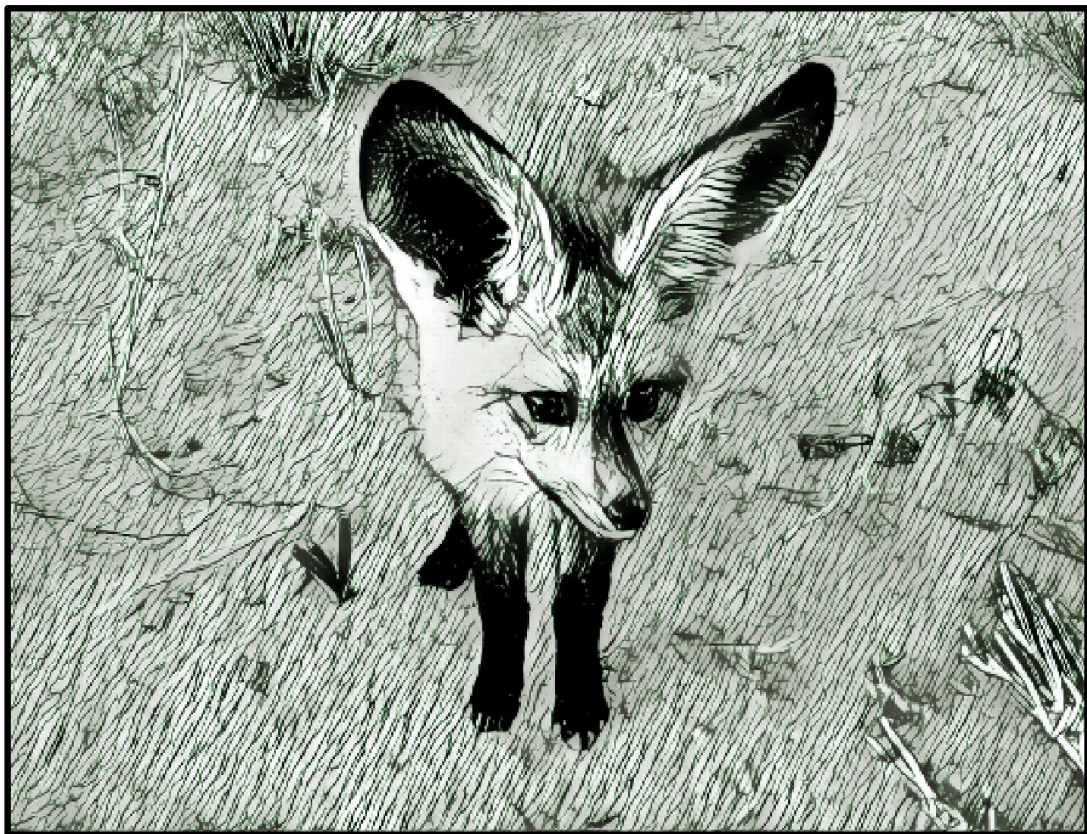


Quantifying perceived risk in a small mesocarnivore, the bat-eared fox

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GENERAL ABSTRACT

The perceived risk of predation can induce anti-predator responses such as the spatial and temporal avoidance of predators. However, such responses come with a level of cost that can potentially have implications for fitness – described as ‘non-lethal effects’. While the non-lethal effects of predators on herbivore prey are well investigated, the non-lethal impacts of predators on mesopredators/mesocarnivores are less understood. Importantly, there is reason to expect mesopredators’ anti-predator responses to be greater than those of herbivores, considering that apex predators represent both predation risk and competition. In this thesis, the effects of temporal, spatial, social and anthropogenic factors on the perceived risk of a small mesopredator, the bat-eared fox (*Otocyon megalotis*), were explored using both experimental and observational approaches. The anti-predator behaviours of this species are virtually undescribed and as large predators, e.g. lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), were historically extirpated from the area, it was unclear if anti-predator responses would have disappeared, or still remain. Using giving-up-density (GUD) experiments, I demonstrated that bat-eared foxes experience greater perceived risk in dark conditions and lower perceived risk in the presence of humans. Vigilance, however, did not appear to vary with these same factors, suggesting that GUDs are capable of detecting more subtle differences in perceived risk. Furthermore, by evaluating how bat-eared foxes use high-cost vigilance (which interrupts other activities) and low-cost vigilance (which occurs simultaneously with other activities), I demonstrated that fox vigilance behaviour is dynamic. Vigilance was generally focused towards that of low-cost, with the occasional use of high-cost vigilance under certain conditions. High-cost vigilance increased with vegetation height, in the presence of adult conspecifics, and in winter. These effects were most likely due to impeded lines of sight, higher levels of competition, and increased social interactions respectively. My results suggest that in areas of low predation risk,

mesopredators retain responses to certain cues of risk, but adapt behaviours to reduce the associated costs, allowing more time to be allocated to other activities. Finally, I determine that personality and plasticity was evident in this population of bat-eared foxes, varying across lunar illumination, wind speed, and temperature. Interestingly, these patterns were only distinct when vigilance was classified as high- and low-cost, and patterns were masked when vigilance types were combined. Individual foxes demonstrated distinct strategies when engaged in high-cost vigilance, where duration of vigilance did not fluctuate among individuals but rate varied significantly. Comparatively, individuals consistently differed in both bout duration and frequency of low-cost vigilance. I propose that the area's low predation pressure is unlikely to constrain individual variation in behaviours. Thus, individual differences in high-cost vigilance may also be adaptive – in contrast to the ecological hypothesis of Favreau et al. (2014), whereby individuals that experience similar ecological conditions behave in a similar manner. Until this study, personality and plasticity in different types of vigilance behaviours has never been demonstrated in mesopredators. Ultimately, my research highlights that when predation pressure is extremely low, it is premature to assume that anti-predator behaviours have been lost. Anti-predator behaviours may still persist, and vary with spatiotemporal changes, in the presence of conspecifics, and amongst individuals. Future research on mesopredator responses to perceived risk should consider investigating different types of vigilance behaviour, as well as the inclusion of individual differences. Combining vigilance types may mask biologically salient differences in personality and plasticity, and distinct behavioural patterns may be undetectable without the consideration of individual variation. Importantly, these differences may be crucial in revealing information on the ecological constraints placed on populations.

Key terms: Giving up densities, Habituated foxes, High-cost vigilance, Individual variation, Low-cost vigilance, Observer effects, *Otocyon megalotis*, Spatiotemporal effects.

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DECLARATION

“I, Rebecca Jane Welch, declare that the PhD research dissertation or interrelated, publishable manuscripts/published articles that I herewith submit for the PhD qualification in Zoology at the University of the Free State is my independent work, and that I have not previously submitted it for a qualification at another institution of higher education.”

“I, Rebecca Jane Welch, hereby declare that I am aware that the copyright is vested in the University of the Free State.”

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CHAPTER 1 GENERAL INTRODUCTION



Ecological communities are comprised of complex linear pathways of interacting species (Fretwell 1987). Predators have far-reaching effects on community dynamics, directly affecting prey species while also indirectly influencing non-prey within their foraging guild, and lower trophic levels through trophic cascading (Estes et al. 2011). The direct effects of predators on prey species within ecological communities include two separate but associated aspects: the lethal effect of predators on their prey (the removal of individuals through predation) and non-lethal effects, whereby prey are not removed from the population, but the presence of predators can alter the behaviour of prey, ultimately resulting in individual fitness reduction (Lima 1998). While the importance of lethal effects on prey population dynamics is indisputable (discussed below), non-lethal effects may also be considerable for recipient species (Lima 1998).

1.1 Lethal effects of predation

Lethal effects are ubiquitous across all environments and are regarded as a key population regulation mechanism (Sinclair et al. 1985; Sinclair and Arcese 1995). In addition to the effects of individual removal from a population, lethal effects can have numerous indirect outcomes for community dynamics. For example, the lethal effects of sharks (*Carcharhinus plumbeus*, *Carcharhinus limbatus*, *Carcharhinus leucas*, *Carcharhinus obscurus*, *Galeocerdo cuvier*, *Sphyrna lewini* and *Sphyrna zygaena*) on their prey maintains diversity in oceanic food webs (Myers et al. 2007), while predation by killer whales (*Orcinus orca*) on sea otters (*Enhydra lutris*) leads to decreased diversity in food webs due to the collapse of kelp forests (Estes et al. 2008). In addition to predator-prey dynamics, lethal effects also encompass intraguild predation events. Intraguild predation is the killing or consuming of potential competitors that utilise similar resources within the same guild, adding further complexity to ecosystems (Polis and Holt 1992; Palomares and Caro 1999; Helldin et al. 2006). Intraguild predation can occur in species of similar size classes, however it more commonly occurs in species of different size classes that use the same resources. The

smaller competitor therefore falls within the prey size class of the larger competitor, and these smaller competitors are known as mesopredators/mesocarnivores (Polis and Holt 1992; Ritchie and Johnson 2009). Certain apex predators are known to persecute mesopredators, often killing without consuming the carcass (Ritchie and Johnson 2009). This type of predation threat can have similar community-level implications to those of conventional predator-prey interactions, with many studies reporting that intraguild predation can lead to suppressed populations of intraguild prey/mesopredators, with consequences for lower trophic levels (Crooks and Soulé 1999; Johnson et al. 2007; Berger et al. 2008).

1.2 Non-lethal effects of predation

To describe the risk of predation, Lima and Dill (1990) use the formula: $P(\text{death}) = 1 - e^{-\alpha d T}$ where α is the predator-prey encounter rate, d the probability of death should an encounter take place, and T the time a prey animal is susceptible to attack. Importantly, prey should be able to accurately assess each of these factors in order to avoid an attack and ultimately death. The presence of a predator can have implications for other species, even in the absence of a direct encounter (Lima 1998). The threat of predation can, for example, have consequences for aspects of reproductive success by influencing 1) encounters with mates (e.g. the moth species, *Pseudaletia unipunct* and *Ostrinia nubilalis*, reduce mate-seeking behaviour in response to predation risk, Acharya and McNeil 1998), 2) reproductive output (e.g. copepods, *Pseudodiaptomus hessei*, have lower clutch sizes in the presence of predators, Wasserman and Froneman 2013), or 3) the timing of egg hatching (e.g. tadpoles, *Hyla regilla* and *Rana cascadae*, hatch at different times depending on the presence of predators, Chivers et al. 2001). Thus, non-lethal effects may also alter population dynamics, albeit in a more subtle manner than direct, lethal impacts.

In addition to influencing reproductive success, non-lethal effects are clear in daily decision-making, related to foraging-safety trade-offs. Therefore, an individual must decide where and when to feed in order to maximise energetic gain, whilst reducing the risk of predation (Lima

and Dill 1990), and this may vary according to the type of predator, the level of risk, individual state, and presence of conspecifics (Creel et al. 2014). As risk is dynamic, fluctuating with time and space, an animal's awareness of their current risk is implicit in managing the optimal trade-off between energy gain and predator avoidance, as fitness can be significantly decreased due to anti-predator behavioural trade-offs (Creel et al. 2007). These trade-offs and decisions can lead to a risk-dependent distribution of prey populations in a landscape (Tolon et al. 2009; Laundré et al. 2010), and cause clear changes on the micro-habitat scale (Kotler et al. 1991). As well as occurring in classic predator-prey interactions, non-lethal effects are also evident in intraguild relationships. The non-lethal effects of intraguild predation can influence the behaviour of subordinate guild members (Périquet et al. 2015; Macdonald 2016), for example, red foxes (*Vulpes vulpes*) are more active during periods of striped hyaena (*Hyaena hyaena*) inactivity (Mukherjee et al. 2009), and red fox food acquisition is curtailed in the presence of dingos (*Canis dingo*, Leo et al. 2015). As a result of persecution, mesopredators actively avoid apex predators (Ritchie and Johnson 2009; Kamler et al. 2013; Macdonald 2016), which may have implications for energetic gain if their own prey species are active in the excluded locations or during these periods of apex predator activity. In the absence of predators, island foxes (*Urocyon littoralis*), are active both diurnally and nocturnally, unlike their mainland relatives, gray foxes (*Urocyon cinereoargenteus*), who coexist with predators and are sedentary during the day (Crooks and Van Vuren 1995). Herbivorous prey have evolved adaptations against predators such as armed defences (Stankowich 2012) or speed (Bro-Jørgensen 2013). Mesopredators, however, are targeted opportunistically and more sporadically and therefore may not be as well adapted for escape as their primary consumer counterparts, therefore non-lethal effects (e.g. behavioural avoidance) may be greater in mesopredators than observed in classical predator-prey interactions (Ritchie and Johnson 2009).

1.2.1. *Spatial effects*

Choosing where to feed depends on how individuals perceive risk, and this risk may vary across a range of physical factors including habitat type, topography, vegetation height or density, and distance to refuge. Distance to refuge considerably alters perceived risk across a wide range of species; for example, small mammals and birds associate vegetative cover with areas of refuge, as cover can conceal them from potential predators (Tchabovsky et al. 2001; Carrascal and Alonso 2006). *Parus* species select feeding sites closer to vegetative cover and higher in the canopy, exhibiting higher levels of vigilance when further from cover (Carrascal and Alonso 2006). Nubian ibex (*Capra nubiana*) associate cliff edges with refuge, reflective of their climbing proficiency, and demonstrate greater perceived risk in open areas further from cliff edges (Hochman and Kotler 2007). Yellow mongooses (*Cynictis penicillata*) use underground burrows as areas of refuge from aerial and large terrestrial predators, and exhibit greater perceived risk when further from underground burrows (le Roux et al. 2009). In comparison, cheetahs (*Acinonyx jubatus*) seek out competition refuges – areas of low lion (*Panthera leo*) density, allowing them to co-exist alongside this competitively superior species (Durant 1998). Although refuge type varies among species, consistent patterns reveal that greater distance from refuge is associated with greater perceived risk.

A prey's ability to detect predators can also influence perceived risk and when lines of sight are obscured, horizontally or vertically by dense vegetation or complex topography, animals may become more reliant on other senses (McCormick and Lönstedt 2013), and perceived risk can increase (Embar et al. 2011). As well as reduced predator detection (Schooley et al. 1996; Arenz and Leger 1999; Whittingham and Evans 2004), perceived risk can also increase under these circumstances due to reduced detection of fleeing conspecifics (Harkin et al. 2000). Gerbils (*Gerbillus andersoni allenbyi*) exhibit greater perceived risk when horizontal sightlines are blocked in the presence of terrestrial predators, and greater perceived risk when vertical sightlines are blocked in the presence of aerial predators

(Embar et al. 2011). In the absence of immediate predation pressure, blocked sightlines still increase perceived risk due to reduced vigilance efficiency (Embar et al. 2011).

The effects of habitat on perceived risk often reflects the hunting mode of predators (Laundré et al. 2010), with species that predominantly face predation threats from aerial predators exhibiting greater levels of risk in open habitats, due to increased predator manoeuvrability (Bowers et al. 1993). Whereas for species that face predation threats from ambush predators, areas of cover can be associated with risk (Underwood 1982). Large herbivores, for example, exhibit greater perceived risk in closed habitats, as these areas may obscure potential predators within (Underwood 1982). Likewise, cheetahs exhibit greater perceived risk when feeding on kills in long grass compared to short grass, due to the reduced detection of threats (Hunter et al. 2007).

Habitat and substrate complexity may also cause changes in perceived risk due to prey evasion abilities (Schooley et al. 1996; Shrader et al. 2008). When the ability of evading a predator is reduced due to increased habitat complexity, perceived risk may increase, as earlier detection of a predator will enable the best possible chance of escape (Schooley et al. 1996; Shrader et al. 2008). For example, Townsend's ground squirrels (*Spemophilus townsendii*) associate greater perceived risk with structurally complex habitats, as juveniles are slower to evade threats (Schooley et al. 1996). Likewise, reductions in escape speed result in greater perceived risk/foraging costs for free-ranging domestic goats (*Capra hircus*) in areas associated with deep sand (Shrader et al. 2008). The relationship between habitat features and perceived risk may not be homogenous across landscapes and species, and choosing where to feed within a landscape is influenced by characteristics of both the predator and prey.

1.2.2. Temporal effects

Choosing when to feed is also influenced by risk (Lima and Dill 1990). For example, during periods of heightened hawk predation, herons (*Ardeidae* spp.) choose to forage during periods of rainfall or at dusk, when hawk activity is reduced, despite the poorer foraging conditions (Caldwell 1986). Beyond vegetation and topological features, lunar or artificial illumination can also have implications for perceived risk (Biebouw and Blumstein 2003; Prugh and Brashares 2010; Prugh and Golden 2014). Lunar illumination can influence encounter and detection rates between predator and prey, and can therefore influence both predator and prey activity patterns (Lima and Dill 1990). Increased illumination can decrease the risk of predation for prey species, given that predators can be more readily detected and evaded by these prey (Packer et al. 2011). However, increased illumination also enhances nocturnal predator vision, wherein well-lit full moon nights increase the ability of predators to detect their prey (Prugh and Golden 2014). The red fox, for example, forages more readily on darker nights to avoid predation by larger apex predators (Mukherjee et al. 2009). Studies have also shown similar patterns for artificial illumination whereby brighter conditions lead to increased perceived risk (Biebouw and Blumstein 2003).

Predator presence can be represented by predator cues (e.g. conspecific and heterospecific alarm calls, predator scat or odour), and studies have shown that in the presence of such cues, perceived risk increases (Schmidt et al. 2008; Leo et al. 2015). Thus, when senses that help detect cues are impeded, perceptions of risk may be altered (Carr and Lima 2010; Ruzicka and Conover 2011; Prugh and Golden 2014). A reduction in predator detection (Carr and Lima 2010) can result in periods of inactivity to avoid the risk of predation (Carter and Goldizen 2003; Hayes and Huntly 2005). For instance, American pikas (*Ochotona princeps*) are considerably less active during periods of increased wind speeds, and when wind speeds exceed 4 m/s they limit activity altogether due to perceived increased predation risk (Hayes and Huntly 2005). Additionally, anthropogenically generated noise can lead to slower responses to predators (Chan et al. 2010). Species that rely on communication for

predator detection demonstrate increased vigilance in the presence of traffic noise, due to both the traffic noise itself, as well as the decreased ability to detect conspecific and heterospecific alarm calls (Kern and Radford 2016; Morris-Drake et al. 2017). Further, weather conditions that can affect olfactory signals and detection may have implications for perceived risk (Dritz 2010; Ruzicka and Conover 2011; Webb et al. 2012). Depositional odours have been shown to increase perceived risk in mesopredators (Leo et al. 2015), and changes, for example, in wind speed or direction may alter the perception of odours by animals (Smee et al. 2008). Thus, visual, auditory, and olfactory cues from predators can induce rapid behavioural responses from prey, and environmental factors that may influence or alter these cues are likely to impact perceived risk.

1.3 The introduction or loss of predators from ecosystems

Human-driven impacts have resulted in predator biodiversity alterations across the globe (Simberloff and Von Holle 1999; Griffin et al. 2013). Given the non-lethal effects predators place on species of lower trophic positions, their loss or introduction into ecosystems is likely to have far-reaching effects. Prey species may exhibit a range of predator-dependent responses, and adaptations to one predator may not be adaptive to all (Edmunds 1974; Relyea 2001). Predators differ in their methods of capture and consumption of prey species and consequently prey species differ in their methods of avoiding detection and capture (Relyea 2001). Vervet monkeys (*Chlorocebus pygerythrus*) are able to co-exist with multiple predators by having developed predator specific anti-predator responses (Seyfarth et al. 1980). For example, in response to leopard (*Panthera pardus*) specific alarms, monkeys will retreat to the safety of trees, whilst in response to martial eagle (*Polemaetus bellicosus*) specific alarms, monkeys will look up (Seyfarth et al. 1980).

In order to restore ecosystems to more natural states, predators are being reintroduced into areas where they had previously been extirpated (Miller et al. 1999). Populations of naïve prey, where effective anti-predator behaviour has not been reinforced, may face challenges

should predators re-colonise or novel predators be introduced (Griffin et al. 2000); thus, understanding the loss of anti-predator behaviour and responses of naïve prey is imperative (Griffin et al. 2000). Ineffective anti-predator defence is exemplified in the invasion biology literature, whereby receiving environments are unnaturally supplemented with non-native predators. In Australia, for example, most mammalian predators have been introduced relatively recently through human incursions (Short et al. 2002). Native prey species can exhibit a wide range of anti-predator defences in response to native predators; however, due to a limited period of co-evolution they have inadequate defences towards introduced predators (Jones et al. 2004). Consequently, introduced predator-prey dynamics are undeveloped and prey species are vulnerable. For example, Eastern quolls (*Dasyurus viverrinus*) face predation from native predators such as masked owls (*Tyto novaehollandiae castanops*) and Tasmanian devils (*Sarcophilus laniarius*), and also from introduced predators such as red foxes and feral cats (*Felis catus*, Jones et al. 2004). Since their introduction in the 1800s, red foxes caused a dramatic decline in the numbers of Eastern quolls on mainland Australia, as Eastern quolls were unable to demonstrate appropriate anti-predator responses to these introduced predators (Jones et al. 2004). This ultimately resulted in their extinction on the mainland in the mid 1960s (Jones et al. 2003).

Since anti-predator behaviours are costly, selection for these behaviours should ultimately reflect the current level of predation risk, and occasionally after the loss of predators, prey can lose anti-predator behaviours (Blumstein and Daniel 2005). However, when predators disappear, prey species sometimes retain certain anti-predator behaviours. These behaviours may become relaxed (Coss et al. 1993), or in some instances persist despite low predation risk (Blumstein and Daniel 2002; Hollén and Manser 2007; Dalerum and Belton 2015). For example, in North America, populations of moose (*Alces alces*), after only one generation, displayed anti-predator behaviour persistence, and demonstrated clear anti-predator behaviours with the reintroduction of wolves (*Canis lupus*; Berger et al. 2001). The retention of anti-predator behaviour without predators has a number of theoretical

hypotheses (Blumstein et al. 2006). The 'ghosts of predators past' hypothesis suggests if a species has demonstrated anti-predator behaviours previously, and if these behaviours are not too costly, then anti-predator behaviours will persist in the absence of predators (Peckarsky and Penton 1988). The 'pleiotropic' hypothesis proposes that the behaviours demonstrated in anti-predator defence may have additional functions and therefore may be retained (Byers 1997). The 'multi-predator' hypothesis highlights that if prey species are subjected to pressures from multiple predators, the presence of one of these predators will be sufficient for anti-predator behaviours to persist, even if the various other predators have been lost (Blumstein et al. 2004). Although some evidence has been demonstrated for the multi-predator hypothesis in tammar wallabies (*Macropus eugenii*), in order to adequately recognise the circumstances under which anti-predator behaviour persists would likely require comparisons made between individuals with distinct evolutionary histories of predator exposure (Blumstein et al. 2006).

The loss of top predators from ecosystems can have numerous dramatic implications for other species (Macdonald 2016). Within the context of mesopredator species, the loss of apex predators is often associated with a rapid increase in mesopredator numbers, known as mesopredator release (Crooks and Soulé 1999). This release has subsequent effects such as higher levels of predation on smaller prey (Ritchie and Johnson 2009), proliferation of diseases (Ostfeld and Holt 2004) and secondary extinctions (Borrvall and Ebenman 2006). However, little is known about the effects on mesopredator species' behavioural adaptations when native predators disappear from an ecosystem.

