Varying degrees of fear: How do large herbivores adjust their anti-predator behaviour in response to different predators?

by

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ABSTRACT

Large predators are returning to areas where they have previously been absent through both predator reintroductions and natural range expansion. As a result, these re/introductions are changing the nature of predator-prey systems, with potential shifts from single to multi-predator environments. In response, prey species must make spatial (i.e. patch use) and behavioural (i.e. vigilance, feeding) adjustments to minimize risk from predators with varying hunting strategies, prey preferences and activity patterns. With this in mind, the broad aim of my study was to determine how perceived predation risk from different large predators affected the spatial and behavioural decisions made by individuals in a community of mammalian herbivore species. To achieve this, I first investigated, how kudu, sable and warthog responded to the introduction of wild dogs into an area with cheetah. In response to this shift from single to multiple predators, all three-herbivores decreased their feeding effort. However, sable (not hunted by cheetah) decreased their feeding intensity more than kudu (preyed upon by cheetah). In contrast, warthog (avoided by cheetah) showed a different feeding pattern, but then displayed a dramatic response to the wild dog introduction in that they disappeared from the study site. These patterns suggest that the magnitude for increasing anti-predator responses to predator introductions may be greater for prey (e.g. sable, warthog) living in initially low risk environments compared to prey species (e.g. kudu) that already have high perceived predation risk from the resident predator (e.g. cheetah). Despite decreasing their feeding effort, all three herbivore species preferred patches located in open grasslands compared to denser vegetation, before and after the wild dog introduction, possibly due to increased predator detection in open areas. In my second experiment, I explored how prey species employed a range of anti-predator behaviours (i.e. vigilance, grouping and temporal shifts in activity) of various combinations to minimize risk from predators with different hunting strategies (ambush vs cursorial) and prey preferences. Overall, herbivores had higher vigilance, moved in larger groups and avoided waterholes at night when exposed to predation risk from lions (ambush predator). In contrast, in response to cheetah and/or wild dogs (cursorial predators), only prey species within the accessible weight range of both these predators (warthog, red hartebeest) moved in larger groups compared to conspecifics in the lion section. They did not however, shift their waterhole use to night to avoid the largely diurnal cheetah and wild dogs. These results suggest that the potential threat of ambushing lions was greater than that of the cursorial cheetah and wild dogs. I then expanded on this experiment by investigating, how prey adjusted their anti-predator behaviour (i.e. vigilance) in response to the alarm calls of con/heterospecifics (i.e. zebra, wildebeest) or to non-hunting predator calls (i.e. lion roars). Overall, red hartebeest and wildebeest living with lions tended to show greater vigilance in response to the lion roars compared to the alarm calls. This suggests that these species perceived the direct cue of lions as a better indicator of risk than the alarm calls. I then compared these responses for prey species living with and without lions. I found that herbivores living with lions had higher vigilance than conspecifics living without lions. Despite a greater overall response in the lion section, herbivores in the lion-free section still significantly increased their vigilance in response to the lion roar. Yet, it was two of the lions' preferred prey species (i.e. zebra, wildebeest) that showed the greatest response. This suggests that species under the greatest threat may maintain innate anti-predator responses to a dangerous but absent predator longer than less preferred prey. Ultimately, my findings indicate that simple cues from dangerous predators can have a greater effect on anti-predator behaviours of prey species than alarm calls. Overall, the results from my PhD highlight that prey respond to changing predation risk after a predator introduction by modifying their fine scale patch use and foraging behaviour. Moreover, prey responses to different predators are not uniform, but reflect differing degrees of danger posed by the predators, resulting in prey using varied combinations of anti-predator behaviours to minimize risk around risky areas. Lastly, non-hunting cues from dangerous predators can trigger strong anti-predator responses from prey living with and without the predator. Ultimately, the results of my three experiments highlight the behavioural plasticity of prey species to reduce predation risk across their fluctuating landscape of fear.

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DECLARATION

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Douglas F Makin
December 2016

PREFACE

The work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from July 2013 to December 2016, under the supervision of Dr. Adrian Morgan Shrader and Dr. Simon Chamaillé-Jammes. This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the authors and has not been submitted in any form to another university. Where use of other work was made, it has been acknowledged in the document.

All work was approved by the University of KwaZulu-Natal's Animal Ethics Committee and permission was obtained from Tswalu Kalahari Reserve to conduct this research.

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CHAPTER ONE

Introduction

Several different factors contribute to how animals make decisions on landscape use and behavioural adjustments (Lima and Dill 1990, Lynch et al. 2014). These include, the distribution, quantity and quality of food resources (Van Beest et al. 2010), competition (Sinclair 1985), landscape features (Schmidt and Kuijper 2015), climatic conditions (Kotler et al. 1991), and predation risk (Lima and Dill 1990). Of these, one of the most important factors driving changing animal landscape use and behaviour is perceived predation risk (Lima and Dill 1990, Caro 2005). In order to avoid predators, prey have to adjust their use of habitats, patches within habitats, and make trade-offs between avoiding predators and obtaining suitable forage required for survival (Lima and Dill 1990). Additionally, predation risk is not uniform across landscapes, but rather fluctuates both temporally and spatially and therefore prey species move across a ‘landscape of fear’ (Laundré et al. 2001a, Laundré et al. 2010). With predators moving back into areas either through reintroductions (Hayward and Somers 2009, Manning et al. 2009) or natural range expansion (Lewis et al. 1999, Fasola et al. 2011), prey species are having to adjust their anti-predator behaviours across both large- (e.g. habitat use) and small-scales (e.g. patch choice). Additionally, these returning predators are potentially shifting predator-prey systems from single to multi-predator environments (Sih et al. 1998, Thaker et al. 2011). Therefore, animals must continually make decisions about where to forage based on this fluctuating ‘landscape of fear’ (Shrader et al. 2008).

In response to changing perceived predation risk, animals can shift their space use (Sih et al. 1998) and adjust their behaviour to minimize risk, while still ensuring that they obtain resources required for survival (Houston et al. 1993). However, these responses will vary for different predators and predator combinations (Thaker et al. 2011). Prey species’ responses to predators will vary with the hunting strategy employed by the predator (e.g. ambush versus cursorial), the predator's activity patterns (e.g. nocturnal or diurnal) and differences in predator prey preferences (Sih et al. 1998, Schmitz and Oswald 2005, Clements et al. 2016). Therefore, prey species will have varying degrees of susceptibility to different predators (Lima 1998, Monterroso et al. 2013). To determine how perceived predation risk from different large predators (lions – *Panthera leo,* cheetah – *Acinonyx jubatus* and wild dogs – *Lycaon pictus*) affected the space use (i.e. patch use) and behaviour (i.e. feeding, vigilance, grouping and temporal activity) of a community of large mammalian herbivores (e.g. sable – *Hippotragus niger*, gemsbok – *Oryx gazella*, plains zebra – *Equus quagga*), I focused my study on the following objectives:

1. Investigate how large herbivores alter their foraging behaviour and patch use in response to the introduction of wild dogs into an area already supporting a cheetah population, thus shifting the environment from a single to a multi-predator system (Chapter 2).
2. Explore how a number of large herbivore species adjust their anti-predator behaviours (i.e. vigilance, group sizes and temporal use) at waterholes (high risk areas) in response to predators with different hunting styles (e.g. ambushing lions vs. cursorial cheetah and wild dogs) and prey preferences (Chapter 3).
3. Determine whether large herbivores consider 1) the alarm calls of conspecifics and/or heterospecifics, or 2) the non-hunting calls of a dangerous predator (lion roars) as a more reliable indicator of predation risk. In addition, explore whether herbivores living with lions show a greater response (i.e. greater vigilance) compared to conspecifics living in a lion-free area (Chapter 4).

Motivation for research

Globally, predators are moving back into areas where they were previously extirpated (Nilsen et al. 2007, Hayward and Somers 2009, Ripple et al. 2014). Examples of these, include, the reintroduction of European lynx (*Lynx lynx*) into parts of Europe , the return of wolves (*Canis lupus*) into parts of North America and Europe (Ripple and Beschta 2004, Theuerkauf and Rouys 2008), and the return of large predators (e.g. lions, wild dogs) into protected areas across southern Africa (Hayward et al. 2007, Davies-Mostert et al. 2009, Hayward and Somers 2009). This has occurred for several reasons, including, the restoration of ecosystem function in reserves devoid of predators, financial benefits of maintaining predator populations for ecotourism purposes, and predator conservation (Ripple and Beschta 2003, Hayward and Somers 2009). The movement of predator species into these areas provides an opportunity to investigate prey species' responses across a variety of temporal and spatial scales (Hayward et al. 2007). However, to date the majority of the studies conducted have almost exclusively focused on single predator systems (e.g. elk, *Cervus canadensis*, responses to wolf reintroduction in Yellowstone; Ripple and Beschta 2006), and comparatively few studies on this topic have been conducted in Africa. This is particularly important given the growing number of large carnivore reintroductions into reserves in Africa (Hayward et al. 2007), and the fact that prey species often coexist with multiple large predator species (Sih et al. 1998).

Laundré et al. (2001a) inferred that following a predator return, a prey species' 'landscape of fear' will likely change in response to risk imposed by the new predator and the existing predators on the landscape. Within a multi-predator system, prey species need to employ a range of predator-specific anti-predator behavioural strategies to minimize predation risk (Lima and Dill 1990, Caro 2005). Thus, the focus of my research was to investigate how a large mammalian herbivore community responded not only to the introduction of a large predator, but also to the presence of different large predators on the landscape.

To address this, I first focused on determining how a number of large herbivore species (e.g. sable, kudu – *Tragelaphus strepsiceros*, warthog – *Phacochoerus africanus*) responded to the introduction of wild dogs into an area already supporting a large cheetah population. I focussed on shifts in the herbivores' space use (e.g. patch) and feeding behaviour. Understanding how foragers make decisions at fine spatial scales is important as it provides insight into larger-scale patterns of habitat use driven by differences in perceived predation risk (Brown 1988, Shrader et al. 2008). Importantly, I was interested in determining how potential prey species respond to a shift from a single to a multi-predator system, and how they modify their behaviour to minimize perceived predation risk from multiple large predators.

A number of studies have illustrated that following a predator return or introduction, prey are potentially naïve in their ability to respond appropriately to the predation risk posed by the predator, thus leading to an inadequate anti-predator response (Blumstein and Daniel 2005, Sih et al. 2010). However, if there is a short duration since predation extirpation (~ 100 years), it would be difficult to ascribe behavioural responses to naivety. For example, an antipredator behaviour expressed in response to a returning predator may be due to the retention of antipredator behaviours for that predator (short evolutionary time period) or towards resident predators that present a similar risk as the returning predator (e.g. cursorial hunters; Chamaillé-Jammes et al. 2014). Thus, teasing apart the degree of naivety of prey species in my study was not possible.

The second focus of my study was to investigate how the same large herbivore species (i.e. eland – *Tragelaphus oryx*; gemsbok, zebra, red hartebeest – *Alcelaphus buselaphus caama*, warthog and wildebeest – *Connochaetes taurinus*) responded to perceived predation risk from different predators (i.e. lions versus cheetah and wild dogs) located in separate but adjacent areas. This allowed me to conduct a comparative study investigating how these prey species employed a range of anti-predator behaviours (i.e. vigilance, grouping and temporal use) in response to the different threats from these predators.

Lastly, I used a manipulative approach to determine if a number of herbivore species (i.e. gemsbok, zebra, red hartebeest and wildebeest) considered alarm calls or non-hunting calls from a dangerous predator (i.e. lions) as more reliable indicators of risk. In addition, I was able to compare the responses of individuals living with and without lions to gain insight into the degree to which these herbivores retain anti-predator behaviours towards a dangerous predator cue in the absence of the predator. This was achieved by recording their vigilance behaviour in response to playbacks of two different herbivore alarm calls (i.e. zebra and wildebeest), and a non-hunting predator call (i.e. lion roars).

Multi-predator-prey systems are complex, with perceived predation risk fluctuating spatially and temporally depending on the predators hunting strategy, prey preferences and diel activity. To counteract this, prey species have a range of anti-predator behaviours to minimize risk while still obtaining necessary resources for survival. Therefore, my research seeks to highlight and add scope to the rapidly developing body of work involved in explaining predator-prey interactions within multi-predator-prey systems.

LITERATURE REVIEW

Prey anti-predator behaviours

Predation risk is a key driver of community dynamics and individual behaviour (Lima and Dill 1990). Many studies of the impacts of predation on prey communities have focused primarily on consumptive effects (i.e. killing of an individual; Rosenzweig and MacArthur 1963). However, expanding on this, Lima (1998), Brown (1988) and Cresswell et al. (2010) emphasized the importance of non-consumptive or non-lethal effects of perceived predation risk in driving changes in prey behaviour. Understanding how perceived predation risk influences predator-prey interactions is important as it allows us to determine how prey species adjust their anti-predator behaviours, shift their space use, and alter their resource acquisition (Kotler et al. 2010).

Several studies have documented the role of non-consumptive predation risk in driving prey space use and behaviour across a variety of environments (Ripple and Beschta 2004, Laundré et al. 2010, Tambling et al. 2012, Chamaillé-Jammes et al. 2014). Moreover, changing habitat use by prey species in response to perceived predation risk has been observed for several species (Brown 1999, Creel et al. 2005, Thaker et al. 2011). For example, Padié et al. (2015) found that roe deer (*Capreolus capreolus*) responded to high perceived predation risk by decreasing their use of risky habitats and reducing distance to cover, but did not shift their overall home range use. At a finer spatial scale, prey species can minimize predation risk by shifting their patch use within habitats (Brown 1988, Brown and Kotler 2004). For example, in response to perceived predation risk, mule deer (*Odocoileus hemionus*) decreased their foraging effort at patches located in dense forest habitats and spent more time feeding from patches located in open grasslands as a means of reducing the risk of ambush from mountain lion (*Puma concolor*; Altendorf et al. 2001).

In addition, prey have adopted different behavioural responses such as increased vigilance (Roberts 1996), gregarious living (Hamilton 1971), and changing their temporal activity (Tolon et al. 2009) to minimize perceived predation risk. However, employing these anti-predator strategies usually involves an associated trade-off cost of decreased time available for other activities (i.e. drinking, foraging, grooming, mate selection; Brown and Kotler 2004, Fortin et al. 2004, Creel et al. 2014).

Vigilance behaviour has been observed to effectively reduce predation risk through improved predator detection (Hunter and Skinner 1998). For example, impala (*Aepyceros* *melampus*) and wildebeest both maintained high levels of vigilance in response to the reintroduction of lions and cheetah in Phinda Resource Reserve as a mechanism for improved predator detection (Hunter and Skinner 1998). In addition, roe deer increased their vigilance in response to high perceived predation risk from lynx to minimize risk in Bavarian National Park, Germany (Eccard et al. 2015).

However, maintaining high levels of vigilance is an expensive behavioural response to high levels of predation risk as it reduces time spent feeding. This was observed in bighorn (*Ovis Canadensis*) sheep, who's foraging efficiency decreased with increased time spent vigilant (Brown et al. 2010). Therefore, high vigilant responses should only be exhibited when the perceived predation risk by an individual is high enough to warrant lower foraging efficiency. In contrast, some studies have pointed out the for some prey species, vigilance and feeding are not mutually exclusive (Fortin et al. 2004). For example, several ungulates are able to actively scan their environment for potential threats while chewing, thus prey can remain vigilant while still processing food (Spalinger and Hobbs 1992).

Another anti-predator behavioural strategy is living in groups (Fitzgibbon 1990, Krause and Ruxton 2002). Grouping behaviour can reduce predation risk by increasing dilution effects (Delm 1990, Schmitt et al. 2014), reducing the 'domain of danger' around individuals (Hamilton 1971), increasing group vigilance (Roberts 1996), and providing cooperative defence against predators (Fortin and Fortin 2009). For example, elk in Banff National Park, responded to perceived predation risk from wolves by increasing their group sizes to increase potential dilution effects (Hebblewhite and Pletscher 2002). In the Serengeti National Park, Tanzania, Thompson's (*Eudorcus thomsonii*) and Grant's (*Nanger granti*) gazelle increased their group sizes to minimize predation risk from cheetah through improved predator detection (Fitzgibbon 1990). In contrast, depending on the species' life history strategies, increasing group size may not reduce perceived predation risk (Jarman 1974). For example, solitary herbivore species often rely on crypsis and remaining concealed in dense vegetation to avoid detection by predators, as such, any significant increase in group size would increase conspicuousness and potentially predation risk (Jarman 1974).

Prey species can also respond to increased predation risk by temporally shifting their behaviour to reduce contact with predators (Lima 1998, Lima and Bednekoff 1999, Creel et al. 2014). For example, voles (*Myodes glareolus*) responded to increased predation risk from diurnal weasels (*Mustela nivalis nivalis*) by temporally shifting their foraging activities towards night, thereby minimizing the overlap of activity with a dangerous predator (Eccard et al. 2008). A key way in which prey species reduce predation risk is through reacting to auditory signals and cues (Shriner 1998, Kitchen et al. 2010, Magrath et al. 2015). These auditory signals and cues consist of conspecific and heterospecific alarm calls, and predator vocalizations (Kitchen et al. 2010). Alarm calling in response to increased perceived predation risk has been recorded for several prey species (Gil-da-Costa et al. 2003, Kitchen et al. 2010, Kuczynski 2015, Magrath et al. 2015).

Alarm calls can convey variable types of information and may code for complex signals, including, predator type (Seyfarth and Cheney 2003), the degree of danger of the predator (Schmidt et al. 2008), and the distance from the signaller to the receiver (Bastian and Schmidt 2008). Individuals do not need to rely solely on the alarm calls from conspecifics, but can also eavesdrop on the alarm calls of heterospecifics. Eavesdropping occurs when individuals who are not the primary target, use information from the alarm signal/call to assess potential risk in their environment (Schmidt et al. 2008). For example, yellow-bellied marmots (*Marmota flaviventris*) and golden-mantled ground squirrels (*Callospermophilus lateralis*) eavesdrop on each other’s alarm calls, and flee to refuges when heard (Shriner 1998).

Ultimately, alarm calls provide public information on predation risk and thus prey species can modify their behaviour to minimize risk (Schmidt et al. 2008). In contrast, predator vocalizations allow for predator-specific information to be gleaned by potential prey species, but many predators don't call while hunting (Hettena et al. 2014). Thus, predator calls may not provide valuable information on increased predation risk (Barrera et al. 2011). For example, western red colobus (*Colobus badius*), western black-and-white colobus (*Colobus polykomos*) and Diana monkeys (*Cercopithecus diana diana*) living in the Taï National Park, did not respond to chimpanzee calls, a primary predator of all three species, possibly due to the fact that chimpanzee's remain silent while hunting and therefore their calls were associated with non-hunting individuals (Zuberbühler et al. 1999). Tasmanian eastern quolls (*Dasyurus viverrinus*) did not increase their use of anti-predator behaviours in response to acoustic cues from foxes (*Vulpes vulpes*), as they potentially did not associate the predator call as a strong indicator of predation risk in their environment (Jones et al. 2004)

Despite this, some prey species do respond to the direct calls of predators (Barrera et al. 2011, Hettena et al. 2014). For example, Diana monkey males responded strongly to the calls of leopard (*Panthera pardus*) and crowned eagle (*Stephanoaetus coronatus*; both key predators of monkeys) by increasing their alarm calling to warn conspecifics (Zuberbühler et al. 1997). Ultimately, the strength of an anti-predator response (e.g. increased vigilance) to conspecific and heterospecific alarm calls and/or predator calls will likely vary depending on the reliability of the degree of risk associated with each call (Kuczynski 2015).

Multi-predator systems

The majority of the studies investigating predator-prey interactions have focused on single predator systems (e.g. Hebblewhite and Pletscher 2002, Peckarsky et al. 2008, Nicholson et al. 2014). Whereas in reality, single predator systems are relatively rare (Relyea 2003). Generally, prey species need to avoid multiple predators of varying degrees of danger (Thaker et al. 2011). Depending on the predators present on the landscape, prey species will employ a suite of anti-predator behaviours to minimize risk (Creel et al. 2014). Prey species therefore often have complex and varied anti-predatory responses to predators and these will vary with the predator species (Relyea 2003), the predators activity patterns (Monterroso et al. 2013), predator prey preferences (Clements et al. 2014) and the state (condition) of the prey (Hayward et al. 2015). For example, Thaker et al. (2011) investigated the anti-predator behaviour of seven ungulate species co-existing within a multi-predator environment. Their findings showed that ungulate species selectively foraged in habitats that were safer from a range of predators, reducing the probability of being killed. Smaller ungulates such as, impala and kudu avoided all areas utilised by large carnivores, while larger ungulates such as plains zebra, buffalo (*Syncerus caffer*) and giraffe (*Giraffa camelopardalis*) only avoided areas utilised frequently by lion and leopard.

