.

Ducatez, S., F. Sayol, D. Sol, and L. Lefebvre. 2018. Are urban vertebrates city specialists, atificial habitat exploiters, or environmental generalists? Integrative and comparative biology **58**:929-938.

Dumont, F., C. Pasquaretta, D. Réale, G. Bogliani, and A. von Hardenberg. 2012. Flight initiation distance and starting distance: biological effect or mathematical artefact? Ethology **118**:1051-1062.

Edwards, A., E. Best, S. Blomberg, and A. Goldizen. 2013. Individual traits influence vigilance in wild female eastern grey kangaroos. Australian Journal of Zoology **61**:332-341.

Elfström, M., A. Zedrosser, O. G. Støen, and J. E. Swenson. 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mammal Review **44**:5-18.

Favreau, F.-R., A. W. Goldizen, H. Fritz, and O. Pays. 2018. Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. Animal Behaviour **135**:165-176.

Fischer, J., B. Brosi, G. C. Daily, P. R. Ehrlich, R. Goldman, J. Goldstein, D. B. Lindenmayer, A. D. Manning, H. A. Mooney, and L. Pejchar. 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment **6**:380-385.

Fischer, J. D., S. C. Schneider, A. A. Ahlers, and J. R. Miller. 2015. Categorizing wildlife responses to urbanization and conservation implications of terminology. Conservation Biology **29**:1246-1248.

Fraser, D., and A. M. MacRae. 2011. Four types of activities that affect animals: Implications for animal welfare science and animal ethics philosophy. Animal Welfare **20**:581-590.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**.

Gabrey, S. W. 1997. Bird and small mammal abundance at four types of waste-management facilities in northeast Ohio. Landscape and Urban Planning **37**:223-233.

Gammage, B. 2012. The biggest Estate on earth: How Aborigines made Australia. Allen & Unwin.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Gélin, U., M. E. Wilson, G. M. Coulson, and M. Festa-Bianchet. 2013. Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos. Animal Behaviour **86**:885-891.

Gonzalo, A., P. López, and J. Martín. 2013. Adaptive forgetting in Iberian green frog tadpoles (Pelophylax perezi): Learned irrelevance and latent inhibition may avoid predator misidentification. Journal of Comparative Psychology **127**:56.

Grueber, C., S. Nakagawa, R. Laws, and I. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of evolutionary biology **24**:699-711.

Heathcote, C. F. 1987. Grouping of eastern grey kangaroos in open habitat. Wildlife Research **14**:343-348.

Inoue, T., S. Nagai, H. Kobayashi, and H. Koizumi. 2015. Utilization of ground-based digital photography for the evaluation of seasonal changes in the aboveground green biomass and foliage phenology in a grassland ecosystem. Ecological informatics **25**:1-9.

Jarman, P. J. 1987. Group size and activity in eastern grey kangaroos. Animal Behaviour **35**:1044-1050.

Jarman, P. J., and G. Coulson. 1989. Dynamics and adaptiveness of grouping in macropods. Kangaroos, Wallabies and Rat-kangaroos'.(Eds G. Grigg, P. Jarman and I. Hume.) pp:527-547.

Jayakody, S., A. M. Sibbald, I. J. Gordon, and X. Lambin. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology **14**:81-92.

Kark, S., A. Iwaniuk, A. Schalimtzek, and E. Banker. 2007. Living in the city: can anyone become an ‘urban exploiter'? Journal of Biogeography **34**:638-651.

Kaufmann, J. H. 1975. Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. Animal Behaviour **23, Part 1**:214-221.

King, W., M. Wilson, T. Allen, M. Festa-Bianchet, and G. Coulson. 2011. A capture technique for free-ranging eastern grey kangaroos (*Macropus giganteus*) habituated to humans. Australian Mammalogy **33**:47-51.

Kretser, H. E., P. J. Sullivan, and B. A. Knuth. 2008. Housing density as an indicator of spatial patterns of reported human–wildlife interactions in Northern New York. Landscape and Urban Planning **84**:282-292.

Lawrence, A. B. 2008. Applied animal behaviour science: Past, present and future prospects. Applied Animal Behaviour Science **115**:1-24.

Lee, E., D. Croft, and D. Ramp. 2010. 26 Flight response as a causative factor in kangaroo–vehicle collisions. Pages 301-311 Macropods: The Biology of Kangaroos, Wallabies, and Rat-kangaroos. CSRIO Publishing.

Letnic, M., and M. S. Crowther. 2013. Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. Oikos **122**:761-769.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour **102**:127-138.

Lowry, H., A. Lill, and B. B. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological reviews **88**:537-549.

Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications **13**:1830-1834.

Matson, T. K., A. W. Goldizen, and D. A. Putland. 2005. Factors affecting the vigilance and flight behaviour of impalas. South African Journal of Wildlife Research **35**:1-11.

McComb, K., G. Shannon, K. N. Sayialel, and C. Moss. 2014. Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proceedings of the National Academy of Sciences **111**:5433-5438.

Miller, K. A., J. P. Garner, and J. A. Mench. 2006. Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. Animal Behaviour **71**:1323-1334.

Norberg, U. M. 2012. Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Springer Science & Business Media.

Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism management **23**:281-293.

Pays, O., G. Beauchamp, A. J. Carter, and A. W. Goldizen. 2013. Foraging in groups allows collective predator detection in a mammal species without alarm calls. Behavioral Ecology **24**:1229-1236.

Pays, O., P. Blanchard, M. Valeix, S. Chamaillé-Jammes, P. Duncan, S. Périquet, M. Lombard, G. Ncube, T. Tarakini, and E. Makuwe. 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. Oecologia **169**:419-430.

Plummer, K. E., K. Risely, M. P. Toms, and G. M. Siriwardena. 2019. The composition of British bird communities is associated with long-term garden bird feeding. Nature communications **10**:2088.

Ramp, D. 2013. Bringing compassion to the ethical dilemma in killing kangaroos for conservation. Journal of bioethical inquiry **10**:267-272.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation **133**:70-80.

Ross, G. A. 2004. Ibis in urban Sydney: a gift from Ra or a pharaoh’s curse. Urban Wildlife: More than Meets the Eye’.(Eds D. Lunney and S. Burgin.) pp:148-152.

Russell, T., B. Bowman, C. Herbert, and J. Kohen. 2011. Suburban attitudes towards the common brushtail possum *Trichosurus vulpecula* and the common ringtail possum *Pseudocheirus peregrinus* in the northern suburbs of Sydney. Australian Zoologist **35**:888-894.

Saïd, S., V. Tolon, S. Brandt, and E. Baubet. 2012. Sex effect on habitat selection in response to hunting disturbance: The study of wild boar. European Journal of Wildlife Research **58**:107-115.

Samia, D. S., S. Nakagawa, F. Nomura, T. F. Rangel, and D. T. Blumstein. 2015. Increased tolerance to humans among disturbed wildlife. Nature communications **6**:8877.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications **4**:367-387.

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. Animal Behaviour, 85(5), 1101-1112.

Soulsbury, C. D., and P. C. L. White. 2016. Human–wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. Wildlife Research **42**:541-553.

Southwell, C. J. 1984. Variability in grouping in the eastern grey kangaroo, *Macropus giganteus* I. Group density and group size. Wildlife Research **11**:423-435.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation **141**:2159-2173.

Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: A meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences **272**:2627-2634.

Stankowich, T., and R. G. Coss. 2005. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology **17**:246-254.

Thibaut, J. W. 2017. The social psychology of groups. Routledge.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation **108**:299-306.

Wallach, A. D., C. N. Johnson, E. G. Ritchie, and A. J. O'Neill. 2010. Predator control promotes invasive dominated ecological states. Ecology Letters **13**:1008-1018.

Watson, J. E., D. F. Shanahan, M. Di Marco, J. Allan, W. F. Laurance, E. W. Sanderson, B. Mackey, and O. Venter. 2016. Catastrophic declines in wilderness areas undermine global environment targets. Current Biology **26**:2929-2934.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior **16**:229-249.

Zhou, Y., C. D. Buesching, C. Newman, Y. Kaneko, Z. Xie, and D. W. Macdonald. 2013. Balancing the benefits of ecotourism and development: The effects of visitor trail-use on mammals in a Protected Area in rapidly developing China. Biological Conservation **165**:18-24.

CHAPTER 5:

HUNTING REDUCES FORAGING AND JUVENILE PLAY IN EASTERN GREY KANGAROOS

Prepared for *Behavioral Ecology*

5.1. ABSTRACT

Hunting wildlife can have significant impacts on populations, over and above the direct loss of those killed. Wildlife respond to the threat posed by hunters by increasing antipredator behavior and altering habitat use to reduce hunting risk, however, these non-consumptive behavioral modifications can impose significant costs to individual fitness and wellbeing. Likewise, human activities that are not intended to cause harm to wildlife, such as ecotourism, can have a similar effect on individuals, causing stress, and reducing fitness-enhancing behaviors. To explore how wildlife navigate landscapes that include a mix of hunting and recreational activities of benign intent, like ecotourism, we analyzed the behavioral activity of eastern grey kangaroos experiencing these disturbances at low and high frequencies. We hypothesized that both disturbances would negatively impact on behavioral activities important for wellbeing, but that the non-consumptive effects of hunting would instigate changes linked to higher fitness costs. We found evidence that recreational disturbance was not as detrimental as hunting as kangaroos spent comparatively longer foraging and resting at sites with recreational disturbance than those which experienced hunting. Furthermore, juveniles participated in play more frequently than those in areas where hunting occurred. Hunting pressure resulted in a decline in time spent foraging and a significant reduction in the play by juveniles, which may have negative implications for wellbeing, leaving individuals vulnerable to mortality from other sources. Our findings provide insight into the ramifications of living in fear, suggesting that potentially significant costs are associated with the reduction in foraging and juvenile play, as well as leading to increased aggression among conspecifics.

5.2. INTRODUCTION

The disruptive effect of hunting is responsible for a multitude of behavioral, social, and physiological changes in populations of target and non-target wildlife (Benhaiem et al. 2008, Ciuti et al. 2012, Lone et al. 2015, Bischof et al. 2018). These changes can occur as a result of the consumptive, predatory nature of hunting, resulting in the direct loss of individuals. To avoid being killed by hunters, wildlife can engage in risk-aversive behaviors to decrease risk (Tigas et al. 2002, Rode et al. 2006, Berger 2007, Gaynor et al. 2018), including altering behavior and avoiding areas of high hunting activity. While these behavioral adaptations to hunting may reduce predation risk, they are likely to cause a significant cost to energy budgets, social learning, animal welfare, individual fitness, and ultimately population-level effects on demography and persistence (New et al. 2013, Say-Sallaz et al. 2019). Considered to be non-consumptive effects, these behavioral modifications can greatly affect daily activities and drive physiological changes, including elevated stress levels associated with a heightened threat (Bryan et al. 2015). It is also possible that elevated stress will lead to increases in agonistic interactions, as has been identified in rats (*Rattus norvegicus domestica*) exposed to stressful situations in peripuberty (Marquez et al. 2013, Veenit et al. 2013). To comprehensively understand the effect of hunting on prey we need to look beyond direct effects and consider the wider costs of living in fear.