1.4 Humans as risks or shields

Irrespective of predator presence, the effects of human presence on species are extensive. Human presence can lead to wide variety of non-lethal effects in animals, including altered vigilance, movement patterns, and changes in foraging and reproductive behaviours (Berger 2007; Proffitt et al. 2009; Ciuti et al. 2012; Nowak et al. 2014). The lethal and non-lethal

effects of humans on mesocarnivores may exceed those placed on other species, as many mesocarnivores are viewed as vermin and are consequently persecuted across their range (Thorn et al. 2012; Humphries et al. 2015; Ramesh et al. 2017). Mesocarnivores, in particular, adapt well to agricultural landscapes due to the extirpation of apex predators from these areas, and thus are highly susceptible to human-wildlife conflict (Ramesh et al. 2017). The non-lethal effects of this active persecution are that mesocarnivores are fearful of humans, often engaging in flight or avoiding human presence altogether (Kaunda 2000). Even in the absence of hunting, species across many trophic levels may still respond to humans. For example, in zoos or areas with recreational game viewing, humans cause greater levels of perceived risk (Tadesse and Kotler 2012), increased vigilance and aggression (Sherwen et al. 2015), reductions in reproductive output (Phillips and Alldredge 2000; Ellenberg et al. 2006), and decreases in fledging weight (Ellenberg et al. 2007).

Interestingly, other studies report that human presence decreases the perceived risk of natural predators, by buffering prey from the risk of predation (Meshesha 2013; Nowak et al. 2014; Geffroy et al. 2015). In these studies, human presence deters predators from the surrounding areas and is described as the 'human shield effect' (Berger 2007). Studies have reported that certain species actively seek areas of human activity to avoid predators (Berger 2007; Meshesha 2013), and in the presence of humans, the predation of certain species decreases (Isbell and Young 1993). However, the human shield effect has typically been recorded for species that humans don't consider as vermin, e.g. herbivores in protected areas (Berger 2007; Geffroy et al. 2015).

1.5 Assessing the non-lethal effects of predation

To evaluate the non-lethal effects of predation on prey species, researchers have used a wide range of methods varying from behavioural observations based on ecological theory, to the evaluation of physiological and neuroendocrine responses.

1.5.1. *Vigilance*

Vigilance is a key behaviour used in response to predation pressure, and the trade-off between vigilance and energy intake has received considerable attention (Lima 1987; Houston et al. 1993; Ferrari et al. 2009). The use of vigilance ultimately results in an individual trading off with another activity to assess the risk of predation, which can come at a cost to energetic gain. This cost can lead to food deprivation and may have implications for survival (Lima and Dill 1990). Vigilance levels generally correlate with both an animal's immediate risk and perceived risk of predation; in areas where predation risk or perceived risk is high, vigilance should increase (Lima 1998; Brown and Kotler 2004; Périquet et al. 2010, 2012). Vigilance levels can vary with fluctuating predator densities, but also with reproductive status, sex, presence of conspecifics, and environmental variables (Childress and Lung 2003; Carr and Lima 2010; Prugh and Golden 2014). For many species, levels of vigilance are influenced by group formation (Elgar 1989; Childress and Lung 2003; Lashley et al. 2014). This phenomenon is largely explained by the 'many-eyes' hypothesis, which allows individual animals to dedicate less time to vigilance, whilst the collective effort of the group avoids a reduction in predator detection (Pulliam 1973), as well as diluting the risk for each individual ('dilution hypothesis', Pulliam and Caraco 1984).

Vigilance is a highly dynamic behaviour influenced by individual experience and motivation (Ferrari et al. 2009). Food-deprived great tits (*Parus major*), for example, focus more on foraging and dedicate less time to vigilance when compared to satiated birds (Krebs 1980). When feeding on high-quality foods, the costs of vigilance increase due to the associated reduced high-quality food intake. Spotted hyaenas (*Crocuta crocuta*), for example, engage in vigilance to detect interspecific threats, and vigilance decreases when feeding on high-quality meats compared to low-quality food such as skin or bone (Pangle and Holekamp 2010). Furthermore, individuals who have been exposed to recent predation risk or predator cues may show heightened vigilance and limited foraging compared to individuals that have not been exposed (Metcalf et al. 1987; Monclús et al. 2006). For example, in response to

predator cues, European rabbits (*Oryctolagus cuniculus*) exhibit heightened vigilance (Monclús et al. 2006), and after exposure to a predator, juvenile Atlantic salmon (*Salmo salar*) feed less and dedicate more time to vigilance compared to individuals who have not been exposed (Metcalf et al. 1987). Likewise, in response to lion calls, cheetahs are more vigilant and less likely to make a kill (Durant 2000).

To reduce the energetic costs of vigilance, certain species are able to engage in vigilance whilst involved in other activities, such as handling food; this form of alertness is known as low-cost or passive vigilance (Illius and Fitzgibbon 1994; Lima and Bednekoff 1999; Unck et al. 2009). It has been suggested that certain species are able to gain sufficient information from their environment without being overtly vigilant, in a 'head-down' position (Quirici et al. 2008). Individuals in a 'head-down' position have been shown to monitor conspecifics (Fernández-Juricic et al. 2005; Quirici et al. 2008), and detect the approach of a predator (Lima and Bednekoff 1999); however, detection is less effective than for 'head-up' alert individuals. Thus, it has been suggested that high-cost/overt vigilance may be more important for anti-predator vigilance whereas low-cost/passive vigilance may be sufficient for conspecific monitoring (Monclús and Rödel 2008). The number of studies measuring low-cost vigilance remains small, and therefore it is premature to draw any conclusions regarding the function, target, and effectiveness of passive vigilance.

1.5.2. *Giving up density experiments*

Perceived risk is often measured by investigating the giving-up-density (GUD) of potential prey species. This method is an experimental approach that uses artificial feeding patches to quantify the foraging costs of a patch (Brown 1988; Kotler and Brown 1990). The GUD represents the density or amount of food remaining in a patch after foraging and is based on the theory that a foraging animal should continue to feed at a patch until its harvest rate no longer exceeds the sum of the energetic, predation, and missed opportunity costs of foraging (Brown 1988). When the energetic and missed opportunity costs remain constant, this

method can be used to assess the foraging costs of predation among patches (Brown 1988). A higher GUD (a less depleted patch) equates to greater perceived risk. GUD experiments have been used to assess perceived risk in both captive and wild populations, in different habitats (Bedoya-Perez et al. 2013), and across taxa, including rodents (Brown 1988; Kotler et al. 1991; Jacob and Brown 2000), ungulates (Shrader et al. 2008; Druce et al. 2009; Iribarren and Kotler 2012), primates (Emerson et al. 2011; Nowak et al. 2014), and a few carnivore species (Mukherjee et al. 2009; Leo et al. 2015). These studies have investigated the effects of multiple factors such as cover (Brown 1988; Jacob and Brown 2000), observer effects (Nowak et al. 2014), illumination (Mukherjee et al. 2009), and predator presence or cues of predator presence (Shrader et al. 2008; Leo et al. 2015). Using this approach enables researchers to monitor perceived risk *in situ* with minimal disturbance, but the method does have disadvantages such as the interference of non-target species (Bedoya-Perez et al. 2013). Patches that are visited by other species may alter results, as perceived risk is likely to vary among species. Additionally, patches that are simultaneously visited by multiple conspecifics can create interesting cost dynamics. For example, visits by multiple individuals may decrease the cost of the patch due to the dilution (Pulliam and Caraco 1984) and many eyes effects (Pulliam 1973), or may increase the cost of the patch due to increased risk of injury or decreased costs of foraging in other areas with fewer competitors (Bedoya-Perez et al. 2013). These limitations can, however, be mitigated with the use of camera traps to monitor artificial sites during operational times, and thus nights with non-target species interference can be removed from analyses and information on the presence of conspecifics incorporated into analyses.

1.5.3. *Movement*

Animals may modify their patterns of movement in order to decrease the risk of encountering predators (Bowyer et al. 1999; Fortin et al. 2005). Prey have been shown to demonstrate erratic and unpredictable movement patterns as a strategy to avoid predators (Bowyer et al. 1999; Fischhoff et al. 2007). It is hypothesised that zebras (*Equus burchelli*), for example,

avoid areas under current use by lions, and demonstrate erratic movements in open areas at night, to reduce the chance of being stalked (Fischhoff et al. 2007). Similarly, it is hypothesised that female Alaskan moose (*Alces alces gigas*) exhibit unpredictable movement patterns prior to giving birth in order to avoid predators (Bowyer et al. 1999), while cheetahs relocate to make kills in areas not occupied by lions (Durant 2000). However, relating movement solely to predator presence may not represent perceived risk strictly speaking, as factors such as food availability and external environmental factors can also influence movement (Fortin et al. 2005). Therefore, studies wishing to relate movement patterns to predator presence should also consider these factors to assure conclusions drawn relate exclusively to predator effects (Fortin et al. 2005).

As well as broad-scale movement patterns, determining the distance at which a prey species flees an approaching predator can also reveal aspects of perceived risk and is described as flight initiation distance (Ydenberg and Dill 1986). Ydenberg and Dill (1986) proposed a model that described factors influencing when a prey flees. They suggested animals would not necessarily flee from a predator at the very moment it was detected, and described a model that not only incorporated fear, but also prey 'goals'. These researchers propose that as predators' approach, prey continually assess whether to stay or flee and that this decision is influenced by factors such as resource density and quality, distance to cover, predator approach speed, and the costs associated with evasion (Ydenberg and Dill 1986; Stankowich and Blumstein 2005). Flight initiation distance is predicted to increase with decreasing resource quality, increased distance to cover, increased speed of approaching predator, and decreased costs of evasion.

1.5.4. *Landscape of fear*

An animal's home range is usually comprised of high- and low-risk areas, which are commonly imperceptible to observers (van der Merwe and Brown 2008). A topographic and temporal map of prey/mesopredator space use, variance in vigilance patterns, and/or

changes in perceived risk can enable researchers to visualise predation threats varying over time and space. Within these maps of risk fluctuation, peaks represent areas of heightened risk and troughs represent areas of refuge (Willems and Hill 2009). Such a time- and space-sensitive description of risk fluctuation is called a 'landscape of fear' (Laundré et al. 2001; Laundré et al. 2010). This approach combines differences in predation risk with the behavioural responses of prey and demonstrates the changing behaviours of individuals in response to predation risk across a landscape, and can be prey/predator specific (Laundré et al. 2001). Different styles of hunting lead to differential success in various habitats: for example, ambush predators hunt more successfully in areas with cover to conceal themselves from prey (Laundré and Hernández 2003), whereas cursorial predators are more adapted to hunting successfully in open habitats (Bowyer et al. 2001). This, therefore, affects predator lethality across a landscape, and prey/mesopredators respond to this lethality with predictable changes in behaviour or time allocation adjustments throughout space and time (Laundré et al. 2010). The development of the landscape of fear model has allowed two concepts – predation risk and response of prey to predation risk – to be combined into one visual representation that is practical for researchers and conservationists (Laundré et al. 2010).

1.5.5. *Population patterns versus the individual*

In investigations of perceived risk, studies can focus on either large-scale population patterns, or on individual patterns (Clutton-Brock and Sheldon 2010). For many years, individual behaviours were grouped to focus on population patterns, and individual variability was considered as non-adaptive noise around a mean (Wilson 1998). However, more recently individual variation has been observed across many species and various behaviours (Sih et al. 2004; Réale et al. 2007), including vigilance (Dannock et al. 2013). Specific methods of evaluating risk can yield both population and individual-level responses, such as vigilance, movement, and physiological and neuroendocrine responses. Studies utilising these methods can either report individual responses or combine individual results to

present average population trends, depending on the question being asked. Other methods, where no distinction is made between individuals, however, are more appropriate for revealing population-level responses, e.g. GUD methods (Bedoya-Perez et al. 2013). Importantly, individual patterns may differ from overall population trends (Nussey et al. 2007), and it is not possible to extrapolate one type of analysis to the other.

When individual variation in behaviours are consistent among individuals, patterns may emerge and demonstrate adaptive behaviours (Sih et al. 2004), such as different levels of vigilance in response to varying levels of predation pressure (Bell and Sih 2007).

Understanding patterns in consistent individual variations can further develop our knowledge of behavioural patterns. Conventionally, behavioural ecologists have been interested in the reasons why animals behave in certain manners, assuming that behaviours are common among individuals and therefore investigating population averages (Dall et al. 2004).

Comparatively, understanding why individuals may differ consistently in behaviours can provide information on the drivers behind these patterns and have been shown to predict, among other things, predator-prey relationships and habitat selection (Réale and Dingemanse 2012). By building on knowledge from individual to population-level patterns, researchers are able to gain a fuller understanding of this phenomenon. Whilst this phenomenon has been demonstrated in birds, fish, reptiles, crustaceans, and captive carnivores, it has seldom been demonstrated in wild carnivores (but see Greenberg and Holekamp 2017).

The majority of research on perceived risk has focused on herbivorous prey animals, but fewer studies have evaluated perceived risk in predators and mesopredators. While some studies have investigated perceived risk in mesopredators using GUD approaches (Mukherjee et al. 2009; Leo et al. 2015) and use of space (Kamler et al. 2013), studies seldom investigate vigilance (but see Durant 2000). Assessing risk perception and responses to risk perception in mesopredators would provide information on how they

respond to the non-lethal effects and competition generated by higher-level predators.

Importantly, this information is essential in understanding ecosystem dynamics and cascades of fear.

1.6 Study species: Bat-eared foxes (*Otocyon megalotis*)

1.6.1. General ecology

Bat-eared foxes (*Otocyon megalotis*) are small (3-5 kg), predominantly nocturnal mesocarnivores (Figure 1.1) that occur in two distinct sub-populations, in East and southern Africa. Group sizes fluctuate and range from 1-10 (Nel et al. 1984; Malcolm 1986), and bat-eared foxes are most commonly observed in monogamous pairs, especially in winter during the mating season (Lamprecht 1979; Malcolm 1986). Bat-eared foxes primarily forage on harvester termites (*Hodotermes mossambicus*, Nel and Mackie 1990; Kok and Nel 1992), and this specialist foraging behaviour promotes co-existence with other canids, and more dominant carnivores due to reduced competition (Bothma et al. 1984). Studies also report that, across their range, a variety of other insects are eaten, including Coleoptera species (Berry 1981; Kuntzsch and Nel 1992), ants (*Ponerinae* spp.), crickets, arachnid species, scorpions, and centipedes, as well as small rodents and lizards (Lamprecht 1979; Andrews and Nesbit Evans 1983; Nel and Mackie 1990). Bat-eared foxes also forage opportunistically on seasonal fruits (Berry 1981; Kuntzsch and Nel 1992), scavenge (Klare et al. 2011), and feed on the eggs or nestlings of ground-dwelling birds (Lamprecht 1979). These foxes primarily detect prey using auditory cues (Malcolm 1986; Renda and le Roux 2017), but also feed opportunistically on acoustically mute species (Malcolm 1986; Grant and Samways 2015).



Figure 1.1. Adult bat-eared fox (photo credit: Stéphanie Périquet).

1.6.2. *Intraguild and interspecific interactions*

Bat-eared foxes face intraguild predation from apex predators, as well as larger mesocarnivores (Pauw 2000; Kamler et al. 2012; Figure 1.2a). Only two studies in a single area (Kamler et al. 2012, 2013) have touched on the non-lethal effects of apex and larger mesopredators on bat-eared foxes. The specialised diet of bat-eared foxes promotes their co-existence with numerous species, such as Cape foxes (*Vulpes chama*, Bothma et al 1984; Kamler et al. 2012) and black footed cats (*Felis nigripes*, Kamler et al. 2015), but also predators, such as lions, leopards, spotted and brown (*Hyaena brunnea*) hyaenas, martial eagles, and black-backed jackals (*Canis mesomelas*) across much of their range (Pauw 2000; Kamler et al. 2012). However, studies have reported numerous killings of bat-eared foxes by all types of co-existing predators including wild-dogs (*Lycaon pictus*), black-backed jackals and golden jackals (*Canis aureus*); these larger predators will kill to eliminate competition but often consume the carcasses too (Rasmussen 1996; Bagniewska and

Kamler 2014; Temu et al. 2017). Birds of prey pose a significant threat to pups, and also sometimes kill adult bat-eared foxes (Malcolm 1986).

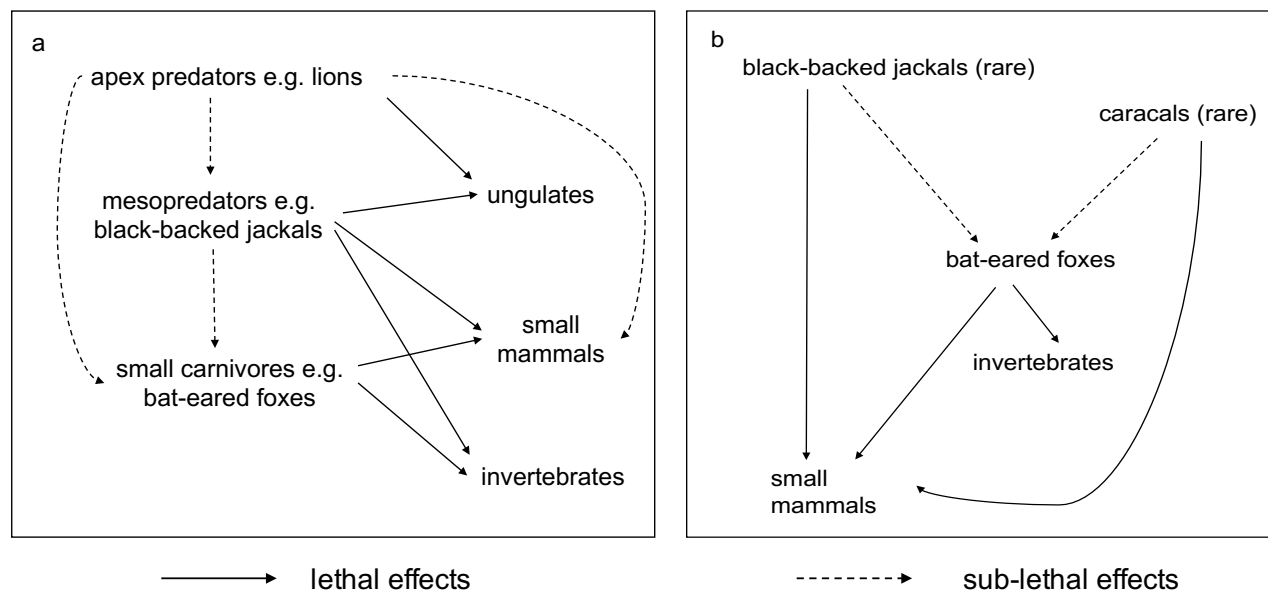


Figure 1.2. a) Major trophic interactions historically for the study system when apex predators were present, and b) current major lethal and sub-lethal effects for bat-eared fox interactions for the study system. Dominant interactions are illustrated, however where sub-lethal effects occur, lethal effects may also infrequently occur.

In response to predation, bat-eared foxes exhibit a number of behavioural adaptations. They demonstrate a preference for short grassland habitats, which facilitates predator detection and avoidance (Lamprecht 1979; Mackie and Nel 1989; Schuette et al. 2013). In the presence of a threat, bat-eared foxes have been observed forming larger groups, mobbing predators (both apex and smaller predators), and barking at predators (Lamprecht 1979; Malcolm 1986; Kamler et al. 2012), as well as evasive behaviours – running to areas of refuge (Lamprecht 1979; Malcolm 1986; Rasmussen 1996). Increased vigilance has been suggested as the key behaviour that triggers group formation (Pauw 2000), but no work has been conducted on their vigilance behaviours. Bat-eared foxes arch their backs when approaching predators and respond to predator movement with an inverted U-shaped tail

and piloerection (Lamprecht 1979; Malcolm 1986). Further, bat-eared foxes do not avoid black-backed jackal core areas when foraging, but instead form larger groups to deter predation (Kamler et al. 2012). However, foxes do avoid jackal core areas when selecting den sites, suggesting black-backed jackals pose a considerable threat to pups (Kamler et al. 2012). Male presence is particularly important at den sites as male foxes will regularly guard den sites and chase away predators (Lamprecht 1979; Pauw 2000; Wright 2006). If more than one adult is present, adult bat-eared foxes will mob predators to deter them from coming near den sites (Pauw 2000). In farmland, predator control (targeting larger carnivore species) has been shown to influence bat-eared fox abundance positively (Blaum et al. 2009), and in the absence of jackals, bat-eared foxes form smaller groups and longevity may increase (Kamler and Macdonald 2006).

1.7 Thesis aims

While much work has investigated the foraging and socio-ecology of bat-eared foxes, the effects of predators on the perceived risk of bat-eared foxes is not well documented. No information exists on how environmental, temporal, and social factors influence the perceived risk of this species, at either the population or individual level. Although a specialised diet promotes co-existence with other species, bat-eared foxes are still involved in antagonistic encounters with larger species, sometimes resulting in death, thus foxes are cautious towards competitively dominant or aggressive species. Additionally, as mesopredators, bat-eared foxes must adequately balance the predation of their own prey, whilst avoiding larger carnivores. Factors that may influence prey detection and foraging success could also influence perceived risk. In this thesis, I aim to assess perceived risk at a site with low predation pressure. At this site, apex predators were extirpated over 100 years ago, and black-backed jackals and caracals are rare, but represent the greatest threat to bat-eared foxes (Figure 1.2b). Predation pressure is thus relatively homogenous across the landscape, allowing for the investigation of landscape, environmental, and social effects that may impact perceived risk over and above the effects of predator presence. Firstly, I use two

different methods (GUD experiments and vigilance assessments) to describe how perceived risk in bat-eared foxes is influenced by spatiotemporal and anthropogenic factors; also investigating how these two methods complement one another (Chapter 2; Welch et al. 2017). Secondly, I examine bat-eared foxes' use of high- and low-cost vigilance. Although predation pressure is largely absent at the study site, bat-eared foxes are unlikely to have lost appropriate anti-predator behaviours, and understanding how foxes utilise high-and low-cost vigilance, and assessing the factors that influence these, may provide clues as to the drivers of these behaviours. Additionally, as behavioural observations are made on a population of habituated bat-eared foxes, I aim to evaluate the influence of observers on vigilance behaviours and whether observers are truly passive (Chapter 3; Welch et al. 2018). Finally, I aim to explore individual patterns in anti-predator behaviours, specifically investigating whether the population exhibits consistent among-individual variation in personality and plasticity in overall, high- and low-cost vigilance. In this assessment, I determine whether patterns in high- and low-cost vigilance reflect those patterns observed for overall vigilance and whether variation in personality and/or individual plasticity is evident (Chapter 4; Welch et al. Under Review).

This thesis is written in 'publication style' - the first and second data chapters are published, and the third data chapter under review. I have maintained format and consistency throughout the thesis. However, each data chapter is written in the style of an individual, stand-alone paper, so although I have tried to reduce repetition where possible, there will still be some repetition throughout the thesis.