Therefore, prey species living in multi-predator systems must exhibit predator-specific behaviours in response to both spatial and temporal shifts in predation risk (Laundré et al. 2001a, Laundré et al. 2010). Particularly, where prey species co-exist with both nocturnal and diurnal predator species (Sih et al. 1998, Relyea 2003). For example,, in southern Spain, rabbits (*Oryctolagus cuniculus*) shifted their temporal use of habitats from feeding in dense vegetation during the day to avoid birds of prey (i.e. red kites – *Milvus milvus*) to open prairies at night to avoid nocturnal ambush predators (i.e. European badgers – *Meles meles*; Moreno et al. 1996).

Within multi-predator systems, predator species can have different hunting strategies/modes. For example, canids such as wolves, hunt large ungulates through cooperative hunting, actively chasing down prey over long distances (Muro et al. 2011). In contrast, felids such as mountain lion and Canadian lynx (*Lynx canadensis*), rely on remaining concealed and ambushing their prey, or silently stalking their prey before chasing them over short distances (Murray et al. 1995). These predators therefore pose different degrees and types of risk to prey species due to their varied hunting strategies (Preisser et al. 2007).

In addition, within a multi-predator-prey system, predators will likely differ with regards to preferred prey species. This will result in the different predators, actively selecting some prey species, while avoiding others (Davidson et al. 2013, Clements et al. 2014). For example, the accessible prey weight range for the African predator guild are; 14-135 kg for cheetah, 1-45 kg for leopard, 32-632 kg for lion, 15-1600 kg for spotted hyena (*Crocuta crocuta*) and 10-289 kg for wild dogs (Clements et al. 2014). Thus, prey species living with different combinations of these predators will likely need to actively avoid the predators that pose the greatest risk to them. For example, in a system containing lions, cheetah and leopards, plains zebra (~175 - 385 kg) would only need to adjust their behaviour to be wary of lions (Hayward and Kerley 2005, Hayward et al. 2006a). In contrast, in the same system, impala (~40 kg) would need to try to reduce predation risk from all three of these predators (Clements et al. 2014). Therefore, in situations where large predators move back into systems, prey species will need to adjust their anti-predator strategies to the returning predators and potentially new predator combinations.

Predators returning to systems

Across many continents, predators are returning to areas after extended periods of absence. This is occurring through natural range expansion (Lewis et al. 1999) and reintroductions (Moll et al. 2016). For example, coyotes (*Canis latrans*) have expanded their geographical range across most of north-eastern North America, including some geographically isolated islands where they have never occurred (Gompper 2002). Across large parts of Europe and northern Africa, golden jackal (*Canis aureus*) have expanded their natural range, moving into new areas, such as, Hungary and Italy (Arnold et al. 2012). Similarly, lynx and wolves have also recolonized their historical geographical range across several European regions over the last 30 years (Chapron et al. 2014).

In addition to natural range expansion, lynx (Schadt et al. 2002, Theuerkauf and Rouys 2008) are being reintroduced into different areas across Europe. Similarly, in North America, wolves (Ripple and Beschta 2003) and bears (Clark et al. 2002) are being reintroduced into systems where they have been absent for over 50 years, while in Australia, dingo (*Canis dingo*) reintroductions into national parks are being proposed to restore an apex predator back into areas where they previously occurred (Allen et al. 2012). Finally, in Africa, lions, leopards, cheetah, wild dogs and spotted hyena are being reintroduced into parts of their historical range. (Hayward et al. 2007, Hayward and Somers 2009, Moll et al. 2016).

In response to a predator return, prey species need to adjust to a changing ‘landscape of fear’ through employing and maintaining appropriate anti-predator behaviours to minimize risk from both the present and returning predators (Dale et al. 1994, Relyea 2003). In some cases the absence of these predators may have led to a loss of previously adaptive anti-predator behaviours within a prey population (Berger 1999). For example, moose (*Alces alces*) when presented with calls from wolves, which had only been absent from their home range for 40 years, did not shift their patch use or avoid risky foraging sites (Berger 1999). In contrast, a moose population co-existing with wolves did respond to the wolf calls by adjusting their patch use and avoiding risky areas to minimize perceived predation risk (Berger 1999). In some predator-free environments, certain anti-predator behaviours for a particular predator can be lost relatively quickly in their absence leading to predator naïve prey populations (Berger 1999, Blumstein 2006). For example, in the absence of predators, costly and redundant anti-predator behaviours are selected against and therefore lost over relatively short periods of time (Blumstein and Daniel 2005). This was observed for macropodid marsupials that exhibited a systematic loss of group-size effects when isolated from predators compared to areas where the predators existed (Blumstein and Daniel 2005). However, even in the absence of predators, some anti-predator behaviours may be retained within a prey population with the presence of other extant predator species (Blumstein 2006, Chamaillé-Jammes et al. 2014). For example, Stankowich and Coss (2007) found that black-tailed deer (*Odocoileus hemionus columbianus*) increased their snorting, foot-stamping and alarm walking behaviour in response to cues from a leopard model which served as a proxy for an extinct jaguar (*Panthera* aff) species. These retained responses could be due to the fact that the deer are hunted by puma, an extant predator species that has a similar body shape to a leopard. (Stankowich and Coss 2007).

Therefore, following a predator return, two proximate mechanisms may be observed. Firstly, a prey species may exhibit a strong innate anti-predator response to the perceived threat leading to the employment of anti-predator behaviours (Laundré et al. 2001a, Laundré et al. 2010). Alternatively, the anti-predator response may be retained within the prey population due to interactions with other predators on the landscape (Blumstein 2006), whereby, certain anti-predator behaviours persist with the loss of some, but not all, of a prey species' predators (multipredator hypothesis; Blumstein 2006). Therefore, following the return of the predator, prey species should employ and maintain appropriate anti-predator behaviours to minimize risk. Secondly, prey species may not recognise the risk posed by the reintroduced predator leading to an inadequate anti-predator response (Kauffman et al. 2007, van der Meer et al. 2015).

THESIS STRUCTURE

The research chapters of this thesis have been written up as stand-alone scientific papers with each chapter containing an Abstract, Introduction, Methods, Results and Discussion. The rationale behind this structure is that I intend to submit each chapter for publication in an international peer-reviewed journal and this structure facilitates the publishing process. In line with this, chapter three is currently in print, in *Animal Behaviour*. Because of this, I have written this chapter using the pronoun "we" instead of "I". However, all the writing is my personal work, with my supervisors providing suggestions and editing. To ease the examination process and remove excess repetition, I have included a single reference list at the end of the thesis. References are formatted using the referencing style of *Ecology*.

Chapter one forms the introduction, including the broad aim and objectives for my research chapters and reviews the current key literature related to the broad concepts covered in the thesis. Chapter two investigates the impact of wild dog introduction on the patch use and feeding behaviour of three large herbivores (kudu, sable and warthog) to assess how prey species respond to a shift from a single to a multi-predator system. Moreover, this chapter highlights the role of multiple predators in driving fine-scale changes in prey species foraging behaviour and space use.

Chapter three further expands on the role of predators in driving prey behaviour, investigating how different large predators (lions vs cheetah and wild dogs) influence the suite of anti-predator behaviours (i.e. grouping, vigilance, temporal activity) of six herbivore species (eland, gemsbok, zebra, red hartebeest, warthog and wildebeest) at waterholes. Chapter four then investigates whether prey species adjust their vigilance behaviour more in response to alarm calls (i.e. zebra and wildebeest) from conspecifics and heterospecifics, or non-hunting predator calls (i.e. lion roars), as more reliable indicators of risk. Having determined that the different prey species react more to the lion roars (see Chapter 4), I then investigated whether prey species living with lion had a greater vigilance response to the lion roars (a key dangerous predator) compared to the conspecifics living in a lion-free area. Finally, chapter five links the results of the different studies into a single overall conclusion. I then provide future research directions that could address some of the key questions generated by my study.

CHAPTER TWO

Predator additions: how do prey species respond to a shift from a single predator to a multi-predator system?

Douglas F. Makin, Simon Chamaillé-Jammes, and Adrian M. Shrader

Abstract

Predators are moving back into systems. In doing so, they can change single predator systems into multi-predator systems. Currently, there is little understanding of how prey species adjust their anti-predator behaviour in response to this type of shift in predation risk. To explore this, we measured giving-up densities (GUDs) in artificial patches for kudu, sable and warthog both before and after a wild dog introduction. Before the introduction, the only predator in the system was cheetah. We found that after the release, none of the prey species adjusted their preference for landscape features (i.e. open grasslands > mixed tree bush-clumps > bush-clumps). However, kudu and sable fed more intensively in open grasslands, and reduced their feeding near denser vegetation. When the wild dogs denned in the study site, potentially increasing contact with the prey species, the feeding effort of kudu decreased significantly across all patches and continued to decrease over time. In contrast, sable and warthog stopped feeding from the patches altogether during this period. The change in feeding intensity by kudu most likely reflects a cumulative anti-predator response to both cheetah and wild dogs, while sable and warthog only respond to the increased risk from the wild dogs. Our findings are the first to record how multiple prey species adjust their anti-predator behaviours when a system changes from a single to a multi-predator system. Moreover, our results provide insight into how risk from different predators within a multi-predator system individually shape prey anti-predator behaviours.

Keywords: feeding effort, GUDs, patch use, predation risk, predator-prey interactions

Introduction

The return of large mammalian predators into ecosystems is becoming increasingly more common (Linnell et al. 2005, Ripple and Beschta 2006, Hayward and Somers 2009, Chapron et al. 2014, Ford et al. 2015). This may be the result of range expansion by the predators, or human facilitated reintroductions aiming at conserving predator species and restoring their ecological functions (Hayward and Somers 2009, Chapron et al. 2014). These returning predators can potentially drive cascading effects within food webs by altering prey behaviour (Knight et al. 2005, Ripple et al. 2014).

Recent studies have investigated prey species' responses to returning large mammalian predators across a variety of temporal and spatial scales (Creel and Winnie 2005, Sand et al. 2006, Laundré et al. 2010). However, the majority of these studies have focused on single predator systems, with many focusing on the return of wolves (*Canis lupus*) and the response of large ungulates that were experiencing virtually no predation risk until wolves returned (Ripple and Beschta 2003, Laundré et al. 2010). Similarly, Tambling et al. (2012) and Moll et al. (2016) studied the response of initially predator-free African buffaloes (*Syncerus caffer*) to the reintroduction of lions (*Panthera leo*). Whereas these studies help frame general questions about the behaviourally-mediated effects of these large predator reintroductions and provide important case studies, single predator systems are generally rare and thus most species face a suite of predators (Hayward and Somers 2009, Thaker et al. 2011, Valeix et al. 2012). Moreover, it remains to be investigated how prey adjust their behaviour in response to an additional predator entering the system and thus shifting it from a single to a multi-predator system.

Within multi-predator systems, prey species need to discriminate between different predators, and employ a range of predator-specific anti-predator strategies to minimize risk (Caro 2005). Prey recognition of cues from a returning predator species is expected to have persisted if closely related predators had remained on the landscape (i.e. the multipredator hypothesis, Blumstein 2006). After recognition, how prey respond to the returning predator will vary depending on how the hunting strategies (e.g. cursorial vs ambush) of the various predators compare. If hunting tactics of the existing and returning predators differ, prey likely adjust their behaviour to find a compromise response to predation risk that minimizes the overall perceived risk (McIntosh and Peckarsky 1999). However, if the relative danger from the predators differs greatly, prey may rather try to avoid the most dangerous predator (i.e. hierarchical response). Conversely, if the different predators use similar hunting tactics the risk they impose on prey would be cumulative. This then could lead to an additive response by prey species whereby prey would maintain similar anti-predator responses to both predators as these responses do not conflict (McIntosh and Peckarsky 1999). Moreover, this cumulative antipredator response by prey species may be observed with an increase in predator abundance, whereby the overall level of risk increases with the addition of a predator that presents a similar type of risk to the resident predator. However, in this situation, the extent to which anti-predator responses (e.g. landscape use) change may depend on the contrast between the initial and combined perceived risk.

This changing perceived risk should be reflected in how prey species utilize patches within habitats, selecting patches that confer the greatest advantage in minimizing predation risk, while still meeting daily energetic demands (Lima and Dill 1990, Owen-Smith 2014). This anti-predator response varies with exposure to different large predator species (Lima and

Dill 1990). Utilizing patches in open grasslands may reduce perceived predation risk in response to predators that rely on stalking and remaining undetected such as lion (Thaker et al. 2011). For example, Périquet et al. (2012) found that, plains zebra (*Equus burchelli*), buffalo, warthog (*Phacochoerus africanus*) and wildebeest (*Connochaetes taurinus*) spent more time utilising grasslands when lions were close (seen within 24 hours in the area) as a means to improve predator detection and increase sight lines. In contrast, utilizing patches near denser vegetation types may be advantageous when avoiding cursorial predators (i.e. wild dogs) that rely on high encounter rates and prefer prey to flee when detected (Mills 1984, Creel and Creel 2002). This was observed in Yellowstone National Park, where elk (*Cervus elaphus)* in response to predation risk from wolves moved away from open meadows and grassland into the cover of coniferous woodlands to avoid detection (Creel et al. 2005). Similarly, female roe deer (*Capreolus capreolus*) in response to predation risk from wolves in the Apennine Mountains, Italy, utilised denser vegetation as a means of avoiding predator detection by remaining concealed (Bongi et al. 2008).

Due to the foraging costs imposed by anti-predator behaviours, prey species that were initially at low risk, and likely displayed lower levels of anti-predator behaviour, have more potential to increase their responses than those initially at higher risk that display stronger anti-predator behaviours. This applies the reasoning underlying the risk-spreading theorem (Houston et al. 1993) to across species comparisons, and predicts that, when faced with additive risk induced by the return of a predator sharing characteristics with predators already present, prey that were initially at lower risk should respond more than those initially at higher risk. Thus, the overall perceived predation risk experienced by the prey species would increase as the general risk level increased with the presence of an additional predator. To the best of our knowledge this prediction has not yet been tested.

To address this, we tested this prediction in a large mammalian multi-predator multi-prey system, exploring how the addition of a predator in an arid African savanna shaped the perceived predation risk of three prey species. At the start of our study, the only predators in the system were cheetah (*Acinonyx jubatus* - solitary cursorial predators that stack close to prey and then chase over 300 m). A pack of 12 wild dogs (*Lycaon pictus* - a pack-hunting cursorial predator that will chase prey up to 3 km) were then introduced a month into the study. To determine how sable antelope (*Hippotragus niger*), kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*), prey species of varying levels of preference by cheetah and wild dogs (Hayward et al. 2006b, Clements et al. 2014), adjusted their anti-predator strategies, we recorded the foraging intensity and landscape use both before and after the wild dog introduction. We did this by measuring giving-up-densities (GUDs) in artificial patches (Brown and Kotler 2004).

We hypothesized that the addition of wild dogs would result in species-specific changes in anti-predator strategies. As GUDs provide a measure of feeding effort at a patch level in response to differences in perceived predation risk, we predicted that (1) if perceived predation risk did not increase following the introduction of the wild dogs, we expected that feeding effort would increase (i.e. lower GUDs) over time as natural forage availability on the landscape declines as the dry season progresses (i.e. period of study; see Shrader et al. 2012), despite a potential increase in predation risk. (2) Feeding effort would decrease more for sable that were less at risk before the wild dog introduction, being a species rarely targeted by cheetah due to their large size. (3) Feeding effort would decrease (i.e. GUDs would be higher) in open grasslands compared to areas near bush-clumps and mixed tree bush-clumps. This would most likely be due to the prey species shifting away from more open areas where they could potentially be seen by the wild dogs, to areas where the ability of the wild dogs to detect prey species would be reduced.

Methods

We conducted our study in Tswalu Kalahari Reserve (Tswalu hereafter), Northern Cape, South Africa (S 27°13’30” and E 022°28’40”). The reserve encompasses 100 000 hectares of restored farmland (Cromhout 2007) located in the southern Kalahari (Roxburgh 2008). The landscape comprises open grasslands containing many small (i.e. 5 to 15 m in diameter) bush-clump and mixed tree bush-clump patches. These patches are dense, thus blocking sightlines, and preventing large herbivores from moving through them. Large mammalian herbivores found on the reserve include kudu, springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), roan (*Hippotragus equinus*) and sable antelope (Appendix 1). In May 2014, Tswalu managers introduced a pack of 14 wild dogs into the 80 000 hectare, western section of the reserve, where cheetahs were the only large predators present. The total number of cheetah in the reserve is not known. However, during our study, we identified 10 individual cheetah within our 12 km^2 study area. This indicates a local density of 0.83 cheetah/km^2, which potentially makes it one of the highest cheetah densities found in small fenced protected areas in South Africa (Lindsey et al. 2011). Despite both these predators being considered cursorial, the fact that cheetah only chase prey for ~300 m, while wild dogs will chase prey for up to 3 km, puts them on extreme ends of the cursorial predator spectrum. Moreover, as cheetah tend to hunt alone or in pairs, while wild dogs hunt in packs, the degree of perceived risk by prey species from these two predators likely differs. Finally, brown hyena (*Hyena brunnea*) also occur, but do not hunt large mammals as they are primarily scavengers (Skinner and Chimimba 2005).

We collected data from May to November 2014, which we divided into four periods related to the presence of potential predators on the landscape. Seasons in the Kalahari are defined by a very long dry season (April/May to November/December) with less than 10 mm of rain falling during this period (Roxburgh 2008), followed by a short wet season (January to March). As a result, our study was restricted to the extended dry season. During the dry season, natural forage availability declines in arid landscapes due to utilisation by large herbivores (Le Houerou 1980, Katjiua and Ward 2006, Shrader et al. 2012). The four time periods we included were 1) one month before wild dog introduction (i.e. cheetah only), 2) one month after the introduction (i.e. cheetah and wild dog present), 3) two months after the introduction (i.e. when the wild dogs denned within our study area), and 4) six months after the introduction (i.e. when wild dogs had finished denning). Wild dogs generally move and hunt extensively across their home ranges throughout the year (Fuller and Kat 1990, Davies-Mostert et al. 2009). However, once they den, they make hunting trips out from the den site, thus acting like central-place foragers. Fuller and Kat (1990) found that in the Serengeti, wild dogs forage between 4 to 9 kilometres out from the den, while Ford et al. (2015) found that wild dogs foraged within 3 kilometres of the den site. As the wild dogs denned between 1 to 4 km from our three sites, this would be likely to increase the encounter rates (Fischhoff et al. 2007, Thaker et al. 2011) and harassment (Creel and Creel 2002) experienced by prey species in our study. By first collecting data when only cheetahs were on the landscape, we could determine the baseline anti-predator strategies (i.e. foraging intensity and landscape use) of these three prey species.

Wild dogs are social coursing predators that, owing to their co-operative hunting strategy, are able to kill a large range of prey of varying body size, ranging in weight from 10 kg to 250 kg (Woodroffe et al. 2007, Clements et al. 2014). Prior to their introduction, the herbivores within the western section had not encountered wild dogs. In contrast, cheetah (N= ~10) had been in the reserve for 20 years, and have an accessible prey weight range of 14 kg to 135 kg (Clements et al. 2014). A comparison of cheetah and wild dog prey weight preferences based on a multisite analysis (Clements et al. 2014) indicates that, warthog (males: 59-103 kg; females: 44-69 kg) fall within the accessible weight range of both predators. Kudu (males: 174-344 kg; females: 112-210 kg) fall within the accessible weight range of wild dog but are taken relative to their availability by cheetah, while sable (males: ~230 kg; females:

180-220 kg) are avoided by cheetah but fall within the upper limit of the accessible prey weight range of wild dog (Clements et al. 2014). Within these accessible prey weight ranges both predators have preferred and avoided prey species (Hayward et al. 2006a, Hayward et al. 2006b). For example, kudu are preferred by wild dogs and taken relative to their availability by cheetah, sable are avoided by cheetah and taken relative to their availability by wild dogs, and warthog are avoided by cheetah and taken relative to their availability by wild dogs (Hayward et al. 2006a, Hayward et al. 2006b). Thus, despite warthog falling within the accessible prey weight ranges of cheetah and wild dogs, they are generally avoided by cheetah (as they are killed relatively less frequently than expected based on their overall abundance) (Hayward et al. 2006a, Hayward et al. 2006b)

To tease apart the separate impacts that cheetah and wild dogs had on the prey species' anti-predator strategies (i.e. foraging and landscape use), we collected GUDs (i.e. amount of food left in a patch once a forager has quit feeding from the patch; Brown 1988, Brown 1999) in artificial patches. Predation risk plays an important part in determining the feeding effort of prey species (Lima 1998, Brown 1999). Specifically, an individual should cease feeding in a patch once the harvest rate (H) is equal to the metabolic (C), predation (P) and missed opportunity costs (MOC) of foraging in that patch (i.e. $H = C + P + MOC$; Brown 1988, Brown 1999). As harvest rate is a direct function of food quantity, GUDs can be used as an index of an animal's quitting harvest rate (Schmidt et al. 1998). Thus, GUDs provide insight into the trade-offs individuals make when seeking to maximize feeding effort while simultaneously reducing predation risk (Brown and Kotler 2004). Therefore, with metabolic and missed opportunity costs constant across patches, greater feeding intensity (i.e. lower GUDs) reflects lower perceived predation risk within an area, while lower feeding intensity (i.e. higher GUDs) reflects greater perceived predation risk (Brown and Kotler 2004).