There is evidence that hunted wildlife respond to different levels of hunting pressure. Roe deer (*Capreolus capreolus*) and elk (*Cervus canadensis*) increase antipredator vigilance during the hunting season (Benhaiem et al. 2008, Jayakody et al. 2008, Ciuti et al. 2012), although little is known of the long-term implications of seasonal stress. Vigilant behaviors are known to suppress other fitness-enhancing activities such as feeding (Quenette 1990, Benhaiem et al. 2008), grooming (Hart et al. 1992, Blumstein et al. 1999), resting (Casas et al. 2009), and mating (Say-Sallaz et al. 2019), and can increase the production of stress hormones which inhibit biological mechanisms resulting in reduced fitness (Wingfield et al. 1997, Bryan et al. 2015). Hunted species also alter their movements to avoid hunters (Wolfe et al. 2000, Benhaiem et al. 2008), so individuals may be incurring the energetic costs of increased locomotion or the potential loss of high-quality resources. However, little is known about how or if hunted species recuperate these losses. Non-consumptive effects may be present even in the absence of direct predation (Blanc et al. 2006). There is good evidence of wildlife modifying their activity budgets in response to non-lethal human disturbance, increasing vigilance in response to disturbances of benign intent, such as tourism or other recreational activities (Duchesne et al. 2000, Schummer and Eddleman 2003, Dyck and Baydack 2004, Wolf and Croft 2010). For example, tourist boats not only decrease feeding behavior of orcas but also change the transition frequency between behaviors (Williams et al. 2006). The study of transitions between behaviors has received little focus in wildlife studies but can provide insights into the mental state of animals beyond the occurrence and duration of behaviors (Rutherford et al. 2004).

The effect of human disturbance on the behavior of eastern grey kangaroos (*Macropus giganteus*) has received little focus. In eastern Australia, kangaroos share much of their range with humans and are increasingly found in national parks, golf courses, sporting ovals, and urban parks (King et al. 2011), where they have habituated to benign human disturbances (Wolf and Croft 2010, Austin and Ramp 2019, In Press). However, in many rural landscapes, they are also subject to harmful disturbances such as hunting, a disturbance which has been present since before European settlement, as kangaroos were sporadically hunted by Indigenous people (Gammage 2012), albeit with different hunting methods and levels of pressure. Since European occupation, kangaroos have increasingly been shot for food (for humans and pets, commercially and for subsistence), sport, or bounties (Boom et al. 2012). The notion of hunting for sport is common and kangaroos are often hunted illegally, a situation that is often justified by normative views of kangaroos as pests in rural and agricultural landscapes (Boom and Ben-Ami 2013, Ramp 2013, Descovich et al. 2015).

The complexities of vigilance behavior and the interplay between group and environmental parameters are well understood in eastern grey kangaroos (Caughley 1964, Coulson 1997, Pays et al. 2007, Carter et al. 2009, Rieucau et al. 2012). Group size has no net effect on the amount of time individuals spend in vigilance. Individuals in larger groups spend less time in antipredator vigilance, however, there is an increase in social vigilance (Favreau et al. 2010). Vigilance is influenced by sex and personality (Pays and Jarman 2008), with shyer females more vigilant than their bolder counterparts (Edwards et al. 2013). The behavior of female kangaroos is also affected by environmental and social factors, with high-intensity vigilance more common when grazing far from cover (Edwards et al. 2013) and longer grazing durations while in the company of known individuals (Carter et al. 2009). However, none of these studies have examined how humans (whether benign or harmful) influence the behavioral repertoires of eastern grey kangaroos. Austin and Ramp (In Press) determined that the intent and frequency of previous kangaroo-human interactions shaped antipredator fleeing behavior, kangaroos that were hunted incorporated humans into their threat assessments, and altered their grouping behavior to avoid the lethal actions of humans (Austin and Ramp 2019). In comparison, those that experienced benign disturbances appear to be habituating to non-lethal disturbances. What is clear is that we know very little of how the non-consumptive effects of hunting and recreational activity translate into costs to foraging and affiliative behaviors, social development, and fitness.

Costs to social development are particularly important yet often elusive. Fear in adults has been shown to decrease juvenile survival rates, particularly for mammals as lactation has high energetic demands (Engelhard et al. 2002). Dedicating more time to vigilance than grazing or affiliative behaviors towards their young can reduce fitness and increase juvenile mortality in kangaroos (Grigg and Jarman 1989, Croft 2004). In wild eastern grey kangaroos, joeys first emerge from the pouch approximately 283 days after birth and are both in and out of the pouch until approximately 320 days when they leave the pouch permanently (Poole 1975). During this period, juvenile mortality is high as young are vulnerable to predation or become estranged from their mothers, leading to starvation (Banks et al. 2000, Croft 2004). There is greater potential for young to be separated from mothers when groups flee from disturbance (Staker 2014). The muscles around the opening of the pouch give the mother control over the opening of the pouch (Dawson 1995). It stands to reason that when mothers are fearful, they will keep their offspring close, and reduce the amount of time young spend out of the pouch. This restriction has the potential to delay development as there are fewer opportunities to learn, develop, play, and explore (Bekoff and Byers

1998, Nowak et al. 2000, Fagen and Fagen 2004). Play fighting is particularly important to juvenile male macropods for socialization and to develop and maintain motor skills (Watson and Croft 1993). To our knowledge, no studies have yet investigated the effect of hunting pressure on parental behavior in macropods.

In this study, our goal was to determine if eastern grey kangaroos adjust their behavioral activity to survive in landscapes where they experience a complex mixture of human disturbances, both recreation of benign intent and hunting at low and high frequencies. To compare behaviors across these disturbance types we deployed remote cameras in hotspots of grazing activity to capture focal samples of free-living eastern grey kangaroos (Austin and Ramp 2019). To investigate the behavioral adjustments of kangaroos in response to different human disturbances we analyzed the frequency of transitions between behaviors across the four disturbance types. If kangaroos are fearful and cautious, we expect to see higher frequencies of transition from high-level vigilance to lower levels of vigilance rather than to grazing or self-maintenance behaviors. However, if kangaroos are relaxed, we predict that vigilance behaviors will primarily transition to grooming or grazing. We predicted that in areas of high recreation activity of benign intent, adult kangaroos would dedicate proportionally more time to grazing and resting behaviors and less time to antipredator vigilance than in areas experiencing hunting, supporting our previously proposed habituation hypothesis (Austin and Ramp 2019). Conversely, we predicted the reverse trend in adult kangaroos experiencing hunting, while also predicting that agonistic interactions would increase and that adult females would prohibit juvenile play behavior.

5.3. METHODS

5.3.1 Site Description

We studied a free-ranging population of eastern grey kangaroos in the surrounds of Wombeyan Karst Conservation Reserve in the Southern Highlands of NSW, adjacent to Kanangra-Boyd National Park, previously described by Austin and Ramp (2019) (Figure 1). The area contains a mix of conservation reserve and private properties over 850 hectares, across which kangaroos are free to move. We previously established that the region included a mix of complex human presence, with areas of low (<1 interaction per week) and high (>1 interaction per week) frequency interaction, and a mix of benign (either ignored or well-intentioned, e.g. tourists taking photographs) and harmful (harassing or shooting) interactions (Austin and Ramp 2019). Consequently, we were able to classify regions by frequency and disturbance type: High Recreation (HR), Low Recreation (LR), Low Hunting (LH), and High Hunting (HH). For the purposes of anonymity, we have not included map locations of each treatment. However, the study area was comprised of 4% HB, 47% LB, 21% LH, and 28% HH.

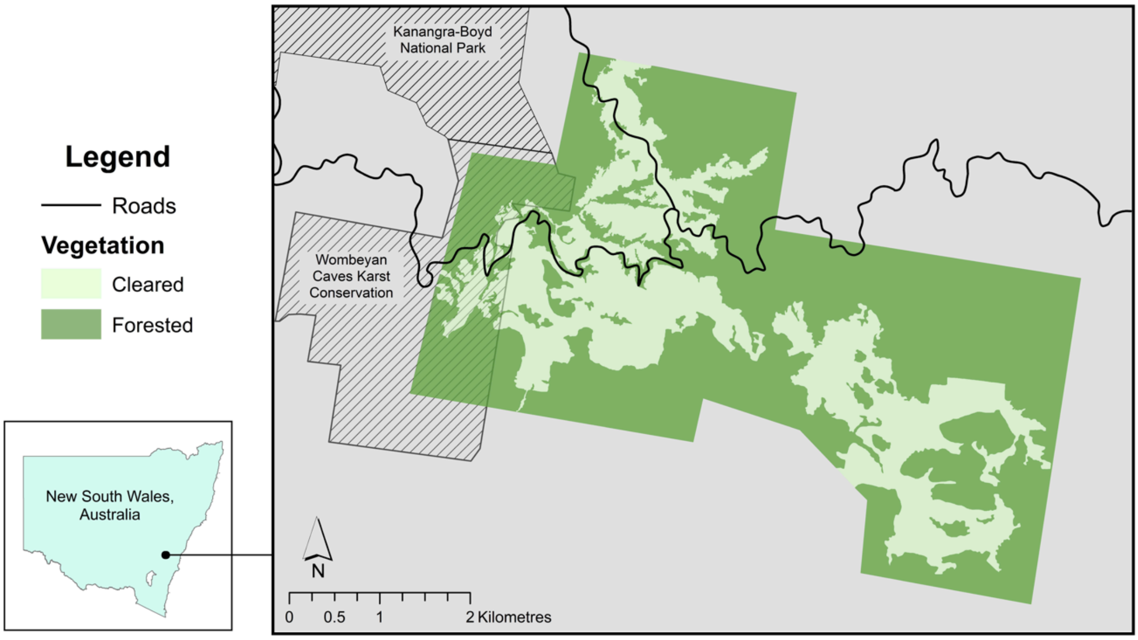


Figure 1. Location of study area within New South Wales, Australia, showing roads and forested and cleared areas within the study area. Property boundaries and human disturbance were omitted to ensure anonymity.