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**CHAPTER 2 HUNTER OR HUNTED? PERCEPTIONS OF RISK
AND REWARD IN A SMALL MESOPREDATOR**



Welch RJ, Périquet S, Petelle MB, le Roux A (2017) *Journal of Mammalogy* 98:1531-1537

2.1 Abstract

Apex predators directly and indirectly influence prey and predators at lower trophic positions (mesopredators). The lethal effect of apex predators on mesopredators is well documented, but they also could affect mesopredators in non-lethal ways. We investigated foraging decisions and perceived risk in the bat-eared fox, a small canid that is often killed by larger terrestrial carnivores and birds of prey. We used giving-up-density (GUD) experiments and observations of vigilance behaviour to assess the influence of temporal, spatial, and anthropogenic factors on perceived risk in a population of bat-eared foxes at the Kuruman River Reserve, Northern Cape, South Africa. GUDs were higher during periods around the new moon and lower in the presence of researchers, suggesting that foxes are warier in darker conditions, but perceive an increase in relative safety in the presence of humans. Vigilance, however, did not vary with these same factors. Observational data revealed foraging success outside the experimental context did not differ with lunar period, implying that higher GUDs associated with new moons were not due to higher missed opportunity costs associated with foraging at patches. These results suggest that GUDs may be capable of detecting more subtle differences in perceived risk when compared to vigilance rates. We highlight the important considerations of using GUDs to examine perceived risk for a predatory species and emphasise that future studies using GUDs should quantify predators' risk-related decisions by documenting missed opportunity costs to determine the implications behind patch-use behaviour.

2.2 Introduction

Animal activity patterns vary across space and time in relation to resource availability (Engqvist and Richard 1991; Overdorff 1996) and level of predation risk (Lima and Dill 1990). For prey species, predation risk is a strong driver of activity patterns through both lethal and non-lethal processes (Lima and Dill 1990; Lima 1998). The non-lethal effects of predator presence are reflected in prey animals' resource exploitation (Périquet et al. 2010)

and vigilance levels (Lima and Dill 1990; Liley and Creel 2008). Much work has been done on perceived risk, which has been shown to operate at many scales (Lima and Dill 1990; Brown et al. 1999) from population (Tolon et al. 2009; Valeix et al. 2009; Kamler et al. 2013) to individual (Roberts 1996; Périquet et al. 2010). Even fine-scale environmental features such as distance to cover (Lima and Dill 1990), ambient light levels (Prugh and Golden 2014), and observer effects (Tadesse and Kotler 2012) can lead to heterogeneous levels of perceived risk within any given habitat. The effects of environmental factors on perceived risk are not similar across taxa, often varying and dependent on the study species and site. For example, prey have been shown to exhibit greater levels of perceived risk in both open and closed habitats (Underwood 1982; Bowers et al. 1993; Schooley et al. 1996), on dark new moon and well-lit full moon nights (Prugh and Golden 2014), and with or without observers (i.e. the impact of a 'neutral' human observer on animal behaviour, Berger 2007; Tadesse and Kotler 2012; Nowak et al. 2014). This contrast hinders universal conclusions regarding perceived risk, highlighting that predator-prey systems are complicated and require, at the very least, consideration of aspects of both predator and prey behaviour.

Most work investigating perceived risk has been conducted on prey species, while less work has investigated perceived risk in predators (but see Schmidt and Schaubert 2007; Mukherjee et al. 2009). Top predators pose a threat not only to herbivores and basal prey species, but also to predators at lower trophic positions (mesopredators, Ritchie and Johnson 2009). Mesopredators perform the role of a predator, but also face the threat of predation by larger carnivores (Kamler et al. 2012). Previously, the majority of studies of mesopredators focused on their role as a predator, and the studies that did consider the effect of top predators on mesopredators generally reported lethal effects. More recently, the non-lethal effects that predators place on mesopredators have been investigated in detail and are seen as important in shaping the behaviour and distribution of mesopredators (Kamler et al. 2013).

Bat-eared foxes are small canids that often coexist with a number of large predator species, and have been identified as a common victim in interspecific killings (Palomares and Caro 1999). Lions, leopards, wild dogs, hyaenas, cheetahs, martial eagles, black-backed jackals, and caracals (*Caracal caracal*) have all been shown to kill bat-eared foxes (Mills 1984; Rasmussen 1996; Macdonald and Sillero-Zubiri 2004; Melville et al. 2004; Kamler et al. 2012). Additionally, predators are known to have non-lethal effects on the behaviour and ecology of these small canids, including increased group size and increased home-range size in the presence of predators (Kamler et al. 2013). Although Kamler et al. (2013) demonstrated these larger-scale spatial and group dynamic effects, perceived risk of predation could also affect mesopredators on a finer scale.

Giving-up-density (GUD) experiments can be used to examine perceived risk and utilise experimental feeding patches to quantify the harvest rate of a foraging animal when it leaves a patch, reflecting the foraging costs of a patch (Brown 1988; Kotler and Brown 1990). A GUD is defined as the density of food remaining in a patch once a forager has stopped exploiting it (Brown 1988), with less-depleted patches having a higher GUD and greater perceived risk, all else being equal. An individual forager should ultimately feed at a patch until its harvest rate no longer exceeds the sum of the energetic, predation, and missed opportunity costs of foraging (Brown 1988). If the energetic costs and missed opportunity costs are constant, this approach can be used to measure the differences in the foraging costs of predation among patches (Brown 1988).

Here, we investigate foraging decisions and risk perception for bat-eared foxes using an experimental GUD approach, complemented by behavioural observations to examine the influence of several environmental features on bat-eared foxes' perceived risk. As this species is a mesopredator, the same factors that lead to increased risk may also cause missed opportunity costs to increase (as prey may become more or less active); thus, we assessed variation in vigilance as well as GUDs. We hypothesised that new moon nights

would result in higher GUDs due to a greater threat of predation, as shown in other nocturnal species (e.g. Biebow and Blumstein 2003), or due to increased hunting opportunities and greater prey availability on new moon nights (Price et al. 1984; Skutelsky 1996; Read and Moseby 2001), which would increase missed opportunity costs at experimental patches. If GUDs are higher on new moon nights, increased vigilance over these same periods would support the increased risk of predation hypothesis, whereas greater out-of-patch foraging success (foraging away from experimental sites) and no or small increases in vigilance on new moon nights would support the increased hunting hypothesis. We hypothesised that microhabitat would have an effect on perceived risk (Bowers et al. 1993). As cursorial predators (black-backed jackal) and birds of prey (e.g. martial eagle, Verreaux's eagle owl, *Bubo lacteus*) were potential predators in the area, we hypothesised that open areas would be associated with higher GUDs and higher vigilance. Finally, humans are typically seen as a threat to predators (Kaunda 2000; Sherwen et al. 2015); therefore, we hypothesised that in the presence of researchers, GUDs and vigilance would be higher.

2.3 Materials and methods

2.3.1. Study site and subjects

We studied a wild population of bat-eared foxes at the Kuruman River Reserve (KRR, 28°59'S, 21°49'E) in the southern Kalahari Desert, Northern Cape, South Africa (Figure 2.1). The reserve vegetation is classified as Kalahari Thornveld (Low and Rebelo 1996), and the three predominant habitats are described as dry river – a largely open area with small clusters of black thorn (*Acacia mellifera*) and camel thorn (*Acacia erioloba*) bushes, dune areas scattered with perennial grasses (*Aristida*, *Eragrostis*, *Schmidtia* and *Stipagrostis* spp), and flat river terraces with expansive areas of driedoring (*Rhigozum trichotomum*) and perdebos (*Galenia Africana*; Figure 2.2). The climate in this region is typically characterised by cold, dry winters (May-September) and hot, wet summers (October-April). Between January 2015 and December 2015, the area experienced an annual rainfall of 282 mm (summer rainfall: 253 mm, winter rainfall: 29 mm), and a temperature range of - 4.6 °C to 41

°C (summer average: 25.5 °C, winter average: 14.8 °C), based on weather data collected on site.

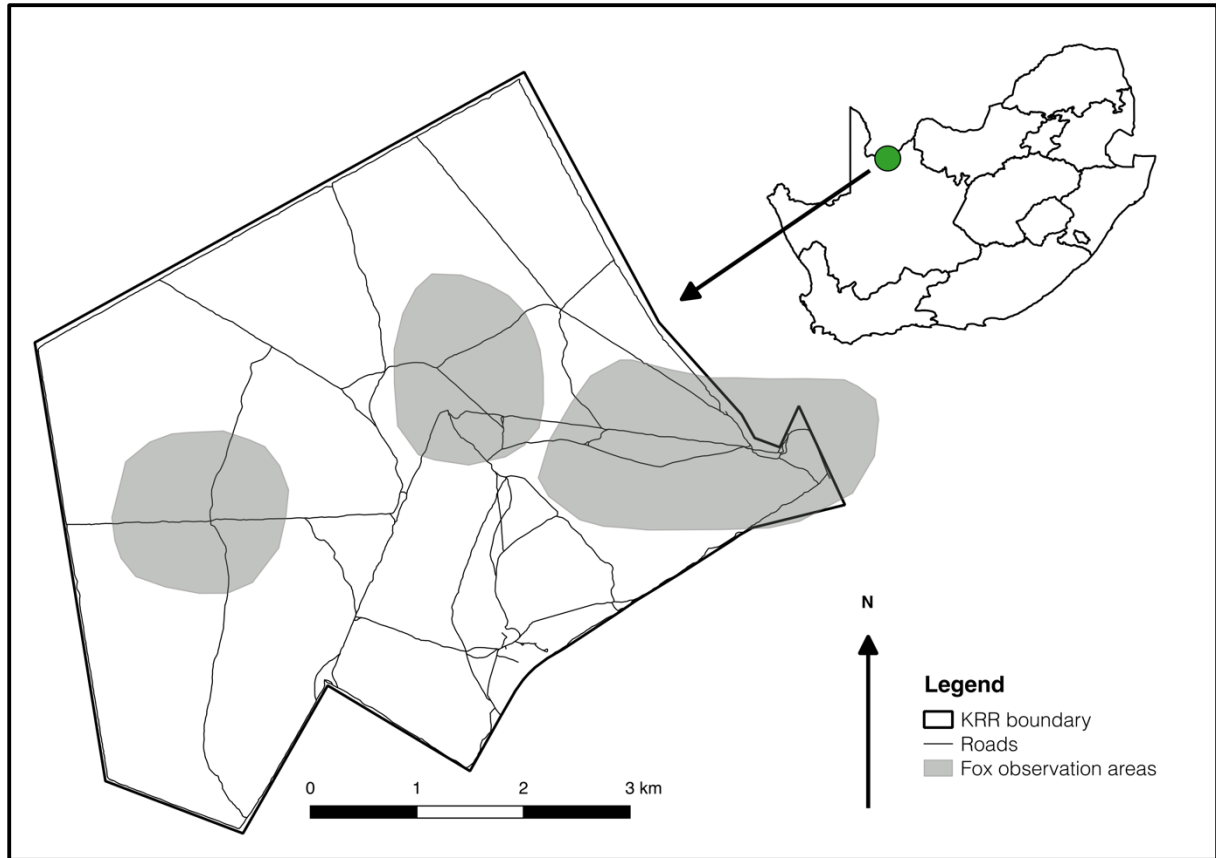


Figure 2.1. Study area location, highlighting behavioural observation areas illustrated by fox home range boundaries (light grey). The upper right image indicates the province boundaries of South Africa, with the study site located in the Northern Cape.

The bat-eared fox is a small (3-5 kg), mainly nocturnal canid with a diet consisting predominantly of insects, as well as some small vertebrates and fruits (Maas and Macdonald 2004; Klare et al. 2011). These foxes form monogamous relationships and will forage either solitarily or with their partner. Although most large predators were absent from our study site in the Kalahari Desert, caracals, black-backed jackals, eagles, Verreaux's eagle-owls, and various dangerous snake species were present.

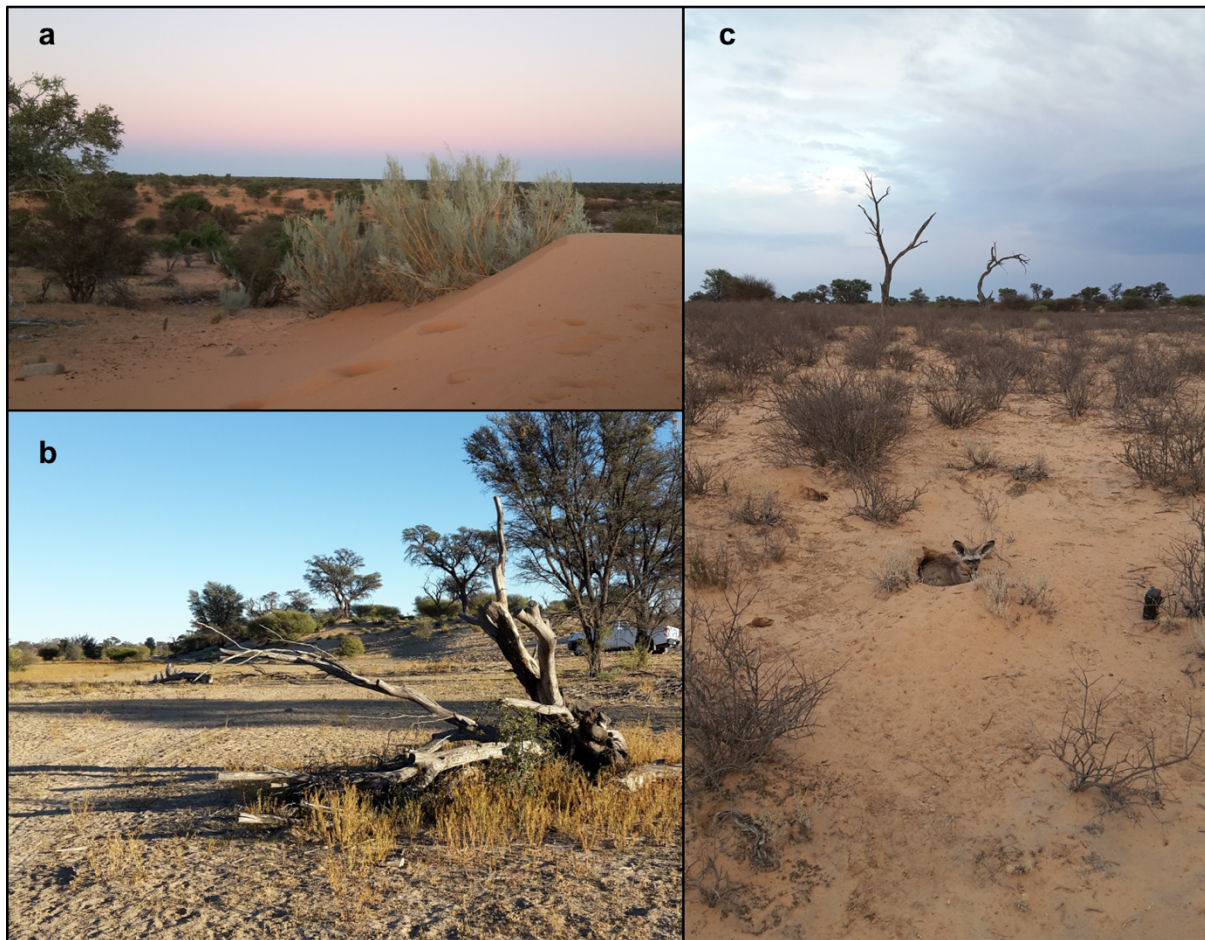


Figure 2.2. The different habitat types at the Kuruman River Reserve, Northern Cape, South Africa, including a) dune areas, b) dry river, and c) flat river terraces.

2.3.2. *GUD experiment settings*

We performed foraging experiments combined with video observations of individual vigilance at experimental feeding patches to understand foraging decisions of foxes in response to perceived risk of predation. Before experiments began, researchers habituated foxes to experimental feeding patches for 10 days. Initially, we placed raisins (a preferred artificial food source, personal observations based on findings during habituation to humans) in experimental patches without an inedible matrix to encourage foxes to forage at patches. Following this, we steadily made the process of finding raisins harder by increasing the volume of inedible matrix (sand). We then created a 4 x 3 grid using galvanised wire over the

top of feeding containers (80 mm x 291 mm x 404 mm), creating 12 openings of approximately 97 mm x 101 mm (Figure 2.3). Additional wire was run along the inside edge of feeding stations to stop sand from being expelled and to create diminishing returns to harvest rates when foxes fed (e.g. Shrader et al. 2008). We needed to ensure the task offered enough rewards to encourage foxes to forage at patches but make the task complex enough so that foxes did not exhaust all items, thus ensuring foxes 'gave up'. Ultimately, we filled containers with six litres of sand and mixed 15 raisins throughout the sand in a random manner. We used 16 experimental feeding patches to measure GUDs and patches were positioned > 50 – 200 m apart to standardise distances between patches. Researchers set experimental feeding patches at dusk (approximately 1800h) and counted the number of remaining raisins (from which we calculated proportion of raisins remaining) in each container every morning (approximately 0730h); these times coincided with peak activity of bat-eared foxes, and avoided interference by diurnal species. Additionally, we positioned camera traps (Bushnell Trophy Cam; Bushnell Co., Philadelphia, Pennsylvania, or Cuddeback Attack IR; Non Typical Inc., De Pere, Wisconsin) at each experimental feeding patch, set to record 60-second videos with 1-second intervals to 1) ensure that only the target species was feeding at these sites, and 2) record the vigilance behaviour exhibited by foxes while using the feeding patch. Distances from feeding patches and angles of cameras were standardised across sites.

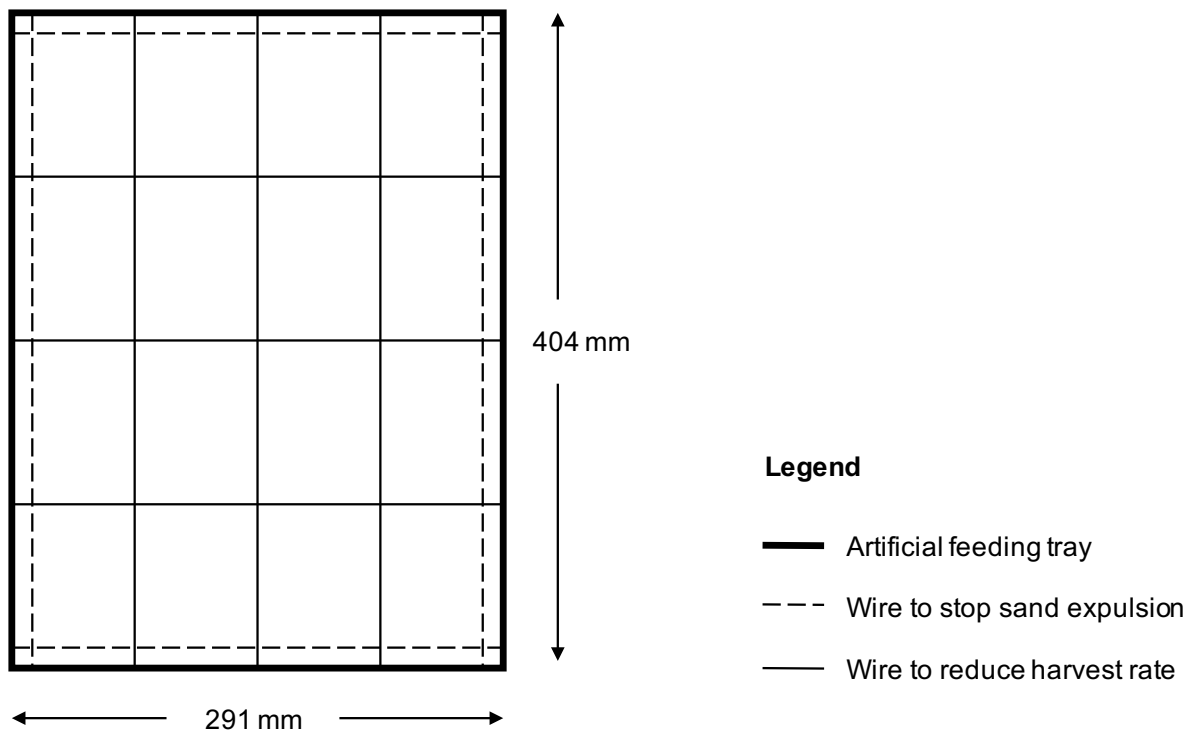


Figure 2.3. Experimental feeding tray set up used in giving up density experiments.

We recorded GUDs (proportion of raisins left) for a total of 40 days across two lunar cycles. To assess the effects of moonlight, we separated data into days that fell within a 5-day period of full moon, new moon, first quarter, and last quarter (the night of the lunar event and two days either side). This ultimately gave us GUD data for a total of 24 days. To assess microhabitat, we placed four experimental feeding patches under large bushes (> 1.5 m in height) and four patches in open areas (approximately 50 m from the nearest cover). We moved these experimental patches to new sites under the same conditions the following lunar cycle, giving a total of eight experimental patches in the open and eight patches under cover across the experiment (Figure 2.4). Additionally, we tested for the effects of presence of a researcher on the foraging costs of predation by comparing GUDs collected on nights where researchers were within a 300-m radius of experimental feeding patches repeatedly throughout the night, to nights where researchers were not present (c.f. Nowak et al. 2014). This was investigated post experiments, when it became apparent that during a number of GUD nights, researchers had been repeatedly in the area conducting other research. On

these nights, one researcher was repeatedly in the area from dusk until dawn, once every couple of hours.

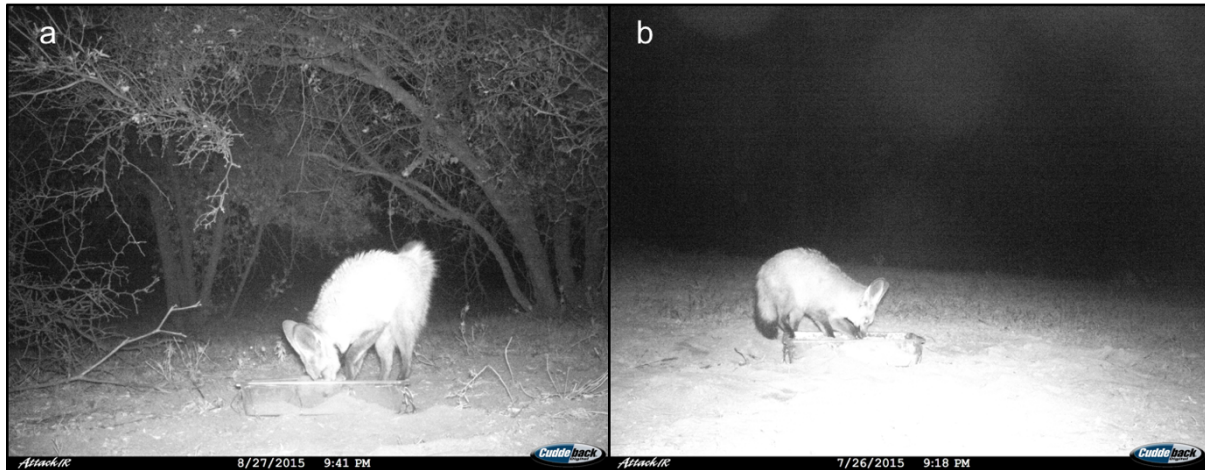


Figure 2.4. Foxes foraging at artificial feeding stations in areas a) associated with cover and b) in open habitat.