For this study, we managed to habituate three prey species (i.e. kudu, sable and warthog) to the artificial patches prior to the wild dog's release. Only adult and subadult sable were recorded in the study sites. Estimated densities of these herbivore species utilising the patches based on camera trap records within the study area (12km^2) were 6 kudu/km^2, 3 sable/km^2 and 3 warthog/km^2. Following two weeks of habituation to the artificial patches, data collection was conducted by positioning the patches across the landscape in open grasslands, next to isolated bush-clumps (3 m x 3 m) and mixed stands of tree bush-clumps (10 m x 10 m). For each herbivore species, we consistently collected GUDs from all 72 artificial patches set up across three sites in the northern section of the reserve. To reduce the possibility of sampling the same individuals from the different prey species, we separated the sites by one kilometre (Owen-Smith and Cain 2007). In addition, these sites were separated by a series of hills thereby limiting the daily movement of herbivore groups between sites. This allowed for replication of patches and individuals. Each site comprised 24 artificial patches, with eight patches placed in open grassland, eight near isolated bush-clumps, and eight near mixed tree bush-clumps for each of the herbivore species. We separated the patches by 20 to 30 metres. Ultimately, the position of these patches in relation to vegetation structure provided varied predation risks (Kotler et al. 2001, Shrader et al. 2008, Stears and Shrader 2015). Specifically, visibility and escape opportunities were limited close to dense vegetation, but may have offered a potential refuge for warthog. However, the denser vegetation could potentially reduce detection by predators, thus reducing predation risk. In contrast, herbivores feeding in open grasslands would have greater sightlines with which to detect approaching predators (but would likely also be seen more easily by predators), and no obstacles that might reduce escape opportunities.

We designed species-specific artificial resource patches for each of the three-herbivore species using plastic packing crates (600 mm x 400 mm x 285 mm; Appendix 2). To provide diminishing returns (Hochman and Kotler 2007), we filled the patch with a matrix of 10 litres of inedible substrate (10 cm long cut pvc tubing). The inclusion of the matrix provides diminishing returns by increasing the feeding effort from the patches as food availability declines and therefore simulates a natural patch whereby food availability and intake rate declines with increased time spent foraging from the patch (Brown 1988). For both kudu and sable, we raised the patches one metre off the ground to exclude smaller herbivore species. In addition, we further adjusted diminishing returns by attaching a wire grid (one horizontal and two vertical strands of wire) over the top of each patch so that the strands were separated by 150 mm on the kudu patches and 200 mm on the sable patches. The wire grid prevented the herbivores from moving their muzzles through the substrate from one side of the patch to the other. As a result, herbivores were unable to push the substrate out and thus reduce the difficulty of feeding in the patch. For warthog, we placed the patches on the ground. We did not attach a wire grid on these patches as it may have caught on the warthogs' tusks.

To ensure that the data reflected the feeding of the target species, we placed Bushnell Trophy Video Cameras with motion and infrared triggers across all sites. Each video camera was positioned to provide a view of and record from more than one patch (recording distance of 1– 40 metres with the field scan feature) thereby allowing us to monitor which herbivore species utilised the patches at each site. In addition, we only included data in the analysis where we could clearly view which of the herbivore species had utilised the patches. Therefore, in the cases where non-target species were observed feeding from the patches (i.e. baboons – *Papio ursinus*) these GUD values were excluded from the dataset. As such the GUD data reflects the feeding effort of the three-target species habituated to the artificial patches. During the study, all 72 patches were utilised by the different herbivore species with varying feeding intensity, and therefore GUD values included in the analysis reflected the use of all patches over time.

Early each morning (06h00), we poured 200 grams of food (Lucerne-based sheep pellets) over the matrix. We then left the patches out all day and sifted out the remaining food (i.e. the GUD) at dusk (i.e. 18h00). This allowed the herbivores sufficient time to utilise the patches. We then replenished the patches and left them out overnight, collecting the remaining pellets (i.e. GUDs) the following morning at 06h00. Patches were put out for the three-herbivore species during all four time periods (i.e. one month before the wild dog release, one, two and six months after release). However, not all the species fed from the trays in all the periods (See results). GUDs were collected from sites where there had been clear feeding activity and thus no GUDs were collected for sites where the herbivores had not visited for a particular day, as these values would not reflect the perceived predation risk experienced feeding from a particular patch but rather that they were not active in the area.

Data Analysis

The distribution of GUD data were not normally distributed and differed for the herbivore species (kudu, sable and warthog). As a result, we used a quantile regression model comparing medians rather than a generalized linear model comparing means (Koenker 2005, Davino et al. 2013) to determine variation in GUDs of the herbivore species between landscape features (mixed tree bush-clumps, bush-clumps, open grassland) and patch use over time (four time periods). For each species, we calculated the average GUD for each landscape feature per site and compared median GUDs for each landscape feature over the four time periods. Quantile regression estimates are more robust against outliers and provides a more comprehensive analysis of the relationship between variables for datasets skewed towards low values than generalized linear mixed effects models (Koenker 2005). To determine where significant differences in GUDs existed for each species across habitats over time, we ran Tukey *post-hoc* tests. All data were analysed in R (R Core Team 2014) using the quantreg package (Koenker et al. 2015). We did not make comparisons between the herbivore species as the artificial species-specific patches were set up differently, and the amount of food the different species would eat would be driven by their body size and the attractiveness of the feeding patches.

Results

For all three-herbivore species, GUDs differed before and after the wild dog introduction (Table 1, Fig. 1). Sable and kudu significantly decreased their overall feeding effort (i.e. GUDs increased) in all patches after the wild dog's release (Fig. 1). Despite sable falling outside the preferred weight range of wild dogs, they decreased their feeding effort by 36% over the six-month period and as such their median GUDs increased from 59 g to 130 g (Fig. 1). After the wild dogs were initially released, sable responded immediately decreasing their feeding effort by 24% across all landscape features (Fig. 1). Similarly, to the sable, kudu reduced their overall feeding effort by 23%, which resulted in their median GUDs increasing from 44 g before the wild dog's release, to 90 g six months later (Fig. 1). However, a small temporary decrease (9%) in GUDs was recorded after the immediate introduction (Fig. 1). Warthog initially increased their feeding effort across patches (i.e. 30%; GUDs dropped from 127 g to 76 g after the wild dogs were released; Fig. 1). However, when the wild dogs denned in the study area a month after release, warthog stopped feeding from the artificial patches (Fig. 1).

Although feeding effort varied for the different herbivore species following the wild dog's introduction, the pattern of landscape feature selection remained the same throughout the study (Table 1). Specifically, kudu and sable showed a clear preference for patches located in open grasslands (i.e. lower GUDs), and showed a stronger avoidance (i.e. higher GUDs) for patches located near bush-clumps and mixed tree bush-clumps (Table 1; Fig. 1). Warthog also maintained a preference for patches in open grasslands before and after wild dog's introduction. However, this was not significantly different (Table 1.).

Table 1. Quantile Regression Model comparing the median giving-up-densities (GUDs) of kudu, sable and warthog in response to landscape features (open grassland, bush-clumps, and tree-bush-clumps) and period before and after wild dogs' release (one month prior – cheetah only, one, two and six months after), including interactions between variables.

Species	Variable	Residual d.f.	d.f.	F	P
Sable	Landscape Feature	304	2	2.71	0.014
	Period	304	2	26.40	<0.001
	Landscape Feature *Period	304	5	1.01	0.405
Kudu	Landscape Feature	679	2	3.10	0.002
	Period	679	3	6.87	<0.001
	Landscape Feature *Period	679	6	0.44	0.845
Warthog	Landscape Feature	469	2	1.45	0.139
	Period	469	1	8.89	<0.001
	Landscape Feature *Period	469	3	0.21	0.973

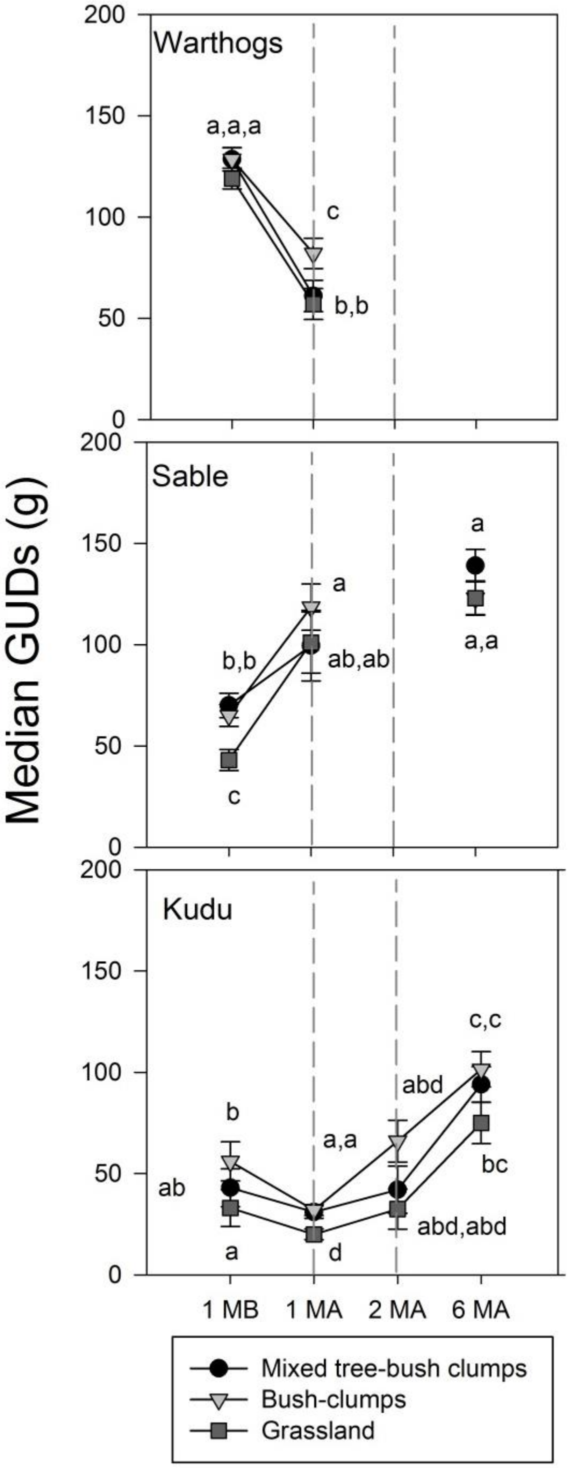

Figure 1. Median GUDs recorded for kudu, sable and warthog before and after the wild dog introduction. Time periods: 1MB – one month before, 1MA – one month after, 2 MA – two months after and 6MA – six months after. Dotted lines represent period when the wild dogs denned in the study area. Bars represent SE. Median GUD values sharing letters are not significantly different, as assessed by the Tukey *post-hoc* comparison tests.

Discussion

In multi-predator systems, prey should develop anti-predator strategies that ultimately limit their overall risk of predation from all predators (Relyea 2003, Thaker et al. 2011). However, what strategies prey species incorporate (e.g. hierarchical, compromise, additive response) when a system shifts from being a single to a multiple predator system, after a predator moves in, is generally unknown. This, however, could be predicted from predator traits such as hunting strategies (McIntosh and Peckarsky 1999) and potentially predator abundance if the hunting strategies of the resident and added predators are similar (Sih et al. 1998). Here, we show how the addition of wild dogs into a single predator system altered the foraging of three prey species that were previously only exposed to predation risk from cheetah. For all three species, the observed changes in response to both predators were not linked to a shift in patch selection near landscape features. Rather, we observed changes in the amount of food consumed from patches suggesting that the addition of wild dogs influenced the foraging/safety trade-off for the three-prey species. Yet, as predation risk from the cheetah and wild dogs differed for each prey species, the mechanisms driving the changes in feeding intensity (i.e. GUDs) were likely different.

Sable and kudu both generally reduced their feeding effort over time after the introduction of the wild dogs. This response was stronger for sable than for kudu, despite sable falling outside of the preferred weight range of wild dogs (Hayward and Kerley 2008, Clements et al. 2014). This matches our prediction that species that were initially less at risk would respond more strongly to the addition of a predator, as their initial low levels of anti-predator behaviour allow them to spend more time feeding. Although cheetah and wild dogs have >70% dietary overlap (Hayward and Kerley 2008), the pack hunting of wild dogs allows them to take larger prey than cheetahs which are unlikely to prey on adult sable based on their preferred weight ranges (Hayward et al. 2006a, Clements et al. 2014). Thus, the introduction of wild dogs into Tswalu has most likely shifted predation risk for sable from safe (virtually no predation, cheetah only) to risky (wild dogs), as wild dogs kill sable based on their availability on the landscape (Hayward et al. 2006b). As a result, despite two predators being on the landscape, the adjustments to sables' anti-predator strategy (i.e. reduced feeding effort) was likely in response to the threat generated by the wild dogs only. This is supported by the fact that the sable moved away from the feeding sites when the wild dogs denned (two months after their release, Fig. 1), possibly due to increased contact with the wild dogs during this period.

In contrast to sable, the feeding effort of kudu changed very little during the first month after the wild dog reintroduction. The small increase in feeding effort in the first month is unlikely to be biologically meaningful (9% increase) before GUDs increased following the wild dog denning event. If it were, it would suggest that their perceived predation risk declined with the presence of wild dogs on the landscape, which is unlikely. Despite this unexplained small initial increase, kudu reduced their overall feeding effort as the study progressed and their exposure to the wild dogs increased during the wild dogs denning period. As this was not associated with changes in patch selection related to woody features, which could modify visibility and detectability, we conclude that, as expected, kudu displayed an additive anti-predator response to the additional threat from the wild dogs. This is particularly noticeable as cheetah density in Tswalu is relatively high, and kudu thus probably already devoted significant effort to anti-predator behaviours. Despite this, they were still able to increase their anti-predator response to compensate for the increased risk from the wild dogs.

Compared to sable and kudu, the warthog displayed significantly different responses to the introduction of the wild dogs. Firstly, they fed more intensively in patches right after the wild dog introduction (30 % increased feeding effort). This was unexpected as warthog while avoided by cheetah are taken relative to their availability by wild dogs and had a relatively high local density (3/km^2) in Tswalu. A tentative explanation for this could be explained by the risk-food-availability trade-off, where warthog increase their feeding effort from patches with the progression of the dry season as natural food availability declines. However, with the denning of the wild dogs in the study site and thus, increased proximity, the increased risk of predation outweighed the benefit of feeding from the artificial patches in the area over that period leading to the patches being abandoned. This remains speculative however. The second way in which the warthog differed to the other species is that they did not return to the feeding sites after the wild dogs had finished denning. There are two possible reasons for this. First, it could be that the warthog moved out of the study sites due to increasing contact with the wild dogs and thus greater perceived risk. If the warthogs left, then this suggests, that they adjusted their anti-predator strategy in response to the increased risk from the wild dog's proximity (i.e. additive response). Alternatively, it could be that the warthogs left the feeding site due to a decline in natural forage with the extension of the dry season. However, if this was the case, one would have expected the larger herbivores to have left the feeding sites first and not returned as larger herbivores are more limited in their ability to obtain adequate food intake as food availability declines (Fryxell 1991). However, this was not observed. Lastly, it could be that warthogs habituated to the artificial feeding patches were killed by the wild dogs. Either way, it seems that increased predation risk had a greater effect on the warthogs than either the kudu or sable antelope. Thus, as with sable, the introduction of wild dogs likely shifted predation risk from safe (avoided by cheetah) to risky (preyed on by wild dogs).

In contrast to the prediction of predation risk driving the observed patterns of patch use, it is possible that the herbivore species' foraging behaviour could have been influenced by a decline in the availability of food on the landscape during the dry season. However, if this were the case, we would then expect feeding effort from the artificial patches to increase (i.e. increased feeding on the greater availability of food in the artificial patches compared to limited food on the landscape) as the dry season progressed. For example, Shrader et al. (2012) found that goats (*Capra hircus*) increased their feeding effort from artificial patches with the progression of the dry season in a semi-desert in the Northern Cape, South Africa. However, this was not observed in our study. In contrast, the feeding effort of the herbivores in the artificial patches declined (i.e. reflecting higher GUDs) as the dry season progressed. Thus, this suggests that a seasonal decline in food availability was not the key driver of the patterns we recorded. Rather, we suggest that changes in perceived predation risk from the cheetah and wild dogs drove the herbivore patch use patterns we recorded.

One possible limitation of this study involves changing group sizes over the study period, which would have influenced the risk-food availability trade-off, as increased group sizes increase time available for feeding (Creel et al. 2014). However, GUDs increased over time following the wild dog's introduction, this suggests, that if group sizes increased it was not sufficient to maintain a similar feeding effort to that recorded before the wild dogs were released. Therefore, the overall perceived predation risk associated with the addition of a predator increased over time.

At the landscape scale, all species foraged more in patches located in the open grasslands compared to those located near bush-clumps/trees, and this pattern did not change after the introduction of wild dogs. Predicting the effect of vegetation structure on predation risk is complex as it integrates the hunting mode of the predator as well as the predator-detection, avoidance and escape strategy of the prey (Kauffman et al. 2007, Gorini et al. 2012). However, visibility is generally a major determinant of safety, as it allows for early detection of the predators and subsequent monitoring, possibly giving time to escape or send pursuit-deterrence signals (Cresswell et al. 2010, Belll et al. 2012). Another possibility includes the fact that wild dogs often use bushes to increase the catchability of prey, as escape options are reduced (Fuller and Kat 1990). In contrast, by foraging close to or within dense vegetation, detection by predators may be reduced (Mech et al. 2001, Creel and Winnie 2005). The fact that all three-species preferred to feed in open grasslands where sightlines were likely greater, both before and after the introduction of the wild dogs, suggests that predator detection reduced perceived predation risk more than hiding from predators does. Moreover, despite cheetah and wild dogs being on the opposite ends of the are cursorial predator spectrum, it seems that the additional predation risk posed by wild dogs was not great enough, nor sufficiently different to the predation risk posed by cheetah to change large-scale landscape use. Thus, the herbivores perceived risk from the two predators to be similar. As a result, with regards to predation risk, the introduction of the wild dogs into the reserve was ultimately similar to just doubling the number of cheetah. However, if an ambush predator such as lion had been introduced, this may have elicited a different anti-predator response as their style of hunting varies considerably from that of cheetah (West et al. 2013). If that was the case, prey may have shifted their patch use to avoid ambushing lions (i.e. hierarchical response).

Predicting prey and ecosystem responses to the return of predators is timely and important, but challenging. Until now most studies have focused on single predator systems and the response of one prey species at a time. This study provides an important step towards extending our knowledge to more complex multi-predator-multi-prey systems. We, however, emphasize that only replication of field studies such as this, grounded in the theory of how prey species adjust their behavioural responses to returning predators within a multi-predator environment, will allow our knowledge to advance at the rapid pace required by the current dynamics of predator returns and reintroductions.

CHAPTER THREE

Herbivores employ a suite of anti-predator behaviours to minimize risk from ambush and cursorial predators

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Abstract

Prey species may adjust their anti-predator behaviours and their combination, to the hunting strategies (e.g. ambush versus cursorial) and the level of risk imposed by different predators. Studies of suites of behaviours across well-defined contrasts of predation risk and type are rare however. Here we explored the degree to which six herbivore species adjusted their anti-predator behaviours to two predator treatments (lion's - *Panthera leo* versus cheetah - *Acinonyx jubatus* and wild dogs – *Lycaon pictus*). We focused on prey behaviour (vigilance, grouping, temporal use) at waterholes. We predicted that if the hunting strategy of the predator was the key driver of anti-predator behaviour, that ambushing lions would elicit a greater response than cursorial cheetah and wild dogs. Alternatively, if predator preference was the main driver, then we expected prey species to adjust their anti-predator behaviours in response to the predators that specifically target them (i.e. preferred prey of the different predators). Overall, we found that the herbivores maintained greater vigilance, generally moved in larger groups, and used waterholes less at dawn, dusk or at night (when lions are active) when exposed to the potential threat of ambushing lions. However, some species preferred by cheetah and/or wild dogs (i.e. red hartebeest, warthog, gemsbok) moved in larger groups in the cheetah and wild dog section. Yet, the magnitude of the differences in group size for these herbivores were small. Thus, we suggest that overall, the potential threat of ambushing lions was the main driver of anti-predator behaviour around waterholes, most likely determined by prey weight preference and the possibility of being ambushed.