5.3.2. Behavioral Observations

Behavioral observation of eastern grey kangaroos across the four disturbance types was recorded using remote cameras (Bushnell Aggressor; Bushnell Corporation, Overland Park, KS, USA) which were deployed in cleared areas previously identified as foraging hotspots where kangaroos were frequently observed (Austin and Ramp, 2019). Cameras were not evenly distributed across disturbance types due to variable landscape topography and the availability of suitable trees to secure cameras. Thirteen cameras were deployed in total: 2 at HB, 4 at LB, 4 at LH, and 3 at HH. Cameras were active from May to December 2017 and programmed to record 60 seconds of video footage when triggered by movement. Videos of mature adults taken between 06:00-10:00 and 15:00-19:00 were identified for analysis to ensure comparisons of behavior were from peak foraging times, as eastern grey kangaroos are crepuscular foragers (Caughley 1964, Kaufmann 1975). To ensure the independence of samples, consecutive observations recorded from the same camera within five minutes were removed prior to analysis. Only individuals in the frame for the entire 60-second video were used. When more than one individual was present, we selected the adult in the foreground of the image as the focal individual. Behavioral observations were analyzed using Behavioral Observation Research Interactive Software (version 7.7.1) (Friard and Gamba 2016). An ethogram was developed that included behavioral states of grazing, self-grooming, resting, aggression, locomotion, and three levels of vigilance (V1, V2, and V3) as described by Colagross and Cockburn (1993) (Supplementary Table S1). Matrices of transition frequencies following each behavior were calculated for each observation so that the total of all frequencies following the one behavioral state was equal to 1. Frequencies were averaged across samples for each disturbance type and processed using Graphviz (http://www.graphviz.org/) to generate flow diagrams for each disturbance type (Supplementary Figure S1).

In addition, observations of mothers with juveniles old enough to spend time out of the pouch, but still dependent on the pouch for safety, were identified. Only observations that satisfied our five-minute rule of independence were used for analysis. The behavioral activity of juveniles was recorded using the behavioral states for play (Bekoff and Byers 1998), allogrooming (Coulson 1997), nursing (Coulson 1997), and exploratory dashes (Johnson 1987), also referred to as ‘hop in a circle’ (Coulson 1997) (Supplementary Table S1).

5.3.3. Statistical Analysis

We compared transition frequencies for behaviors following grazing, grooming, V1, V2, and V3 between all disturbance types using goodness of fit tests with significance values computed with 2,000 iterations of Monte Carlo simulations. To visually explore differences between disturbance types, we generated flow diagrams to represent differences in transition frequency for all combinations of disturbance type: HB: LB, HB:LH, HB:HH, LB:LH, LB:HH, and LH:HH. For each combination, we calculated the difference in transition frequency by subtracting one from the other. For clarity, we only plotted transition behaviors where the difference between disturbance types was generally larger than 10% (with some exceptions).

We initially included camera location as a random variable to account for nested effects, however, likelihood ratio testing found that no evidence of camera location affecting the duration of behaviors across disturbance types. We, therefore, compared the time individuals spent in each behavioral state using generalized linear models, employing the negative binomial family from R package '*MASS*' (Venables and Ripley 2002) to account for overdispersion evident in the data. We ran these models for each behavioral state: grazing, grooming, V1, V2, V3, and resting. We also compared the logged bout length of behavioral states each time they occurred using linear mixed models, excluding the first and last behavioral events for each observation. The observation identification code was included as a random variable to account for individuals contributing more than one occurrence of a behavior in the analysis. A linear model was run for resting as the behavior did not occur twice within the one sample. Fleeing and aggression were excluded from analyses as they only occurred infrequently.

To explore differences in juvenile play behavior among disturbance types, we calculated the proportion of time juveniles spent inside or outside the pouch for all observations where young were present for the duration of the observation. Proportions were compared across disturbance types using a binomial generalized linear model. Differences in the duration of mother/young behaviors between disturbance types were analyzed with generalized linear models from the negative binomial family. Separate models were run for each behavior: nursing, allogrooming, play, and exploratory dashes.

5.4. RESULTS

5.4.1. Behavioral Transitions

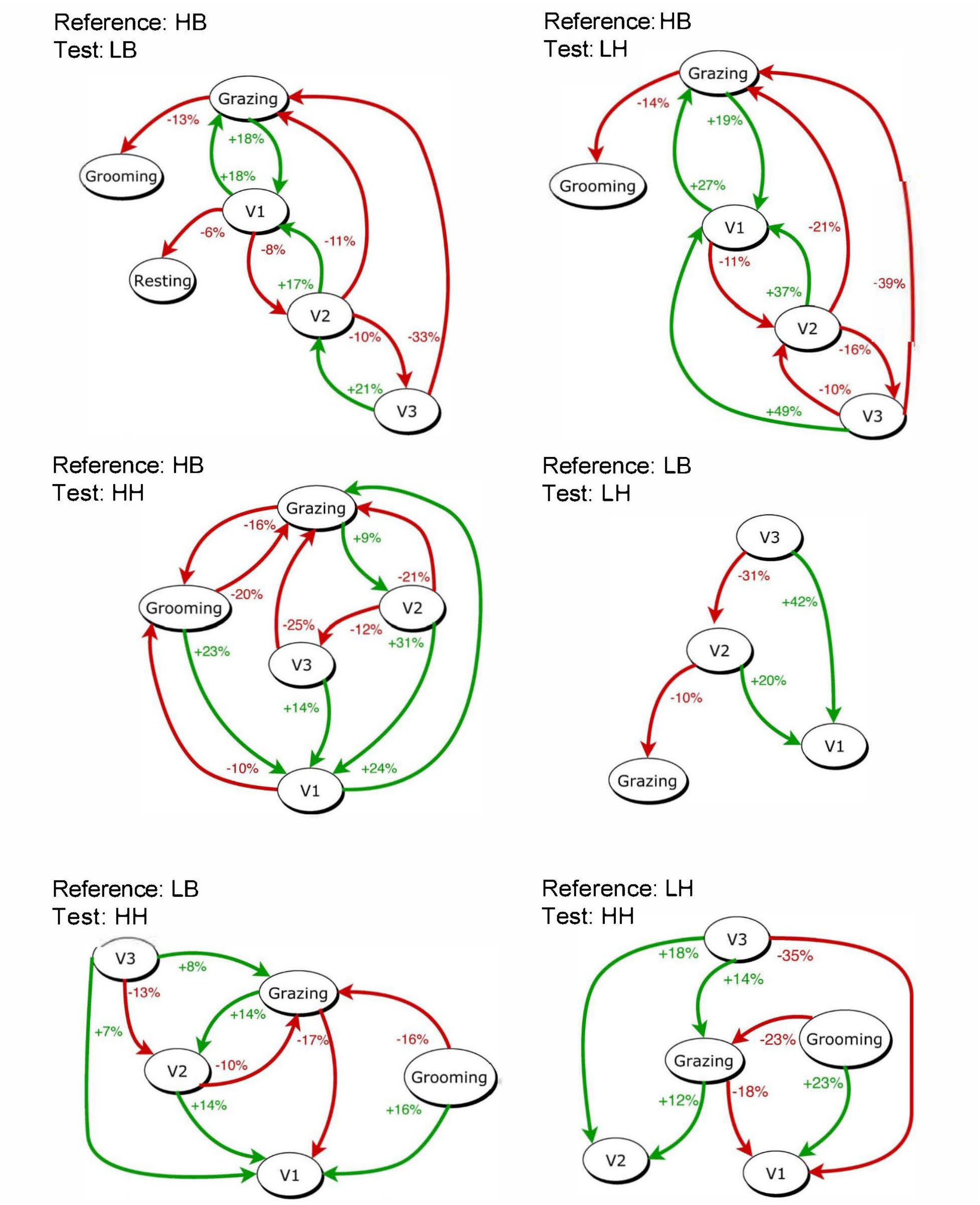
A total of 707 observations of adult eastern grey kangaroo behavior were analyzed across the four disturbance types: 134 from HB, 196 from LB, 188 from LH, and 189 from HH. Transition frequencies of follow-on behaviors showed distinct patterns across disturbance types. The frequency of each behavior following grazing and all levels of vigilance (V1, V2, and V3) were significantly different between HB and the other three disturbance types (Table 1). The differences in behaviors following grazing arose from higher frequencies of transitions from grazing to grooming at HB than at all other sites and lower frequencies from grazing to V2 (HH) or V1 (LR, LH) (Figure 2). Compared to HB, all other disturbance types had lower transition frequencies from both V2 and V3 to grazing. V2 and V3 were instead more likely to transition to a lower level of vigilance (V1).

At HH, the frequencies of behaviors following grooming were significantly different from those at all other disturbance types (Table 1). At HH, the frequency of V1 following grooming was significantly higher than that at HB, LB, and LH, whereas the frequency of grooming instead transitioning to grazing was higher at HB, LB, and LH than at HH (Figure 2). The comparison of behavioral transitions between LB and LH only found significant differences in the frequency of behaviors following V2 and V3. Compared to LB, the probability of transitioning from either V3 or V2 to V1 was substantially higher at LH (Figure 2). The transition frequencies at HH were also significantly different to LB and LH for behaviors following grazing ($p < 0.001$, $p < 0.001$) and V3 ($p = 0.001$, $p < 0.001$). The probability of V1 following grazing was lower at HH than LB and LH but frequencies from grazing to V2 or V3 were higher (Figure 2). The frequency of grazing following V3 was higher at HH than both LB and LH. At LB the frequency of V2 following V3 was higher than at HH but the opposite was seen between LH and HH where the transition from V3 to V2 was higher at HH. The frequency of V3 transition to V1 was considerably lower at HH than LH.

Table 1. P-values of Chi-Squared goodness of fit tests for comparisons of transition frequencies of following behaviors between disturbance types.

	PRECEDING BEHAVIORS				
	GRAZING	GROOMING	V1	V2	V3
HB:LB	0.004	0.103	0.001	<0.001	<0.001
HB:LH	0.003	0.231	<0.001	<0.001	<0.001
HB:HH	<0.001	<0.001	<0.001	<0.001	0.001
LB:LH	0.410	0.182	0.198	0.001	<0.001
LB:HH	<0.001	0.001	0.216	0.01	0.001
LH:HH	<0.001	<0.001	0.237	0.115	<0.001

Figure 2. Flow diagrams highlighting the notable differences in following behaviors between disturbance types. Red lines indicate a decrease in transition probability between the reference disturbance type and the test disturbance type. Green arrows indicate a higher transition probability at the test disturbance type than at the reference disturbance type.



5.4.2. Activity Budgets

We detected significant differences in activity budgets for adult kangaroos across all disturbance types. From 60-second sampling observations, we found that kangaroos spent the majority of the observation grazing (Figure 3). Individuals at HB spent significantly longer grazing that was observed at other disturbance types (LB: p = 0.002, LH & HH; p < 0.001). Individuals at HB spent less time vigilant (V1, V2) or expressing aggressive behaviors than at all other disturbances (Figure 3). Compared to HH, kangaroos at HB also spent significantly more time resting and grooming (p = 0.001, p = 0.001). Individuals that experienced high levels of hunting spent significantly less time grazing and grooming than those at LB (p = 0.011, p = 0.004) and less grooming than at LH (p = 0.036) and instead spent more time in intermediate (V2) and high level vigilance (V3) than at all other disturbance types [HB (p < 0.001, p < 0.001), LB (p < 0.001, p = 0.008) and LH (p < 0.001, p < 0.001)]. The portion of time spent resting was significantly lower at HH than LB (p = 0.017). Similar activity budgets were observed for LB and LH, the only difference observed was in the proportion of time individuals spent in aggressive behavior, being lower at LB than LH (p < 0.001).