2.3.3. Behavioural data

From the video recordings, we extracted the proportion of time spent foraging, the proportion of time spent vigilant, and the rate of vigilance (vigilant glances/min). Vigilance was defined as whenever a fox ceased foraging (or another mutually exclusive activity) and lifted their head with ears erect and forward to scan the area (Nel and Bester 1983). We collected behavioural data from the moment foxes began interacting with experimental feeding patches until the foxes left the patch.

Additionally, to evaluate foraging success away from experimental patches, we followed individual foxes for two hours once per week. Number of items consumed were recorded and used to estimate foraging rates (number of items consumed per minute) over full and new moon phases. Bat-eared foxes were habituated to observer presence and we were able to follow foraging foxes from a distance of 1-2 m when collecting behavioural data.

All protocols were assessed by The University of the Free State's ethical committee and were in accordance with The University of the Free State's ethical standards protocol under the ethical clearance number 11/2013. The Department of Nature Conservation approved all fieldwork under permit number 476/2/2013. All research conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2016).

2.3.4. *Statistical analyses*

All analyses were conducted in R (R Development Core Team 2016), using the package lme4 (Bates et al. 2015). Data exploration was conducted based on the guidelines described in Zuur et al. (2010). Model assumptions were confirmed by plotting residuals against fitted values, and versus covariates in the model and covariates not in the model (Zuur and Ieno 2016). For all models we used Likelihood Ratio Tests (LRTs) to assess goodness of fit of the global model compared to the null model (intercept only with an identical random effects structure). All figures show mean values and standard error unless stated otherwise.

We used generalised linear mixed effects models (GLMMs) to assess the relationship between GUDs and spatiotemporal variables. We used a binomial error distribution with a logit link to model GUDs (i.e. proportion of raisins left at each experimental feeding patch each morning). We included the categorical variables microhabitat (cover versus open), lunar phase (full moon, new moon, and intermediate), and human presence (nights where researchers were repeatedly within a 300-m radius of experimental feeding patches versus nights where researchers were not present) as fixed effects, and site identity as a random effect. We had limited data for both waxing and waning periods (two days for each period). As there was no significant difference in the number of raisins left between waxing and waning periods (Wilcoxon rank-sum test, $W = 69$, $df = 22$, $P = 0.976$), these were pooled into an 'intermediate' category (defined as periods in-between full and new moon).

To assess how vigilance related to GUDs, we used a GLMM with binomial error distribution and a logit link with GUDs as the response variable. Proportion of time spent foraging, proportion of time spent vigilant, and vigilance rate were initially included in the models. However, proportion of time spent vigilant and vigilance rate were highly correlated so the least significant of the two was removed, leaving proportion of time spent foraging and rate of vigilance included in models as fixed effects. Site identity was included as a random effect.

We used a GLMM to evaluate the effect of moonlight, cover, and human presence on vigilance rate. We used a Poisson error distribution and a log link to model the number of vigilance bouts, and the log of the total time was included as an offset. We included lunar phase (full, new moon, or intermediate), microhabitat (cover and open), and human presence (present or absent) as fixed effects and site identity as a random effect.

Mean foraging success over the full and new moon phases ($n = 21$ per moon phase) was assessed using a Wilcoxon rank-sum test (as the data were not normally distributed).

2.4 Results

We used a total of 155 GUD data points, as of the 192 GUD data points (eight experimental feeding patches per night for 24 nights) 37 were discarded from analyses either because bat-eared foxes did not visit the feeding patches ($n = 28$), or another species fed from the patch ($n = 9$). The average proportion of raisins left across all GUDs was 0.696 ± 0.267 (mean \pm SD); 0.580 ± 0.268 on full moon nights, 0.721 ± 0.262 on intermediate moon nights, 0.805 ± 0.218 on new moon nights, 0.641 ± 0.259 on nights with 'researcher present,' 0.745 ± 0.265 on nights with 'researcher absent,' 0.666 ± 0.277 for areas associated with cover, and 0.730 ± 0.252 for open areas.

2.4.1. Effects of spatial and temporal factors on GUDS

A model including moon, microhabitat, and human presence was significantly better than the null model ($X^2 = 115.800$, $df = 4$, $P < 0.001$). Lunar phase ($X^2 = 79.017$, $df = 2$, $P < 0.001$) and researcher presence ($X^2 = 11.015$, $df = 1$, $P < 0.001$) had significant effects on GUDs. GUDs were higher over new moon periods (parameter estimate \pm SE: 0.997 ± 0.112 ; $P < 0.001$; Figure 2.5) and intermediate periods (0.439 ± 0.156 ; $P < 0.01$; Figure 2.5) and lower on nights where humans had been present (-0.373 ± 0.112 ; $P < 0.001$; Figure 2.6). Microhabitat had no effect on GUDs ($X^2 = 0.579$, $df = 1$, $P = 0.447$).

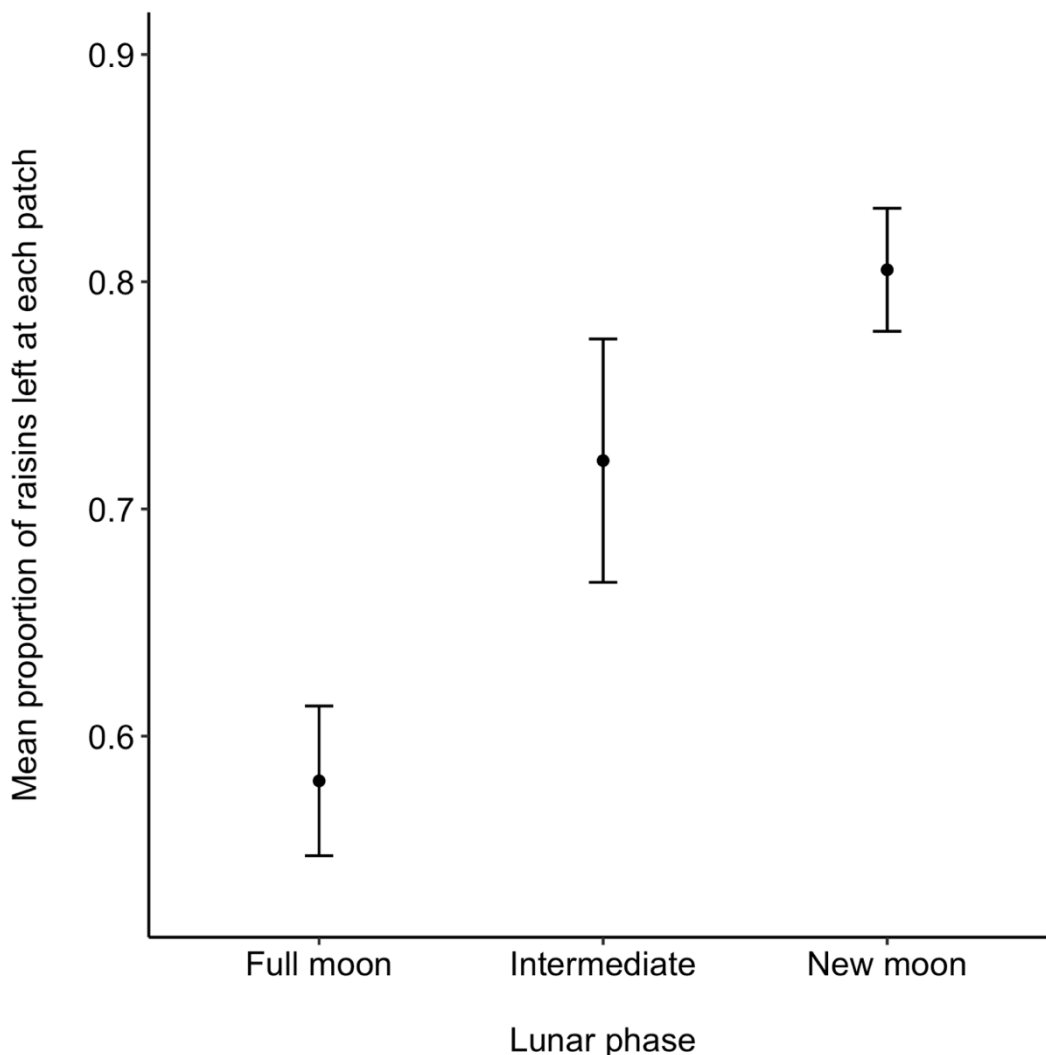


Figure 2.5. Differences in bat-eared fox giving-up-densities at experimental feeding patches observed between full moon, new moon, and intermediate phases in the Kalahari Desert.

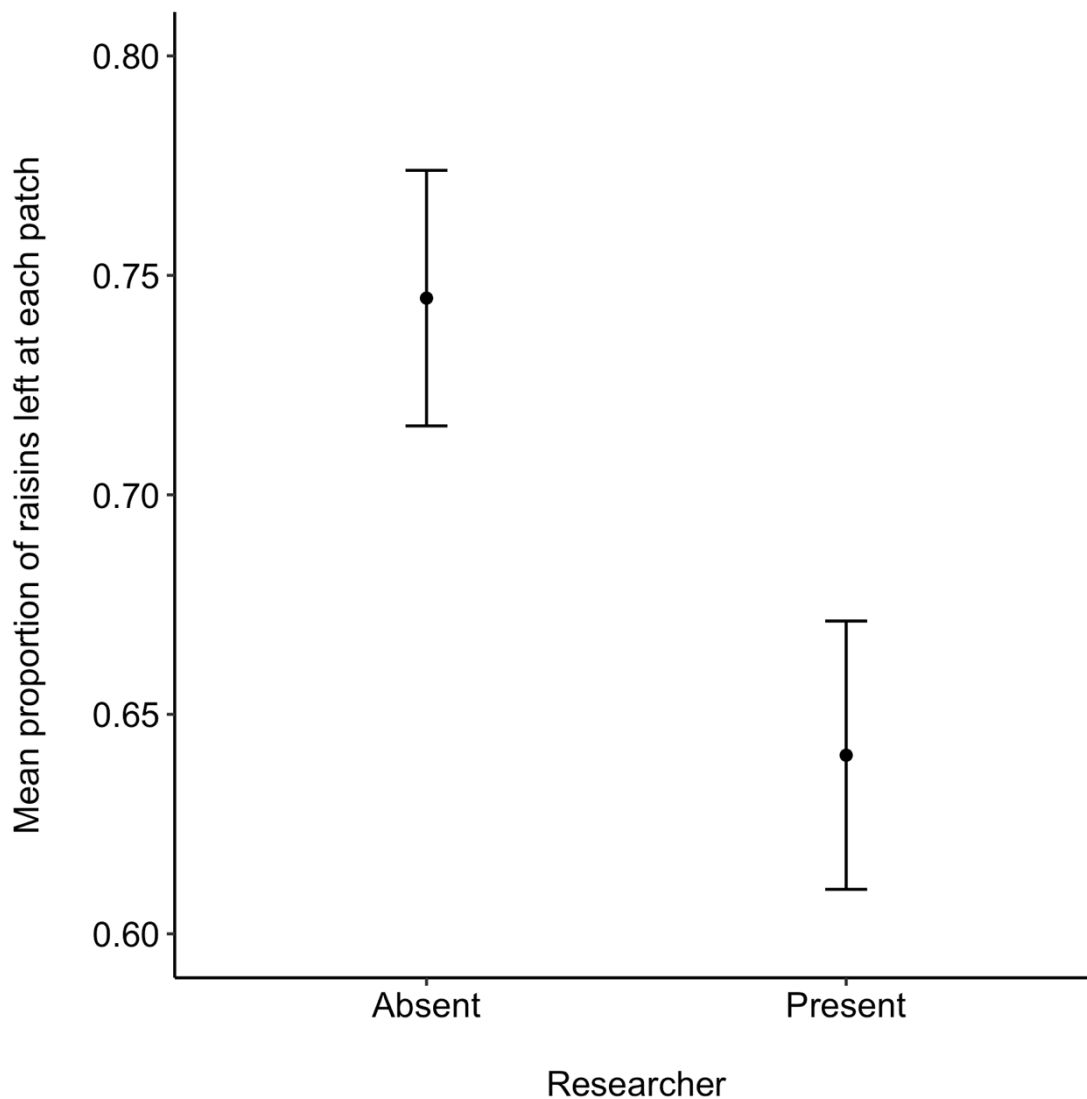


Figure 2.6. Differences in bat-eared fox giving-up-densities at experimental feeding patches observed during the presence and absence of researchers in the Kalahari Desert.

2.4.2. Behavioural analyses

When investigating the relationship between GUDs with foraging time and vigilance, a model including rate of vigilance and proportion of time spent foraging at patches was significantly better than the null model ($\chi^2 = 103.410$, $df = 2$, $P < 0.001$). Results show that GUDs increased as foraging time at experimental patches decreased (-2.124 ± 0.225 ; $P < 0.001$),

but that there was no significant relationship between GUDs and rate of vigilance. A model assessing the link between moon, microhabitat, researcher presence, and vigilance rate as the dependent variable was not significantly better than the null model ($X^2 = 6.936$, $df = 4$, $P = 0.139$), indicating that none of these factors were good predictors of vigilance. Lastly, foraging rate (away from GUD experimental patches) did not differ between new and full moon nights ($W = 225$, $df = 40$, $P = 0.921$; Figure 2.7). Foraging rate was 4.812 ± 4.789 on full moon nights (mean number of items consumed $\pm SD$) and 3.931 ± 3.057 on new moon nights.

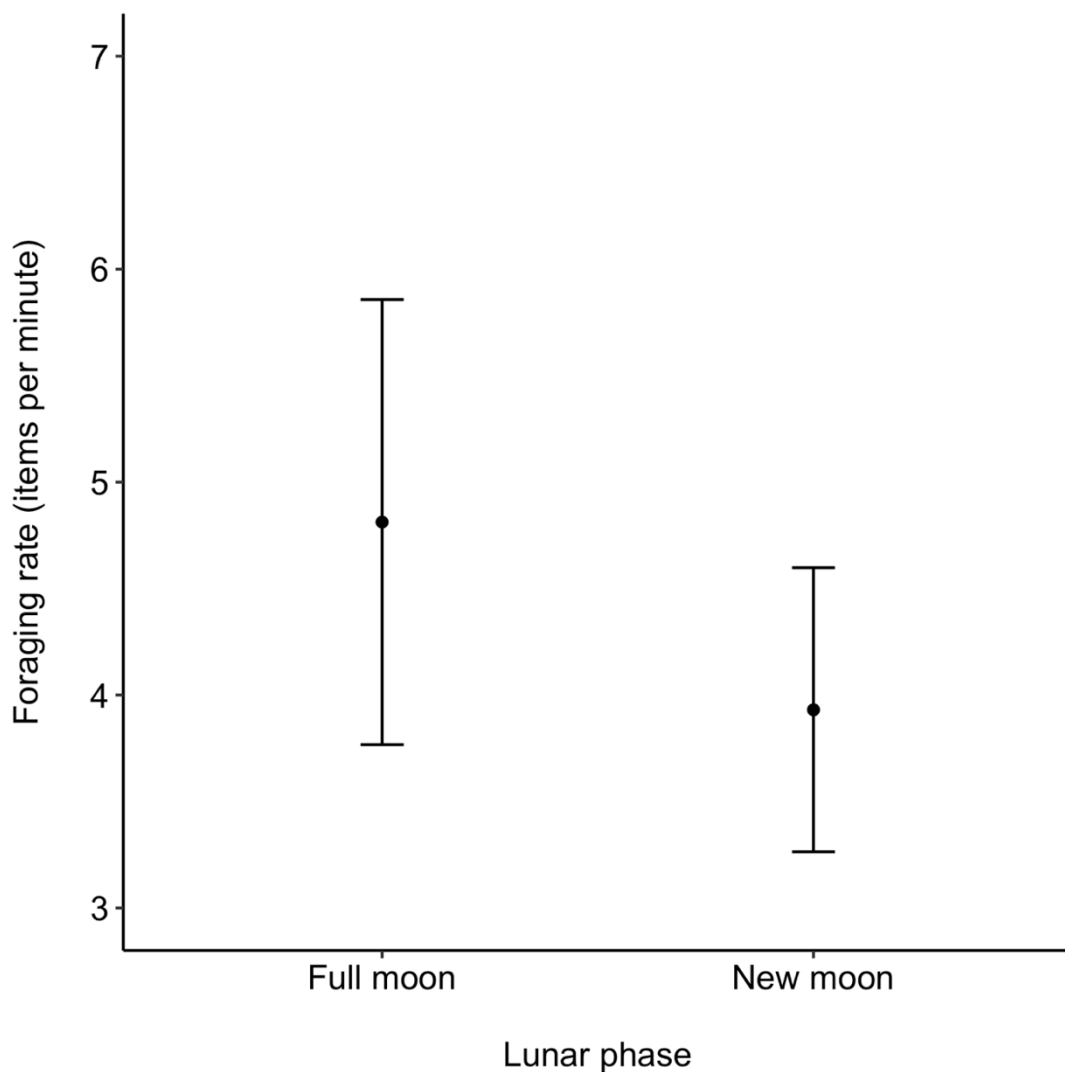


Figure 2.7. Bat-eared fox foraging rates away from experimental feeding patches, compared between full moon and new moon phases in the Kalahari Desert.

2.5 Discussion

Our study highlights that bat-eared foxes demonstrate patch-use behaviour that most likely reflects perceived risk. In line with our expectations, bat-eared foxes demonstrated higher GUDs during dark, new moon nights. In addition, our findings indicate that the presence of researchers resulted in lower GUDs and that microhabitat did not have implications for GUDs or vigilance.

GUDs were higher over new moon periods, translating to either greater perceived risk of predation over these periods, or that alternatively, these periods were associated with higher levels of prey activity. Observational data indicated foraging success was not affected by lunar phase, suggesting that missed opportunity costs did not differ with lunar phase.

Although the activity levels of many bat-eared fox prey items such as moths, rodents, reptiles, scorpions, and other invertebrates (Price et al. 1984; Skutelsky 1996; Tigar and Osborne 1999; Read and Moseby 2001) have been shown to vary with lunar phase, this does not appear to impact the foraging rates of bat-eared foxes (whether positively or negatively). Therefore, we suggest that our results reveal variation in perceived risk and that bat-eared foxes perceive risk to be greater in darker conditions. Some studies suggest that well-lit, full moon conditions decrease the risk of predation for certain herbivorous prey species given that predators can be more readily detected and evaded (Biebow and Blumstein 2003; Nersesian et al. 2012). This study suggests that the same factors may influence the risk perception of small mesopredators. It is important to note that the time of night may affect lunar illumination, but was not considered in this study.

GUDs were significantly lower on nights when researchers were repeatedly within 300 m of experimental feeding patches. Human presence has been shown to alter animal's risk-taking decisions, as humans following habituated animals could be regarded by the study animals as providing some form of buffer against predation risk (human shield effect, Berger 2007;

Nowak et al. 2014). In South Africa, humans persecute both black-backed jackals and caracals due to livestock conflicts (Thorn et al. 2012), resulting in increased wariness towards humans (Kaunda 2000). Our presence may therefore have buffered against predation risk from these species. Isbell and Young (1993) demonstrated that leopards preyed less on vervet monkeys when in the presence of humans. Likewise, Nowak et al. (2014), who used a similar GUD approach, demonstrated that samango monkey's (*Cercopithecus mitis erythrarcus*) perceived risk of terrestrial predators was significantly reduced in the presence of humans. The observer effect detected here could be direct (foxes perceive risk to be lower in the presence of researchers) or indirect (the presence of humans may impact upon missed opportunity costs by influencing prey behaviour). It is important to consider this may have influenced GUDs. However, we observed foxes eating the typical range of prey and the successful capture of larger prey items in our presence (Jacobs and le Roux 2016). How perceived risk and prey behaviour interact in the presence of observers could not be answered in this study.

Contrary to our hypothesis, there was no effect of microhabitat on perceived risk. We predicted that areas associated with more cover would be associated with lower perceived risk, as cover can decrease the probability of being detected by cursorial predators (Creel and Creel 2002), and previous observations have reported bat-eared foxes retreating to thick shrub when evading predators (Mills and Hes 1997). Cover has been shown to have both positive and negative effects, as cover can either conceal predators or shield prey. Mule deer (*Odocoileus hemionus*) have been shown to demonstrate higher levels of risk in open areas, which has been attributed to the greater hunting success of cursorial predators in these areas (Bowyer et al. 2001). Conversely, cover can be associated with increased perceived risk due to decreased detection of predators (Underwood 1982; Schooley et al. 1996). Bat-eared foxes have powerful auditory senses (Renda and le Roux 2017) and thus most likely use hearing as another sense to detect predators. The non-significant effect of microhabitat could thus be due to the fact that hearing is used more readily in areas of

vegetation, and is not affected by lines-of-sight. Additionally, vegetation could offer foraging opportunities (S. Périquet and A. le Roux, pers. obs.) and therefore may not pose solely as a threat to foxes.

Previous studies have highlighted that spatial and temporal variation in the occupancy of intraguild predators can influence perceived risk (e.g. Berger and Gese 2007; Mukherjee et al. 2009). The presence and spatial distribution of intraguild predators may influence perceived risk in bat-eared foxes, but we did not quantify such effects at this site and assumed that, if present, the intraguild competition would be low and relatively homogenous across the site. Lastly, an aspect that was not explicitly investigated in this study is the effect of sociality on perceived risk. Previous studies have highlighted that the presence or absence of conspecifics can cause changes in perceived risk (e.g. Roberts 1996). As bat-eared foxes form monogamous pair-bonds, we expect that perceived risk may differ in the presence and absence of partners. This is a factor that we were unable to test with our data, as foxes appeared to be alone during GUD experiment footage and were generally alone during behavioural observations. Future research should assess the impact of sociality on perceived risk in bat-eared foxes.

This study demonstrates that, at least in our research area, perceived risk in bat-eared foxes varies with lunar phase and human presence. This site presents a relatively unique situation where foxes were habituated to human presence, and therefore care must be taken when comparing to systems where mesopredators are not habituated. Using a GUD approach for predators can be challenging, as foraging experiments rely on constant missed opportunity costs to assess fear. Without quantifying foraging success across different situations, the missed opportunity costs for predators may differ and results may therefore not represent perceived risk. However, here we demonstrate if missed opportunity costs are quantified, a GUD approach can detect subtle differences in perceived risk more readily than vigilance

rates. If foraging success can be quantified to demonstrate constant missed opportunity costs, we recommend this method as a way to assess perceived risk in mesopredators.