Keywords: group size, hunting strategies, predator-prey interactions, prey preferences, temporal activity, vigilance

Introduction

Prey possess a whole suite of behaviours that they may employ to reduce predation risk (Lima and Dill 1990, Caro 2005). In particular, vigilance and grouping are flexible behaviours that can be used to reduce risk, though they come with associated costs. For example, increased vigilance allows individuals to detect attacks earlier, providing a greater chance of escaping (Lima and Bednekoff 1999), but often reduces food intake rate (Fortin et al. 2004). Living in larger groups allows individuals to potentially benefit from dilution, collective vigilance, and/or deterrence effects (Beauchamp 2003, Schmitt et al. 2014), but could increase intra-group competition (Krause and Ruxton 2002). Because of these costs, prey are not expected to always display a full suite of antipredator behaviours, but rather to finely adjust anti-predator behaviours to the level of risk, by prioritizing certain behaviours over others (e.g. vigilance, grouping, temporal shifts; Creel et al. 2014).

Predation risk varies both temporally and spatially across the landscape. This translates into a ‘landscape of fear’ (Laundré et al. 2001b), that is shaped by differences in the prey’s perception of the likelihood of meeting a specific predator (e.g. predator density, similar landscape use between predator and prey, shared time of activity), and of the likelihood of being killed when attacked (i.e. ‘threat’ of the predator). However, as not all predators are the same, prey species likely adjust the extent to which they utilise different anti-predator behaviours (e.g. vigilance levels, group size) in response to different predators or predator combinations.

One factor that likely greatly influences anti-predator strategies is the hunting strategy of a predator. For instance, large mammalian predators are usually classified as either cursorial or stalking/ambush predators. Cursorial predators roam over large areas looking for prey, and then approach prey rapidly and silently when found (Creel and Creel 2002, Pomilia et al. 2015). As a result, their distribution in the landscape is generally unpredictable, and thus prey tend not to associate specific places with predation risk from these species (see discussion in Preisser et al. 2007). On the contrary, ambush predators rely on places were the likelihood of meeting prey is high, relying on small scale vegetation cover, rather than speed, to approach prey (Preisser et al. 2007). Thus, areas attracting prey usually also attract ambush predators, and thus prey should increase their anti-predator behaviour when using these areas (Valeix et al. 2009a). For example, within arid and semi-arid environments that we study here, water sources attract both large mammalian herbivores and their ambush predators such as lions (de Boer et al. 2010, Valeix et al. 2010, Thaker et al. 2011, Ogutu et al. 2014).

In addition to a predator's hunting strategy, prey species likely also consider the degree of threat posed by a specific predator. Predators tend to target prey species within specific body size ranges (for lion: Hayward 2006, Hayward et al. 2011, Clements et al. 2014). Thus, some predators will be more of a threat than others. For example, lions are more likely to attack a 290-340 kg zebra (*Equus quagga)* as opposed to a 40-70 kg impala (Aepyceros melampus; Hayward and Kerley 2005). As a result, prey species should increase the extent to which they utilise specific behaviours (e.g. increase vigilance levels) in response to their primary predators, compared to more peripheral predators. Yet, an overarching factor that greatly influences predation risk is the overlap in the activity patterns of predators and prey (i.e. whether they are nocturnal or diurnal; Kronfeld-Schor and Dayan 2003). To minimise contact with predators, prey species can shift their temporal use of the landscape to periods when predators are least active. For example, in Hwange National Park, most ungulate species appear to avoid coming to drink at night when lions are in the vicinity of the waterholes (Valeix, Fritz, Loveridge et al., 2009).

Here we explore the degree to which prey species adjust their anti-predator strategies in response to different predators. We focused our observations at waterholes in a semi-arid ecosystem as a model of key interaction areas between predators and prey, and studied the anti-predator behaviour (grouping, vigilance, time of use) of six large herbivore species (i.e. eland, *Taurotragus orynx*; gemsbok, *Oryx gazalla*; plains zebra, red hartebeest, *Alcelaphus busealaphus caama*; warthog, *Phacochoerus africanus*; blue wildebeest, *Connochaetes taurinus*) at these waterholes. We did this in two sections of the same reserve that were separated by fences, one with only lions (ambush predators), the other with cheetah and wild dogs (both cursorial predators), and no lions.

In many ecosystems, lions select and kill in areas close to water (de Boer et al. 2010, Valeix et al. 2010, Thaker et al. 2011, Ogutu et al. 2014). Cheetah and wild dog may also do this, but their presence near waterholes might be less predictable as their cursorial hunting strategies likely increase their use of areas away from water sources, more so than lions (e.g. Ndaimani et al. 2016). Thus, we predicted that if hunting strategy was a key driver of prey anti-predator behaviour, lions would elicit a greater anti-predator response from prey species compared to the less spatially predictable cheetah and wild dogs. This could either be through all the prey species showing greater changes in their anti-predator behaviours (e.g. increased vigilance and larger groups) and/or adjusting their temporal activity patterns in response to lions compared to cheetah and wild dogs. Alternatively, if anti-predator behaviours of prey species are driven more by predator prey preference, then we would expect individual prey species to make greater adjustments in the anti-predator behaviours in response to the predators that specifically target them (i.e. prey falling within the predator's preferred prey weight range) compared to predators where the prey species falls outside the predator's prey weight range. This could then result in species-specific differences both within and between the predator sections.

Methods

Ethical Note

The university of KwaZulu-Natal approved all aspects of the research design (Ethics code: 058/14/Animal).

Data Collection

We conducted our study in Tswalu Kalahari Reserve (Tswalu hereafter) in the Northern Cape, South Africa (S 27°13'30" and E 022°28'40") from October 2013 to April 2015. The fenced reserve encompasses 1000 km^2 of restored farmland (Cromhout, 2007) located in the southern Kalahari (Roxburgh 2008). Tswalu has a mean annual rainfall of 250 mm, with an extended dry season lasting from May to September/October where there is less than 10 mm rainfall (Roxburgh 2008). Large mammalian herbivores found in the reserve include kudu, springbok (*Antidorcus marsupialis*), gemsbok, eland, sable (*Hippotragus niger*), zebra, red hartebeest, warthog, and wildebeest.

Tswalu is divided into two adjacent sections which support different large predator populations, but are separated by ~50 metres comprising a road and two predator fences. The western section of the reserve (200 km^2) contains lion (N= 24), while the eastern section (800 km^2) contains populations of cheetah (N ~10) and wild dog (N = 14). Habitat types across both sections are similar, made up of *Digitaria polyphylla* dominated hills, *Stipagrostis uniplumis* dominated plains and valleys, and *Anthephora pubescens* dominated sand dunes (see Van Rooyan, 1999). Likewise, both sections have a similar mean annual rainfall (mm), with 326 ±

40 mm falling within western section compared to 345 ± 42 mm within the eastern section recorded over a nine-year period. We limited data collection to the herbivore species that occurred in both sections of the reserve. These included eland, gemsbok, zebra, red hartebeest, warthog and wildebeest. The herbivores living in the two sections face different levels of predation risk due to the hunting strategy employed, their activity patterns, and the prey weight preferences of the different predator species (Hayward et al. 2007, Hayward and Slotow 2009). Lion are stalk and ambush predators that are predominantly active at night, while cheetah and wild dogs are mostly diurnal and hunt by chasing down their prey (Hayward and Somers 2009). Comparing prey weight preferences from a multi-site analysis, Clements et al. (2014) determined that lion have an accessible prey weight class range of 32 kg - 632 kg and therefore all six herbivores species monitored in our study fall within their prey weight range. However, they tend to prefer prey weights of between 92 kg and 632 kg (Clements et al. 2014)Clements, Tambling, Hayward, & Kerley, 2014) with wildebeest and zebra often preferentially targeted over other prey (Sinclair et al. 2003). In contrast, cheetah and wild dogs have smaller accessible prey weight ranges of between 14 kg – 135 kg (with a peak weight mode of 36 kg; Hayward, Hofmeyr, O'Brien, & Kerley, 2006) and 10 kg – 289 kg (peak weight modes of 16-32 kg and 120-140 kg; Hayward, Hofmeyr, O'Brien, & Kerley, 2006), respectively. Therefore, only warthog and red hartebeest fall within the accessible range of cheetah, while all of the herbivores, with the exception of eland, fall within the accessible prey range of wild dogs (Clements, Tambling, Hayward, & Kerley, 2014). Within these accessible prey weight ranges only warthog fall within the preferred prey weight range of both cheetah and wild dogs (Clements, Tambling, Hayward, & Kerley, 2014). Despite discrepancies in prey weight range preferences, cheetah and wild dogs have the highest recorded dietary overlap (73.5%; Hayward and Kerley 2008) of the large African predator guild and therefore present a significant cumulative predation risk to shared prey species. Within Tswalu, lion prey upon wildebeest

and gemsbok (Roxburgh, 2008), while cheetah prey on red hartebeest and springbok, and wild dogs prey on kudu, red hartebeest and impala (Makin, n.d).

Throughout the study, all three predator species were observed utilising waterholes. Moreover, lions were active at waterholes predominantly at night and during crepuscular periods (80% of observations). In contrast, cheetah and wild dogs were more diurnal, visiting waterholes during the crepuscular periods and during the day (65% and 70% of observations, respectively).

To assess the anti-predator strategies used by the different prey species in response to the different predators, we deployed Bushnell video camera traps with heat-motion sensors at five waterholes in the cheetah and wild dog section, and three waterholes in the lion section. Camera traps were attached to trees at a height of one metre above the ground. This ensured that each camera's field of view extended from the ground up to over 2.5 metres. Camera traps were placed so that they had a clear view of the entire waterhole. This enabled all individuals visiting the waterholes to be recorded. Only videos showing clearly discernible individuals were included in the data analysis.

We limited the chances of collecting data from the same individual's multiple times within a single recording event, by first noting when individuals left the field of view. We then waited 30 minutes before collecting data from groups of the same species comprising the same number of individuals (i.e. potentially the same group) that entered the field of view (Linkie and Ridout 2011, Tambling et al. 2015). Previous studies have suggested that 30 minutes represents a sufficient trade-off between recording the same individual multiple times and missing new individuals (Rovero et al. 2005, Tambling et al. 2015).

We analysed the video camera data recording: 1) herbivores species, 2) time of day (Day: 0600 – 1700, Crepuscular: 0400 – 0600 and 1700 – 1900, Night: 1900 – 0400), 3) typical group size (i.e. reflection of the animal's rather than the human observers experience within the group; calculated as Sigma(n2)/sigma(n), with n group size of group; Jarman 1974), 4) predator section (lion versus cheetah and wild dogs), and 5) proportion time individual herbivores within groups were vigilant at waterholes. We followed the approach of Périquet et al. (2010) where vigilance was monitored for a focal animal within the centre of each group. We did this as central individuals are less likely to be killed than individuals on the periphery, thus any increase in vigilance by central individuals will likely reflect an increase in vigilance for all individuals within the group. We considered an animal to be vigilant when it stood in an upright position, head alert and actively scanning with ears held forward. All individuals recorded were adult members of the group. As females with juveniles will maintain higher levels of vigilance to protect dependent offspring we focused on the vigilant responses of females without juveniles (Périquet et al. 2010). Additionally, the study was conducted following a severe drought year and therefore there was little recruitment into the different herbivore populations during this period, with most breeding groups consisting of only adults and sub-adults from the previous year (Makin Pers. Obs.).

We recorded the proportion time each individual spent vigilant at waterholes over a 10-minute period or over the entire time herbivore groups were drinking at a waterhole if it was less than 10 minutes. We defined both of these time periods as an observation. Vigilance was recorded for individuals within groups that were in close proximity to the waterhole (i.e. drinking or standing on the water’s edge). Within the lion section, we recorded 85 wildebeest, 23 eland, 91 gemsbok, 147 zebra, 36 red hartebeest and 88 warthog observations, while in the cheetah and wild dog section we recorded 182 wildebeest, 76 eland, 222 gemsbok, 78 zebra, 187 red hartebeest, and 275 warthog observations.

Statistical analysis

For each herbivore species, we compared the effect of predator section (i.e. lion versus cheetah and wild dog) and the interaction between predator section and herbivore species on changes in the anti-predator behaviours of typical group size and proportion of time spent vigilant using generalized linear models (GLM) with Poisson and binomial errors, respectively. To keep the model simple, we did not include group size as a predictor of the proportion of time spent vigilant. Preliminary analyses showed that there was no relationship for 5 out of the 6 species (all $P > 0.10$), with only red hartebeest showing a slight positive relationship between individual vigilance and increasing group size ($z = 3.86$, $P < 0.01$), but this was of a very small magnitude (Lion section: $y = 0.03x + 0.33$; Cheetah and wild dog section: $y = 0.03x + 0.11$). For each herbivore species in each predator section, we visually displayed the diel distribution of visits to waterholes using kernel-based density plots. In addition, we tested for the statistical significance of differences between predator sections by fitting a GLM with Poisson distributed errors with the number of herbivore observations recorded at a waterhole within each time-period (night, crepuscular, day) as the response variable, and time period and predator section as explanatory variables, including interactions between variables. Warthog were not recorded visiting waterholes at night in the lion section and therefore could not be compared for this time period. All analysis was performed using R 3.21 (R Core Team 2014) using the lme4 package (Bates et al. 2012), MASS package (Venables and Ripley 2002) and the multcomp package (Hothorn et al. 2008).

Results

Typical group sizes varied significantly between herbivore species ($x^2_{10} = 732.7$, $P < 0.01$), between the predator sections ($x^2_6 = 51.5$, $P < 0.01$) and for the interaction between herbivore species and the different predator sections ($x^2_5 = 51.4$, $P < 0.01$). Overall, group size did not differ between the sections for eland ($z = -1.72$, $P = 0.08$; Fig. 1a). Zebra ($z = 2.12$, $P = 0.03$)

and wildebeest ($z = 5.05$, $P < 0.01$) maintained larger groups in response to lion compared to cheetah and wild dogs. In contrast, gemsbok ($z = -2.18$, $P = 0.03$), red hartebeest ($z = -2.37$, $P = 0.018$) and warthog ($z = -3.45$, $P < 0.01$) maintained slightly larger groups in response to cheetah and wild dogs than in response to lion (Fig. 1a).

All the herbivore species tended to be more vigilant at waterholes within the lion section compared to within the cheetah and wild dog section (Fig. 1b). Differences, however, were only statistically significant for gemsbok ($z = 2.52$, $P = 0.01$), red hartebeest ($z = 3.54$, $P < 0.01$) and warthog ($z = 2.88$, $P < 0.01$) groups, and not for eland ($z = 1.69$, $P = 0.09$), zebra ($z = 1.92$, $P = 0.06$) or wildebeest ($z = 0.94$, $P = 0.35$; Fig. 1b).

Gemsbok, zebra and wildebeest were predominantly diurnal at waterholes in both predator sections (Fig. 2). However, when we compared the differences in temporal waterhole use (day, crepuscular, night) for the same species across sections, we found statistically significant differences in the waterhole use of gemsbok ($z = -2.58$, $P = 0.01$), zebra ($z = -2.48$, $P = 0.02$) and wildebeest ($z = -2.14$, $P = 0.03$). Specifically, in the lion section, these herbivores visited the waterholes less during the night ($z = -10.98$, $z = -5.161$, $z = -3.63$; all, $P < 0.01$, respectively) and during crepuscular periods ($z = 3.58$, $z = 3.59$, $z = 3.35$, all, $P < 0.01$, respectively) than they did in the cheetah and wild dog section. There were no statistically significant differences in temporal use of waterholes for eland (Night - $z = -0.12$, $P = 1.00$; Crepuscular – $z = -0.12$, $P = 1.00$; Day – $z = -0.36$, $P = 0.998$), red hartebeest (Night - $z = 0.69$, $P = 0.982$; Crepuscular – $z = -0.33$, $P = 0.999$; Day – $z = -0.29$, $P = 0.997$) and warthog (Crepuscular – $z = 0.03$, $P = 1.00$; Day – $z = -0.26$, $P = 0.998$; Fig. 2).

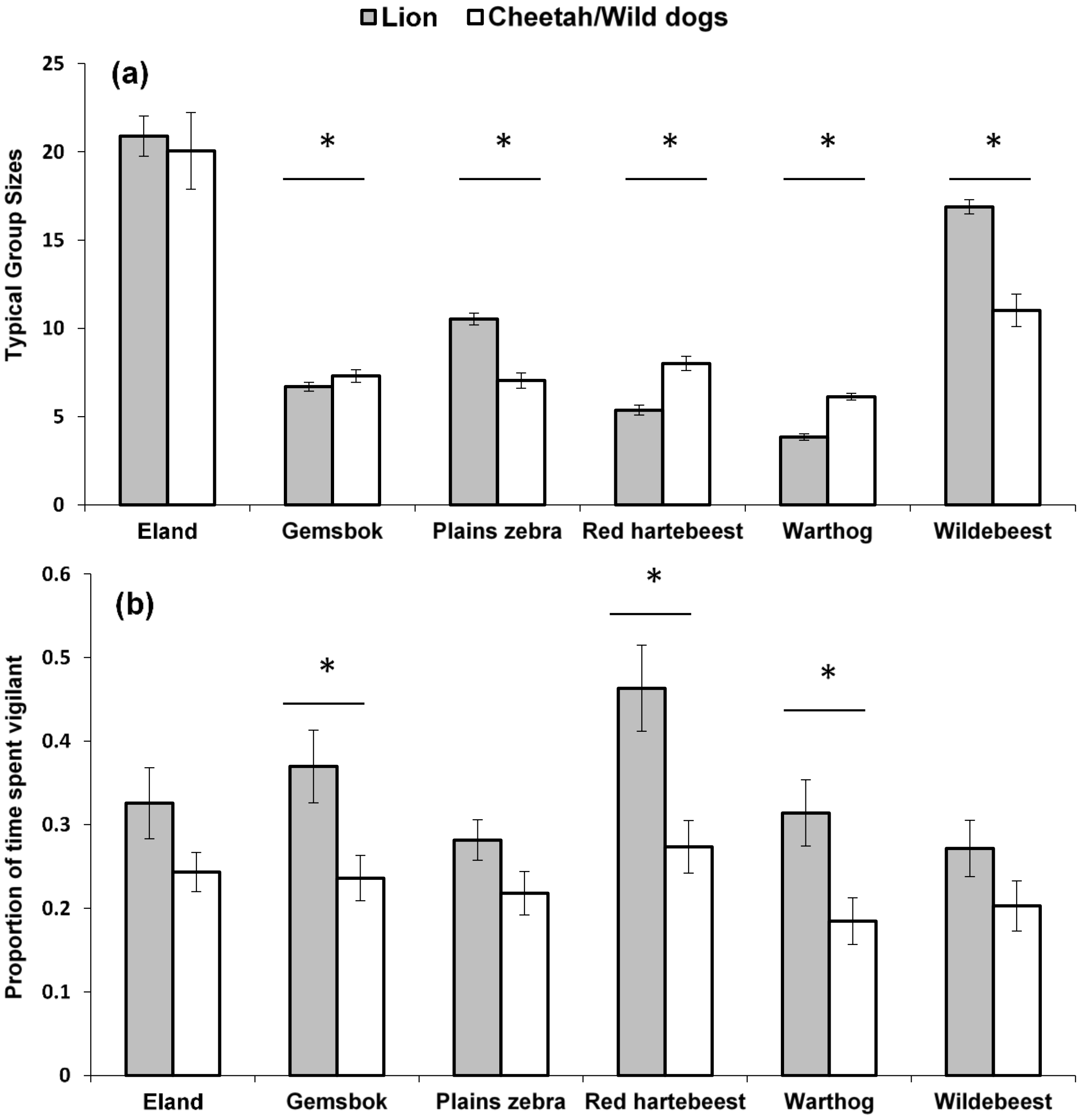


Figure 1. **(a)** Typical group sizes and **(b)** mean proportion time herbivore groups were vigilant at waterholes comparing the two different predator sections (lion versus cheetah and wild dogs). Bars represent SE. * denotes significant differences across predator sections.