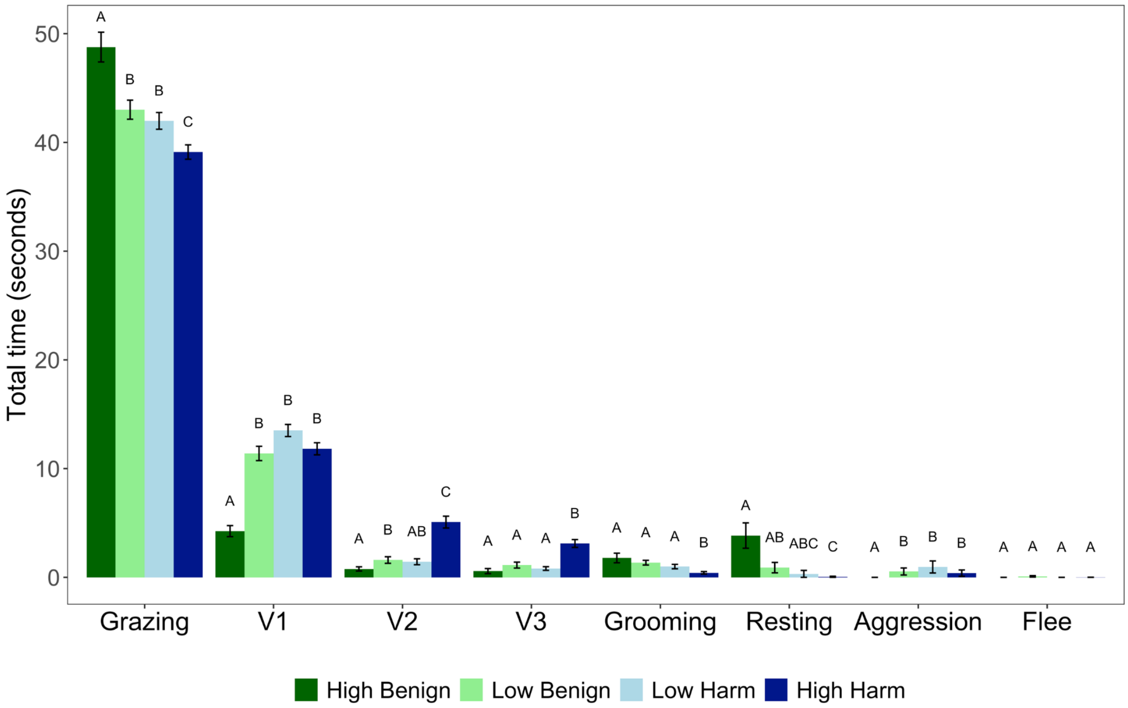


Figure 3. Mean time spent in each behavioral state across disturbance types. Error bars represent standard error. Letters denote significant differences at p < 0.05.

We detected significant differences in the bout duration of each behavioral state across disturbance types with the exception of grooming where no significant difference was detected. We found that the mean duration of grazing events varied significantly across disturbance types (Figure 4, Table 2) and significantly decreased as disturbances moved from recreational disturbances to hunting (Figure 4). Bouts of V1 were significantly longer at LB than at all other disturbance types and LH bouts of V1 were longer than at HB (Figure 4, Table 2). Bouts of V2 were significantly longer when recreational disturbances were encountered at low frequencies than when they were encountered frequently. Similarly, bout of V2 were longer at HH than HB (Table 2). Bouts of high-level vigilance (V3) were significantly longer at HH than both LB and LH (Table 2, Figure 4).

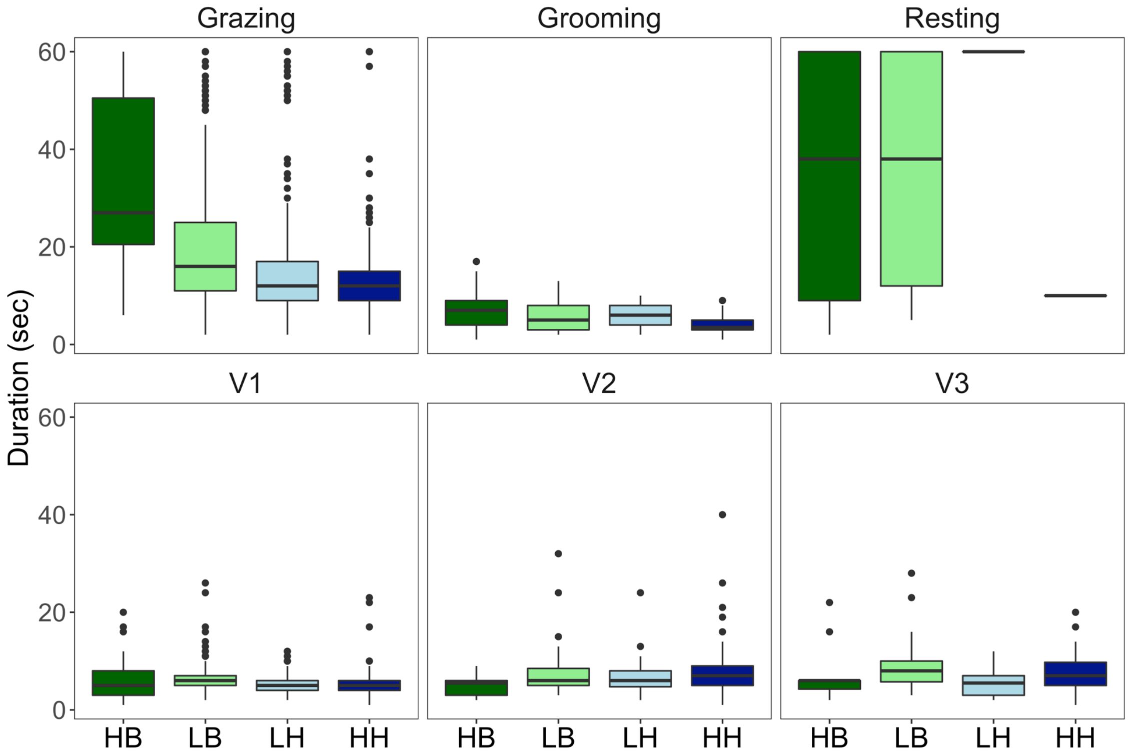


Figure 4. Duration of each behavioral state (Grazing, Grooming, Resting, V1, V2, and V3) across disturbance types; HB: High Benign, LB: Low Benign, LH: Low Harm, and HH: High Harm.

Table 2. Wald value and 95% confidence intervals for the comparison of logged mean duration of behavioral events Grazing, V1, V2, V3, and Grooming between disturbance types (HB: High Benign, LB: Low Benign, LH: Low Harm, and HH: High Harm).

		Grazing	**V1**	**V2**	**V3**	**Grooming**
HB	**LB**	-0.446 (-0.573, -0.318)	0.023 (0.161,0.366)	0.362 (0.071, 0.653)	0.253 (-0.145,0.650)	-0.099 (-0.364,0.166)
	LH	-0.756 (-0.884,-0.628)	0.109 (0.009,0.209)	0.234 (-0.062,0.530)	-0.230 (-0.620,0.160)	-0.049 (-0.349,0.251)
	HH	-0.948 (-1.075,-0.820)	0.051 (-0.050,0.152)	0.305 (0.045,0.566)	0.088 (-0.267,0.443)	-0.395 (-0.743,0.047)
LB	**LH**	-0.310 (-0.424,-0.197)	-0.155 (-0.229,-0.080)	-0.128 (-0.372,0.115)	-0.483 (-0.777,-0.189)	0.050 (-0.229,0.329)
	HH	-0.502 (-0.645,-0.389)	-0.212 (-0.288,-0.136)	-0.057 (-0.255,0.142)	-0.165 (-0.412,0.082)	-0.300 (-0.626,0.034)
LH	**HH**	-0.192 (-0.305,-0.078)	-0.058 (-0.130,0.015)	0.071 (-0.134,0.277)	0.318 (0.085,0.551)	-0.346 (-0.705,0.012)

5.4.3. Juvenile Play Behavior

We identified 245 observations of mothers and pouch young (HB= 92, LB= 101, LH = 22, and HH = 30). Pouch young from HB were in their mother's pouch for 24% of the samples which was significantly lower than at other disturbance types (LB: p = 0.014, LH: p = 0.001, and HH: p = 0.001) (Figure 5). The proportion of young in pouch was higher at LH than LB (41% and 68%, p = 0.024) and 87% of joeys observed at HH were in their mother's pouch for the duration of the observation, this was significantly more than at both frequencies of recreational activity (HB: p = 0.001, LB: p = 0.003) but no significant difference was detected between LH and HH (p = 0.126).

Pouch young at HB spent longer in bouts of allogrooming, nursing, playing, and exploratory dashes than individuals at other disturbance types (Figure 5). These behaviors did not occur at HH and could not be included in the analysis. The mean duration of bouts of nursing and playing was not affected by the frequency of benign recreational activity (p = 0.117, p=0.072) and durations of nursing at LB were significantly higher than at LH (p = 0.002). Exploratory dashes were not observed at LH or HH, however, the mean duration of exploratory dashes at HB was significantly longer than at LB (p < 0.001).

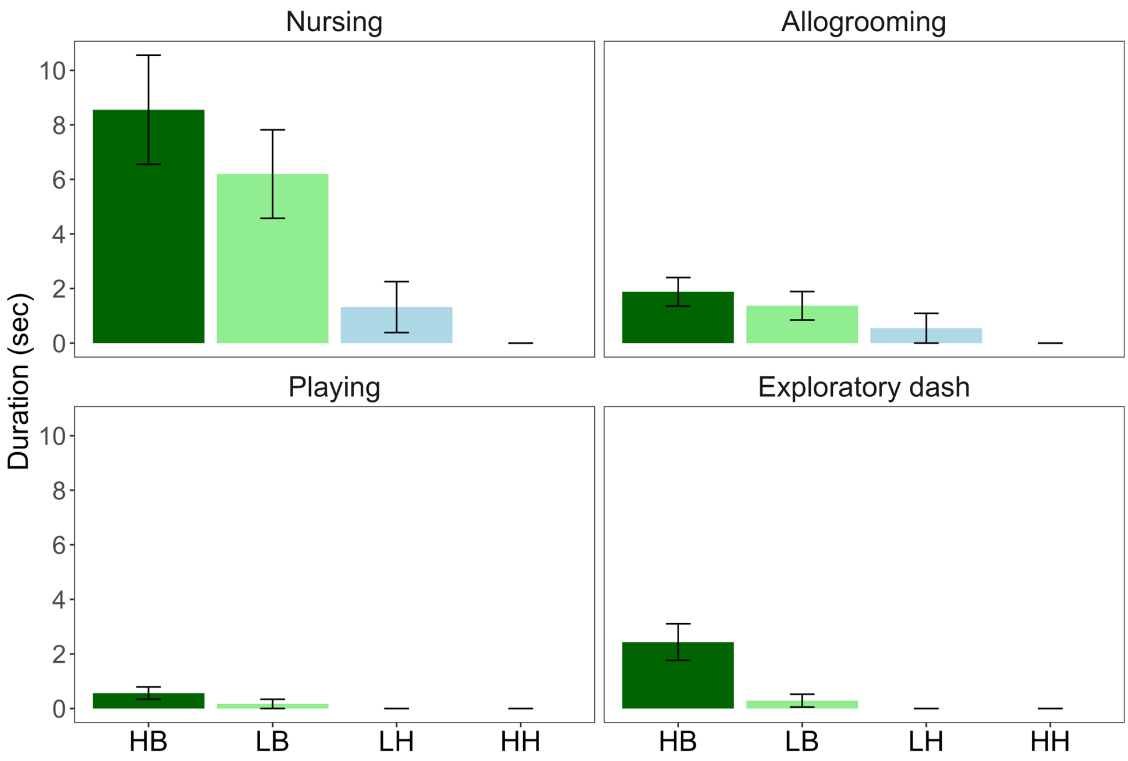


Figure 5. Mean duration of time (seconds) that pouch young spent nursing, allogrooming, playing or performing exploratory dashes per observation across disturbance types; HB: High Benign, LB: Low Benign, LH: Low Harm, and HH: High Harm). Error bars represent standard error.