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**CHAPTER 3 THE INFLUENCE OF ENVIRONMENTAL AND
SOCIAL FACTORS ON HIGH- AND LOW-COST VIGILANCE IN BAT-
EARED FOXES**



Welch RJ, le Roux A, Petelle MB, Périquet S (2018) Behavioral Ecology and Sociobiology

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3.1 Abstract

Vigilance is commonly used to assess anti-predator behaviour; however, the majority of studies assess only high-cost vigilance, which interrupts any other activities. Low-cost vigilance, by comparison, allows animals to be vigilant whilst engaged in other activities, thereby reducing the cost of vigilance. Here, we investigate the use of high- and low-cost vigilance in relation to environmental and temporal factors in a wild population of the bat-eared fox, a small mesopredator, using behavioural observations of eight habituated animals. We hypothesised that vigilance would increase with tall, dense vegetation, high wind speeds, and low ambient light, and that vigilance would decrease in the presence of conspecifics and over the period of a single observation session. Overall, bat-eared foxes spent significantly more time engaged in low-cost vigilance than in high-cost vigilance. High-cost vigilance increased with vegetation height, in the presence of adult conspecifics and in winter. We suggest these effects are due to impeded lines of sight with increases in vegetation height, increased competition in the presence of conspecifics, and increased social interactions in winter. Low-cost vigilance was highest at the start of observational sessions, and we suggest that this is due to observer effects, as foxes demonstrated increases in both high- and low-cost vigilance specifically towards observers during this time. This study demonstrates that foxes are highly dynamic in their vigilance behaviour. Due to the low predation pressure in the study area, the use of mostly low-cost vigilance may be sufficient in this environment, and thus foxes can allocate more time to other activities. Our results indicate that, in this environment, vigilance may be driven by factors other than predation risk, but that foxes may still respond to certain cues of predation risk. Ultimately, in areas of low predation risk, species susceptible to predation may retain responses to cues of risk, but adapt behaviours to reduce the associated costs.

3.2 Introduction

Foraging theory predicts that animals strive to find the optimal balance in the trade-off between foraging success and predator avoidance (Lima and Dill 1990). Typically, this trade-off can vary depending on food type and availability (Beauchamp 2009), predation risk (Lima and Bednekoff 1999), social dynamics (Elgar 1989; le Roux et al. 2009), vegetation type (Tchabovsky et al. 2001; Devereux et al. 2006), and abiotic factors such as ambient illumination, temperature, and wind speed (Elgar 1989; Carr and Lima 2010; Prugh and Golden 2014). Both vegetation type and abiotic variables can impede visual and auditory senses and have been shown to be important in shaping perceived risk (Biebouw and Blumstein 2003; Hayes and Huntly 2005; Prugh and Golden 2014).

Vigilance levels continue to be a common way of assessing perceived risk (le Roux et al. 2009; Périquet et al. 2010). However, most studies focus on high-cost vigilance, or vigilance that interrupts other activities such as foraging (Lima and Bednekoff 1999). A small number of studies have additionally investigated low-cost vigilance, which enables other behaviours to continue while an animal is scanning for potential threats (Unck et al. 2009; Périquet et al. 2012). Being able to remain vigilant whilst engaged in other behaviours considerably reduces the cost of vigilance, as there is less of a trade-off between the two behaviour types (Illius and Fitzgibbon 1994; Bednekoff and Lima 2005). High-cost vigilance, however, has been shown to be more important in areas of high predation risk (Unck et al. 2009).

Mesopredators occupy a trophic position in which they are not only predators, but are also prey to or killed by larger predators (Ritchie and Johnson 2009). Therefore, mesopredator vigilance patterns might be affected by perceived predation risk, however studies remain rare, and almost no research exists on high- and low-cost vigilance in mesopredators (but see le Roux et al. 2009). For social mesopredators, individuals must balance detection of predators and prey as well as finding mates or conspecifics.

Bat-eared foxes are small (3-5 kg), socially monogamous, largely nocturnal mesopredators that feed predominantly on termites, but also on other insects, rodents and fruits (Nel 1990; Maas and Macdonald 2004). Bat-eared foxes have both diurnal and nocturnal predators, including terrestrial species such as black-backed jackal, and avian threats such as martial eagle (Malcolm 1986), and are common victims in interspecific killings (Palomares and Caro 1999). Previous studies have shown that bat-eared foxes exhibit anti-predator responses in terms of social behaviour (e.g. mobbing) and home-range use (Kamler et al. 2012, 2013), but their vigilance patterns remain unclear (Chapter 2; Welch et al. 2017).

This study aims to investigate high- and low-cost vigilance in bat-eared foxes, specifically focusing on factors potentially influencing vigilance: perceived predation risk, social factors, and observer effects. If perceived predation risk has an effect, we expect vegetation height and density (impaired visibility in dense and high vegetation, Devereux et al. 2006; Embar et al. 2011; Emerson et al. 2011), lunar illumination (impaired visibility during new moon nights, Biebouw and Blumstein 2003) and wind (impaired hearing with high wind speeds, Hayes and Huntly 2005) to have an effect on vigilance. Social factors can also influence vigilance, whereby the presence of conspecifics has been demonstrated to either increase or decrease individual vigilance, due to competition (Shrader et al. 2007) and the 'dilution effect' (Pulliam and Caraco 1984; Dehn 1990) respectively. Bat-eared foxes are known as social foragers (Lamprecht 1979), and we would therefore expect that the presence of conspecifics should lower individual vigilance rather than increasing it. Observers have been shown to influence perceived risk in even habituated animals (Nowak et al. 2014), and in the case of bat-eared foxes, the presence of observers appears to reduce perceived risk (Chapter 2; Welch et al. 2017). However, fine-scale analysis of vigilance patterns might reveal changes throughout the observational period, and bat-eared foxes should be expected to gradually habituate to the presence of an observer over the course of an evening.

Specifically, we predicted that vigilance would increase 1) in higher, denser vegetation, 2) in high wind conditions and 3) in lower levels of ambient light. As bat-eared foxes are social foragers, we hypothesised that vigilance would decrease 4) in the presence of conspecifics and 5) at times of the year when social interactions were more frequent. In addition, we expected that observer effects would be evident in 6) a gradual decrease in observer-directed vigilance over the course of a single observation session.

3.3 Materials and methods

3.3.1. Study site and species

Behavioural observations were conducted at the Kuruman River Reserve (KRR, 28°59'S, 21°49'E) in the southern Kalahari Desert, Northern Cape, South Africa, on a wild but habituated (prior to the start of this study) population of bat-eared foxes. The climate in the region is distinguished by a hot, wet summer period (October-April) and cold, dry winters (May-September). The average annual rainfall for this area is 264 mm (2010-2015, KRR weather station). Based on the descriptions of Low and Rebelo (1996), the vegetation classification for this area is Kalahari Thornveld, and consists of three principal habitats, namely dune areas comprised of undulating dunes and perennial grasses (*Aristida*, *Eragrostis*, *Schmidtii* and *Stipagrostis* spp), flat river terraces with two predominant species, perdebos and driedoring, and dry riverbed, which is predominantly open habitat, interspersed with small camel thorn and black thorn bushes.

Bat-eared foxes are predominantly nocturnal and are relatively common in the study area (several individuals seen on a daily basis). Most large predators were historically extirpated from the area. Black-backed jackals and caracals remain in the area, but are hunted on the surrounding farmlands. Thus, predation pressure in the study area was low, and black-backed jackals and caracals are rarely seen at the study site (three per annum and two per annum respectively, based on unpublished data from 2015) despite a large sampling effort (Kalahari Meerkat Project 2017). Recorded mortality events of study individuals was as a

result of disease (one confirmed case, two suspected). Another predominant cause of death in the area is due to road accidents (R. Welch, pers. obs.). We recorded no mortality events due to predation.

3.3.2. *Behavioural data*

Bat-eared foxes were habituated to observers and followed on foot from approximately 1-2 m while collecting behavioural data (c.f. le Roux et al. 2009). Foxes were collared and observers radio-tracked individuals to find their location prior to behavioural investigations. Observers followed each fox once a week for a period of two hours ('follows' hereafter). Monthly 'all-night follows' were done where reiterative 2-hour follows were conducted throughout the night with 1-hour rest periods in between. A total of 164 follows were completed on eight adult bat-eared foxes (five males, three females) between August 2015 and April 2016. On average, 18 follows were conducted per individual (range: 6-48). Follow data were collected directly on a Samsung handheld tablet using the program Cybertracker (www.cybertracker.org).

To assess anti-predator behaviour, we conducted 10-minute vigilance focals ('focals' hereafter, c.f. Favreau et al. 2014) before and after every follow. A total of 270 focals were completed for the aforementioned eight foxes between August 2015 and April 2016. On average, 34 focals were conducted per individual (ranging from 6-77). Vigilance focal data were collected using voice recordings that were later transcribed and collated. Focals focused solely on vigilance behaviour (bout rate and duration). The possible cause of vigilance (observer, social i.e. other foxes in the vicinity, potential predator, or unknown), the presence of conspecifics (no conspecifics, habituated individuals, unhabituated individuals, or pups), and the type of vigilance (high cost – individuals stopped any other activity to be vigilant with head held high; low cost – individuals vigilant scanning while engaged in other activities like movement or foraging) were recorded (c.f. Unck et al. 2009). For this study, all high-cost vigilance events interrupted foraging, and low-cost vigilance occurred

simultaneously with movement behaviours predominantly, but also marking behaviours, grooming, and consuming large prey items. All food-motivated vigilance events (i.e. clearly listening/looking for food) were discarded. Additionally, focals were assigned a type, either 'pre' or 'post' follow. Pre-focals were recorded at the beginning of observation periods before the follow (approximately 1830h-2000h) and post-focals were recorded after follows. On nights where data were collected throughout the night, all vigilance focals after the first follow were categorised as 'post'. Despite differences in the time of night at which they were recorded, post-focals did not differ in proportion of time vigilant (Kruskal-Wallis, $X^2 = 0.450$, $df = 3$, $P = 0.930$) or rate of vigilance ($X^2 = 1.415$, $df = 3$, $P = 0.702$) and therefore were pooled as post-focal data. Focals shorter than five minutes were discarded from analyses. During the focals, foxes were in constant line of sight and if they were out of sight for more than one minute, the focal was restarted.

3.3.3. *Vegetation effects*

In order to assess the effects of vegetation height and density on vigilance, vegetation data were collected for every vigilant event and additionally for non-vigilant events (when foxes were foraging). Vegetation density was categorised into 'sparse' (bare ground or roots of perennial species more than 1 m apart) or 'dense' (roots of perennial species less than 50 cm and up to 1 m, c.f. Périquet and le Roux 2017). Vegetation height was categorised into 'low' (lower than the eyeline of a moving fox) or 'high' (higher than the eyeline of a moving fox). Vegetation data were collected during focals for each vigilant event. For non-vigilant events, five randomly selected non-vigilant events were selected post-hoc from follow data associated with the focal (i.e. on the same night). These points had associated GPS locations (recorded during the follow) and these locations were visited the following day to describe vegetation using the methods above.

3.3.4. *Abiotic factors*

All focals were assigned environmental variables (lunar illumination index and wind speed) and a temporal variable (season). A lunar illumination index (0-1) was obtained from <http://aa.usno.navy.mil/data/docs/MoonFraction.php> for our study location. For each focal, we assigned a lunar illumination index equal to the lunar illumination if the moon was above the horizon at the time of the observation and zero otherwise. Nights with full cloud cover were removed from analyses, as this could have confounded lunar illumination. Wind speeds (0-6 m/s) were extracted from data collected every hour at a weather station on site. Seasons were categorised as spring (September-November), summer (December-February), autumn (March-May), and winter (June-August).

3.3.5. *Statistical analyses*

All analyses were performed in R (R Development Core Team 2016), using the lme4 package (Bates et al. 2015). Data exploration was carried out and model assumptions verified by following the protocol described in Zuur et al. (2010) and Zuur and Ieno (2016). Graphs were created using the ggplot2 package (Wickham 2009) in R and report actual data rather than predicted model results. All graphs show mean and standard error unless stated otherwise.

3.3.5.1 Behavioural data

To investigate whether bat-eared foxes spent a greater proportion of their vigilance time invested in low-cost vigilance, we used a Chi-square goodness of fit test. Expected proportions were based on the assumption that vigilance would be divided evenly between low- and high-cost vigilance.

3.3.5.2 Vegetation effects

To assess how the probability of high- and low-cost vigilance changed with vegetation height and density, we used generalised linear mixed effects models (GLMMs) with binomial error

distribution and a logit link (logistic regression) with the response variable being set to vigilant (1) or not vigilant (0). Vegetation height (high or low) and vegetation density (dense or sparse) were set as main effects. Individual fox was included as a random effect.

3.3.5.3 Abiotic factors

We used GLMMs with a binomial error distribution and a logit link to investigate how time spent in high-cost vigilance (as a proportion of focal time) varied with lunar illumination, wind speed, season, and focal type. Individual fox was included as a random effect. Interactions between variables were investigated, however these were non-significant and therefore removed from models. The analyses were repeated for low-cost vigilance. We used GLMMs with a Poisson error distribution and a log link to investigate how the rate of high- and low-cost vigilance varied with the same abiotic factors as already described. To correct for over-dispersion an observation level random effect was added (Elston et al. 2001; Harrison 2014).

3.3.5.4 Social effects

To compare how proportion of time spent in high- and low-cost vigilance, and high- and low-cost vigilance rate varied with the presence of conspecifics, we selected a random sample of 20 vigilance focals with no conspecifics present and compared them to all vigilance focals with habituated conspecifics present ($n = 16$), unhabituated conspecifics present ($n = 14$), and pups present ($n = 21$) using a Kruskal-Wallis test (as data were not normally distributed). Post-hoc analyses were applied using Wilcoxon rank-sum tests for each pairwise combination and a Bonferonii correction was applied.

3.3.5.5 Observer-directed vigilance

We used GLMMs with a binomial error distribution and a logit link to investigate how both high- and low-cost observer-directed vigilance (as a proportion of focal time) varied with focal type including individual fox as a random effect. We used GLMMs with a Poisson error distribution and a log link to investigate how the rate of high- and low-cost observer directed

vigilance varied with focal type including individual fox as a random effect. To assist with over-dispersion an observation level random effect was added (Elston et al. 2001; Harrison 2014).

3.4 Results

3.4.1. Behavioural data

A total of 270 vigilance focals were recorded, including 140 pre-focals and 130 post-focals. Within these focals, 1526 vigilant events were documented, to which 63 % the cause was unknown, 11 % of events were caused by conspecifics, 23 % were caused by human observers, and the remaining 3 % were caused by non-threatening heterospecific species (e.g. common duiker, *Sylvicapra grimmia*). Bat-eared foxes spent a significantly higher proportion of time invested in low-cost vigilance than in high-cost vigilance ($X^2 = 6.760$, $df = 1$, $P < 0.01$), with high-cost vigilance accounting for only 37 % of time spent vigilant.

3.4.2. Vegetation effects

The probability of engaging in high-cost vigilance decreased in low vegetation, but vegetation density had no effect (Table 3.1). Neither vegetation height nor density had a significant effect on the probability of engaging in low-cost vigilance (Table 3.1).

3.4.3. Abiotic factors

Lunar illumination and wind speed did not have a statistically significant effect on the proportion of time spent in either high- or low-cost vigilance (Table 3.1). Season had no impact on the proportion of time spent in low-cost vigilance, but the proportion of time spent in high-cost vigilance was lower in spring than in winter (Table 3.1). The proportion of time spent engaged in low-cost, but not high-cost, vigilance was greater for pre-focals when compared to post-focals (Table 3.1; Figure 3.1).

Table 3.1. Model coefficients (β) illustrating the relationship between high- and low-cost vigilance with vegetation, abiotic factors, and observers for bat-eared foxes in the Kalahari Desert. For categorical variables, the intercept denotes the reference level category (high vegetation, dense vegetation, winter, and post-focal respectively).

Factors	Variables	β	SE	Z	P
Vegetation					
High-cost	Intercept	0.235	0.473	0.497	= 0.619
	low height	-0.699	0.198	-3.524	< 0.001
	sparse density	0.194	0.195	0.997	= 0.319
Low-cost	Intercept	-0.052	0.349	-0.151	= 0.880
	low height	0.151	0.200	0.758	= 0.449
	sparse density	-0.333	0.207	-1.610	= 0.107
Abiotic factors					
High-cost					
<i>Proportion of time</i>	Intercept	-3.704	0.431	-8.600	< 0.001
	moon	-0.788	0.486	-1.621	= 0.105
	wind	-0.280	0.163	-1.715	= 0.086
	spring	-1.161	0.469	-2.473	< 0.05
	summer	-0.944	0.542	-1.743	= 0.081
	autumn	-1.259	0.822	-1.532	= 0.125
	pre-focal	-0.406	0.351	-1.155	= 0.248
<i>Rate</i>	Intercept	-4.782	0.209	-22.840	< 0.001
	moon	-0.388	0.255	-1.524	= 0.128
	wind	-0.054	0.085	-0.640	= 0.522
	spring	-1.031	0.234	-4.407	< 0.001
	summer	-0.909	0.272	-3.344	< 0.001
	autumn	-1.131	0.425	-2.661	< 0.01

	pre-focal	-0.152	0.180	-0.847	= 0.397
Low-cost					
<i>Proportion of time</i>	Intercept	-5.226	0.535	-9.765	< 0.001
	moon	0.338	0.587	0.576	= 0.565
	wind	0.358	0.193	1.853	= 0.064
	spring	-0.897	0.575	-1.559	= 0.119
	summer	-1.158	0.677	-1.710	= 0.087
	autumn	-1.591	1.007	-1.579	= 0.114
	pre-focal	1.217	0.427	2.853	< 0.01
<i>Rate</i>	Intercept	-6.059	0.280	-21.680	< 0.001
	moon	0.173	0.307	0.563	= 0.573
	wind	0.133	0.100	1.336	= 0.181
	spring	-0.368	0.298	-1.236	= 0.216
	summer	-0.407	0.352	-1.154	= 0.249
	autumn	-0.718	0.530	-1.354	= 0.176
	pre-focal	0.794	0.222	3.570	< 0.001
Observer effects					
High-cost					
<i>Proportion of time</i>	Intercept	-8.178	0.496	-16.483	< 0.001
	pre-focal	0.817	0.427	1.912	= 0.056
<i>Rate</i>	Intercept	-7.911	0.377	-20.990	< 0.001
	pre-focal	0.637	0.302	2.110	< 0.05
Low-cost					
<i>Proportion of time</i>	Intercept	-8.448	0.449	-18.950	< 0.001
	pre-focal	1.759	0.472	3.726	< 0.001
<i>Rate</i>	Intercept	-8.122	0.292	-27.820	< 0.001
	pre-focal	1.310	0.298	4.390	< 0.001

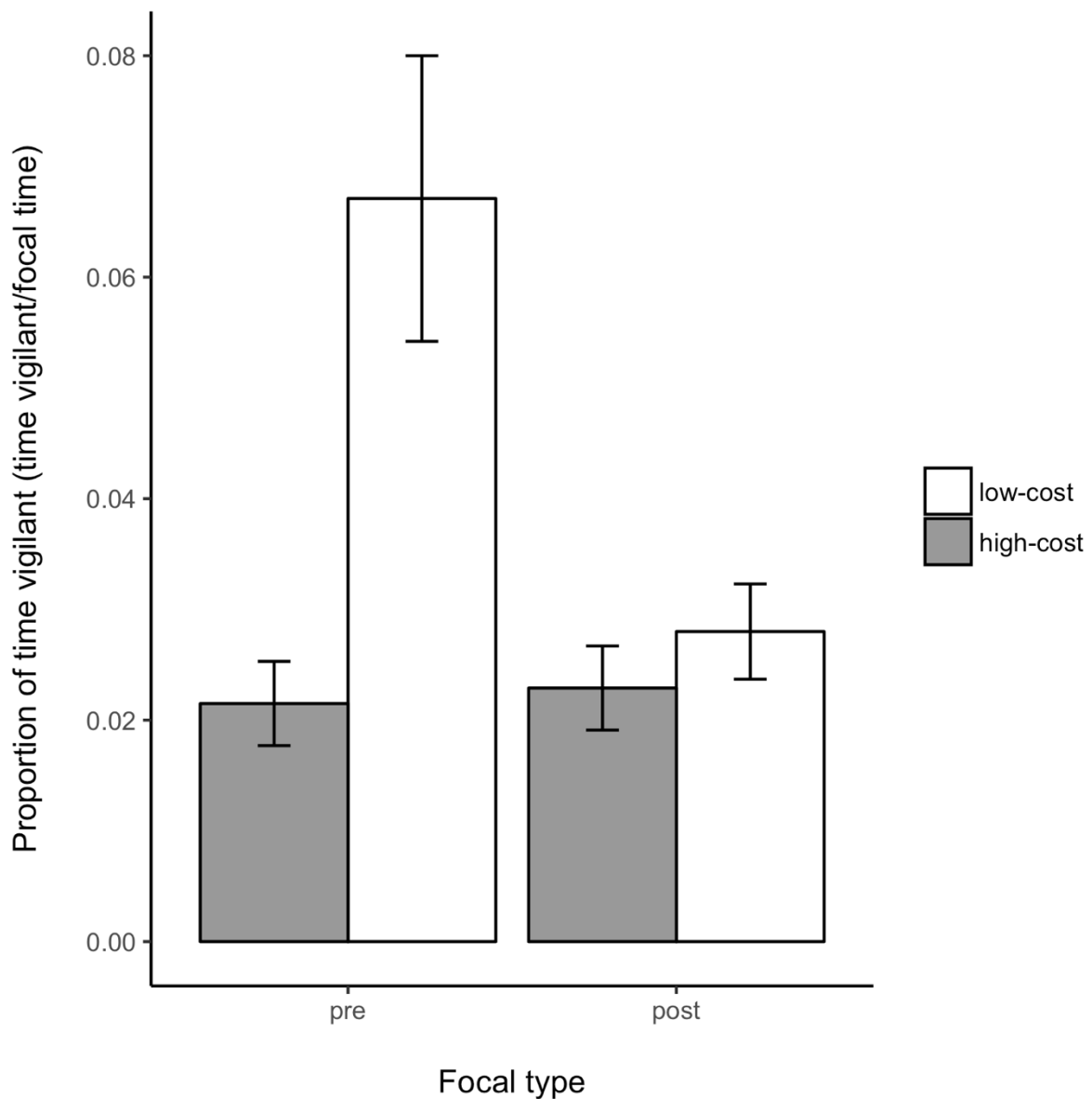


Figure 3.1. Bat-eared fox high- and low-cost vigilance (as a proportion of focal time) before and after 2-hour observation sessions (error bars represent standard error).

Lunar illumination and wind speed did not have a statistically significant effect on high- or low-cost vigilance rate. Season did not have a statistically significant effect on low-cost vigilance rate, but high-cost vigilance rate was lower in spring, summer and autumn than in winter (Table 3.1; Figure 3.2). High-cost vigilance rate was not affected by focal type, but the

rate of low-cost vigilance was greater for pre-focals (0.008 ± 0.001 , mean \pm SE) when compared to post-focals (0.003 ± 0.001 ; Table 3.1).