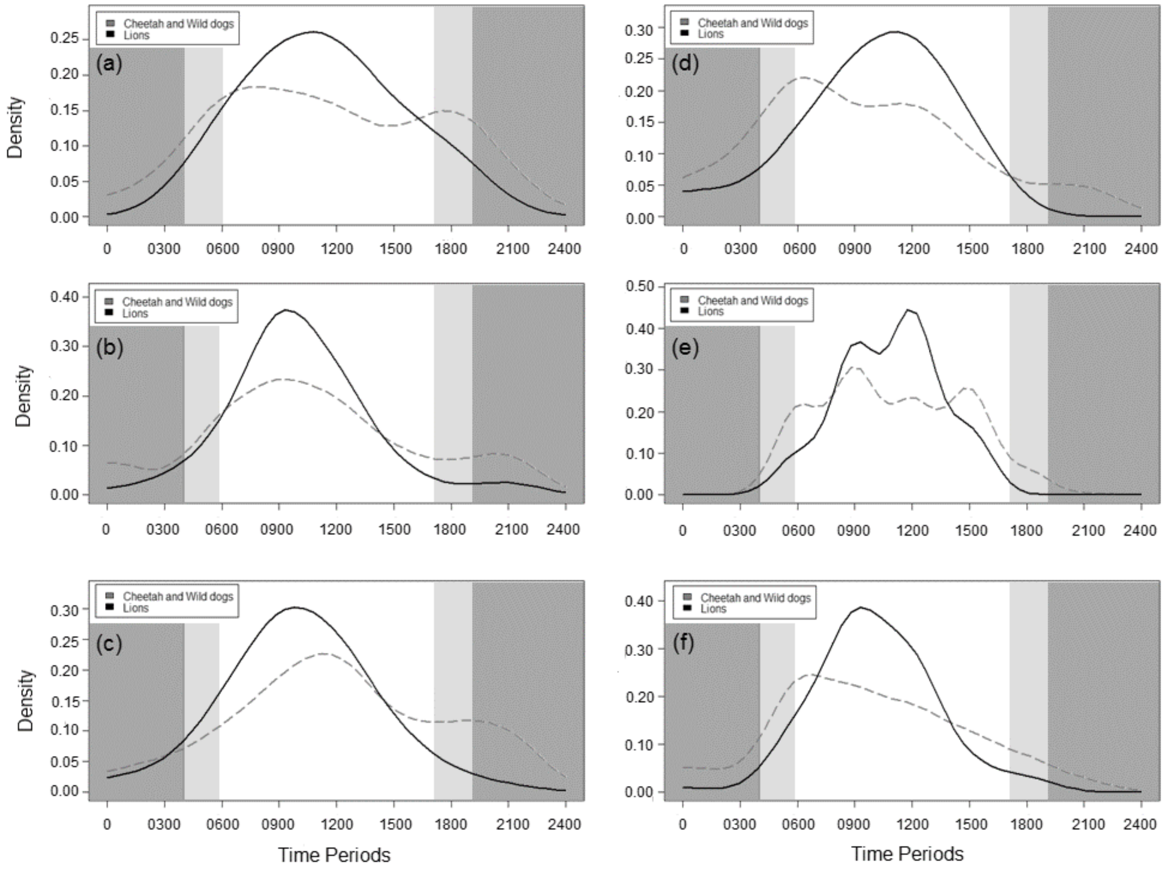


Figure 2. Density kernel plots estimating the daily activity patterns of **(a)** eland, **(b)** gemsbok, **(c)** zebra, **(d)** red hartebeest, **(e)** warthog and **(f)** wildebeest at waterholes comparing different predator sections (Cheetah and Wild dog - dotted grey line versus Lions – solid black line) and time periods (Night – dark grey, Crepuscular – light grey, Day – White).

Discussion

In response to predators, prey species can adjust their behaviour in several ways to reduce risk (Lima and Dill 1990, Caro 2005, Creel et al. 2014). However, as not all predators impose the same threat, the behavioural strategies utilised by prey will likely vary in response to different predator hunting modes (i.e. ambush versus cursorial), overlap in activity patterns (i.e. nocturnal versus diurnal), and their prey preferences. We found that the anti-predator behavioural strategies of six herbivore species differed between the lion, and cheetah and wild dog sections. Overall, lions had the greatest effect suggesting that the threat of this ambush predator around waterholes was a key driver of the observed anti-predator behavioural adjustments of most of the herbivores.

It is possible, however, that the differences in anti-predator behaviours we recorded were driven by landscape differences between the sections. Though, the two sections were only separated by ~50 m, had identical history of land use, similar climates/rainfall, and similar topography (Cromhout, 2007; Van Rooyan, 1999). As a result, we believe that it more likely that the behavioural differences between the two sections were driven by differences in predation risk posed by the two sets of predators.

Across African landscapes, lions are one of the most dangerous predators that herbivores can encounter. The combination of their large body size and group-hunting tactics mean that they can successfully kill a number of species ranging from warthogs up to larger-bodied herbivores including buffalo (550-700 kg), giraffe (700-1400 kg) and in some cases even elephants (even up to 7 years old; 700-900 kg; Hanks 1972, Loveridge et al. 2006). Moreover, lion actively select habitats close to waterholes and therefore present a significant risk to herbivores aggregated around these water sources (Valeix et al. 2009a, de Boer et al. 2010).

Comparing differences in the herbivore species' anti-predator behaviours between predator sections, we found that the majority of the herbivore species adjusted their behaviours so as to minimise the risk of attack from ambushing lions. This was evident in that all the herbivore species maintained greater vigilance in the lion section (significantly so for gemsbok, red hartebeest and warthog) compared to the cheetah and wild dog section. This could also be partly caused by the fact that vigilance may not be so necessary in the face of cursorial predators that often ‘test’ herds for vulnerable animals (Creel and Creel 2002). Moreover, all herbivores preferred to utilise waterholes during midday when lions tended to be less active (Valeix et al. 2009b, Tambling et al. 2015). The fact that zebra, wildebeest (both preferred prey of lions) and gemsbok reduced their night time usage of waterholes in the lion section indicates that these species adjusted their activity patterns to reduce contact with lions. In addition, both zebra and wildebeest moved in larger groups in the lion section compared to the cheetah and wild dog section. Thus, these species increased the use of their range of anti-predator behaviours against their main predator, lions. This was similar to Valeix et al. (2009b) who found that in Hwange National Park, wildebeest and zebra increased their group sizes with the long-term risk of encountering lion around waterholes.

As all the herbivores species in our study fall within the prey weight range of lions, it is difficult to tease apart which factors are driving the observed behavioural differences between the herbivores in the two predator sections. However, as the main species making these adjustments (i.e. zebra and wildebeest) are generally preferred prey species of lions, we suggest that it is likely the combination of prey preference of the lions (Sinclair et al. 2003) and heightened predation risk at the waterholes (i.e. possibility of being ambushed) that lead to adjustments to these and the other species’ anti-predator strategies (de Boer et al. 2010).

In contrast to the general response towards lions, we found that red hartebeest, warthog (both accessible prey of cheetah and wild dog; Hayward et al. 2006b, Marker et al. 2007) and gemsbok (within the prey range of wild dogs; Hayward et al. 2006a, Hayward et al. 2006b) moved in larger groups at waterholes in the cheetah and wild dog section. This suggests that these herbivores were responding to the combined threat from cheetah and wild dog. Yet, all three of these herbivore species also fall within the prey range of lions. A potential reason for why these herbivores maintained larger groups in the presence of cheetah and wild dogs is that it is possible that the combined risk from these predators was greater than the risk from lions alone. This may have been due to more frequent contact with cheetah and wild dogs as opposed to lions. Within the lion section, there were only two prides of lions. In contrast, in the cheetah and wild dog section there were a minimum of 10 cheetahs, each moving separately (Makin pers. obs.), and one pack of wild dogs (i.e. 11 potential encounters with predators). Moreover, as cheetah and wild dogs are predominately active during the day (Hayward and Somers 2009), and thus a greater overlap in the activity patterns of these predators and their prey, it is possible that by moving in larger groups these herbivores reduced the combined risk from both predators (Clements, Tambling, Hayward, & Kerley, 2014).

Despite this, the magnitude of the differences in group size for all six-herbivore species were small with a difference of only a few individuals in typical group sizes between the predator sections. This suggests that group size may in fact not be a major adaptive response to increased predation risk from predators at waterholes in Tswalu. If this is the case, then this suggests that all the herbivores in our study adjusted their anti-predator behaviours more in response to the potential threat from the two prides of ambushing lions as opposed to the cursorial cheetah and wild dogs. Additional support for this, comes from the fact that herbivores preferred by cheetah and wild dogs did not shift to utilising water holes during the night, when these predators were less active (Hilborn et al. 2012, Ford et al. 2015), but see Cozzi et al. (2012). One possibility for this is that there may have been costs that prevented these herbivores from doing this, but it is unclear what these costs may be.

In conclusion, we found that the herbivores tended to display stronger anti-predator behaviour in response to lions (i.e. greater vigilance, larger groups, and temporal shift in water hole usage) than when living with cheetah and wild dogs. This suggests that the cursorial hunting strategy of cheetah and wild dogs imposed lower perceived risk around waterholes compared to the stalk and ambush strategy adopted by lions. Ultimately, our study represents one of the few studies that directly addresses the effect of hunting mode on prey behaviour, using a powerful semi-experimental design. Moreover, our results support the common assertion that ambush predators are likely to induce stronger non-consumptive effects on prey than cursorial predators (Middleton et al., 2013; Preisser, Orrock & Schmitz, 2007).

Yet, as predation risk varies across the landscape (Shrader et al. 2008, Laundré et al. 2010), behavioural strategies utilised to reduce this risk likely also vary spatially. As waterholes represent key interaction areas between predators and prey, the suite of behaviours utilised by each species we recorded likely reflect those best suited against ambush predators. However, as the possibility of ambush likely declines as herbivores move away from waterholes, herbivores possibly adjust their anti-predator behaviours to reduce the use of behaviours that decrease risk from ambush predators and increase those that are better suited against roaming cursorial predators. Observations in landscapes with multiple predators using contrasted hunting strategies will be required to test this hypothesis. However, in such a landscape, Thaker et al. (2011) found that all prey species tended to avoid the activity areas of ambush, but not of cursorial, predators. They also found that prey responded more to habitat-cues than to actual predator distribution. See Schmitz (2007) for further discussion on additive or substitutive effects in multi-predator systems.

Despite focusing on a number of anti-predator behaviours, there are others we did not consider, for instance multi-scale habitat use (e.g. Padié et al. 2015) or reactive responses (e.g. Courbin et al., 2016). Our study, however, highlights an important point, namely that ecologists (including ourselves) need to move beyond focusing on a limited set of behaviours (e.g. just vigilance) when studying prey species’ responses to predation risk. This will be difficult, but is required, as highlighted by our results, animals do not reduce risk by simply adjusting one or two behaviours, but rather exploit and combine an array of anti-predator behaviours.

CHAPTER FOUR

Alarm calls or predator calls: which elicit stronger responses in ungulate communities living with and without lions?

Abstract

Conspecific and heterospecific alarm calls, and predator vocalizations convey information on predator presence and thus potential risk. Generally, prey tend to respond more to alarm calls as they are indicators of greater risk. However, sometimes the threat from specific predators is great enough that prey respond to any indicator of the predator's presence (e.g. non-hunting vocalisations). However, as predator and prey distributions do not always overlap, some individuals live in areas where these dangerous predators are absent. This begs the question, do prey species still respond more strongly to alarm calls of con/heterospecifcis when exposed to a predator call from a dangerous key predator? In addition, would the prey species' response (e.g. vigilance) be greater than or less than that of prey already living with these predators? To answer these questions, I conducted several playback experiments to test whether large herbivore species (i.e. zebra, wildebeest, red hartebeest, gemsbok) living with a dangerous predator (i.e. lions) responded more (i.e. increased their vigilance) to conspecific and heterospecific alarm calls, or to the vocalizations of lions. Overall, red hartebeest and wildebeest living with lions tended to show greater vigilance in response to the lion roars compared to the alarm calls. This suggests that these species perceived the direct cue of lions as a better indicator of risk than the alarm calls. Having established this, I then tested whether the herbivores living with lions increased their vigilance more to lion roars compared to conspecifics living in a lion-free section of the same reserve. I found that herbivores living with lions had higher vigilance than conspecifics living without lions. Despite a greater overall response in the lion section, herbivores in the lion-free section still significantly increased their vigilance in response to the lion roar. Yet, it was two of the lions' preferred prey species (i.e. zebra, wildebeest) that showed the greatest response. This suggests that species under the greatest threat may maintain innate anti-predator responses to a dangerous but absent predator longer than less preferred prey. Ultimately, my findings indicate that simple cues from dangerous predators can have a greater effect on anti-predator behaviours of prey species than alarm calls.

Keywords: anti-predator behaviour, auditory cues, vigilance

Introduction

A key challenge faced by prey species is to reduce predation risk (Lima and Dill 1990). Proactively, they can do this by moving in groups, increasing their vigilance, and limiting the time they spend in dangerous areas across the landscape (Caro 2005). Additionally, they can react to cues of immediate predation risk, by responding to the alarm calls of con – or heterospecifics, and to the vocalizations of predators themselves (Hettena et al. 2014, Magrath et al. 2015). However, the degree to which prey respond to these different auditory signals will vary depending on the reliability of the signals as indicators of risk (Rainey et al. 2004, Kitchen et al. 2010) and previous experience with predators (Blumstein et al. 2008). Generally, prey tend to respond more to conspecific and heterospecific alarm calls, than they do to predator vocal cues (Schmidt et al. 2008, Magrath et al. 2015). For example, Eastern chipmunks (*Tamias striatus*) decreased their feeding behaviour in response to heterospecific titmouse (*Baeolophus bicolor)* alarm calls but not to the direct call of broad-winged hawks (*Buteo platypterus),* their primary predator (Schmidt et al. 2008). Similarly, coots (*Fulica atra*) spent significantly more time vigilant in response to the alarm calls of conspecifics compared to a predator call (dog bark; Randler 2006). In another example, Tammar wallabies (*Macropus eugenii*) responded to the playbacks of conspecifics’ foot thumps, as an anti-predator signal, but did not respond to the vocalization of wedge-tailed eagles (*Aquila audax*), a resident predator (Blumstein et al. 2000).

A potential reason that prey may react more to alarm calls than predator vocalizations is that they tend to be indicators of greater risk (Barrera et al. 2011, Magrath et al. 2015). For example, alarm calls provide information on predator detection, state (i.e. actively hunting) and identity, thus providing public information on local risk (Schmidt et al. 2008, Kitchen et al. 2010). Therefore, in response to these alarm calls, prey species should have higher perceived predation risk and increase their investment in anti-predator behaviours (i.e. vigilance; Schmidt et al. 2008). In addition, many predators rely on stealth and surprise while hunting (Preisser et al. 2007). Thus, hunting predators are unlikely to give away their location, proximity and potential identity to prey species by calling (Barrera et al. 2011). As a result, the vocalisations of predators tend to suggest that the predator is not hunting, and thus deemed to be less of a threat by prey (Barrera et al. 2011, Hettena et al. 2014).

However, some studies have found that prey species elicit a strong anti-predator response to the non-hunting vocalisations of predators (e.g. Karpanty and Wright 2007, Hettena et al. 2014). For example, racoons have been found to spend less time foraging after hearing dog barks (Suraci et al. 2016). In addition, elephant (*Loxodonta africana*) herds increased their bunching behaviour and alertness in response to male lion (*Panthera leo*) roars (McComb et al. 2011). Furthermore, black-casqued hornbills (*Ceratogymna atrata*) increased their call rates in response to crowned eagle (*Stephanoaetus coronatu*) shrieks (Rainey et al. 2004). A unifying feature of these different predators is that they all present a significant risk to the prey species studied (Rainey et al. 2004, Suraci et al. 2016). Thus, it seems that cues from key/dangerous predators can also signal risk and trigger increased anti-predator responses from prey species.

Worldwide, predators are moving back into ecosystems, either via natural range shifts (Banks et al. 2002) or through reintroductions (Hayward and Somers 2009). As a result of these movements, prey species are now coming into contact with predators that historically have been absent on the landscape (Mech et al. 2001, Sand et al. 2006, Sih et al. 2010). In some cases, prey have lost their anti-predator responses to these 'returning' predators (Blumstein 2006), while in other situations, they still react to the cues of these predators (Blumstein et al. 2009, Chamaillé-Jammes et al. 2014). For those prey species that retain their anti-predator behaviours, a key question that arises is, when faced with returning dangerous predators, do these individuals still react to these predator's calls, or do they rather consider conspecific and heterospecific alarm calls as better indicators of risk?

In African systems, lions (*Panthera leo*) are key apex predators (Owen-Smith and Mills 2008, Davidson et al. 2013, Courbin et al. 2016). Due to their large size and cooperative hunting strategies, they present a significant risk to a broad range of herbivores (Scheel and Packer 1991, Hayward and Kerley 2005). In addition, lions are stalk and ambush predators that opportunistically use ambush sites to target and kill prey (Hopcraft et al. 2005). Thus, they present a major predation risk to herbivores that co-exist with them on the landscape (Valeix et al. 2009a). As such, prey species need to employ and maintain anti-predator behaviours to minimize this risk (Valeix et al. 2009a, Courbin et al. 2016, Traill et al. 2016). However, do prey species that no longer interact with lions on the landscape still respond to cues from this dangerous predator?

To address these questions, I first compared changes in vigilance in a number of ungulate species (i.e. gemsbok – *Oryx gazelle*; zebra – *Equus quagga*; red hartebeest - *Alcelaphus buselaphus caama* and wildebeest - *Connochaetes taurinus*) living with lions (a key predator) in response to con/heterospecific alarm calls, and lion roars. I predicted that, all four-herbivore species would increase the proportion time they spent vigilant in response to the alarm calls (i.e. zebra and wildebeest), as they are key indicators of risk. Alternatively, as lions are dangerous predators, herbivores may show a greater increase in vigilance in response to the lion roars as they indicate the presence of a dangerous predator. Having found that the herbivores reacted more towards the lion roars (see results), I exposed individuals not living with lions to lion roars, and conspecific and heterospecific alarm calls, and recorded changes in vigilance levels. I predicted that if these herbivores retained their anti-predator behaviours for lions (an absent but dangerous predator), then, similar to those individuals living with lions, they would react strongly towards the lion roars. Alternatively, if they had lost their predator recognition of lion calls, then they should not react to lion roars, but still react to the alarm calls, as they would function as an indicator of general risk.

Methods

I conducted this study in Tswalu Kalahari Reserve, Northern Cape, South Africa (S 27°13'30" and E 022°28'40"). The reserve is divided into two separate, but adjacent sections that support the same herbivore species but different predators. The western section (20 000 hectares) contains 24 lions, while the eastern section (80 000 hectares) supports a minimum of 10 cheetahs and a pack of 14 wild dogs (i.e. lion-free). Herbivores living in the cheetah and wild dog's section have not come into contact with lions for over 100 years (Roxburgh 2008). Within Tswalu, waterholes are widely distributed across the landscape and offer the only source of permanent ground water. Thus, they are heavily utilised by herbivore species. For this study, I limited my data collection to four herbivore species that were found in both predator sections. These included, gemsbok, red hartebeest, zebra and wildebeest. Calculated herbivore species densities based on aerial census data were 1.3 and 2.4 gemsbok/km^2, 0.63 and 1.2 red hartebeest/km^2, 1 and 0.8 wildebeest/km^2 and 0.2 and 1 zebra/km^2 within the lion-free and lion section, respectively. To quantify how these herbivores adjusted their vigilance in response to differences in perceived predation risk, I used a playback experiment to manipulate the auditory landscape of fear. Herbivore alarm calls (zebra and wildebeest) and predator calls (lion roars) were played at eight different waterholes (five within the cheetah and wild dogs section and three within the lion section; Fig. 1) from January 2015 to April 2015.

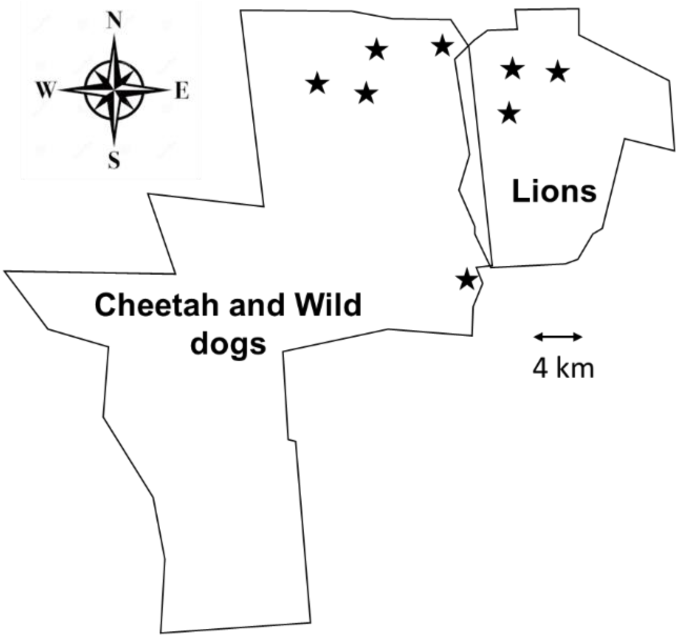


Figure 1. Location of waterholes used for the playback experiments within Tswalu.