5.5. DISCUSSION

This study found that hunted populations of eastern grey kangaroos spent less time grazing and significantly more time in antipredator vigilance than those which were not hunted. Kangaroos that experienced high frequencies of shooting spent significantly more time in V2 and V3 than at other sites. For kangaroos, vigilance does not always exclude energy acquisition as individuals can survey the surrounding area while chewing (Favreau et al. 2015), however, throughout this study V2 and V3 consistently excluded chewing. When vigilance excludes energy acquisition, increased vigilance has the potential to negatively impact individual fitness (Quenette 1990, Fortin et al. 2004, Benhaiem et al. 2008, Casas et al. 2009). The reduction of grooming and resting observed in individuals living under fear of hunting may be contributing to increased ectoparasite load (Weaver and Aberton 2004, Staker 2014) or physiological stress which can result in mortality from sources other than hunting (Peckarsky et al. 2008, Bryan et al. 2015). The non-consumptive effect of hunting can have a detrimental effect on populations, potentially leading to local extinctions (Peckarsky and McIntosh 1998, Orrock et al. 2008) which can alter wider communities within the ecosystem (Laundre et al. 2001, Lone et al. 2014).

The commercial kangaroo industry prioritizes the harvest of large adults and discourages shooting mothers with pouch young. However, mothers are often targeted by landholders who cull kangaroos as a damage mitigation measure to suppress population numbers. Targeted demographics are not the only individuals within a population to express a fear of humans. Large male brown bears are targets for trophy hunting, but, mothers with young alter their behavior at the commencement of hunting season, even though they are protected from hunting by law (Ordiz et al. 2012). We found that the behavior of pouch young and mothers was impacted by hunting at both low and high frequencies. We found that only 45% of pouch young at these sites were out of their mother's pouch at the time of sampling. We did not record any juveniles playing at either LH and HH and did not observe nursing or allogrooming at HH. Being restricted to the pouch may reduce opportunities for juveniles to play and explore the environment which could impair the development of foraging and antipredator behaviors potentially increasing juvenile mortality rates. It is possible that these developmentally beneficial behaviors occurred in hunted populations but were performed at different times of the day or locations in the landscape, such as in the safety of forested woodland. However, the occurrence of these behaviors at comparative times and locations where the disturbance was of a benign intent implies that hunting could negatively impact juvenile development and consequent survival. Other studies have detected hunted species altering their daily activity patterns in response to human disturbance, often shifting to nocturnal activity to avoid disturbances (Gaynor et al. 2018). This study was not designed to detect any changes in site selection or modification to daily activity patterns that may be occurring in this population. To determine if kangaroos are compensating for the reduction of grazing, grooming, resting, or playing during peak foraging times, further study into the daily activities of hunted populations is required to determine whether these behaviors are occurring outside of the crepuscular period of peak foraging activity.

The study of transitions between behaviors has received little focus in wildlife studies but we found that multi-step processes of behavior were capable of providing insight into the mental state of animals beyond the occurrence and duration of behaviors. Compared to all other disturbance types, kangaroos at High Benign were more likely to return to grazing following bouts of intermediate or high vigilance. At HH we observed a higher frequency of transitions from grazing to V2 than at HB; these individuals were performing a higher level of vigilance when initially breaking from grazing indicating a higher level of fear. Compared to HB, kangaroos that experienced high levels of hunting exhibited a reduction in transition frequencies in both directions between grazing and grooming. This indicates that individuals are in a high state of alert as individuals performed vigilance both before and after vulnerable behaviors such as grazing and grooming.

There are countless studies documenting the negative non-consumptive effects of tourism and recreational activity on wildlife species (Duchesne et al. 2000, Schummer and Eddleman 2003, Dyck and Baydack 2004). However, we found no evidence that recreational disturbance negatively impacted the behavior of eastern grey kangaroos. Individuals that experienced high frequencies of disturbance of benign intent appeared to be desensitized to human disturbances and spent more time grazing, resting, and grooming than those which experienced the disturbance at lower frequencies. Notably, mothers at HB do not appear to be overprotective of their young: juveniles were out of the pouch more frequently, undertook more exploratory dashes, and played for longer than those from other disturbance types. If kangaroos are desensitized to human disturbances there may be additional benefits if the disturbance also deters natural predators (Berger 2007, Atickem et al. 2014). The goal of this study was to make comparisons between the behaviors of kangaroos at sites where human disturbance varies in frequency and intent. The study of a control population of eastern grey kangaroos in temperate Australia that have never encountered human disturbance is almost impossible to locate, as people occupy the entire range of the species. As a result, we are unable to formulate conclusions regarding the effect of disturbance comparative to undisturbed populations of kangaroos, where recreation or hunting was truly novel, instead relying on the comparison of behavioral responses of kangaroos across the spectrum of these interactions.

5.5.1 Conservation Implications

To our knowledge, this is the first study to consider the non-consumptive effects of recreational hunting, whether for sport or damage mitigation, on macropod species. Our findings provide insight into the ramifications of living in fear, suggesting that potentially significant costs are associated with the reduction in foraging and juvenile play, as well as leading to increased aggression among conspecifics. Problematically, there is no documented quantification of the extent of recreational hunting across the range of eastern grey kangaroos, although anecdotally it would appear to be widespread. Furthermore, we know that recreational hunting sits alongside, and is probably dwarfed by, the commercial killing of free-ranging kangaroos (Boom et al. 2012). How the effects observed here manifest in areas targeted for commercial killing is currently unknown, as there are likely considerable differences in the intensity and duration of killing, as well as differences in the proportion of individuals left un-shot. However, it is possible, although speculative, that if surviving individuals experience declines in fitness then these declines should be factored into regional growth rates and estimates of sustainable killing quotas. Adhering to the precautionary principle, we recommend that further investigation be conducted into the non-consumptive effects of the hunting of macropods, namely the health and juvenile survival rates of populations experiencing both recreational and commercial hunting.

5.6. REFERENCES

Atickem, A., Loe, L. E., & Stenseth, N. C. 2014. Individual heterogeneity in use of human shields by mountain nyala. Ethology, **120 (7)**:715-725.

Austin, C. M., and D. Ramp. 2019. Behavioural plasticity by eastern grey kangaroos in response to human behaviour. Animals **9**:244.

Austin, C. M., and D. Ramp. In Press. Flight responses of eastern grey kangaroos to benign or harmful human behaviour. Ecology and Evolution.

Banks, P. B., A. E. Newsome, and C. R. Dickman. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. Austral Ecology **25**:283-291.

Bekoff, M., and J. A. Byers. 1998. Animal play: Evolutionary, comparative and ecological perspectives. Cambridge University Press.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour **76**:611-618.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters **3**:620-623.

Bischof, R., C. Bonenfant, I. M. Rivrud, A. Zedrosser, A. Friebe, T. Coulson, A. Mysterud, and J. E. Swenson. 2018. Regulated hunting re-shapes the life history of brown bears. Nature Ecology & Evolution **2**:116.

Blanc, R., M. Guillemain, J.-B. Mouronval, D. Desmonts, and H. Fritz. 2006. Effects of non-consumptive leisure disturbance to wildlife. Revue d'écologie.

Blumstein, D. T., C. S. Evans, and J. C. Daniel. 1999. An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*. Animal Behaviour **58**:351-360.

Boom, K., and D. Ben-Ami. 2013. Kangaroos at a crossroads: Environmental law and the kangaroo industry. Environmental and Planning Law Journal **30**:162-181.

Boom, K., D. Ben-Ami, D. B. Croft, N. Cushing, D. Ramp, and L. Boronyak. 2012. 'Pest' and resource: a legal history of Australia's kangaroos. Animal Studies Journal **1**:17-40.

Bryan, H. M., J. E. G. Smits, L. Koren, P. C. Paquet, K. E. Wynne-Edwards, M. Musiani, and J. Grindstaff. 2015. Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. Functional Ecology **29**:347-356.

Carter, A. J., O. Pays, and A. W. Goldizen. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behavioral Ecology and Sociobiology **64**:237-245.

Casas, F., F. Mougeot, J. Viñuela, and V. Bretagnolle. 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. Animal Conservation **12**:346-354.

Caughley, G. 1964. Social Organization and Daily Activity of the Red Kangaroo and the Grey Kangaroo. Journal of Mammalogy **45**:429-436.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. Plos One **7**:e50611.

Colagross, A., and A. Cockburn. 1993. Vigilance and grouping in the eastern gray kangaroo, *Macropus giganteus*. Australian Journal of Zoology **41**:325-334.

Coulson, G. 1997. Repertoires of social behaviour in captive and free-ranging grey kangaroos, *Macropus giganteus* and *Macropus fuliginosus* (Marsupialia: Macropodidae). Journal of Zoology **242**:119-130.

Croft, D. B. 2004. Kangaroo management: individuals and communities. Australian Mammalogy **26**:101-108.

Dawson, T. J. 1995. Kangaroos : biology of the largest marsupials / Terence J. Dawson ; illustrated by Anne Musser and Jillian Hallam. UNSW Press, Sydney.

Descovich, K., I. McDonald, A. Tribe, and C. Phillips. 2015. A welfare assessment of methods used for harvesting, hunting and population control of kangaroos and wallabies. Animal Welfare **24**:255-265.

Duchesne, M., S. D. Côté, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation **96**:311-317.

Dyck, M. G., and R. K. Baydack. 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. Biological Conservation **116**:343-350.