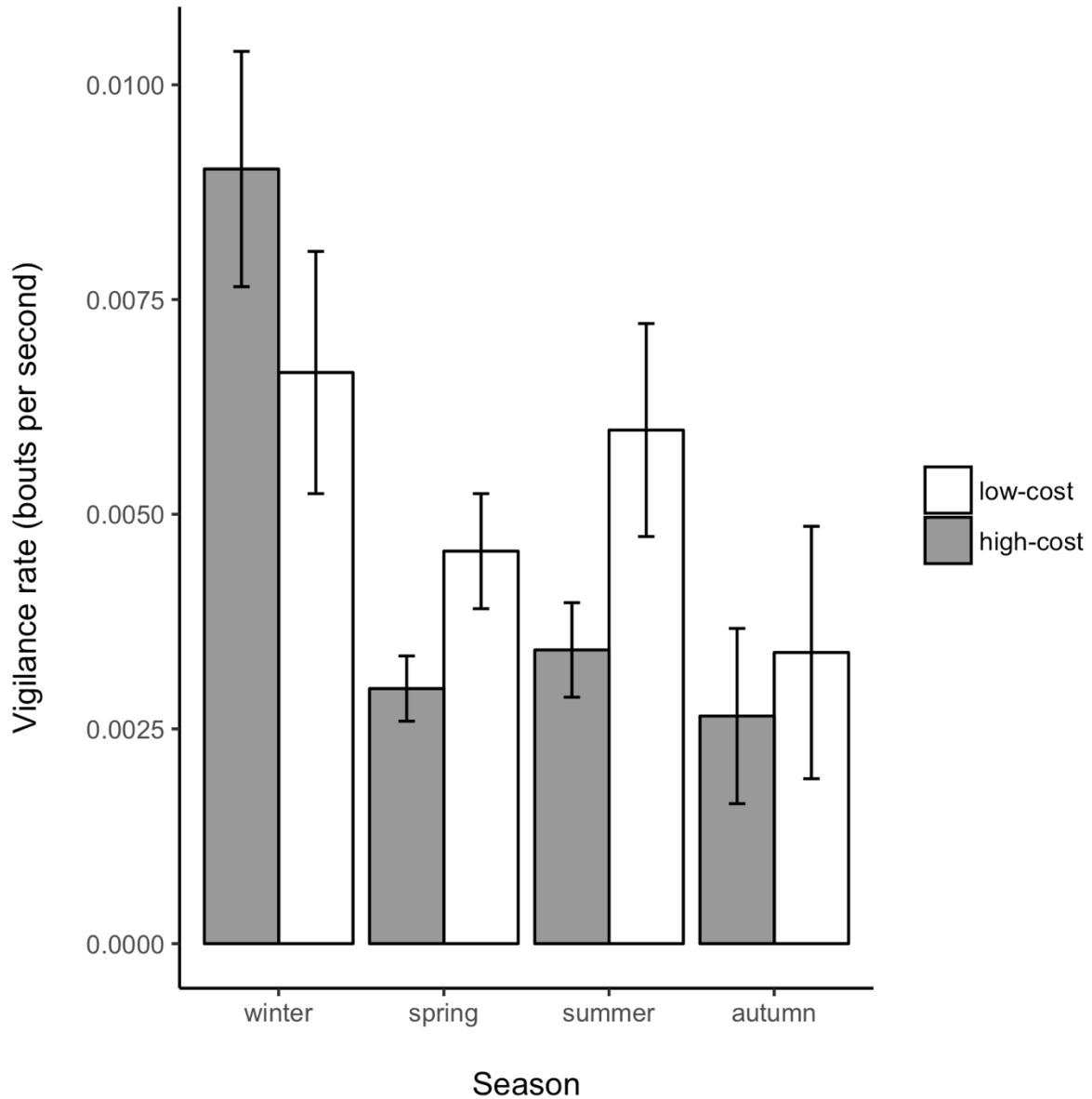


Figure 3.2. Bat-eared fox high- and low-cost vigilance rate (bouts of vigilance per second) across seasons (error bars represent standard error).

3.4.4. Social effects

The proportion of time invested in high- ($X^2 = 6.606$, $df = 3$, $P = 0.856$) and low- ($X^2 = 5.033$, $df = 3$, $P = 0.169$) cost vigilance did not vary among different social contexts. However, high-

cost vigilance rate varied significantly between different social contexts ($X^2 = 14.636$, $df = 3$, $P < 0.01$), being highest in the presence of habituated conspecifics (0.011 ± 0.006) vs. no conspecifics (0.003 ± 0.005 ; $W = 277$, $df = 34$, $P < 0.001$), and vs. pups (0.002 ± 0.005 ; $W = 262$, $df = 35$, $P < 0.01$; Figure 3.3a). There was no difference in low-cost vigilance rate among the different social contexts (habituated conspecifics 0.002 ± 0.008 , unhabituated conspecifics 0.002 ± 0.003 , pups 0.008 ± 0.012 and alone 0.005 ± 0.015 ; $X^2 = 3.425$, $df = 3$, $P = 0.331$; Figure 3.3b).

3.4.5. *Observer-directed vigilance*

The proportion of time engaged in high-cost observer-directed vigilance did not vary between the two focal types. High-cost observer-directed vigilance rate was higher in the pre-focal (Table 3.1; Figure 3.4). The proportion of time engaged in low-cost observer-directed vigilance was higher in the pre-focal (0.008 ± 0.002 vs 0.003 ± 0.001 ; Table 3.1), as was low-cost observer-directed vigilance rate (Table 3.1; Figure 3.4).

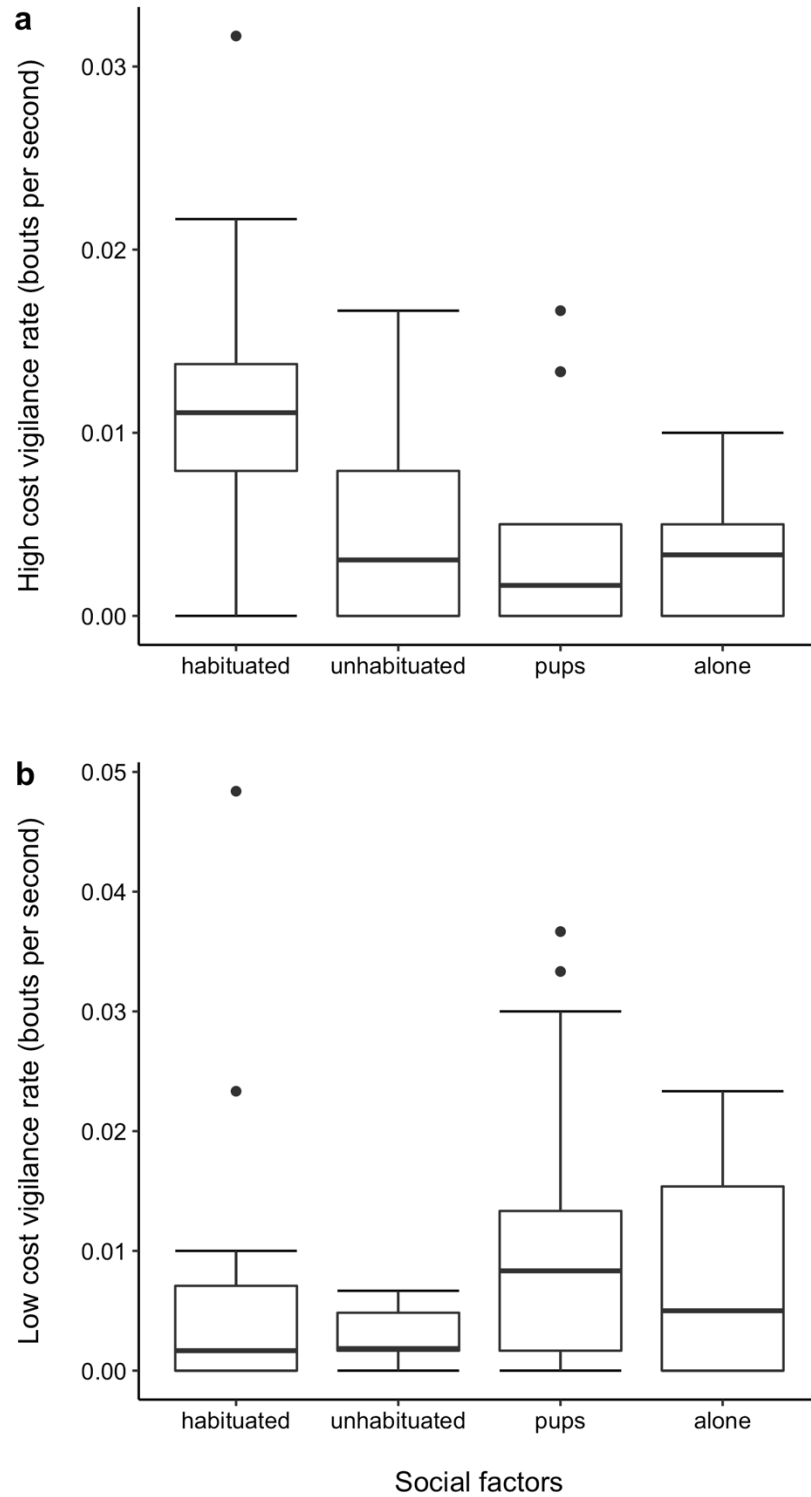


Figure 3.3. Bat-eared fox a) high-cost vigilance rate and b) low-cost vigilance rate in the presence and absence of conspecifics. Plot represent medians with interquartile range, whiskers represent 1.5 x interquartile range and outliers are points outside this range, Y axes are truncated so data are presented within text.

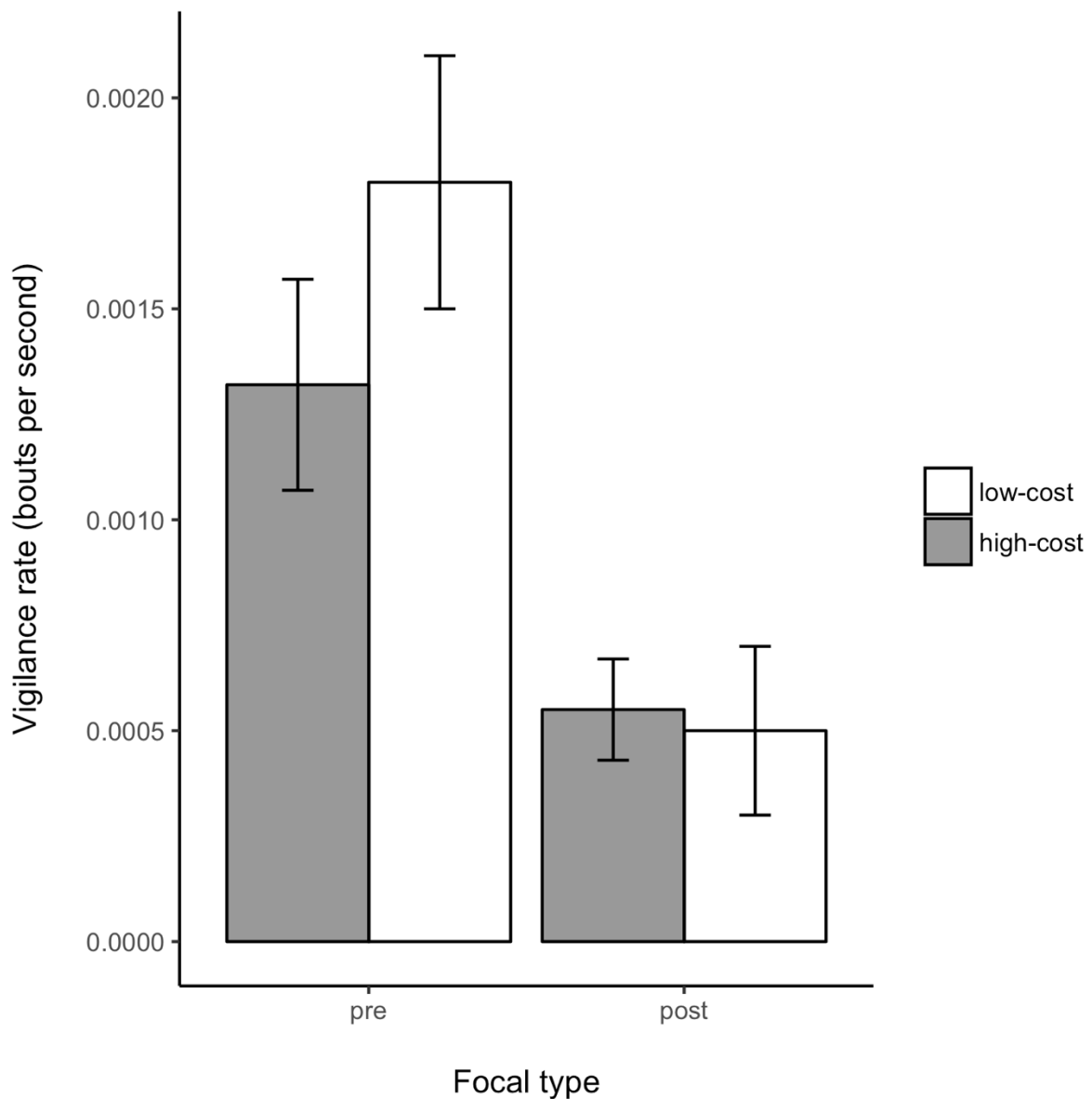


Figure 3.4. Bat-eared fox high- and low-cost observer-directed vigilance rate (bouts per second) before and after 2-hour observation sessions (error bars represent standard error).

3.5 Discussion

Our results showed that bat-eared foxes invested most of their vigilance effort into low-cost vigilance. High-cost vigilance has been shown to be more important in areas where perceived risk is greater (Unck et al. 2009), and therefore the use of predominantly low-cost vigilance may indicate that perceived risk is generally low in this environment, as suggested

by the absence of any recorded mortalities due to predation. Due to low predation pressure, low-cost vigilance may be sufficient, and thus foxes can allocate more time to foraging. Bat-eared foxes are unlikely to have lost appropriate anti-predator behaviours altogether, despite low predation pressure, and the use of high-cost vigilance under certain situations (in tall vegetation, in the presence of adult conspecifics, during winter and towards observers at the start of observation sessions) may, however, suggest these factors are associated with greater perceived risk.

Tall vegetation significantly increased the probability of high-cost vigilance, but not of low-cost vigilance, which suggests bat-eared foxes do not associate areas of tall vegetation with sites of refuge, as found for other fox species (Hall et al. 2013). As vegetation height categories were associated with line of sight, we consider that greater vigilance in higher vegetation is due to obscured line of sight and thus difficulty in detecting potential dangers, and similar patterns have been shown in other studies (Bednekoff and Blumstein 2009). Increased vigilance in tall vegetation suggests that, despite the lack of potential predator sightings, ambush predators may still pose as a perceived threat to bat-eared foxes, or that foxes still respond to certain cues of predation risk, despite predators being largely absent. Previous studies have highlighted that even after the loss of predators, prey may still retain appropriate anti-predator behaviours (Blumstein 2006). Increases in vigilance with vegetation height may also have been associated with the presence of hidden conspecifics.

Previous studies have reported that both lunar illumination and wind speed affect perceived risk of predation in certain species e.g. tamar wallabies (Biebouw and Blumstein 2003) and brush-tailed rock-wallabies (*Petrogale penicillata*, Carter and Goldizen 2003). Additionally, recent research suggests that bat-eared foxes rely on hearing as their predominant sense (Renda and le Roux 2017), but that wind speed does not influence their ability to detect prey (S. Renda et al. unpubl. data). We therefore suggest auditory processes may be involved in the detection of predators but that the generally low wind speeds (0-6 km/h) recorded during

our observations were not enough to significantly impair their capability of detecting potential predators.

High-cost vigilance rate, but not low-cost, was influenced by social factors and bat-eared foxes were more vigilant in the presence of habituated conspecifics than they were when foraging alone or with pups. Previous work has highlighted that increased vigilance in the presence of conspecifics may be related to competition over food and conspecific monitoring (Beauchamp 2001, 2009; Lung and Childress 2007; Shrader et al. 2007), and social vigilance has been highlighted to be particularly pertinent in areas of low predation pressure (Hirsch 2002). Lower levels of vigilance in the presence of pups suggests that predation risk may not be the biggest driver of vigilance in areas with low predation pressure. If predation risk had posed a considerable threat, we would have expected increased vigilance in the presence of pups as demonstrated in previous studies (Lung and Childress 2007; Lashley et al. 2014). We suggest that pups did not compete over food with adults, as adults regularly provisioned them with food, and their survival influences adult fitness (Trivers 1972). Additionally, our results showed vigilance was greater in winter. We suggest this may be related to increased social interactions during this time (R. De Bruin et al. unpubl. data). Bat-eared foxes are monogamous and pair bonding occurs during winter months (Nel 1984), and due to the foraging behaviour of foxes, no trade-off is experienced between foraging and mate-guarding (Wright et al. 2010). We therefore suggest that bat-eared foxes may perceive greater resource competition during this time and increase vigilance in the presence of conspecifics for mate guarding/seeking extra pair mating, or possibly due to increased competition in the presence of conspecifics (Beauchamp 2001). Unfortunately, as most partners were unhabituated at this study site, pairs were rarely observed foraging together in our presence making the validation of this hypothesis difficult with our data. We therefore recommend that future studies test this idea with pairs of habituated foxes. Furthermore, our results indicated that winter was the only season where high-cost was greater than low-cost vigilance and we suggest this is due to greater day-time activity and foraging during this

season (Lourens and Nel 1990). Our results indicate that mate association or competition may be some of the costliest activities in an environment with low predation pressure.

Greater low-cost vigilance was observed during the pre-focal (at the start of observation sessions, before the follow) compared to post-focals. Other studies have indeed reported that time of day or night changes in vigilance patterns can be attributed to predation risk in birds, in areas where predation risk is evident (McNamara and Houston 1986), and in marsupials, in areas where predation risk is not evident e.g. quokkas (*Setonix brachyurus*, Blumstein et al. 2001). At our study site, large predators are absent, and jackals and caracals are persecuted in the surrounding areas, therefore presence is extremely rare. This implies that the observed increased vigilance early in the night may be related to bat-eared fox cautiousness towards observers. Both high- and low-cost observer-directed vigilance was greater during the pre-focal than the post-focal, indicating that our initial presence certainly had an effect on foxes. The presence of observers close to habituated animals is said to be neither positive nor negative, but studies have highlighted that observer effects may indeed occur, albeit subtle and difficult to detect (McDougall 2012; Nowak et al. 2014). Therefore, the general increase in low-cost vigilance observed in pre-follow focals may have been an artefact of our presence, as bat-eared foxes may have been generally wary in our presence initially and subsequently relaxed with time (McDougall 2012). Previous studies have demonstrated that the presence of observers on habituated animals may or may not directly alter the behaviours being assessed (Crofoot et al. 2010; McDougall 2012), and this is something that should be considered when interpreting the results from this study.

In conclusion, our study reveals that in areas with low predation pressure, vigilance behaviour is concentrated towards low-cost vigilance, with the use of high-cost vigilance under certain conditions. This study demonstrates that vigilance can indeed be investigated in habituated animals, but that care must be taken to ensure that data collection commences at a point when animals are fully relaxed around human observers. Previous studies have

demonstrated that species can retain appropriate anti-predator behaviours long after the loss of predators from an ecosystem (Blumstein 2006), and thus vigilance is unlikely to be completely lost in an environment with low (but possible) predation risk. Mesocarnivores (and prey in general), in areas of low predation risk, may retain responses to certain cues of risk, but may adapt behaviours to reduce the associated costs. Future studies should aim to assess the use of high- and low-cost vigilance for bat-eared foxes in areas with greater predation risk to assess whether the partitioning of time to each type of vigilance differs from this study, and evaluate how high- and low-cost vigilance may vary with spatiotemporal factors. We conclude that the drivers of vigilance in areas with low predation risk may be more related to factors other than predation risk, such as the presence of conspecifics and observers, but that foxes may still respond to certain cues of predation risk.

3.6 Acknowledgements

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3.7 References

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**CHAPTER 4 INDIVIDUAL DIFFERENCES IN PERSONALITY AND
PLASTICITY IN BAT-EARED FOX VIGILANCE BEHAVIOUR**



Welch RJ, Petelle MB, Périquet S, le Roux A (Under Review) Animal Behaviour

4.1 **Abstract**

Vigilance behaviour is influenced by both intrinsic and extrinsic factors, and variability in vigilance may affect individual fitness due to the associated costs of this behaviour. We used a behavioural reaction norm approach to assess differences in personality and plasticity in vigilance behaviours across lunar illumination, wind speed, and temperature in a small mesocarnivore, the bat-eared fox. We found little evidence of different personality or plasticity in overall vigilance behaviours of individuals. However, when separated into high- and low-cost vigilance, individual differences became apparent. Foxes behaved similarly with regards to the duration of high-cost vigilance (vigilance that interrupts other activities), but exhibited personality differences in the rate of high-cost vigilance. Comparatively, foxes demonstrated personality differences in both the rate and duration of low-cost vigilance (vigilance that occurs simultaneously with other activities). We also found individual differences in plasticity for high-cost vigilance rates and low-cost vigilance (both rate and duration) across environmental factors. Low-cost vigilance may serve multiple functions and does not preclude other behaviours, and we suggest that due to lower costs, we may see the adaptive emergence of different strategies in this behaviour. We suggest that the presence of individual differences in high-cost vigilance may be attributed to the areas low predation pressure, which is unlikely to constrain individual variation in behaviours. Additionally, this study highlights the importance of investigating different types of vigilance behaviours, as combining vigilance types may mask salient individual differences in personality and plasticity patterns.

4.2 **Introduction**

In contrast to morphological phenotypes, behavioural phenotypes can be rapidly adapted to fluctuating environments, where temporal and environmental cues can guide the expression of a particular behaviour (Hazlett 1995; Mery and Burns 2010; Snell-Rood 2013). From an evolutionary perspective, behavioural traits should be flexible to maximise fitness across

spatiotemporal environmental variation, and enable individuals to respond accordingly to environmental changes (Hazlett 1995). Such behavioural plasticity is demonstrated across a wide range of taxa and behaviours. For example, activity levels may vary with lunar illumination (Mukherjee et al. 2009; Cozzi et al. 2012), and vigilance behaviours co-vary with factors such as habitat cover, lunar illumination, and wind speed (Carter and Goldizen 2003; Jayakody et al. 2008). Previously, individual behavioural variation was considered as non-adaptive 'noise' around a behavioural mean (Wilson 1998). However, the ecological forces that lead to morphological and behavioural variations in co-existing species and populations (niche specialisation), can likewise act upon individuals within the same population (Wilson 1998). Individual strategies may be evident in personality differences – i.e. consistent individual differences in behaviour across time or contexts (Sih et al. 2004; Dingemanse et al. 2007), and in plasticity – i.e. individual differences in response to environmental variability (Dingemanse et al. 2010). For example, personality differences may be represented by the presence of consistently bold or shy individuals in a population, and plasticity differences may be represented by individual differences in behavioural responses to varying levels of predation.