I used zebra (‘Kwa-ha’ sounds and loud snorts) and wildebeest (grunts and snorts) alarm calls (Estes 1991) as they were two commonly occurring herbivore species found at waterholes across both predator sections of Tswalu. In addition, both zebra and wildebeest have distinctive alarm calls/snorts and frequently call when they have detected a potential threat (Estes 1991, Stensland et al. 2003). As a non-hunting predator cue from a dangerous predator, I used lion roars. Lions are ambush predators, thus they rely on silence and stealth to hunt prey (Schaller 2009). Moreover, lions tend to roar to advertise territorial ownership, locate pride members, strengthen bonds and intimidate rivals (Estes 1991). As a control call, I used black cuckoo (*Cuculus clamous clamous*) calls as they are a resident bird species in the reserve that called frequently around the waterholes in both predator sections. Whereas, some prey species have predator-specific alarm calls (i.e. different calls for terrestrial vs aerial predators; Enstam and Isbell 2002), zebra and wildebeest have a set alarm call type to warn of predation risk (Estes 1991, Leuthold 2012).

To prevent pseudoreplication in the playback experiments through using a single exemplar (i.e. individual recording) from a stimuli class as a representative of the entire class itself (Kroodsma et al. 2001), I used three exemplars of each call type. In addition, I randomized the order in which calls were played at waterholes, such that the same playback treatments were not played consecutively (Hettena et al. 2014). I played the different calls through two Boashan horn speakers (Model: SK-610) attached to short stakes (~ 1 metre) set out near bushes (100 metres) away from the waterhole (Fig. 2). Playback calls were obtained through the Macaulay Library (Cornell Lab of Ornithology, Ithaca, USA). I played the calls at amplitudes deemed to simulate the natural call of the animal and this was maintained throughout the duration of the study (100 decibels – lion roar; Webster et al. 2012), 75 decibels – zebra and wildebeest, 65 decibels – black cuckoo control). The peak intensity of calls (dB) were checked at 1 metre away from the speakers using a handheld Lutron Digital Sound Level Meter (Model: SL-4001). The calls were played from a 5-core Sound of India amplifier (Model number: 5CA-4040) powered by a 12 V car battery (Leisure Pak, Model: FNL 464). During observations I positioned myself within a bush-hide located 100 metres away from the waterhole which was sufficiently far enough away to minimize the effects of potential observer disturbance (Fig. 2; Khoury 2013).

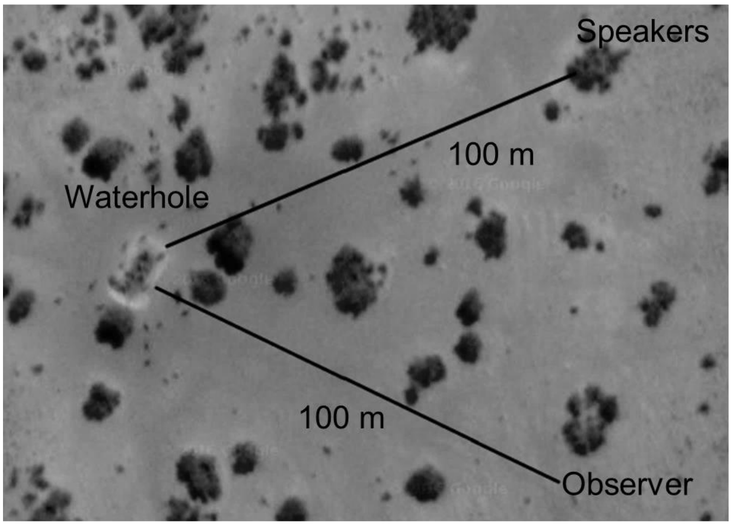


Figure 2. Example of the auditory playback experimental design with speakers placed 100 m away from the waterholes near cover. The observer was positioned 100 m away in a hide with a clear view of the entire waterhole. Dark spots are bush and tree clumps.

I played the different randomly selected playback calls once the focal herbivores had moved towards the waterhole and began drinking. Playback calls (20-30 seconds in length) were played every ten minutes at the waterhole for 2 hrs for a single exemplar of each call type (Khoury 2013). To prevent waterholes from being considered as consistently dangerous, thereby reducing the chances of herbivores using them, I did not play calls at each waterhole consecutively, but rather randomized the days when playback calls would be played. This meant that each waterhole had a minimum of two rest days between playbacks when no calls were played. Thus, for each waterhole, 1 of 3 exemplars of each call type (con/heterospecific alarm calls, lion calls and black cuckoo calls) was randomly selected and played over a 2hr period for a given day for a particular waterhole. Thus, a total of 8 waterholes, 4 different call types and 3 repeats of each call type were used, totalling 96 playbacks.

Vigilance behaviour is defined as the primary adaptive response to reduce perceived predation risk through actively scanning the environment for potential threats (Delm 1990). Thus, while vigilance behaviour can have other functions such as searching for mates and resources (Beauchamp 2015), within the context of this study, vigilance behaviour to reduce risk is key, as waterholes are dangerous areas where predators target prey species. To determine how herbivores responded to the different playback calls, I recorded the vigilance of individuals compared to a control call (black cuckoo) to assess the magnitude of change in perceived predation risk at waterholes (Delm 1990, Beauchamp 2015). I used the focal sampling technique to monitor the vigilance behaviour of individuals within groups (Altmann 1974). For each individual, I recorded the proportion time spent vigilant at waterholes for a maximum of 20 minutes or over the entire duration if herbivores spent less than 20 minutes drinking from waterholes (Périquet et al. 2010). I focussed on individuals centrally located within each group. As these individuals are unlikely to be killed before individuals on the group periphery, any increase in vigilance for central individuals likely reflects an increase in vigilance for the entire group (Périquet et al. 2010). Vigilance was defined as the focal animal standing, head up, alert, and actively scanning their environment. To avoid potential confounding group-size effects through recording the vigilance of individuals across different sized breeding groups, I recorded the vigilance of individuals from similar sized breeding groups ($\bar{x}$ = 8 ± 2 SE individuals) for each herbivore species. The mean proportion time spent vigilant by the herbivore species in response to each of the playback calls (i.e. wildebeest, zebra, control and lion) was then compared across the two predator sections (lion vs cheetah and wild dogs).

Data Analysis

The proportion time spent vigilant at waterholes was compared for each herbivore species (gemsbok, zebra, red hartebeest and wildebeest) in response to the different playback calls (zebra, wildebeest, lion, control) comparing across the two predator treatments (lion vs lion-free). I used a generalized linear mixed effects model (GLMM) with binomial errors (Zuur et al. 2009), incorporating proportion vigilance as the response variable, and playback call type and predator section as the explanatory variables, and waterhole identity as a random factor, including interactions between variables. For each waterhole, the proportion time spent vigilant was averaged for each two-hour sampling period for each species present at the waterhole. Thus, the mean proportion time spent vigilant reflects the average time spent vigilant by all herbivore species groups over a 2-hour sampling period, thereby, reducing the risk of pseudo-replication through repeated measures. I ran Tukey *post-hoc* tests to determine where significant differences in proportion time spent vigilant existed comparing the same herbivore species across predator sections and herbivore responses to each of the different playback calls within predator sections.

Results

Comparing the overall vigilance responses to the different call types, I found that prey generally responded more to the lion roars than to the alarm calls of wildebeest and zebra (Table 1). Overall, compared to the control, the mean proportion of time spent vigilant (± SE) increased significantly for gemsbok (27 ± 12% up to 73 ± 4%), zebra (17 ± 3% up to 66 ± 4%), and wildebeest (33 ± 5% up to 59 ± 2%), but not for red hartebeest (38 ± 6% up to 75 ± 6%) after I played the lion roars (Table 1). In contrast, in response to the conspecific/heterospecific alarm calls compared to the control, only gemsbok (64 ± 7% - wildebeest alarm and 74 ± 5% - zebra alarm) and zebra (67 ± 5% - wildebeest alarm and 56 ± 3% zebra alarm) significantly increased their vigilance in response to both calls (Table 1). Wildebeest only increased their vigilance (52 ± 14%) in response to their own alarm call, while red hartebeest only responded to the zebra alarm, slightly decreasing their vigilance in response from 39 ± 4 % (control call) to 35 ± 3% (zebra alarm) (Table 1).

Table 1. Generalized linear mixed effects model (GLMM) comparing the proportion of time spent vigilant by gemsbok, zebra, red hartebeest and wildebeest at waterholes in response to the lion roars and zebra and wildebeest alarm calls, comparing across the two predator sections (lions versus cheetah and wild dogs), including interactions between variables.

Species	Playback Calls	Estimate	Z	P	Sig
Gemsbok	Intercept	-0,154	-0,329	0,742	
	Lion	2,716	5,606	<0.001	***
	Wildebeest	2,581	4,960	<0.001	***
	Zebra	2,155	4,280	<0.001	***
	Lion vs Cheetah/Wild dog sections	1,377	2,319	0,020	*
	Lion Call: Cheetah/Wild dogs	-2,115	-3,259	0,001	**
	Wildebeest Call:Cheetah/Wild dogs	-2,309	-3,466	<0.001	***
	Zebra Call:Cheetah/Wild dogs	-0,821	-1,289	0,197	
Zebra	Intercept	0,552	1,570	0,116	
	Lion	1,909	6,844	<0.001	***
	Wildebeest	2,004	6,546	<0.001	***
	Zebra	1,500	4,886	<0.001	***
	Lion vs Cheetah/Wild dog sections	-0,399	-0,822	0,411	
	Lion Call: Cheetah/Wild dogs	0,124	0,331	0,740	
	Zebra Call:Cheetah/Wild dogs	-0,445	-0,760	0,447	
Red Hartebeest	Intercept	0,425	0,692	0,489	
	Lion	0,615	0,735	0,462	
	Wildebeest	-0,052	-0,092	0,926	
	Zebra	-0,818	0,308	0,006	**
	Lion vs Cheetah/Wild dog sections	0,229	0,308	0,758	
	Lion Call: Cheetah/Wild dogs	0,123	0,139	0,889	
Wildebeest	Intercept	1,045	1,833	0,066	
	Lion	2,033	5,256	<0.001	***
	Wildebeest	-1,721	-2,204	0,027	*
	Zebra	-0,475	-1,286	0,198	
	Lion vs Cheetah/Wild dog sections	-1,809	-2,260	0,023	*
	Wildebeest Call:Cheetah/Wild dogs	4,449	4,975	<0.001	***
	Zebra Call:Cheetah/Wild dogs	1,226	2,662	0,007	**

In response to the lion roars, zebra, red hartebeest and wildebeest within the lion section increased their vigilance more than conspecifics in the lion-free section (Fig. 3). Within the lion section, mean vigilance increased more than 40% for zebra, 70% for red hartebeest, and 25% for wildebeest in response to the lion roars compared to the control playback (Fig 3). Although, gemsbok increased their mean vigilance by more 50% in response to the lion roar, this did not differ significantly from conspecifics in the lion-free section (Fig. 3). In comparison, within the lion-free section, only zebra and wildebeest significantly increased their mean vigilance in response to the lion roars (increasing by 35 and 25%, respectively), while gemsbok and red hartebeest did not significantly increase their vigilance compared to the control playback (Fig. 3).

In response to the herbivore alarm calls, gemsbok in the lion's section maintained higher vigilance in response to the zebra and wildebeest alarm calls than con-specifics in the lion-free section (Fig 3). Likewise, zebra (in response to the wildebeest call) and red hartebeest (in response to the zebra call) in the lion section had higher vigilance than con-specifics in the lion-free section (Fig 3). There was no significant difference in the mean vigilant responses between zebra across predator sections in response to the alarm call from conspecifics. Furthermore, there was no significant difference between the mean vigilant responses of red hartebeest and wildebeest in response to the wildebeest alarm call, comparing across lion and lion-free sections (Fig.3). Interestingly, in response to the control call, gemsbok and red hartebeest in the lion-free section maintain higher levels of vigilance compared to conspecifics in the lion section (Fig. 3).

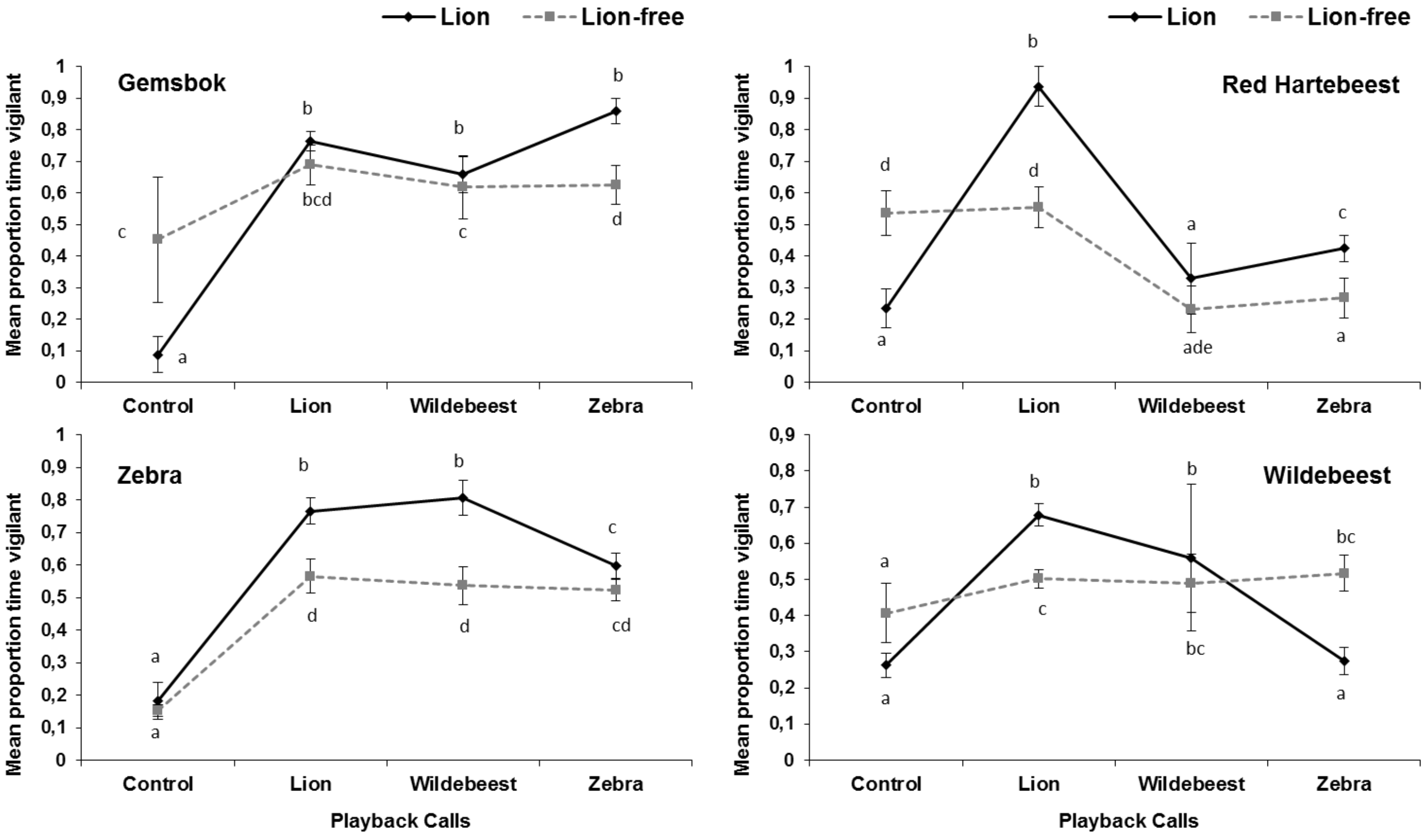


Figure 3. Mean proportion of time spent vigilant by a) gemsbok, b) zebra, c) red hartebeest, and d) wildebeest at waterholes within the two predator treatments (i.e. lions, lion-free). Vigilance levels of these species are shown after playbacks of a black cuckoo (control), lion roars, and wildebeest and zebra alarm calls (snorts). Bars represent SE. Mean proportion vigilance values sharing letters are not significantly different, as assessed by the Tukey *post-hoc* comparison tests.

Discussion

Auditory cues (i.e. con/heterospecific alarm calls and predator calls) are easily heard by prey species (Schmidt et al. 2008). Therefore, if these cues provide information on the location of a predator, its proximity and potential state, then reacting to these cues (e.g. increasing vigilance) should minimize an individual's predation risk (Kuczynski 2015). Comparing the auditory cues as indicators of increased predation risk, several studies have highlighted that prey species react more strongly to conspecific and heterospecific alarm calls compared to predator sounds (Griffin et al. 2000, Blumstein et al. 2008, Hettena et al. 2014). However, some species seem to react more to cues given off by dangerous predators than alarm calls (Rainey et al. 2004, Barrera et al. 2011). In line with these latter studies, I found that the overall broad pattern of vigilant responses supported the findings that dangerous predator cues may indicate greater risk than the con/heterospecific alarm calls. However, these responses were species-specific and varied significantly across the different predator sections. Overall, wildebeest and red hartebeest living with lions adjusted their vigilance more in response to lion roars (i.e. non-hunting predator cue) compared to conspecific and/or heterospecific alarm calls. Although, zebra and gemsbok significantly increased their vigilance in response to the lion roar within the lion section, they also responded strongly to the con/heterospecific alarm calls. Specifically, gemsbok responded as strongly to the wildebeest and zebra alarm calls as they did to the lion roar, while zebra responded as strongly to the wildebeest call as to the lion roar. In the lion-free area, both zebra and wildebeest tended to have an equal increase in vigilance in response to both the alarm calls and the lion roars. Both zebra and wildebeest (preferred prey of lions) in the lion-free section significantly increased their vigilance in response to the lion roars, while surprisingly gemsbok (also a preferred prey of lions) and red hartebeest did not. Interestingly, both gemsbok and red hartebeest elicited a stronger vigilant response to the control call in the lion-free section compared to conspecifics in the lion section.

Rainey et al. (2004) proposed the ‘information precision hypothesis’ in support of the stronger anti-predator response to predator vocalizations, which suggests that in contrast to alarm calls, the information contained in predator cues provides more accurate spatial information on predator location. When interpreting the reliability of alarm calls, the alarm signal may represent the signaller’s perception of risk, rather than the listeners. Whereas, a predator call provides accurate information on the exact type and location of a predator, rather than the general vicinity signalled through alarm calling (Rainey et al. 2004). Therefore, for a many species, direct cues on predator location can be more useful, and thus have a greater reduction on predation risk than an indirect cue (van der Veen 2002, Rainey et al. 2004). For example, Gil-da-Costa et al. (2003) found that howler monkeys (*Alouatta palliate*) rapidly responded to the calls of recently reintroduced harpy eagles (*Harpia harpyja*), increasing the mean amount of time they spent vigilant compared to the alarm calls of other bird species (Gil-da-Costa et al. 2003). In addition, Rainey et al. (2004) found that black-casqued hornbills had an increased frequency of call responses to a direct predator call (crowned eagle) compared to eavesdropping on the alarm calls of heterospecific monkeys. In response to the playback calls of red-tailed hawks (*Buteo jamaicensis*), Zenaida doves (*Zenaida aurita*) had higher levels of vigilance compared to the alarm signals of conspecifics (Barrera et al. 2011). Across these systems, these predators presented a significant predation risk to these prey species and therefore, prey were shown to respond to cues from these predators.

The results of my study provide some support to the suggestion that prey species can consider non-hunting predator cues more important that the alarm calls of conspecifics and heterospecifics. This was true for red hartebeest and wildebeest in the lion section, as they maintained higher levels of vigilance in responses to the lion roar than either herbivore alarm call. This suggests that for these species, lion roars were an indicator of greater risk than the alarm calls within the lion's section. This indicates that cues from dangerous key predators on the landscape can be important determinants of prey anti-predator responses.

Comparing the strength of the herbivore' vigilant responses to the different alarm calls revealed an interesting interaction between zebra and wildebeest within the lion section. Both zebra and wildebeest fall within the preferred prey class of lion (Hayward and Kerley 2005). However, in response to the alarm calls, zebra increased their vigilance in response to both zebra and wildebeest alarm calls, with a stronger vigilance response to the wildebeest alarm. In comparison, wildebeest only increased their vigilance in response to conspecifics. A study investigating the mixed-species herds of zebra and wildebeest, observed that a single wildebeest moving with a herd of zebra would result in the zebra decreasing their vigilance by 50% (Schmitt et al. 2014). One possible explanation for this is that wildebeest are more preferred by lions, thus making them more of a target for lions attacking the herd (Schmitt et al. 2014, Hayward pers. com.). Wildebeest were killed proportionally more than they were available (26% across 38 sites) by lion compared to 15% across 40 sites for zebra (Hayward and Kerley 2005). Another possibility is that wildebeest employ anti-predator behaviours that improve their early predator detection such that zebra rely on cues from wildebeest as reliable sources of anti-predatory information, potentially more so than conspecifics (Schmitt et al. 2014).