Edwards, A. M., E. C. Best, S. P. Blomberg, and A. W. Goldizen. 2013. Individual traits influence vigilance in wild female eastern grey kangaroos. Australian Journal of Zoology **61**:332-341.

Engelhard, G. H., A. N. Baarspul, M. Broekman, J. C. Creuwels, and P. J. Reijnders. 2002. Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. Canadian Journal of Zoology **80**:1876-1886.

Fagen, R., and J. Fagen. 2004. Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos*. Evolutionary Ecology Research **6**:89-102.

Favreau, F.-R., A. W. Goldizen, and O. Pays. 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proceedings of the Royal Society B: Biological Sciences **277**:2089-2095.

Favreau, F.-R., O. Pays, H. Fritz, M. Goulard, E. C. Best, and A. W. Goldizen. 2015. Predators, food and social context shape the types of vigilance exhibited by kangaroos. Animal Behaviour **99**:109-121.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos **107**:172-180.

Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution **7**:1325-1330.

Gammage, B. 2012. The biggest Estate on earth: How Aborigines made Australia. Allen & Unwin.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Grigg, G. C. and P. Jarman. 1989. Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons.

Hart, B. L., L. A. Hart, M. S. Mooring, and R. Olubayo. 1992. Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. Animal Behaviour **44**:615-631.

Jarman, P. J. 1987. Group-size and activity in eastern grey kangaroos Animal Behaviour **35**:1044-1050.

Jayakody, S., A. M. Sibbald, I. J. Gordon, and X. Lambin. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology **14**:81-92.

Johnson, C. N. 1987. Relationships between mother and infant red-necked wallabies (*Macropus rufogriseus banksianus*). Ethology **74**:1-20.

Kaufmann, J. H. 1975. Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. Animal Behaviour **23, Part 1**:214-221.

King, W., M. Wilson, T. Allen, M. Festa-Bianchet, and G. Coulson. 2011. A capture technique for free-ranging eastern grey kangaroos (*Macropus giganteus*) habituated to humans. Australian Mammalogy **33**:47-51.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology-Revue Canadienne De Zoologie **79**:1401-1409.

Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos **123**:641-651.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour **102**:127-138.

Márquez, C., Poirier, G. L., Cordero, M. I., Larsen, M. H., Groner, A., Marquis, J., ... & Sandi, C. 2013. Peripuberty stress leads to abnormal aggression, altered amygdala and orbitofrontal reactivity and increased prefrontal MAOA gene expression. Translational Psychiatry, **3**:e216-e216.

New, L. F., D. J. Moretti, S. K. Hooker, D. P. Costa, and S. E. Simmons. 2013. Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). Plos One **8**:e68725.

Nowak, R., R. H. Porter, F. Lévy, P. Orgeur, and B. Schaal. 2000. Role of mother-young interactions in the survival of offspring in domestic mammals. Reviews of Reproduction **5**:153-163.

Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation **152**:21-28.

Orrock, J. L., J. H. Grabowski, J. H. Pantel, S. D. Peacor, B. L. Peckarsky, A. Sih, and E. E. Werner. 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology **89**:2426-2435.

Pays, O., and P. J. Jarman. 2008. Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo? Behavioral Ecology and Sociobiology **62**:757-767.

Pays, O., P. J. Jarman, P. Loisel, and J.-F. Gerard. 2007. Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? Animal Behaviour **73**:595-604.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, and O. J. Schmitz. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology **89**:2416-2425.

Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia **113**:565-576.

Poole, W. 1975. Reproduction in the two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). II. Gestation, parturition and pouch life. Australian Journal of Zoology **23**:333-353.

Quenette, P. 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica **11**:801-818.

Ramp, D. 2013. Bringing compassion to the ethical dilemma in killing kangaroos for conservation. Journal of Bioethical Inquiry **10**:267-272.

Rieucau, G., P. Blanchard, J. G. Martin, F.-R. Favreau, A. W. Goldizen, and O. Pays. 2012. Investigating differences in vigilance tactic use within and between the sexes in eastern grey kangaroos. Plos One **7**:e44801.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation **133**:70-80.

Rutherford, R. B., Quinn, M. M., & Mathur, S. R. (Eds.). 2004. Handbook of research in emotional and behavioral disorders (Vol. 642). New York: Guilford Press.

Say-Sallaz, E., S. Chamaillé-Jammes, H. Fritz, and M. Valeix. 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. Biological Conservation **235**:36-52.

Schummer, M. L., and W. R. Eddleman. 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. The Journal of Wildlife Management:789-795.

Staker, L. 2014. Macropod Husbandry, Healthcare and Medicinals--Volumes One and Two. Lynda Staker.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation **108**:299-306.

Veenit, V., Cordero, M. I., Tzanoulinou, S., & Sandi, C. 2013. Increased corticosterone in peripubertal rats leads to long-lasting alterations in social exploration and aggression. Frontiers in Behavioral Neuroscience, **7**:26.

Venables, W., and B. Ripley. 2002. Statistics and computing. Modern applied statistics with S. Springers, New York, USA.

Watson, D. M. 1998. Animal play: Evolutionary, comparative and ecological perspectives. Cambridge University Press.

Watson, D. M., and D. B. Croft. 1993. Playfighting in captive red-necked wallabies, *Macropus rufogriseus banksianus*. Behaviour **126**:219-245.

Weaver, H. J., and J. G. Aberton. 2004. A survey of ectoparasite species on small mammals during autumn and winter at Anglesea, Victoria. Page 205 *in* Proceedings of the Linnean Society of New South Wales. Linnean Society of New South Wales.

Williams, R., D. Lusseau, and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation **133**:301-311.

Wingfield, J. C., K. Hunt, C. Breuner, K. Dunlap, G. S. Fowler, L. Freed, and J. Lepson. 1997. Environmental stress, field endocrinology, and conservation biology. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge:95-131.

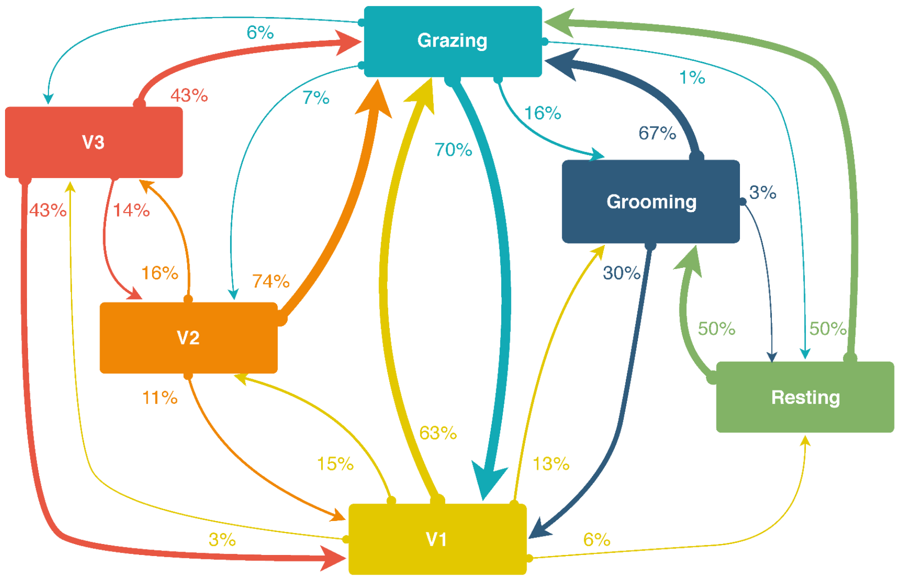
Wolf, I. D., and D. B. Croft. 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. Applied Animal Behaviour Science **126**:75-84.

Wolfe, S. A., B. Griffith, and C. A. G. Wolfe. 2000. Response of reindeer and caribou to human activities. Polar Research **19**:63-73.

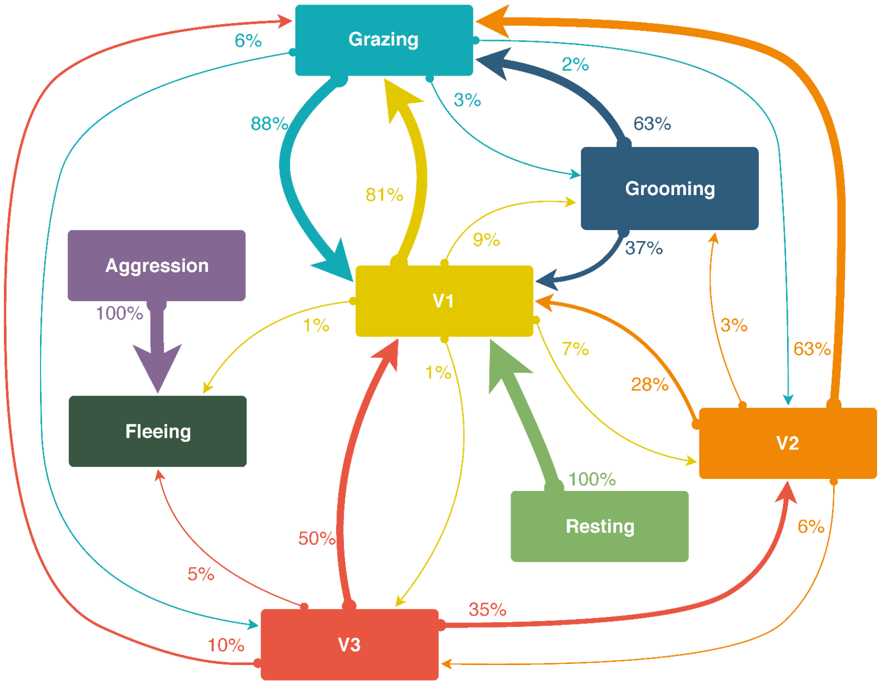
5.7. SUPPLEMENETRY MATERIAL

Supplementary Figure S1: Flow diagram of transition frequencies for following behaviors at each disturbance type. Arrow thickness is weighted according to transition frequency.