Favreau et al. (2014) state that two contrasting hypotheses explain the presence or absence of individual differences in personality and plasticity in specific populations. The ecological hypothesis suggests that individuals experiencing similar ecological circumstances (e.g. habitat or predation risk) should behave in a similar manner (i.e. absence of different personalities and plasticity). For example, when constraints are high (foraging in large groups, poor-quality patches, or under high risk of predation), individuals behave in a similar manner, sharing the same optimal behavioural phenotypes (Favreau et al. 2014). Behaving in the same, optimal manner reduces individuals' risk of making mistakes. Thus, significant ecological pressures (e.g. high predation pressure or low food availability) are likely to constrain variation, as will high costs of a particular behaviour. In contrast to this, the behavioural hypothesis describes that even if similar ecological constraints are experienced,

individual animals should demonstrate behavioural variation (differences in personality) and additionally may vary in response to environmental factors (differences in plasticity), improving individual fitness through variability, regardless of the environmental context. Support for both theories exist in nature: female eastern grey kangaroos (*Macropus giganteus*) behave similarly in response to external factors (both social and ecological, Favreau et al. 2014), supporting the ecological theory. By contrast, red knots (*Calidris canutus islandica*) demonstrate plasticity differences in levels of vigilance in response to perceived predation risk, whereby certain individuals are highly plastic in levels of vigilance depending on perceived risk, whereas other individuals are constrained in their plasticity (Mathot et al. 2011). Development of this behavioural variation is thought to be a way of managing environmental uncertainty (Mathot et al. 2012).

Anti-predator behaviours – directly impacting death or survival – are under extreme selection pressure (Lima and Dill 1990). Not only must predators be detected and avoided, but other behaviours need to be maintained for an individual to increase fitness. Vigilance, in its broadest sense, is described as – ‘a motor act which corresponds to a head lift interrupting the ongoing activity, and followed by a visual scanning of the environment’ (Quenette 1990). Thus, vigilance explicitly conflicts with any other activity, leading to a trade-off between increased vigilance and other functions such as foraging, mating, and socialising. However, such ‘high-cost’ vigilance is not the only manner in which prey animals can detect predators. The use of both high- and low-cost vigilance (which occurs simultaneously with other behaviours, such as moving or chewing) has been demonstrated in a number of species including yellow mongoose (le Roux et al. 2009), ungulates (Illius and Fitzgibbon 1994; Blanchard and Fritz 2007; Périquet et al. 2012), Cape ground squirrels (*Xerus inauris*, Unck et al. 2009), and bat-eared foxes (Welch et al. 2018). High-cost vigilance is predicted to be more common in high-risk areas (Lima and Bednekoff 1999; Unck et al. 2009). In this context, individuals would be predicted to behave in a similar manner, to avoid predation (Lima and Bednekoff 1999). Comparatively, low-cost vigilance may be a mere precursor to

high-cost vigilance (Lima and Bednekoff 1999), and the lack of behavioural trade-offs suggest that engaging in low-cost vigilance does not necessarily relate to the riskiness of a specific time or place (Blanchard and Fritz 2007). Individuals may therefore exhibit more variability in low-cost vigilance, in relation to intrinsic rather than extrinsic factors.

A previous study demonstrated the effects of environmental variables on bat-eared fox vigilance at the population level, where lunar illumination and wind speed had little effect on population-level vigilance (Welch et al. 2018). However, even in the absence of population-level plasticity, patterns may be discerned at the individual level (Nussey et al. 2007). Here we therefore aim to assess whether individual differences in personality and plasticity exists in vigilance behaviours of the bat-eared fox.

We first investigated the effect of a change in environmental conditions on overall vigilance (pooling high- and low-cost vigilance together). Specifically, we assessed for the presence of individual differences in personality and plasticity across lunar illumination, wind speed, and temperature using a behavioural reaction norm approach (Nussey et al. 2007; detailed in methods). As overall vigilance may mask patterns in different types of vigilance, we repeated investigations for both high- and low-cost vigilance separately. We predicted that high-cost vigilance would not vary in this population because overall predation risk was low, i.e. individual foxes would not exhibit different personalities or vary in their responses to environmental variation, conforming to the ecological hypothesis (Favreau et al. 2014). Low-cost vigilance however, may vary significantly among individuals as it is not necessarily associated with immediate danger, i.e. individual foxes will exhibit different personalities and vary in their response to environmental variation, as individuals may differ in motivation or state, thus conforming to the behavioural hypothesis (Favreau et al. 2014).

4.3 Materials and methods

4.3.1. *Study site and species*

We conducted behavioural observations on a wild, habituated population of bat-eared foxes in the Kuruman River Reserve (KRR, 28°59'S, 21°49'E) in the southern Kalahari Desert, Northern Cape, South Africa. Summers (October-April) are characterised as hot and wet, and winters (May-September) characterised as cold and dry. The average annual rainfall for this area is 264 mm (2010-2015, KRR weather station). The vegetation for this region is classified as Kalahari thornveld (Low and Rebelo 1996). For a more detailed description of the surrounding vegetation see Welch et al. (2017) or Périquet and le Roux (2017).

Predation pressure is generally low, with large predators absent for over 100 years, whilst smaller predators such as black-backed jackal and caracal are present, but rare.

4.3.2. *Behavioural observations*

From August 2015 to April 2016, we followed individual bat-eared foxes on foot at a distance of approximately 1-2 m. An observer followed each fox once a week for a 2-hour period ('follows' hereafter). Once a month, 'all-night follows' were conducted, consisting of 2-hour follows repeatedly throughout the night with 1-hour periods in between where no data were collected. Additionally, vigilance focals ('focals' hereafter) were conducted on eight adult foxes (five males, three females). Focals consisted of 10-minute observation periods before and after every 2-hour follow (classified as 'pre' and 'post' focals). For all-night follows, all focals after the first follow were categorised as post-follow. During focals, the start and end of all vigilance bouts were voice-recorded and later transcribed to determine vigilance rates and durations. Each bout was classified as high- or low-cost, and the target of directed glances was specified (observer, conspecific, unknown, etc.). High-cost vigilance was defined as the individual lifting its head and stopping foraging, while low-cost vigilance was when an individual lifted its head but continued to engage in another activity (e.g. movement

or handling prey items, c.f. Unck et al. 2009; Welch et al. 2018). A total of 225 vigilance focals were completed. On average, 28 focals were conducted per individual (range: 5-63).

4.3.3. *Environmental data collection*

We assigned environmental variables (lunar illumination index, wind speed, and temperature) to each focal. We acquired lunar illumination indices, on a scale of 0-1 (where 0 indicates total darkness and 1 indicates brightest nocturnal illumination conditions), from <http://aa.usno.navy.mil/data/docs/MoonFraction.php> for our study location. If the moon was below the horizon at the time of the observation, we assigned a lunar illumination index of zero-value. Overcast nights were removed from analyses to accurately assess the impact of lunar illumination. A weather station on site recorded wind speeds (0-6 m/s) and temperatures (1.5 °C to 37.4 °C) every hour.

4.3.4. *Statistical analyses*

The presence of different individual personalities and plasticity in behaviour are demonstrated using a behavioural reaction norm approach (Réale et al. 2007; Dingemanse et al. 2010), where behavioural traits are plotted against environmental variables. Using this approach, four scenarios are possible: 1) non-existent personality and individual plasticity demonstrated by no differences in intercepts or slopes, 2) personality but no among-individual differences in plasticity, illustrated by different intercepts with parallel slopes in response to environmental factors, 3) individual differences in plasticity but no personality demonstrated by similarities in intercept but variation in slope, and 4) personality and individual differences in plasticity illustrated by differences in both intercept and slope (Nussey et al. 2007; Dingemanse et al. 2010).

All statistical analyses were performed in R (R Development Core Team 2016). We used generalised linear mixed effects models (GLMMs), in lme4 package (Bates et al. 2015), to assess for individual differences in personality and plasticity of behavioural responses. We

used a Poisson error distribution with a log link to model duration (number of seconds vigilant within a 10-minute period) engaged in and rate (number of bouts within a 10-minute period) of overall, high-cost and low-cost vigilance with environmental factors (lunar illumination, wind speed, and temperature) and focal type (pre or post) as fixed effects. While some post focals occurred later in the night (during full-night follows), we were able to pool the data from all post focals. These focals did not differ in duration of vigilance (Kruskal-Wallis, $X^2 = 0.450$, $df = 3$, $P = 0.930$) or rate of vigilance ($X^2 = 1.415$, $df = 3$, $P = 0.702$). We included individual fox identity and observer identity as random effects in the GLMMs. An additional observation level random effect was added to duration models to assist with overdispersion (Elston et al. 2001; Harrison 2014). Only vigilance focals that were recorded for the full 10 minutes were included in analyses. Temperature data were centered to assist with convergence. Moon and wind data were not centered as data were skewed, and thus there was little benefit in the standardisation of these variables. To assess for personality differences, repeatability was estimated for the six random intercept models using the rptPoisson for count data from the package rptR (Stoffel et al. 2017) with 1000 permutations. Repeatability is used to measure personality (measured on a scale of 0-1), and is a value of how much the phenotypic variance is attributed to individual differences (i.e. whether or not individuals have different intercepts).

To investigate for individual differences in plasticity, we fit random slope models for each environmental variable separately (also known as individual by environment -I x E- models) and compared these to random intercept models using Log-likelihood ratio tests (LRTs) to assess for the significance of adding environmental variables into random effects. Model assumptions were verified following the procedure described in Zuur et al. (2010) and Zuur and Ieno (2016) using the R package DHARMA (Hartig 2017).

4.4 Results

4.4.1. *Personality (consistent individual differences)*

We found no individual fox repeatability for duration spent in overall vigilance across environmental variables ($r = 0.017$, $SE = 0.025$, $P = 0.200$), or for the rate of overall vigilance ($r = 0.033$, $SE = 0.035$, $P = 0.075$). Similarly, there was no repeatability for the duration of time in high-cost vigilance across environmental variables ($r = 0.039$, $SE = 0.040$, $P = 0.091$). However, we did find low, but significant repeatability for the rate of high-cost vigilance ($r = 0.104$, $SE = 0.071$, $P < 0.01$), indicating the presence of different personalities. We found low repeatability across environmental variables for duration ($r = 0.090$, $SE = 0.063$, $P < 0.05$) and rate ($r = 0.081$, $SE = 0.066$, $P < 0.01$) engaged in low-cost vigilance, indicating the presence of difference personalities for both measures.

4.4.2. *Plasticity (individual differences in response to environmental variability)*

We did not find any significant I x E interactions for any environmental variable for the duration of overall vigilance (Table 4.1; Figure 4.1 a-c), indicating the absence of individual differences in plasticity across environmental fluctuations. For rate of overall vigilance, we found a significant interaction between individual and lunar illumination, but not for wind speed or temperature (Table 4.1; Figure 4.1 d-f).

Similarly, we also found no individual differences in plasticity in duration of high-cost vigilance for lunar illumination, wind speed, or temperature (Table 4.1; Figure 4.2 a-c). We did, however, find evidence of individual differences in plasticity in the rate of high-cost vigilance across lunar illumination, wind speed, and temperature (Table 4.1; Figure 4.2 d-f), indicating that individuals demonstrated different patterns of high-cost vigilance rate as lunar illumination, wind speed and temperature varied.

For the duration of time engaged in low-cost vigilance, we found significant I x E interactions between individual and wind speed, and between individual and temperature, but not for

lunar illumination (Table 4.1; Figure 4.3 a-c), indicating individual variation in plasticity for the duration of time engaged in low-cost vigilance as wind and temperature varied. For low-cost vigilance rate, we found significant I x E interactions between individuals and all three environmental variables, and thus individuals demonstrated differences in plasticity for low-cost vigilance rate across lunar illumination, wind speed, and temperature (Table 4.1; Figure 4.3 d-f).

Table 4.1. Generalised linear mixed-effects models (GLMMs) with and without I x E interactions with lunar illumination, wind speed and temperature on the duration and rate bat-eared foxes engaged in overall vigilance, as well as high-cost and low-cost vigilance (all models also include focal type as a fixed effect). Significance was tested with log-likelihood ratio tests (LRT). Significant interactions between individual and environment are in bold.

Factors	Models	Log-likelihood	df	LRT	P
Overall vigilance					
<i>Duration</i>					
moon	M1.1: model with fox ID	-1010.1	6		
	M1.2: model with fox ID x moon	-1009.3	8	1.676	= 0.433
wind	M2.1: model with fox ID	-1010.9	6		
	M2.2: model with fox ID x wind	-1010.9	8	0.051	= 0.975
temperature	M3.1: model with fox ID	-1008.6	6		
	M3.2: model with fox ID x temperature	-1008.0	8	1.170	= 0.557
<i>Rate</i>					
moon	M4.1: model with fox ID	-646.62	5		
	M4.2: model with fox ID x moon	-643.35	7	6.552	< 0.05
wind	M5.1: model with fox ID	-649.64	5		

	M5.2: model with fox ID x wind	-648.11	7	3.049	= 0.218
temperature	M6.1: model with fox ID	-642.62	5		
	M6.2: model with fox ID x temperature	-639.64	7	5.965	= 0.051
High-cost vigilance					
<i>Duration</i>					
moon	M7.1: model with fox ID	-710.25	6		
	M7.2: model with fox ID x moon	-710.24	8	0.021	= 0.990
wind	M8.1: model with fox ID	-711.55	6		
	M8.2: model with fox ID x wind	-711.28	8	0.535	= 0.765
temperature	M9.1: model with fox ID	-709.47	6		
	M9.2: model with fox ID x temperature	-708.33	8	2.290	= 0.318
<i>Rate</i>					
moon	M10.1: model with fox ID	-516.67	5		
	M10.2: model with fox ID x moon	-512.68	7	7.973	< 0.05
wind	M11.1: model with fox ID	-522.27	5		
	M11.2: model with fox ID x wind	-517.40	7	9.727	< 0.01

temperature	M12.1: model with fox ID	-510.45	5		
	M12.2: model with fox ID x temperature	-497.97	7	24.960	< 0.001
Low-cost vigilance					
<i>Duration</i>					
moon	M13.1: model with fox ID	-773.38	6		
	M13.2: model with fox ID x moon	-773.15	8	0.460	= 0.794
wind	M14.1: model with fox ID	-771.18	6		
	M14.2: model with fox ID x wind	-766.06	8	10.235	< 0.01
temperature	M15.1: model with fox ID	-770.99	6		
	M15.2: model with fox ID x temperature	-766.99	8	8.007	< 0.05
<i>Rate</i>					
moon	M16.1: model with fox ID	-623.93	5		
	M16.2: model with fox ID x moon	-619.53	7	8.803	< 0.05
wind	M17.1: model with fox ID	-618.07	5		
	M17.2: model with fox ID x wind	-594.86	7	46.531	< 0.001
temperature	M18.1: model with fox ID	-634.32	5		
	M18.2: model with fox ID x temperature	-605.28	7	38.086	< 0.001

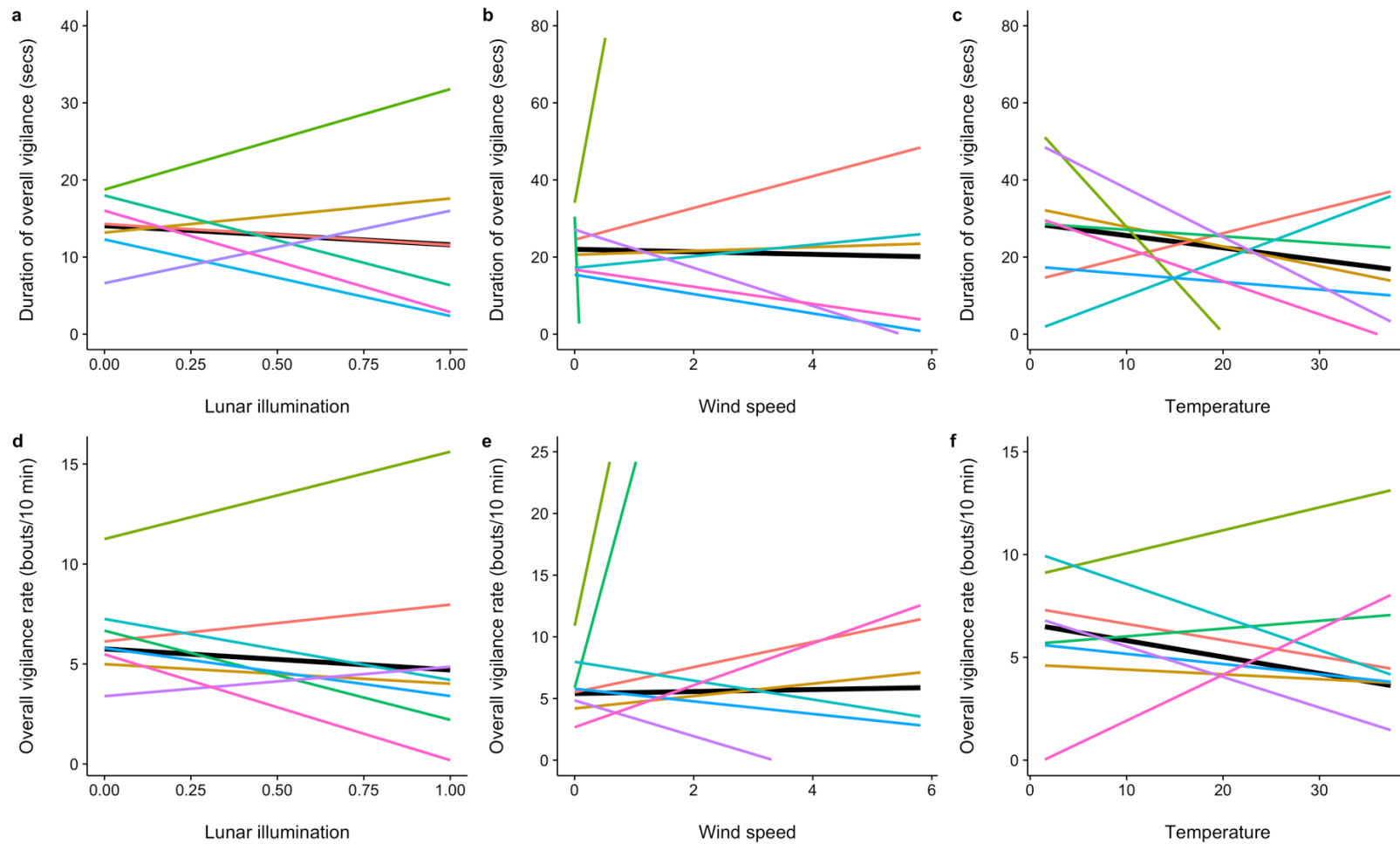


Figure 4.1. Patterns of I x E interactions for overall vigilance time across a) lunar illumination, b) wind speed and c) temperature, and overall vigilance bouts across d) with lunar illumination, e) wind speed and f) temperature for individual bat-eared foxes in the Kalahari Desert. The bold black lines represent population-level response, and individual foxes are illustrated by colours.

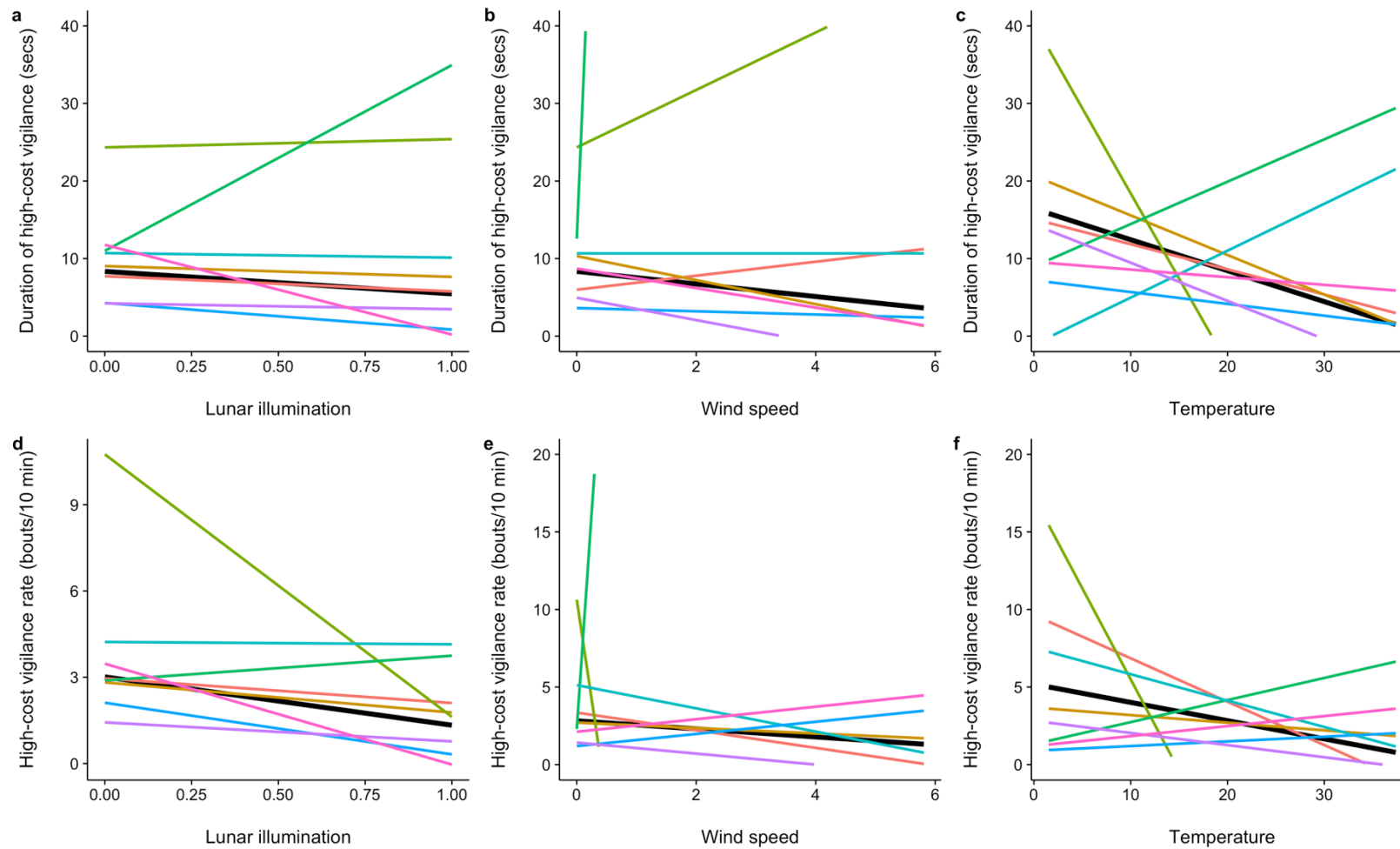


Figure 4.2. Patterns of I x E interactions for high-cost vigilance time across a) lunar illumination, b) wind speed and c) temperature, and high-cost vigilance bouts across d) with lunar illumination, e) wind speed and f) temperature for individual bat-eared foxes in the Kalahari Desert. Black line reveals population-level response, and individual foxes are illustrated by colours.