Based on these findings, it is possible that zebra rely on the alarm calls of wildebeest as more important sources of information on predation risk at waterholes in Tswalu than the alarm calls from conspecifics. Whereas, wildebeest potentially have alternative vigilance methods (i.e. improved hearing, smell; Schmitt et al. 2014) that allows them to minimize risk by responding to the alarm calls of conspecifics without having to eavesdrop on zebra alarm calls. Alternatively, the information conveyed in wildebeest alarm calls could provide more accurate and reliable information on predation risk than zebra calls, with both wildebeest and zebra (often occurring within mixed herds) relying on these alarm calls to manage potential predation risk. Both, gemsbok and zebra maintained high levels of vigilance in response to both the alarm calls and the lion roar. This suggests that the perceived predation risk at waterholes of these two species is high, and they utilise a wide range of auditory signals as indicators of risk. Whereas, wildebeest and red hartebeest consider the lion roars in the lion section as important cues of greater predation risk resulting in an increase in their vigilant responses.

In the absence of predators, prey species have been observed to lose previously adaptive anti-predator behaviours over time (Blumstein 2006). However, some species retain these anti-predator behaviours and therefore respond quickly and appropriately to cues from these predators (Blumstein et al. 2009, Chamaillé-Jammes et al. 2014). These innate anti-predator behavioural responses may be due to interactions with other extant predators on the landscape (Blumstein 2006). Alternatively, the loss of these behaviours may only occur after extended periods of isolation from the predator (Sih et al. 2010). The results of my study indicated that red hartebeest, wildebeest and zebra responded to the lion roars more strongly within the lion section than the same herbivores species living without lions. This suggests that the effect of lion present on the landscape coupled with spatial information obtained from the lion roar provided a greater indicator of potential risk than the call in the absence of the predator. Similarly, Berger (2007) found that elk (*Cervus canadensis*) and bison (*Bison bison*) displayed increased vigilant responses to wolf (*Canis lupus*) calls in areas where wolves had been reintroduced compared to wolf-free areas.

Despite lower levels of vigilance from the herbivores in the lion-free section, I found that zebra and wildebeest in this section significantly increased their vigilance in response to the lion roar. This suggests that although lions are absent from the landscape, their auditory cues still indicated potential risk to these herbivores. This increased anti-predator response may be due the fact that lions are the main predator of both of these herbivores (Hayward and Kerley 2005). Thus, it seems that they have retained their anti-predator responses for this dangerous ambush predator (Valeix et al. 2009a). Similarly, Dalerum and Belton (2014), found that both naïve and lion exposed populations of impala, wildebeest and warthog responded to auditory calls of lion by increasing their vigilance. Therefore, these prey species retained adaptive anti-predator behaviours for lion even in the absence of the predator, potentially due to genetic inheritance or exposure to continued predation pressure from other large extant predators (Dalerum and Belton 2014). This is similar to mule deer (*Odocoilus hemionus*) in the East River Valley, USA, where they responded to wolf vocalizations despite the fact that wolves have been absent from the area for over 100 years, possibly due to predation risk from coyotes (*Canis latrans*) and puma (*Puma concolor*), therefore retaining their anti-predator behaviours to cues from wolves (Hettena et al. 2014). In contrast, black-tailed deer (*Odocoilus hemionus sitkensis*) strongly modified their threat-sensitive foraging in response to a wolf cue (absent dangerous predator) more so than a black bear cue (*Ursus americanus* – less dangerous present predator), thus showing an innate anti-predator response to a dangerous predator that black-tailed deer co-evolved with. Therefore, prey can also retain recognition of and respond to absent predators for several generations, even when closely related predator species are absent (Chamaillé-Jammes et al. 2014).

Although gemsbok and red hartebeest fall within the preferred weight range of lion (Clements et al. 2014), neither species significantly increased their vigilance in response to the lion roar within the lion-free area. This was particularly surprising for gemsbok as based on a multi-site analysis they are the most preferred prey of lion (Hayward and Kerley 2005). This may be due to the fact that neither gemsbok or red hartebeest are water dependent species (Smit et al. 2007), therefore they potentially interact less with lion near ambush sites (i.e. waterholes). In contrast, zebra and wildebeest are both water dependent and therefore likely have higher perceived predation risk around these ambush sites and respond more strongly to cues from lions. Therefore, in the absence of lions, it is possible that there is not the same evolutionary pressure on gemsbok and red hartebeest to maintain predator recognition of lion calls.

One interesting observation, is the high vigilant responses observed for gemsbok and red hartebeest in response to the control call within the lion-free section. The high vigilant responses by these two species in response to the black cuckoo calls suggested that they maintain a higher baseline level of vigilance compared to conspecifics in the lion's section. This was surprising as gemsbok are avoided by cheetah and wild dogs while red hartebeest are taken relative to availability by cheetah and avoided by wild dog (Hayward et al. 2006a, Hayward et al. 2006b). Thus, a higher baseline vigilance should have been observed in the lion section where both species are preferred prey of lion (Hayward and Kerley 2005). The factors driving this observation are unclear. However, it may be possible that the sample size for the vigilant responses to the control call in the lion-free section were small, thus, explaining the high variability around these mean values for the control call for these prey species.

Ultimately, the findings from this study indicate that prey species can rely on the information contained in alarm calls and predator vocalizations to assess and manage predation risk. While, most studies have pointed to alarm calls as indicators of greater risk than predator calls (Shriner 1998, Magrath et al. 2015), this study suggests that auditory cues from dangerous key predators reflect high levels of predation risk, thus prompting prey species to react by employing anti-predator behaviours. Moreover, this can extend to prey species that no longer live with key predators (Blumstein 2006, Sih et al. 2010). Specifically, the predation risk associated with a cue from an absent but dangerous predator can trigger a strong innate anti-predator response in prey species that are preferentially targeted by the predator (for olfactory cues see; Chamaillé-Jammes et al. 2014). Alternatively, these anti-predator behavioural responses to dangerous but absent predators can be retained in prey populations when other extant predators are present on the landscape (i.e. cheetah and wild dogs in this study; Blumstein 2006). Therefore, with the return of predators into systems, prey species are potentially able to recognize predator cues as indicators of risk and adjust their anti-predator behaviours to minimize risk.

CHAPTER FIVE

Conclusion

The broad aim of my PhD was to determine how risk from different large predators affected the space use (i.e. patch use) and behaviour (i.e. feeding, vigilance, grouping and temporal activity) of a community of large mammalian herbivores. To investigate this, I recorded how different herbivore species adjusted their vigilance, group sizes, and temporal activity patterns in response to the predators' different hunting strategies, diel activity and prey preferences.

In my first experiment, I investigated how sable (*Hippotragus niger*), kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) adjusted their patch use and feeding behaviour in response to the introduction of wild dogs (*Lycaon pictus*). A key aspect of this introduction, was that it shifted the system from a single predator (cheetah – *Acinonyx jubatus* only) to a multi-predator (cheetah and wild dogs) environment. My second experiment, investigated how eland (*Tragelaphus oryx*), gemsbok (*Oryx gazella*), zebra (*Equus quagga*), red hartebeest (*Alcelaphus buselaphus caama*), warthog and wildebeest (*Connochaetes taurinus*) adjusted their suite of anti-predator behaviours (i.e. vigilance, grouping, temporal activity) to minimize predation risk from either lion (*Panthera leo*), or cheetah and wild dogs. Finally, in my third experiment I recorded changes in vigilance to determine whether gemsbok, zebra, red hartebeest, and wildebeest found alarm calls from conspecifics and heterospecifics (i.e. zebra and wildebeest), or non-hunting predator vocalizations (i.e. lion roars) to be greater indicators of predation risk. Having determined this, I then explored whether herbivores living in a lion-free section elicited the same vigilance response to the lion roars as conspecifics living with lions.

The results of my first experiment (Chapter 2) demonstrated, that the herbivore species responded differently to the introduction of wild dogs by modifying their patch use and feeding behaviour. Specifically, the magnitude of the response to the introduction was greater for those species (e.g. sable) that initially had lower risk in the single predator system (i.e. they were outside the prey weight preference of cheetah; Hayward et al. 2006a), compared to species (e.g. kudu) that are preferred prey of cheetah. This was likely because sable living in an initially low risk environment (cheetah only) had increased time for foraging and therefore would have a greater potential to increase their anti-predator response to predation risk from wild dogs (Houston et al. 1993). In contrast, kudu were likely already maintaining high levels of anti-predator behaviour for cheetah and thus the magnitude by which they could increase their anti-predator response for wild dogs was reduced compared to that of sable (Houston et al. 1993). Although warthog are avoided by cheetah and taken relative to their availability by wild dogs (Hayward et al. 2006b), they ceased feeding from the patches when the wild dogs denned, indicating that the increased proximity increased their perceived risk of predation.

Despite the shift from a single to a multi-predator system, prey species did not alter their broad-scale habitat use. Rather, they preferred to feed from patches located in open grasslands before and after the introduction of wild dogs, possibly due to improved predator detection in more open areas (Chapter 2). Similar to my findings, white-tailed deer (*Odocoileus virginianus*) showed an increased avoidance of denser vegetation in response to perceived predation risk from wolves (*Canis lupus*), where wolves, despite being a cursorial predator, were more successful hunting when using denser vegetation to approach the deer undetected (Kunkel and Pletscher 2001). This suggests that perceived predation risks from cheetah and wild dogs associated with landscape features were likely similar, and that the risk posed by wild dogs was not sufficiently great or different enough to that of cheetah to result in a shift in broad-scale habitat use.

In response to the different hunting strategies of lion (stalk and ambush), and cheetah and wild dogs (cursorial), prey species varied their use of and combination of anti-predator behaviours (i.e. vigilance, grouping, temporal shifts; Chapter 3). Overall, prey species co-existing with lions had higher vigilance at waterholes compared to conspecifics living with cheetah and wild dogs. However, herbivore species adjusted their group sizes and moved in larger groups in response to perceived predation risk from the resident predators. For example, both zebra and wildebeest (preferred prey of lion; Hayward and Kerley 2005) maintained larger groups in the lions section. Surprisingly, warthog and red hartebeest, avoided or taken relative to their availability by cheetah and wild dogs (Hayward et al. 2006a, Hayward et al. 2006b) lived in larger groups in the cheetah and wild dog section.

When comparing the temporal use of waterholes however, prey species only adjusted their use of waterholes in response to the largely nocturnal/crepuscular lion (Schaller 2009), and not the diurnal cheetah and wild dogs (Hayward and Slotow 2009). This was likely due to the increased risk posed by ambushing lions around waterholes where the risk from these predators is high (Valeix et al. 2009a, de Boer et al. 2010). Similar to the findings from this study, Ross et al. (2013) found that bearded pigs (*Sus barbatus*) preyed on by clouded leopards (*Neofelis diardi* - nocturnal ambush predator) shifted their temporal activity towards the day and avoided being active at night when overlaps of activity with leopards were high. In comparison, bearded pigs living in a leopard-free area were almost entirely nocturnal, thus this temporal shift in activity likely reflects an attempt to reduce predation risk from a dangerous ambush predator (Ross et al. 2013). Other studies have illustrated that prey make shifts from day to night to minimize risk from predators (Eccard et al. 2008, Crosmary et al. 2012). For example, roe deer (*Capreolus capreolus*) avoided risky habitats during the day in response to hunting pressure but selected for the same habitats at night when the risk was lower (Padié et al. 2015).

In contrast, herbivores living with cheetah and wild dogs did not shift their use of waterholes to night to minimize interactions with the largely diurnal cheetah and wild dogs

(Hayward and Slotow 2009). This may be due to the lower probability of herbivores encountering these cursorial predators at waterholes compared to conspecifics co-existing with ambushing lions (Preisser et al. 2007). Thus, it is likely that the potential predation risk costs from cheetah and wild dogs were not sufficiently high enough for prey species to make a temporal shift in their use of waterholes. Ultimately, the findings from this study highlight the complex array and combination of anti-predator behaviours utilised by prey species to minimize predation risk from different large predators (Caro 2005, Creel et al. 2014).

To expand on the findings from the first two studies (i.e. Chapters 2 and 3), I then asked the question, do prey species consider alarm calls from conspecifics and heterospecifics as a greater indicator of risk compared to the non-hunting vocalizations of a key predator? (Chapter 4). To answer this, I used a manipulative approach to record the vigilance responses of gemsbok, zebra, red hartebeest and wildebeest to the playback calls of two herbivore alarms (i.e. zebra and wildebeest) and lion roars (i.e. non-hunting vocalisation). Most studies investigating prey responses to auditory cues have indicated that alarm calls are better indicators of predation risk (Zuberbühler et al. 1999, Schmidt et al. 2008, Magrath et al. 2015) than predator vocalizations. However, I found that red hartebeest and wildebeest maintained higher levels of vigilance in response to the lion roars than the zebra and wildebeest alarm calls.

While predator calls give away the predator’s exact location and therefore, predators are unlikely to vocalize while hunting (Zuberbühler et al. 1997, Rainey et al. 2004), some prey species do respond to a direct predator call, increasing their use of anti-predator behaviours, particularly, if the call is made by a key dangerous predator (Barrera et al. 2011, Hettena et al. 2014). For example, male Gulf toadfish (*Opsanus beta*) responded to acoustic cues from their primary predator, bottlenose dolphins (*Tursiops truncatus*), by reducing their calls rates by 50% thus reducing the chance of being detected (Remage-Healey et al. 2006). Likewise, lion present a significant threat to prey species on the landscape, their large body size coupled with their ambush and cooperative hunting strategies make them dangerous predators for a wide range of prey species (Hayward and Kerley 2005, Schaller 2009). As such, in my study the lion roars elicited a strong overall vigilant response by prey species.

Having established that the herbivores respond strongly to the lion roars, I then asked, do prey species living with lions elicit a stronger vigilant response to the lion roars compared to conspecifics in the lion-free area? My findings indicated that the herbivores living with lions respond more strongly than conspecifics not living with lions. However, despite this both zebra and wildebeest in the lion-free section responded strongly to the lion roars. This suggests that it is possible that they retained their anti-predator behaviours as they are preferred prey of lions (Mills and Shenk 1992). Thus, despite the absence of lion, they react to lion roars to minimize risk from cues from this dangerous predator. Potential explanations for the retention of these anti-predator behaviours are that they persist within prey populations when other predators are present on the landscape (i.e. multipredator hypothesis; Blumstein et al. 2009). Thus, the risk from cheetah and wild dogs may have been sufficient for prey species to retain appropriate anti-predator responses to lions (Blumstein 2006). Alternatively, these prey species may have retained appropriate anti-predator behaviours over a few generational periods of lion absence (Chamaillé-Jammes et al. 2014), possibly through genetic inheritance of these anti-predator behaviours (Dalerum and Belton 2014).

Understanding, how prey species adjust to a new ‘landscape of fear’ driven by shifts from single to multi-predator systems is important. Prey species living within these multi-predator systems employ a diverse range of anti-predator behaviours to minimize risk from different large predators (Sih et al. 1998, Thaker et al. 2011). These can include, 1) modifying space use (i.e. patches) and feeding behaviour (Chapter 2), increasing vigilance, forming larger groups, and making shifts in the temporal use of risky areas (Chapter 3), and adjusting anti-predator responses to auditory cues from con/heterospecifics and predators as indicators of varying predation risk (Chapter 4).

The findings from my PhD, highlight that prey respond to a new ‘landscape of fear’ generated through a predator introduction by altering their small-scale foraging decisions and patch use to minimize risk from multiple predators. Moreover, prey vary their anti-predator responses to different large predators with differing degrees of risk and therefore must maintain a combination of anti-predator behaviours to effectively minimize risk while still acquiring necessary resources. Lastly, prey species modify their behaviour (i.e. increase vigilance) in response to cues from dangerous predators and that predator cue recognition can extend to prey species no longer living with the predator. Ultimately, adjustments in these behaviours can have repercussions on ecosystem functioning via changes in broader landscape use. Some studies have indicated that changes in herbivore anti-predator behaviours (e.g. landscape use) can lead to behaviourally-mediated trophic cascades (Fortin et al. 2005, Peterson et al. 2014, Ford 2015, Suraci et al. 2016). However, the results of my PhD suggest that for these trophic cascades to be initiated in a newly restored multi-predator system, the predator entering the system needs to be sufficiently different from (e.g. habitat use, hunting strategy, prey preference) or present greater predation risk than the resident predator. For example, the reintroduction of wild dogs in Laikipia, Kenya, was predicted to generate a trophic cascade through high suppression levels of dik dik (*Madoqua guentheri*; Ford et al. 2015). However, browsing pressure by dik dik was similar before and after the wild dogs returned (Ford et al. 2015). Therefore, the return of an apex predator does not necessarily lead to a trophic cascade despite strong top-down effects. Thus, an understanding of the ecology of the different predators, and the potential threats that they pose to the resident prey species, will go a long way in contributing to our understanding of the broad implications of the return of predators into systems.

FUTURE RESEARCH

The results from my data chapters (Chapters 2 - 4) provide a platform on which future research projects can be built. This is especially true with regards to the impacts that returning predators can have, as they alter predator-prey dynamics through shifts from single to multi-predator systems.

Individual effects of predators

Considerable research has been done comparing before and after responses of prey to single large predator reintroductions (Creel et al. 2005, Fischhoff et al. 2007, Nicholson et al. 2014). For example, several studies investigated the responses of elk (*Cervus canadensis*), caribou (*Rangifer tarandus)* and moose (*Alces alces*) to wolf (*Canis lupus*) reintroductions comparing behavioural responses and landscape use of prey before and after their return (Laundré et al. 2001a, Ripple and Beschta 2004, Nicholson et al. 2014). However, comparatively few studies have been able to tease apart the individual effects of predators within multi-predator systems. By focusing on the individual impacts of predators, we will be better able to understand the likely asymmetrical degree of predation risk presented by the different predators. Moreover, this may allow us to determine the role of each predator in shaping the 'landscape of fear' of prey species and how these impacts may drive changes in landscape use (i.e. potential trophic cascades). Differences in landscape use by the different prey species could then be linked back to the varied hunting modes (ambush vs cursorial), prey preferences, and activity patterns of the different predators (Hayward and Kerley 2008).

In my study (Chapter 2), the threat from the introduced wild dogs was perceived to be similar to that of the resident cheetah (i.e. both diurnal cursorial hunters), despite the different hunting strategies (i.e. cheetah chase for ~300 m, wild dogs chase for ~ 3 km). What would be interesting to investigate is how prey species adjust their landscape use, and anti-predator behaviours in response to the introduction of a predator with a completely different hunting strategy. For example, the introduction of an ambush predator into a system that had a resident cursorial predator, or vice versa. This was tested for two gerbil species (*Gerbillus allenbyi* and *Gerbillus pyramidum*) in response to perceived predation risk from an aerial (owls) and a terrestrial predator (vipers; Kotler et al. 1992). In response to predation risk from owls, gerbils avoided open areas and reduced their foraging activity to minimize risk. However, when faced with predation risk from vipers in closed microhabitats, gerbils were forced to spend more time in open areas to avoid vipers increasing their chances of owl predation (Kotler et al. 1992). Therefore, the hunting strategies of the different predators facilitated one another, such that, gerbils could not forage and be safe from both predators simultaneously (Kotler et al. 1992). A similar pattern has been observed for darter fish (*Etheostoma nigrum*), that leave refuges under rocks when faced with predatory crayfish (*Orconectes rusticus*), and in doing so, increase their risk of predation by small mouth bass (*Micropterus dolomieui*) in open water (Rahel and Stein 1988). Similarly, roe deer face predation risk from lynx (*Lynx lynx*) an ambush predator that favours dense vegetation and hunting by humans that rely on open areas for greater sightlines, thus roe deer experienced contrasting conflicting risk from multiple predators (Lone et al. 2014)

Therefore, the introduction or return of predators potentially places conflicting demands on prey species such that changing their behaviour and habitat use to minimize risk from one predator, increases their risk from another predator. Information on how large terrestrial mammalian herbivores deal with these potential conflicting demands through predator facilitation is largely unknown, and thus, is a key question to be answered with the movement of different predators back into ecosystems. In addition, conflicting anti-predator demands from multiple predators have also been observed through human impacts (Lone et al. 2014). Hunting pressure by humans, forces prey to modify their behaviour to minimize risk.