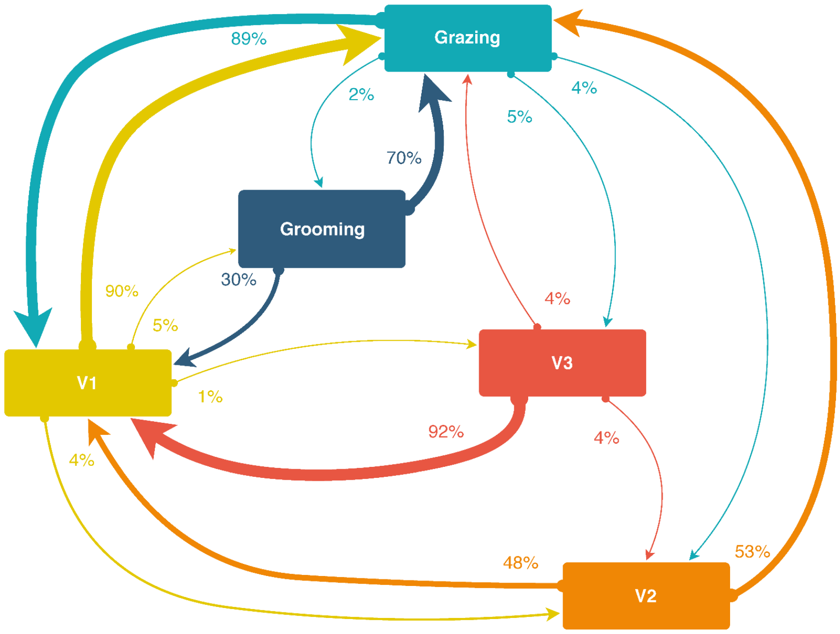
High Benign



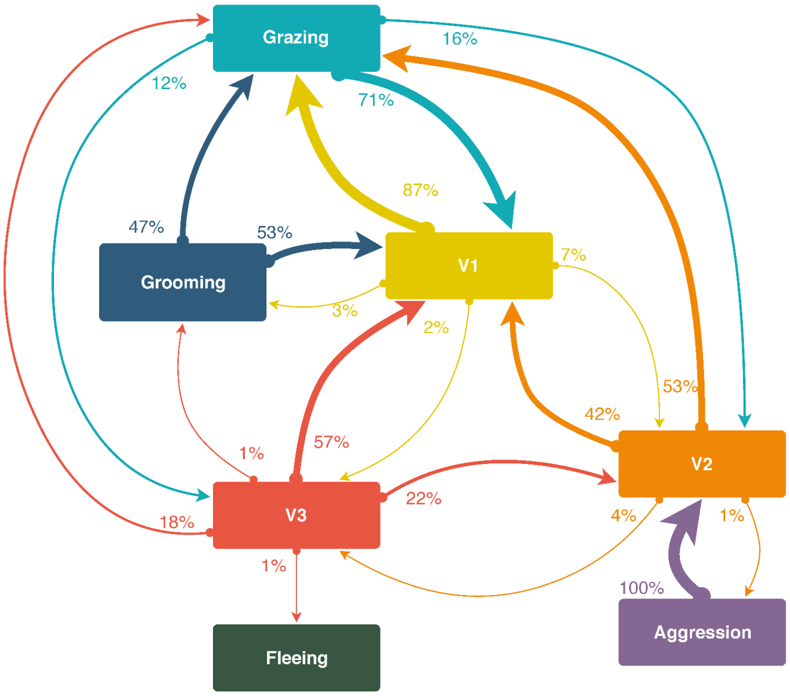
Low Benign



Low Harm



High Harm



Supplementary Table S1: Behavioral ethogram for eastern grey kangaroos.

Behavior	Definition
Vigilance #1	Low level vigilance on all fours with head up (Jarman 1987, Colagross and Cockburn 1993)
Vigilance #2	Intermediate vigilance with arms off the ground, back hunched (Jarman 1987)
Vigilance #3	Body is fully erect with back straight (Jarman 1987)
Resting	All four limbs and belly on the ground, head can be raised or resting on the ground (Jarman 1987)
Grazing	On all fours, chewing with head down (Jarman 1987)
Grooming	Moistens body or arms with tongue. Rubs face with moistened paws (Kaufmann 1975). Scratches body with front limbs
Allogrooming	Interaction between mother and joey where one is licking the other
Playing	Mother and joey slapping or making contact with one another without noticeable aggression (Kaufmann 1975, Coulson 1997).
Aggression	Two adult males lean back on their tails and use legs to kick one another. May involve coughing (Kaufmann 1975)
Exploratory dash	Joey moves quickly conducting exploratory dashes short distance from mother and returning (Watson 1998)
Fleeing	Use feet to propel itself forward, arm do not make contact with the ground (Kaufmann 1975)

CHAPTER 6:

GENERAL DISCUSSION AND THESIS SUMMARY

For wildlife to persist in landscapes shared with humans it is crucial that they respond appropriately to novel threats and opportunities. The persistence of populations at regional scales may mask the complexity of challenges species face when adjusting to local processes. Comprehensive information on the costs and benefits of these responses to individuals and populations is necessary to properly understand the implications for the conservation and survival of these species. As a consequence, the studies presented in this thesis were designed to explore the responses of eastern grey kangaroos to human disturbances in countryside landscapes, addressing this previously ignored element of macropod behaviour, ecology, and conservation. Overwhelmingly, these studies suggest that behavioural responses vary according to the intent (benign or harmful) and frequency (low or high) of human disturbances. Combined, they highlight the adaptability and plasticity of kangaroo behaviour that facilitate behavioural changes in response to disturbance of benign intents while enabling antipredator responses to mitigate harmful disturbances. A species' ability to correctly assess the risk associated with interacting with humans in countryside landscapes can provide improved foraging opportunities and novel habitats at a time when wilderness is decreasing at an astonishing rate. In this chapter, the key results and implications of these findings are discussed, along with future research directions.

6.1. RESPONSES TO HARMFUL DISTURBANCE

The studies included within this thesis identified that eastern grey kangaroos are adapting to life in countryside landscapes where they experience both benign and harmful disturbances at fine scales. For hunted populations, whether hunted for recreation or damage mitigation, it is essential that kangaroos incorporate humans into their landscape of fear and employ successful behaviours to survive. There is good evidence from other herbivore species of the importance of this responsiveness. The behavioural plasticity of ungulate species has allowed for the development of finely-tuned adaptive responses, which, in turn, allows individuals to alter their movements and behaviours in response to differing levels of hunting (Manor and Saltz 2003, Jayakody et al. 2008, Saïd et al. 2012, Bonnot et al. 2013, Lone et al. 2015). By studying kangaroos under a range of human disturbance conditions, I detected similar behavioural flexibility to that previously shown in ungulates in eastern grey kangaroos, who altered their spatial arrangement and grouping under different human disturbances at fine scales (Chapter 3). The plasticity of these responses fits traditional forms of associative learning: habituation to the absence of consequences from a stimulus (human presence) at sites with benign human disturbance while associating negative consequences from the same stimulus at neighbouring sites with harmful human disturbances (Chapter 4).

My findings provide support for the hypothesis that kangaroos are learning from previous interactions with humans, incorporating humans into their landscape of fear, particularly when previous encounters were of harmful intent (Chapter 4). Importantly, the frequency of harmful experiences with humans significantly affected their perception of risk. Kangaroos that experienced low levels of recreational hunting spent longer assessing the potential threat than those who experienced higher hunting frequencies, who fled almost immediately after detecting human presence. Likewise, the flight response to an approaching human provided a detailed understanding of how kangaroos assess the conditions that represent safety in hunted landscapes. Animals generally feel safer and tolerate closer approaches when they are closer to refuges, such as a burrow or thick vegetation, which facilitate escape from predators (Dill and Houtman 1989, Bonenfant and Kramer 1996). I found that in a landscape where kangaroos previously experienced harmful interactions with humans consistently perceived humans as posing a risk regardless of their distance from safety. I hypothesised that this could be due to the predatory behaviour of hunters, who typically target exposed individuals, found in the open with unobstructed sightlines (Chapter 4). My findings provide strong evidence that it is the nature of past interactions with humans that alters kangaroo perceptions of fear: not only are humans perceived as posing different levels of threat, but the contribution of environmental and group parameters to risk perception is modified by human disturbance. Individuals do not necessarily have to experience a negative interaction with humans to exhibit fearful behaviour, socially acquired predator avoidance strategies have been observed in tammar wallabies (*Macropus eugenii)* presented with visual predator stimuli (Griffins and Evans 2003).

Hunting has well established consumptive effects on targeted populations, including altered sex ratios and lower population density which can increase the risk of local extinction. Similarly, I found a reduction in the number of young at foot and subadults in groups of eastern grey kangaroos who experience harmful disturbances such as hunting and harassment (Chapter 3). The decline in this demographic group could be due to increased juvenile mortality rates as a result of poorer parental care and over-protection, manifesting in ontogenetic issues that drive environment naivety and delayed motor training during the early stages of development (Chapter 5).

Antipredator behavioural responses which seek to mitigate the consumptive effects of hunting can contribute to non-consumptive effects. The non-consumptive effects of hunting can have a similarly detrimental effect on populations, perpetuating animal welfare harms and potentially exacerbating local extinction risk (Peckarsky and McIntosh 1998, Orrock et al. 2008), which can subsequently alter wider communities within the ecosystem (Laundre et al. 2001, Lone et al. 2014). When vigilance precludes energy acquisition, increased vigilance has the potential to negatively impact individual fitness (Quenette 1990, Fortin et al. 2004, Benhaiem et al. 2008, Casas et al. 2009). In this regard, I found that hunted populations of eastern grey kangaroos spent less time grazing and significantly more time displaying antipredator vigilance than those who were not hunted. Increased vigilance may see species altering their periods of activity to compensate for reduced energy acquisition during peak foraging times. The longer assessment distances I observed when high-quality resources were present in areas of high hunting activity could be a reflection of this (Chapter 4), as individuals were less willing to surrender high-quality resources to flee from disturbance. Competition for resources and a lack of social stability could also explain the increase in agonistic behaviours observed at sites experiencing hunting (Chapter 5), supporting the hypothesis of Jaremovic and Croft (1991) that competition for resources may be a driver of aggression in female eastern grey kangaroos.

This study is the first to consider the non-consumptive effects of recreational hunting, whether for sport or damage mitigation, on eastern grey kangaroos. My results provide insight into the ramifications of living in fear, suggesting that potentially significant costs are associated with the reduction in foraging and juvenile play, as well as leading to increased aggression among conspecifics. It is difficult to assess what the costs of these behavioural responses are to eastern grey kangaroos as a species, as there is no documented quantification of the extent of recreational hunting across their range. Anecdotally, recreational hunting would appear to be widespread, with the enforcement of laws regarding the killing of wildlife, including kangaroos, being considerably relaxed in recent years (Department of Planning Industry and Environment 2018). Furthermore, I know that recreational hunting sits alongside, and is probably dwarfed by, the commercial killing of free-ranging kangaroos (Boom et al. 2012). The manifestation of these observed effects in areas targeted for commercial killing is currently unknown, as there are likely considerable differences in the intensity and duration of killing, as well as differences in the proportion of individuals who survive. These effects are yet to be studied for any species harvested as part of the commercial kangaroo industry, and as such these effects are not currently factored into regional growth rates and estimates of sustainable killing quotas. Sustainable quotas are currently determined by surveys of population size and only consider the direct consumptive impacts of harvesting on kangaroo populations (Office of Environment and Heritage 2017). The reduction of grooming and resting I observed for hunted individuals may be contributing to increased ectoparasite load (Weaver and Aberton 2004, Staker 2014) and/or physiological stress, which can result in mortality from sources other than hunting (Peckarsky et al. 2008, Bryan et al. 2015). On the basis of my findings and adhering to the precautionary principle, I recommend further investigation be conducted into the non-consumptive effects of the hunting of macropods, namely the health and juvenile survival rates of populations experiencing both recreational and commercial hunting. Outcomes of such investigation would ensure that the wellbeing of kangaroos and their conservation can be considered with full knowledge of how hunting affects their survival.