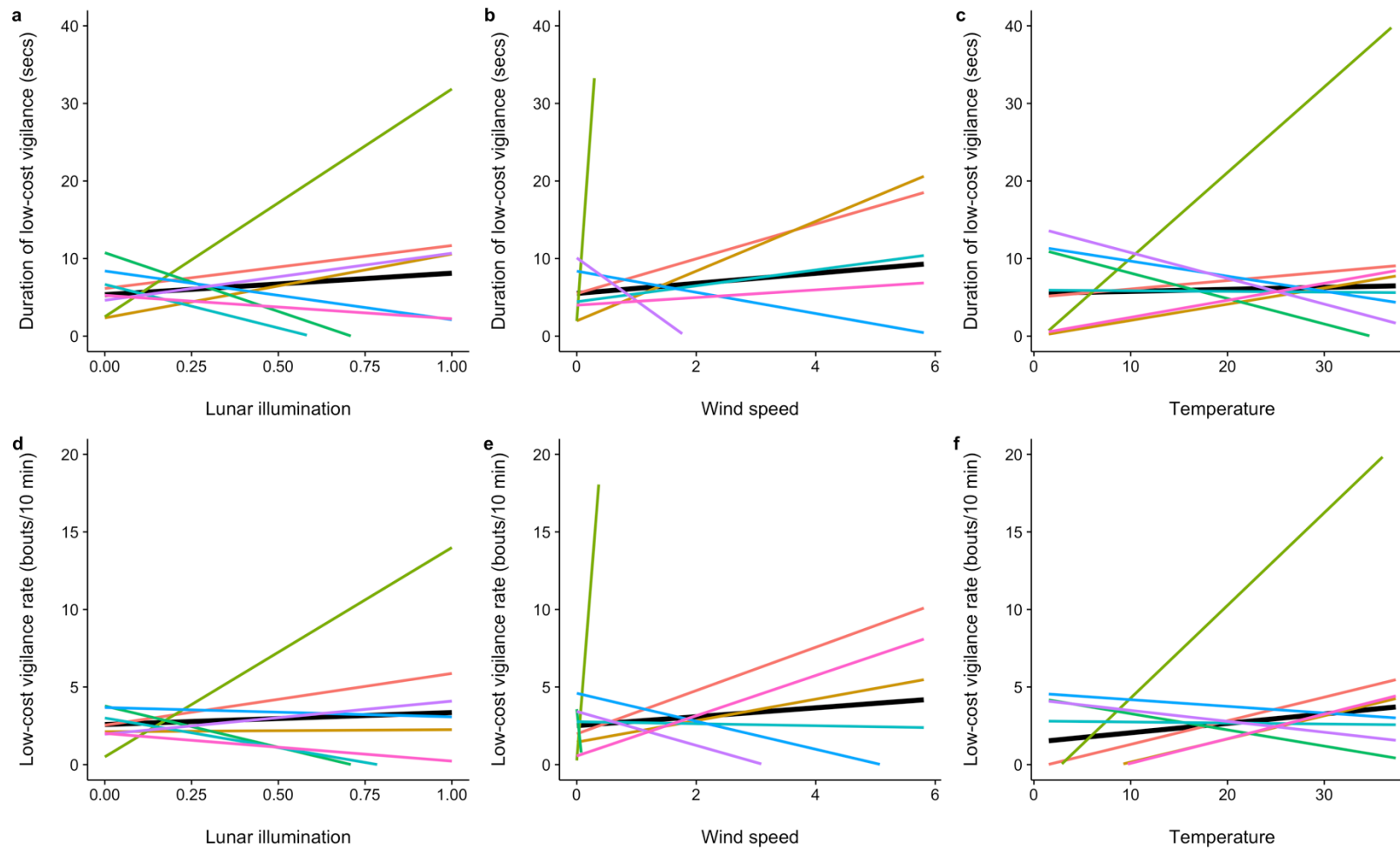


Figure 4.3. Patterns of I x E interactions for low-cost vigilance time across a) lunar illumination, b) wind speed and c) temperature, and low-cost vigilance bouts across d) with lunar illumination, e) wind speed and f) temperature for individual bat-eared foxes in the Kalahari Desert. Black line reveals population-level response, and individual foxes are illustrated by colours.

4.5 Discussion

We investigated for the presence of individual differences in personality and plasticity for overall vigilance, as well as high- and low-cost vigilance across lunar illumination, wind speed, and temperature in bat-eared foxes. Our results highlighted that distinctive patterns occurred for different types of vigilance. Overall vigilance appeared to follow the ecological hypothesis (general absence of individual differences in personality and plasticity), whereas adjustments in high- and low-cost vigilance offered greater support for the behavioural hypothesis (evidence of individual differences in personality and plasticity).

4.5.1. *Personality*

When assessing overall vigilance, we detected no personality differences, however we identified personality differences in high-cost vigilance rate, as well as for the duration and rate of low-cost vigilance. Risk-associated behaviours have been shown to consistently vary among individuals for other species, e.g. threespined sticklebacks (*Gasterosteus aculeatus*, Bell 2005; Bell and Sih 2007), and eastern grey kangaroos (Favreau et al. 2014). High-cost vigilance interrupts feeding and thus is generally external-stimuli driven (Blanchard and Fritz 2007). Ecologically, high-cost vigilance is therefore associated with greater threats or current risk (Monclús and Rödel 2008; Unck et al. 2009), and thus we would expect individuals to behave in a similar manner to avoid death. Our study reveals that individual foxes behaved in a similar manner with respect to the duration of high-cost vigilance, but differences were demonstrated for the rate of high-cost vigilance. This suggests that some individuals may consistently use longer, infrequent bouts of vigilance, whereas other individuals use shorter, more frequent bouts of vigilance, and that personality differences are demonstrated by these distinct high-cost vigilance strategies. The presence of personality differences for high-cost vigilance contradicts our initial hypothesis, but supports other research indicating personality traits in high-risk areas (Bell 2005). Individual foxes may be more or less bold in high-risk situations (Bell 2005) or may have different perceptions of risk (Dammhahn and Almeling

2012). Alternatively, this may be associated with the area's low predation risk, where behavioural variation in anti-predator behaviours may not be constrained (Mathot et al. 2011), thus potentially leading to the individual differences observed here. While low predation pressure may have allowed for the development of significant individual variation in our study population, it is important to note that overall vigilance and high-cost vigilance duration did not vary among individuals. Ecological theory predicts that trade-offs on foraging success are imposed by the duration of vigilance (i.e. the more time spent vigilant, the less time there is to forage). Although bat-eared foxes may be using different strategies, ultimately the duration of vigilance is similar. These different strategies may offer different advantages; more frequent, shorter bouts will increase predator detection (Cresswell et al. 2003), but will be more conspicuous (le Roux et al. 2009), and thus infrequent, longer bouts offers greater crypsis, but may not be as efficient at predator detection. Thus, if the duration of vigilance remains similar, distinct strategies may even be evident in areas of high predation risk. Ultimately the patterns demonstrated in high-cost vigilance support the behavioural hypothesis.

Bat-eared foxes also exhibited personality differences in low-cost vigilance, also supporting the behavioural hypothesis, although it must be noted that repeatability (the measure of personality) was relatively low (Bell et al. 2009). Low-cost vigilance does not necessarily conflict with other activities and has been described as a monitoring behaviour that can occur during an animal's 'spare time' (Illius and Fitzgibbon 1994; Blanchard and Fritz 2007). As this type of vigilance is not necessarily associated with imminent danger, we would expect to see personality differences arise, as individuals may perceive environmental cues or risks differently (Dammhahn and Almeling 2012) based on motivation, state, or past experiences (McNamara and Houston 1996; Dingemanse and Wolf 2013). Unck et al. (2009) suggest that the use of low-cost vigilance may be less effective than high-cost vigilance, but we suggest that this type of vigilance is useful in lower-risk areas. Low-cost vigilance is the dominant form of vigilance exhibited by foxes in this area (Welch et al. 2018), and thus may

be an important strategy in low predation risk areas. High-cost vigilance may be more important when perceived risk increases and may explain why foxes switch to high-cost vigilance under these circumstances (Lima and Bednekoff 1999; Unck et al. 2009). This however, requires further investigation. Another factor that may warrant investigation in future studies is the sex of foxes. This study was unable to investigate this factor adequately due to low sample size, but this may be an important determinant of individual differences.

4.5.2. *Plasticity*

Similar to our personality results, investigating overall vigilance masked plasticity patterns that became evident when focusing on high- and low-cost vigilance separately. For overall vigilance, individual differences in plasticity were only observed for vigilance rate across lunar illumination. Comparatively, for high-cost vigilance rate, individual plasticity varied across all environmental factors in our study. Thus, while individual responses to these environmental factors did not vary in terms of the duration of time engaged in overall and high-cost vigilance, individual variation in plasticity was evident regarding the rate of overall and high-cost vigilance bouts across these factors. Individuals differentially made use of more frequent, shorter glances and infrequent, longer glances across the different environmental variables, thus supporting the behavioural hypothesis. Lunar illumination, wind speed, and temperature can be associated with perceived risk, as bat-eared foxes may be less able to detect predators in dark and/or windy conditions (Biebouw and Blumstein 2003; Carr and Lima 2010), and cold temperatures can increase predator energy requirements increasing risk due to increased hunting (Careau et al. 2007). Environmental variables can have complex consequences for predator-prey dynamics and individuals are likely to differ in what they perceive as risky (Dammhahn and Almeling 2012), but it is important to note that individuals did not vary in the duration of overall or high-cost vigilance across environmental factors. Foxes ultimately paid similar costs in terms of time spent vigilant, despite environmental variability, indicating a similar population-level response to perceived risk.

Individual differences in plasticity were also present for low-cost vigilance. Individuals varied in both duration of time vigilant across wind speed and temperature, and rate of vigilance across lunar illumination, wind speed, and temperature. These results again providing support for the behavioural hypothesis. Low-cost vigilance is not necessarily associated with immediate threats and may have multiple purposes such as monitoring the environment, monitoring conspecifics, looking for escape paths, or identifying food (Blanchard and Fritz 2007). Thus, it is not surprising that this type of vigilance varies across environmental factors, as these factors can affect perceived risk (Biebouw and Blumstein 2003; Careau et al. 2007; Carr and Lima 2010), potential food availability/conspecific competition (Mellanby 1939; Briers et al. 2003; Lang et al. 2006), as well as conspecific communication (Kern and Radford 2016). Individuals likely vary in how they perceive risk (Dammhahn and Almeling 2012), in their energetic state or motivation (McNamara and Houston 1996; Dingemanse and Wolf 2013), and in their experiences (Dingemanse and Wolf 2013), which may all contribute to individual plasticity in low-cost vigilance across environmental factors. Due to the lower costs associated with this type of vigilance, individual variation would incur minimal consequences to other activities (Unck et al. 2009). However, as this is one of the few studies to investigate low-cost vigilance, the drivers behind this behaviour still remain largely unknown.

This study highlights the importance of investigating individual differences in personality and plasticity in behaviour across multiple environmental gradients. We explicitly demonstrate that by investigating overall vigilance, patterns in individual strategies are masked, and the importance in examining different types of vigilance is highlighted. With this behavioural study, we can only speculate as to the drivers of personality and plasticity in this environment where predation pressure is relaxed. The mechanisms behind personality and plasticity are many and include an individual's experiences (Dingemanse and Wolf 2013), differences in energetic state or motivation, environmental uncertainty, and perception of

environmental cues (Wolf et al. 2008). We suggest that the area's low predation pressure may allow for the development of individual variation, as this low predation pressure is not likely to constrain anti-predator behaviours. However, if the duration of vigilance is similar among individuals, comparable behavioural variation may even be expected in high-risk areas. Importantly, we demonstrate that by combining vigilance types, distinct individual strategies that could influence fitness may be overlooked. These patterns, however, may be important in understanding vigilance behaviours.

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CHAPTER 5 GENERAL DISCUSSION



5.1 Highlights of the current study

Prior to this study, the anti-predator behaviours of bat-eared foxes in the wild were virtually undescribed. It was unknown how this mesopredator perceives and responds to risk, and whether anti-predator behaviours persist after the extirpation of larger predators. Ultimately, my research has demonstrated that even when predation pressure is extremely low, it is premature to assume that anti-predator behaviours have been lost. Perceived risk may still be present, and this risk may vary on a spatiotemporal scale.

Typically, experimental manipulation with mesocarnivores can be problematic in natural environments, as quantifying foraging costs can be challenging; factors that may influence perceived risk may also influence foraging opportunities. In this study, however, I was able to quantify missed opportunity costs by assessing foraging success in conjunction with the assessment of risk perception. Thus, I was able to demonstrate small changes in a mesocarnivore's perceived risk associated with lunar phase and human presence.

Importantly, the results from this chapter indicate that GUDs are capable of detecting subtle differences in the perceived risk of mesocarnivores, more readily than vigilance behaviours. There are many ways to assess perceived risk, and by collecting both GUD and vigilance data at foraging stations, I highlighted that different methods to assess perceived risk can provide diverse results, and thus researchers should not assume different methods yield comparable data. Ultimately, the patch use behaviours of bat-eared foxes demonstrate that, even in an area with low predation pressure, environmental and anthropogenic factors influence perceived risk, and thus anti-predator behaviours are maintained. In areas where predators have been lost, anti-predator behaviours may still persist, explained by the pleiotropic hypothesis (Byers 1997), the multi-predator hypothesis (Blumstein et al. 2004), and the ghosts of predators past hypothesis (Peckarsky and Penton 1988). Although not explicitly tested in this thesis, my findings suggest the ghosts of predators past hypothesis may be evident. The ghosts of predators past hypothesis suggests that if anti-predator

behaviours have been demonstrated previously and are not too costly, the persistence of these behaviours is likely. By focusing predominantly on low-cost vigilance, fox anti-predator behaviours are retained but the associated costs are low.

Low-cost vigilance is an important behaviour to investigate as it allows simultaneous activities to take place, but is seldom studied. The exclusion of this measure may mask subtleties in how animals perceive risk and the subsequent management of this risk. The predominant use of low-cost vigilance in this study may suggest that, in addition to a risk detection role, it may also serve other purposes. Interspecific competition for food may occur between bat-eared foxes and Cape foxes, aardwolves (*Proteles cristata*), and aardvarks (*Orycteropus afer*), and bat-eared foxes were occasionally observed chasing away competitors (R. Welch, pers. obs.). The pleiotropic hypothesis states that anti-predator behaviours are retained if they have additional functions. I suggest that if mesopredators are able to simultaneously detect competitors and predators, the continuation of anti-predator behaviours is likely adaptive. In areas of low risk, the predominant use of low-cost vigilance may be effective, despite the suggested reduced quality of this type of vigilance in other studies (Lima and Bednekoff 1999; Unck et al. 2009). The results demonstrated in my study suggest that mesocarnivore behaviours may be adapted in areas of low risk to reduce the costs associated with vigilance behaviours, whilst not losing these behaviours altogether. To the best of my knowledge, such a pattern has not been reported before and therefore my study highlights potential strategies used by mesocarnivore species in areas of low predation risk.

Observer presence has been shown to both increase perceived risk (Tadesse and Kotler 2012) and decrease perceived risk (Nowak et al. 2014). In this study, GUD results demonstrated that the presence of observers, in the surrounding area, appeared to lower perceived risk, whereas during vigilance focals vigilance was heightened in the presence of observers initially, but decreased over the course of an observation period. The presence of

observers certainly had an effect, but knowing the exact influence our presence had on foxes was difficult to ascertain. I suggest that on a broad scale, the presence of humans may decrease perceived risk due to buffering foxes from the risk of predation (Berger 2007; Nowak et al. 2014), but that when foxes are in close proximity to observers (2-5 m), any noise or movement made by observers may be a source of distraction, and that foxes habituate to this over the course of an observation period.

Furthermore, this is the first study to demonstrate individual differences in personality and plasticity in a wild population of mesocarnivores. I found that individuals use distinct strategies with respect to both high-cost and low-cost vigilance. Other studies have reported that animals may use different strategies with respect to anti-predator behaviours (Lima 1990; Blumstein et al. 2010) and that this may be associated with distinct foraging behaviours (Gall and Fernández-Juricic 2009), predator attacks (Jones et al. 2007, 2009), and conspecific monitoring (Dawkins 2002). Some individuals within populations, for example, rely on early detection and speed to evade predators, whereas others minimise time spent in exposed areas. When both strategies are successful their development is adaptive (Blumstein et al. 2010). At any one time, animals cannot be aware of all alternative options available to them, and gathering information on all alternative options requires time, energy and comes at a cost (Mathot et al. 2011). Thus, it has been suggested that the development of individual strategies is a way to manage environmental uncertainty. Areas with high predation pressure may pose even greater uncertainty with respect to predator presence. Thus, if the development of personality is adaptive for high-cost vigilance in this environment, it may well be adaptive in areas of risk (Mathot et al. 2012). By constraining time spent vigilant, but varying the rate, leads to different strategies that may offer distinct benefits, such as crypsis or increased predator detection (Cresswell et al. 2003; le Roux et al. 2009). In this study, individuals demonstrated similar durations of overall and high-cost vigilance (predicted by ecological theory). However, personality was demonstrated by the

use of different strategies when rate of vigilance was considered, and studies may therefore overlook personality differences if only duration of vigilance is considered.

Throughout the thesis, subtle distinctions were highlighted between chapters. Interestingly, differences in perceived risk were found across lunar illumination using GUDs, but not for vigilance at the population level. GUDs represent the state of the last fox who fed at foraging stations (and thus may not be representative of the population). The energetic state of an individual may influence how they use a patch (Bedoya-Perez et al. 2013), and individuals who are in an energetically poor state may select to feed more vigorously at a patch even if perceived risk is greater. Differences in vigilance across lunar illumination were recorded among individuals, and importantly, personality may also influence patch-use behaviour. Bolder individuals may perceive areas as having lower risk and occupy patches for longer (Réale and Festa-Bianchet 2003). Thus, the GUD results may be representative of a ‘snapshot’ into perceived risk of a few select individuals. The results from chapter 4 then demonstrate that these among-individual differences in vigilance across lunar illumination are consistent over time. This highlights the importance of individual behaviours in studies of perceived risk, and that without their consideration distinct behavioural patterns may be masked. Additionally, habitat effects were not observed in chapter 2, but were observed in chapter 3, whereby vigilance increased with tall vegetation. A major difference between the two methods is that food availability was equal at GUD patches, however under natural foraging conditions it may be expected to vary. If food availability was lower in areas of tall vegetation compared to other areas (and thus individuals foraged less) the costs of vigilance would be lower.

5.2 Future research

There is enormous opportunity for future investigations into perceived risk in mesopredators. Importantly, this study has highlighted that vigilance behaviours are concentrated towards low-cost vigilance and I have suggested this was predominantly due to low predation risk.

However, this has yet to be tested and future studies should therefore aim to repeat these investigations by using a similar approach. Researchers should investigate the role of spatiotemporal cues on perceived risk, as well as the use of high- and low-cost vigilance in high predation risk areas for bat-eared foxes, and for other mesopredators in both high- and low-risk areas. If patterns are dissimilar in high-risk areas, this may suggest that the predominant use of low-cost vigilance is due to low predation pressure and would suggest evidence for the ghosts of predators past hypothesis (Peckarsky and Penton 1988).

Furthermore, no information currently exists on mesocarnivore predator detection, and I have proceeded on the assumption that the visual modality is important in anti-predator responses. However, it is unclear whether predators are predominantly detected using visual, auditory, or olfactory cues. Bat-eared foxes are primarily acoustic foragers who detect prey using auditory cues (Malcolm 1986; Renda and le Roux 2017). If predators are likewise predominantly detected through auditory cues, it may suggest that bat-eared foxes are able to adequately detect predators whilst engaged in other activities. The use of high-cost vigilance may occur when a secondary sense is required and thus only used in perceived high-risk situations. Other studies have shown that species use different senses to detect predators. Tammar wallabies, for example respond to visual but not auditory predator cues (Blumstein et al. 2000). Using an experimental approach to determine which sensory cues provide the most salient information on predators can be employed, similar to that used by Blumstein et al. (2000). Researchers could present study individuals with taxidermic mounts of predators to assess responses to visual stimuli, playbacks of predator sound to investigate responses to acoustic stimuli, and finally predator scat or urine to assess responses to olfactory stimuli.

Mesopredators may face threats from terrestrial carnivores, aerial predators, and venomous snakes. In other prey species, responses to different types of predator can vary (Seyfarth et al. 1980; Manser et al. 2001; Furrer and Manser 2009), and 'functionally referential'

vocalisations may be used to warn conspecifics (Macedonia and Evans 1993; Manser 2001). Initial investigations revealed that bat-eared foxes fled from aerial and terrestrial predator simulations, but mobbed snake simulations whilst emitting a snorting vocalisation (R. Welch, pers. obs.). Unfortunately, due to the loss of the study population to disease, I was unable to continue with these investigations. However, initial findings suggest that responses may differ depending on the type of threat, and that bat-eared foxes appear to respond to unfamiliar sounds before visual cues were available. Investigating this further could provide information on the detection of predators, perceived risk in the presence of predators, and responses to predator presence.

I was able to demonstrate that vigilance increased in the presence of conspecifics. Due to bat-eared fox partners being predominantly unhabituated, conspecifics seldom foraged with partners in our presence. Thus, I was unable to assess whether the cause of vigilance in the presence of conspecifics could be attributed to mate detection, competition, or conspecific monitoring (Beauchamp 2001; Cameron and du Toit 2005; Fernández-Juricic et al. 2005). Future work should emphasise the importance of habituating a larger proportion of the study population, where possible. Research could then investigate the group size effect and ascertain functions of social vigilance in small mesocarnivores. In the presence of multiple conspecifics, I would expect anti-predator vigilance to decrease due to the many eyes and dilution hypotheses (Pulliam 1973; Pulliam and Caraco 1984), but social vigilance to increase due to competition (Lung and Childress 2007; Shrader et al. 2007; Beauchamp 2009) or mate guarding (Wright et al. 2010). Habituating a larger proportion of individuals would additionally allow for the investigation of personality and plasticity in the presence of conspecifics, as individual variation in vigilance has been shown to differ depending on group size in other species (Dannock et al. 2013). Additionally, as mesopredators must actively find their own prey, whilst avoiding predation, future studies may wish to investigate how time is budgeted between foraging and anti-predator behaviours. This would allow researchers to directly assess this trade-off in relation to spatiotemporal factors. However, I

suggest that rate of vigilance is still investigated, as exploring duration alone may mask differences in individual behaviours/strategies. Lastly, as different methods of assessing perceived risk may demonstrate distinct patterns, future studies may therefore wish to employ multiple methods to assess perceived risk in mesopredators, allowing researchers to gain a fuller understanding of this phenomenon.

This thesis has furthered our knowledge on perceived risk in bat-eared foxes, and has highlighted further gaps in this field regarding this species and mesocarnivores in general. Investigating perceived risk at a site with low predation pressure allowed for the investigation of factors other than predator presence, which was considered to be relatively homogenous across the landscape. Importantly, my research has demonstrated that in areas of low predation pressure perceived risk still exists and varies on a spatiotemporal scale. The costs of anti-predator behaviours may be reduced and patterns of individual anti-predator responses can vary significantly. Importantly, by combining vigilance types, distinct behavioural patterns may be masked. By understanding under what conditions, and in which species high- and low-cost vigilance, and consistent among-individual variation develop, will further our knowledge on the drivers and evolutionary foundations of these behaviours.

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