6.2. RESPONSES TO DISTURBANCE OF BENIGN INTENT

Several prey species have been shown to exploit humans directly or indirectly to avoid predation or secure resources (McKinney 2002, Gilroy and Sutherland 2007, Lesmerises et al. 2017). Non-lethal and benign human activities can create protective areas for prey species by excluding their predators through the 'human shield effect' (Berger 2007, Atickem et al. 2014). Through this mechanism, evidence suggests that many prey species seek close proximity to human settlements because their predators are fearful of humans and avoid those regions (Berger 2007, Atickem et al. 2014). The 'human shield effect' has been observed in antelope (*Tragelaphus buxtoni*), who relocate to nearby human settlements to exploit lower densities of spotted hyenas (*Crocuta crocuta*) (Atickem et al. 2014). This has also been observed in female brown bears (*Ursus arctos*) with cubs who exploit the protection of tourists and spend longer feeding when tourists were present, as human presence discourages aggressive males (Nevin and Gilbert 2005). Likewise, I found that eastern grey kangaroos were at higher densities in areas of frequent benign human activity than at other disturbance types across my study landscape (Chapter 3). Although there may be unmeasured reasons why densities were higher at these sites, this evidence suggests that kangaroos can habituate to benign presence and may benefit from being shielded from lethal human activity occurring in the surrounding landscape (Berger 2007). The frequency of benign human interactions did not significantly alter assessment distances, implying that behavioural responses to benign human disturbances are consistent, even when the disturbance is encountered infrequently. These results provide support for the notion that kangaroos are rapidly developing tolerance to benign human disturbances as has been documented in a variety of wildlife species (Samia et al. 2015). Among many examples, previous research has shown that repeated presentation of a consistently benign stimulus leads to rapid habituation in marmosets (Dacier et al. 2006) and bears (Elfström et al. 2014). Further investigation into the behavioural responses of kangaroos to benign human disturbances is required to directly test this habituation hypothesis.

Habituating to benign disturbance has economic benefits, enabling individuals to avoid the costs of fleeing in response to non-threatening disturbances; namely the loss of resources and unnecessary expenditure of energy (Ydenberg and Dill 1986). However, species that appear to be habituating to non-threatening recreational activity may still be disrupted by human disturbances. There are countless studies documenting the non-consumptive effects of tourism and recreational activity, often negatively impacting wildlife species (Duchesne et al. 2000, Schummer and Eddleman 2003, Dyck and Baydack 2004), including kangaroos (Wolf and Croft 2010). However, I found no evidence that recreational disturbance negatively impacted the behaviour of eastern grey kangaroos. Individuals that experienced high frequencies of disturbance of benign intent appeared to be desensitised to human disturbances and spent more time grazing, resting, and grooming than those which experienced the disturbance at lower frequencies.

6.3. FUTURE DIRECTIONS

Existing literature describes species' responses to human presence along gradients of intensity, typically using human density as a metric of disturbance. However, little attention is paid to the context or frequency of human-wildlife interactions, which may better explain behavioural responses. The studies included in this thesis investigated the effect of different types of human disturbance, varying in intent and frequency, to provide insight into the behavioural responses of kangaroos that facilitate adaptation to complex learning environments. There is nothing to suggest that this plasticity would be unique to kangaroos, as numerous species experience negative consequences of human actions, like hunting, while also benefiting from benign interactions and resource provision. For example, brown bears are hunted and harassed when they encroach into urban areas, but they also experience benign interactions as they are highly sought after subjects for wildlife ecotourism (Nevin and Gilbert 2005, Støen et al. 2015). Research has already identified that brown bears experience positive and negative effects of human activity but are yet to investigate how individuals who experience both disturbances are managing the complexities of sharing landscapes with humans.

The location chosen for this study is representative of countryside New South Wales, where the intent and frequency of interactions with kangaroos can vary considerably at fine scales. However, there is a clear imperative to extend my study design and approach to different kinds of locations across the range of eastern grey kangaroos to explore the generality of my findings and to contribute further to understanding the adaptations of kangaroos to human disturbances. Although my study methodologies were unable to distinguish individuals, invasive additions to my methods, such as tagging, that would enable the tracking of behaviour of marked individuals as they navigate this complex landscape. This would provide further information on the plasticity of behaviours and personalities of individuals. This information would further clarify how individuals perceive varying levels of fear within the landscape and whether individuals develop this knowledge of the landscape through social learning or previous experiences.

Despite this, I found strong evidence that non-consumptive behavioural effects associated with hunting have non-trivial costs that may impact on individual wellbeing and fitness (Chapter 5). However, further studies are needed to quantify how these non-consumptive costs impact on the health and welfare of individuals and to determine whether individuals alter their daily activity patterns to either avoid humans or compensate for a reduction in hunting during peak grazing periods. Other such shifts in activity patterns have been observed in hunted species, including shifting to nocturnal activity in order to increase temporal avoidance from human disturbance (Gaynor et al. 2018). Significantly, I found that in areas where hunting occurs there were few situations in which pouch young ventured out of the pouch to play, either through choice or by suppression by protective mothers. Future studies tracking individual movements and behaviours could be extended to investigate the causes of non-consumptive juvenile mortality in hunted populations and any impact this might have on population growth.

6.4. CONCLUSION

Eastern grey kangaroos are adapting to landscapes shared with humans; habituating to human interactions that do not seek to cause harm and developing antipredator responses to avoid the harmful effects of shooting. Kangaroos that experience interactions with humans with benign intent, such as recreational activities and passive land sharing, did not develop fearful attitudes towards humans in my studies and appeared to associate benign disturbances with a lack of negative consequence. This is further supported by the apparent attraction of kangaroos to sites with high tourist activity, a reduction in antipredator vigilance, and the frequent observation of juvenile play behaviour. These adaptations allow individuals to access reliable resources and obtain protection from harmful disturbances, such as hunting and predation, which are less likely to occur in recreational and tourist zones. Where hunting and harassment occurs, I found that kangaroos perceive humans as threatening, resulting in lower densities and increases in antipredator vigilance, appearing to come at the cost of grazing and self-maintenance behaviours. While these adaptations allow them to persist in shared landscapes, living in fear may negatively impact individual fitness and increase juvenile mortality. The comprehensive effects of living in fear must be fully accounted for and quantified to ensure that hunting and harassment do not avoidably contribute to local extinctions.

6.5. REFERENCES

Atickem, A., L. E. Loe, and N. C. Stenseth. 2014. Individual heterogeneity in use of human shields by mountain nyala. Ethology **120**:715-725.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour **76**:611-618.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters **3**:620-623.

Bonenfant, M., and D. L. Kramer. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. Behavioral Ecology **7**:299-303.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research **59**:185-193.

Boom, K., D. Ben-Ami, D. B. Croft, N. Cushing, D. Ramp, and L. Boronyak. 2012. 'Pest' and resource: a legal history of Australia's kangaroos. Animal Studies Journal **1**:17-40.

Bryan, H. M., J. E. G. Smits, L. Koren, P. C. Paquet, K. E. Wynne-Edwards, and M. Musiani. 2015. Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. Functional Ecology **29**:347-356.

Casas, F., F. Mougeot, J. Viñuela, and V. Bretagnolle. 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. Animal Conservation **12**:346-354.

Dacier, A., R. Maia, D. Agustinho, and M. Barros. 2006. Rapid habituation of scan behavior in captive marmosets following brief predator encounters. Behavioural Processes **71**:66-69.

Department of Planning Industry and Environment. 2018. Licence to Harm Kangaroos.

Dill, L. M., and R. Houtman. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology **67**:233-235.

Duchesne, M., S. D. Côté, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation **96**:311-317.

Dyck, M. G., and R. K. Baydack. 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. Biological Conservation **116**:343-350.

Elfström, M., A. Zedrosser, O. G. Støen, and J. E. Swenson. 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mammal Review **44**:5-18.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos **107**:172-180.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Gilroy, J. J., and W. J. Sutherland. 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends in Ecology & Evolution **22**:351-356.

Griffin, A. S., & Evans, C. S. 2003. Social learning of antipredator behaviour in a marsupial. Animal Behaviour, **66**:485-492.

Jaremovic, R., and D. Croft. 1991. Social organization of eastern grey kangaroos in southeastern New South Wales. II. Associations within mixed groups. Mammalia **55**:543-554.

Jayakody, S., A. M. Sibbald, I. J. Gordon, and X. Lambin. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology **14**:81-92.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology-Revue Canadienne De Zoologie **79**:1401-1409.

Lesmerises, F., C. J. Johnson, and M. H. St-Laurent. 2017. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. Ecology and evolution **7**:845-854.

Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos **123**:641-651.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour **102**:127-138.

Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications **13**:1830-1834.

McKinney, M. L. 2002. Urbanization, Biodiversity, and ConservationThe impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. BioScience **52**:883-890.

Nevin, O. T., and B. K. Gilbert. 2005. Measuring the cost of risk avoidance in brown bears: further evidence of positive impacts of ecotourism. Biological Conservation **123**:453-460.

Office of Environment and Heritage. 2017. New South Wales Commercial Kangaroo Harvest Management Plan 2017–2021, Department of Planning and Environment (NSW), Sydney.

Orrock, J. L., J. H. Grabowski, J. H. Pantel, S. D. Peacor, B. L. Peckarsky, A. Sih, and E. E. Werner. 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology **89**:2426-2435.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, and O. J. Schmitz. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology **89**:2416-2425.

Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia **113**:565-576.

Quenette, P. 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica **11**:801-818.

Saïd, S., V. Tolon, S. Brandt, and E. Baubet. 2012. Sex effect on habitat selection in response to hunting disturbance: The study of wild boar. European Journal of Wildlife Research **58**:107-115.

Samia, D. S., S. Nakagawa, F. Nomura, T. F. Rangel, and D. T. Blumstein. 2015. Increased tolerance to humans among disturbed wildlife. Nature Communications **6**:8877.

Schummer, M. L., and W. R. Eddleman. 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. The Journal of Wildlife Management:789-795.

Staker, L. 2014. Macropod Husbandry, Healthcare and Medicinals--Volumes One and Two. Lynda Staker.

Støen, O.-G., A. Ordiz, A. L. Evans, T. G. Laske, J. Kindberg, O. Fröbert, J. E. Swenson, and J. M. Arnemo. 2015. Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). Physiology & Behavior **152**:244-248.

Weaver, H. J., and J. G. Aberton. 2004. A survey of ectoparasite species on small mammals during autumn and winter at Anglesea, Victoria. Page 205 *in* Proceedings of the Linnean Society of New South Wales. Linnean Society of New South Wales.

Wolf, I. D., and D. B. Croft. 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. Applied Animal Behaviour Science **126**:75-84.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior **16**:229-249.