However, these modifications may facilitate the hunting success of natural predators (Lone et al. 2014). Thus, determining how humans impact predator-prey systems is another key question that should be further investigated (Proffitt et al. 2009, Ciuti et al. 2012).

A theoretical framework within which to explore the different behavioural responses of prey species to individual predators in multi-predator systems was suggested by McIntosh and Peckarsky (1999). Mechanisms determining the outcomes of these interactions between prey and multiple predators will depend on type of risk posed by each predator species (McIntosh and Peckarsky 1999). One possibility, is a hierarchical response where the risk from one predator significantly outweighs the risk from others. In these situations, prey species adopt predator avoidance strategies to minimize risk from the dominant predator on the landscape (McIntosh and Peckarsky 1999). A second potential response occurs when the risk from two predators is equivalent but avoiding one increases risk from the other (predator facilitation). If this occurs, then prey species will adopt a compromise anti-predator response to minimize risk from both predators. Lastly, if the risk from different predators is similar and the anti-predatory responses to them do not conflict, than prey likely show an accumulative response to multiple predators (McIntosh and Peckarsky 1999).

This framework has been tested for mayflies (*Baetis bicaudatus*) in response to predation risk from drift-feeding trout (*Salvelinus fontinalis*) and benthic-feeding stoneflies (*Megarcys signata*; McIntosh and Peckarsky 1999). However, it has not been tested within large mammalian multi-predator-prey systems. The results of my study showed that the herbivores adopted a cumulative anti-predatory response to the combined risk posed by two cursorial predators. However, I was unable to test all the interactive effects of multiple predators on prey behaviour. Therefore, exploring whether prey have hierarchical, compromise, or cumulative anti-predator responses to minimize risk within multi-predator systems would be important to predict the type and magnitude of the anti-predator behaviours employed by prey species. An understanding of how prey species react to different predators in multi-predator systems could provide key insight into how predators shape herbivore space use and thus potential impacts on the landscape.

Predator calls and retaining anti-predator behaviours

A limitation of my last study (Chapter 4), was that I only focussed on one predator (i.e. lions). Thus, an interesting question that remains is, do prey species react to the calls of all their predators or is the anti-predatory reaction restricted to their key/most dangerous predator? To explore this, I would suggest, using the calls of a range of predator species that differ with regards to their predation risk (e.g. low to high risk), and recording the behavioural adjustments of prey species to these different calls. This would determine the extent to which predator threat influences the use of non-hunting auditory cues by prey species. It could be that prey respond only to the auditory cues from the top predator, or predators that use specific hunting modes. For example, are the non-hunting calls from ambush predators considered greater indicators of risk compared to the non-hunting calls of cursorial predators? Further studies are also required to assess the degree and nature of the information coded for in the playback of auditory cues, to assess if different levels of information are being gleaned from the vocalizations. This would require further research into the acoustic features of vocalizations and would allow for greater standardization of playback experiments if the degree of information or the reliability of auditory cues could be determined.

Management implications: Predicting impacts of introducing predators

In the absence of predators, prey species can retain anti-predator behaviours through genetic inheritance over several generations (Chamaillé-Jammes et al. 2014), or through interacting with similar extant predators on the landscape (Blumstein et al. 2009). Across the globe, predators are entering systems, yet in many cases we are unsure of the impacts these predators will have. It is obvious that they will have direct lethal effects (i.e. killing), yet the large-scale changes to landscape use of the prey species and the potential impacts these changes may have on vegetation and ecosystem functioning are unclear.

In some instances, the reaction to predators moving into systems has been dramatic. For example, wolf reintroduction into Yellowstone National Park, triggered a trophic cascade, whereby elk shifted their habitat use avoiding riparian areas following wolf reintroduction, this lead to the subsequent restoration of aspen (*Populus tremuloides*) populations (Ripple and Beschta 2003). In response to lion reintroduction in Addo Elephant National park, buffalo (*Syncerus caffer*) herds amalgamated to form larger groups and shifted their habitat use to more open areas thus avoiding denser vegetation associated with ambushing lions (Tambling et al. 2012).

A key challenge for managers is understanding how prey species will react to the introduction of a predator, and the potential knock-on effects that may result due to this introduction. One possible way to gain some insight into potential changes would be to use playbacks of predator cues and monitor the behavioural changes of prey (e.g. habitat use, feeding intensity, temporal shifts) prior to the predator being released. This may then enhance predictive capabilities, and thus understanding, of the impacts that a returning predator may have on prey populations, and the potential cascading effects on the ecosystem. Managers could then use this information to assess whether the potential impacts are acceptable and/or even desirable.

REFERENCE LIST

Allen, B. L., P. J. Fleming, M. Hayward, L. R. Allen, R. M. Engeman, G. Ballard, and L. K.-P. Leung. 2012. Top-predators as biodiversity regulators: contemporary issues affecting knowledge and management of dingoes in Australia.*in* G. Lameed, editor. Biodiversity Enrichment in a Diverse World. DigitalCommons, University of Nebraska-Lincoln.

Altendorf, K. B., J. W. Laundré, C. A. L. González, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy **82**:430-439.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour **49**:227-266.

Arnold, J., A. Humer, M. Heltai, D. Murariu, N. Spassov, and K. Hacklaender. 2012. Current status and distribution of golden jackals Canis aureus in Europe. Mammal Review **42**:1-11.

Banks, P. B., K. Norrdahl, and E. Korpimäki. 2002. Mobility decisions and the predation risks of reintroduction. Biological Conservation **103**:133-138.

Barrera, J. P., L. Chong, K. N. Judy, and D. T. Blumstein. 2011. Reliability of public information: predators provide more information about risk than conspecifics. Animal Behaviour **81**:779-787.

Bastian, A., and S. Schmidt. 2008. Affect cues in vocalizations of the bat, Megaderma lyra, during agonistic interactions. The Journal of the Acoustical Society of America **124**:598-608.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes (2011). R package version 0.999375-42.

Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. Behavioural Processes **63**:111-121.

Beauchamp, G. 2015. Animal vigilance: monitoring predators and competitors. Academic Press.

Belll, S., E. D. McCoy, and H. R. Mushinsky. 2012. Habitat structure: the physical arrangement of objects in space. Springer Science & Business Media.

Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proceedings of the Royal Society of London B: Biological Sciences **266**:2261-2267.

Berger, J. 2007. Carnivore repatriation and holarctic prey: narrowing the deficit in ecological effectiveness. Conservation Biology **21**:1105-1116.

Blumstein, D. T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology **112**:209-217.

Blumstein, D. T., L. Cooley, J. Winternitz, and J. C. Daniel. 2008. Do yellow-bellied marmots respond to predator vocalizations? Behavioral Ecology and Sociobiology **62**:457-468.

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

Blumstein, D. T., J. C. Daniel, A. S. Griffin, and C. S. Evans. 2000. Insular tammar wallabies (Macropus eugenii) respond to visual but not acoustic cues from predators. Behavioral Ecology **11**:528-535.

Blumstein, D. T., E. Ferando, and T. Stankowich. 2009. A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators. Animal Behaviour **78**:873-878.

Bongi, P., S. Ciuti, S. Grignolio, M. Del Frate, S. Simi, D. Gandelli, and M. Apollonio. 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of zoology **276**:242-251.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology **22**:37-47.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research **1**:49-71.

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

Brown, N. A., K. E. Ruckstuhl, S. Donelon, and C. Corbett. 2010. Changes in vigilance, grazing behaviour and spatial distribution of bighorn sheep due to cattle presence in Sheep River Provincial Park, Alberta. Agriculture, Ecosystems & Environment **135**: 226-231.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press.

Chamaillé-Jammes, S., H. Malcuit, S. Le Saout, and J.-L. Martin. 2014. Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. Oecologia **174**:1151-1158.

Chapron, G., P. Kaczensky, J. D. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, and O. Anders. 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science **346**:1517-1519.

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

Clark, J. D., D. Huber, and C. Servheen. 2002. Bear reintroductions: lessons and challenges: invited paper. Ursus **13**:335-345.

Clements, H. S., C. J. Tambling, M. W. Hayward, and G. I. Kerley. 2014. An objective approach to determining the weight ranges of prey preferred by and accessible to the five large African carnivores. PLoS ONE **9**:e101054.

Clements, H. S., C. J. Tambling, and G. I. H. Kerley. 2016. Prey morphology and predator sociality drive predator prey preferences. Journal of Mammalogy:1-9.

Courbin, N., A. J. Loveridge, D. W. Macdonald, H. Fritz, M. Valeix, E. T. Makuwe, and S. Chamaillé-Jammes. 2016. Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. Oikos **125**:829-838.

Cozzi, G., F. Broekhuis, J. W. McNutt, L. A. Turnbull, D. W. Macdonald, and B. Schmid. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology **93**:2590-2599.

Creel, S., and N. M. Creel. 2002. The African wild dog: behavior, ecology, and conservation. Princeton University Press.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology **25**:773-784.

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

Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour **69**:1181-1189.

Cresswell, W., J. Lind, and J. L. Quinn. 2010. Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. Journal of Animal Ecology **79**:556-562.

Cromhout, M. 2007. The ecology of the African buffalo in the eastern Kalahari region, South Africa. University of Pretoria.

Crosmary, W.-G., M. Valeix, H. Fritz, H. Madzikanda, and S. D. Côté. 2012. African ungulates and their drinking problems: hunting and predation risks constrain access to water. Animal Behaviour **83**:145-153.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology **63**:644-652.

Dalerum, F., and L. Belton. 2014. African ungulates recognize a locally extinct native predator. Behavioral Ecology:1-8.

Davidson, Z., M. Valeix, F. Van Kesteren, A. J. Loveridge, J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. PLoS ONE **8**:e55182.

Davies-Mostert, H. T., M. G. L. Mills, and D. W. Macdonald. 2009. A critical assessment of South Africa's managed metapopulation recovery strategy for African wild dogs. Reintroduction of top-order predators:10-42.

Davino, C., M. Furno, and D. Vistocco. 2013. Quantile regression: theory and applications. John Wiley & Sons.

de Boer, W. F., M. J. Vis, H. J. de Knegt, C. Rowles, E. M. Kohi, F. van Langevelde, M. Peel, Y. Pretorius, A. K. Skidmore, and R. Slotow. 2010. Spatial distribution of lion kills determined by the water dependency of prey species. Journal of Mammalogy **91**:1280-1286.

Delm, M. M. 1990. Vigilance for predators: detection and dilution effects. Behavioral Ecology and Sociobiology **26**:337-342.

Eccard, J. A., J. K. Meißner, and M. Heurich. 2015. European Roe Deer Increase Vigilance When Faced with Immediate Predation Risk by Eurasian Lynx. Ethology **121**:1-11.

Eccard, J. A., J. Pusenius, J. Sundell, S. Halle, and H. Ylönen. 2008. Foraging patterns of voles at heterogeneous avian and uniform mustelid predation risk. Oecologia **157**:725-734.

Enstam, K. L., and L. A. Isbell. 2002. Comparison of responses to alarm calls by patas (Erythrocebus patas) and vervet (Cercopithecus aethiops) monkeys in relation to habitat structure. American Journal of Physical Anthropology **119**:3-14.

Estes, R. 1991. The behavior guide to African mammals. University of California Press Berkeley.

Fasola, L., J. Muzio, C. Chehébar, M. Cassini, and D. W. Macdonald. 2011. Range expansion and prey use of American mink in Argentinean Patagonia: dilemmas for conservation. European Journal of Wildlife Research **57**:283-294.

Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, and D. Rubenstein. 2007. Habitat use and movements of plains zebra (Equus burchelli) in response to predation danger from lions. Behavioral Ecology **18**:725-729.

Fitzgibbon, C. D. 1990. Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Animal Behaviour **39**:1116-1126.

Ford, A. T. 2015. The mechanistic pathways of trophic interactions in human-occupied landscapes. Science **350**:1175-1176.

Ford, A. T., J. R. Goheen, D. J. Augustine, M. F. Kinnaird, T. G. O'Brien, T. M. Palmer, R. M. Pringle, and R. Woodroffe. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology **96**:2705-2714.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320-1330.

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

Fortin, D., and M.-E. Fortin. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Animal Behaviour **78**:887-892.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Fuller, T. K., and P. W. Kat. 1990. Movements, activity, and prey relationships of African wild dogs (Lycaon pictus) near Aitong, southwestern Kenya. African Journal of Ecology **28**:330-350.

Gil-da-Costa, R., A. Palleroni, M. D. Hauser, J. Touchton, and J. P. Kelley. 2003. Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. Proceedings of the Royal Society of London B: Biological Sciences **270**:605-610.

Gompper, M. E. 2002. Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of North-eastern North America by Coyotes The expansion of the coyote's geographical range may broadly influence community structure, and rising coyote densities in the suburbs may alter how the general public views wildlife. Bioscience **52**:185-190.

Gorini, L., J. D. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. Nilsen. 2012. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Review **42**:55-77.

Griffin, A. S., D. T. Blumstein, and C. S. Evans. 2000. Training captive-bred or translocated animals to avoid predators. Conservation Biology **14**:1317-1326.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology **31**:295-311.

Hanks, J. 1972. Growth of the African elephant (Loxodonta africana). African Journal of Ecology **10**:251-272.

Hayward, M. 2006. Prey preferences of the spotted hyaena (Crocuta crocuta) and degree of dietary overlap with the lion (Panthera leo). Journal of zoology **270**:606-614.

Hayward, M. W., G. J. Hayward, C. J. Tambling, and G. I. Kerley. 2011. Do lions Panthera leo actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? PLoS ONE **6**:e23607.

Hayward, M. W., M. Hofmeyr, J. O'Brien, and G. I. H. Kerley. 2006a. Prey preferences of the cheetah (Acinonyx jubatus) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? Journal of zoology **270**:615-627.

Hayward, M. W., and G. I. Kerley. 2005. Prey preferences of the lion (Panthera leo). Journal of zoology **267**:309-322.

Hayward, M. W., and G. I. Kerley. 2008. Prey preferences and dietary overlap amongst Africa's large predators. South African Journal of Wildlife Research **38**:93-108.

Hayward, M. W., G. I. Kerley, J. Adendorff, L. C. Moolman, J. O'brien, A. Sholto-Douglas, C. Bissett, P. Bean, A. Fogarty, and D. Howarth. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. Oryx **41**:205-214.

Hayward, M. W., J. O'Brien, M. Hofmeyr, and G. I. Kerley. 2006b. Prey preferences of the African wild dog Lycaon pictus (Canidae: Carnivora): ecological requirements for conservation. Journal of Mammalogy **87**:1122-1131.

Hayward, M. W., S. Ortmann, and R. Kowalczyk. 2015. Risk perception by endangered European bison Bison bonasus is context (condition) dependent. Landscape Ecology **30**:2079-2093.

Hayward, M. W., and R. Slotow. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research **39**:109-125.

Hayward, M. W., and M. Somers. 2009. Reintroduction of top-order predators. John Wiley & Sons.

Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology **80**:800-809.

Heltai, M., L. Szemethy, J. Lanszki, and S. Csányi. 2000. Returning and new mammal predators in Hungary: the status and distribution of the golden jackal (Canis aureus), raccoon dog (Nyctereutes procyonoides) and raccoon (Procyon lotor) in 1997–2000. Beiträge zur Jagd-und Wildforschung **26**:95-102.

Hettena, A. M., N. Munoz, and D. T. Blumstein. 2014. Prey responses to predator's sounds: a review and empirical study. Ethology **120**:427-452.

Hilborn, A., N. Pettorelli, C. D. L. Orme, and S. M. Durant. 2012. Stalk and chase: how hunt stages affect hunting success in Serengeti cheetah. Animal Behaviour **84**:701-706.

Hochman, V., and B. P. Kotler. 2007. Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behavioral Ecology **18**:368-374.

Hopcraft, J. G. C., A. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559-566.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal **50**:346-363.

Houston, A. I., J. M. McNamara, and J. M. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society of London B: Biological Sciences **341**:375-397.

Hunter, L., and J. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour **135**:195-211.

Jarman, P. 1974. The social organisation of antelope in relation to their ecology. Behaviour **48**:215-267.

Jones, M. E., G. C. Smith, and S. M. Jones. 2004. Is anti-predator behaviour in Tasmanian eastern quolls (Dasyurus viverrinus) effective against introduced predators? Animal Conservation **7**:155-160.

Karpanty, S. M., and P. C. Wright. 2007. Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. Pages 77-99 Primate anti-predator strategies. Springer.

Katjiua, M., and D. Ward. 2006. Cattle diet selection during the hot-dry season in a semi-arid region of Namibia. African Journal of Range and Forage Science **23**:59-67.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecology Letters **10**:690-700.

Khoury, R. E. 2013. Eavesdropping : how do vervet monkeys perceive the alarm calls of other species? University of KwaZulu-Natal.

Kitchen, D. M., T. J. Bergman, D. L. Cheney, J. R. Nicholson, and R. M. Seyfarth. 2010. Comparing responses of four ungulate species to playbacks of baboon alarm calls. Animal Cognition **13**:861-870.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature **437**:880-883.

Koenker, R. 2005. Quantile regression. Cambridge university press.

Koenker, R., S. Portnoy, P. T. Ng, A. Zeileis, P. Grosjean, and B. D. Ripley. 2015. Package ‘quantreg’.

Kotler, B. P., L. Blaustein, and J. S. Brown. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. Pages 199-206 *in* Annales Zoologici Fennici. JSTOR.

Kotler, B. P., J. Brown, S. Mukherjee, O. Berger-Tal, and A. Bouskila. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proceedings of the Royal Society of London B: Biological Sciences **277**:1469-1474.

Kotler, B. P., J. Brown, A. Oldfield, J. Thorson, and D. Cohen. 2001. Foraging substrate and escape substrate: patch use by three species of gerbils. Ecology **82**:1781-1790.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology **72**:2249-2260.

Krause, J., and G. D. Ruxton. 2002. Living in groups. Oxford University Press.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics **34**:153-181.

Kroodsma, D. E., B. E. Byers, E. Goodale, S. Johnson, and W.-C. Liu. 2001. Pseudoreplication in playback experiments, revisited a decade later. Animal Behaviour **61**:1029-1033.

Kuczynski, A. M. 2015. Assessment of predation risk in the environment: Use of acoustic and visual cues. Texas Tech University.

Kunkel, K., and D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. The Journal of Wildlife Management **65**:520-530.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001a. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology **79**:1401-1409.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001b. Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology **79**:1401-1409.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal **3**:1-7.

Le Houerou, H. N. 1980. Browse in Africa: the current state of knowledge. ILCA.

Leuthold, W. 2012. African ungulates: a comparative review of their ethology and behavioral ecology. Springer Science & Business Media.

Lewis, J. C., K. L. Sallee, and R. T. Golightly Jr. 1999. Introduction and range expansion of nonnative red foxes (Vulpes vulpes) in California. The American midland naturalist **142**:372-381.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience **48**:25-34.

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

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619-640.

Lindsey, P., C. J. Tambling, R. Brummer, H. Davies-Mostert, M. Hayward, K. Marnewick, and D. Parker. 2011. Minimum prey and area requirements of the Vulnerable cheetah Acinonyx jubatus: implications for reintroduction and management of the species in South Africa. Oryx **45**:587-599.

Linkie, M., and M. Ridout. 2011. Assessing tiger–prey interactions in Sumatran rainforests. Journal of zoology **284**:224-229.

Linnell, J. D., H. Brøseth, E. J. Solberg, and S. M. Brainerd. 2005. The origins of the southern Scandinavian wolf Canis lupus population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. Wildlife Biology **11**:383-391.

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

Loveridge, A. J., J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2006. Influence of drought on predation of elephant (Loxodonta africana) calves by lions (Panthera leo) in an African wooded savannah. Journal of zoology **270**:523-530.

Lynch, E., J. M. Northrup, M. F. McKenna, C. R. Anderson, L. Angeloni, and G. Wittemyer. 2014. Landscape and anthropogenic features influence the use of auditory vigilance by mule deer. Behavioral Ecology:aru158.

Magrath, R. D., T. M. Haff, P. M. Fallow, and A. N. Radford. 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biological Reviews **90**:560-586.

Manning, A. D., I. J. Gordon, and W. J. Ripple. 2009. Restoring landscapes of fear with wolves in the Scottish Highlands. Biological Conservation **142**:2314-2321.

Marker, L., A. Dickman, C. Wilkinson, B. Schumann, and E. Fabiano. 2007. The namibian cheetah: Status report. Cat News **3**:4-13.

McComb, K., G. Shannon, S. M. Durant, K. Sayialel, R. Slotow, J. Poole, and C. Moss. 2011. Leadership in elephants: the adaptive value of age. Proceedings of the Royal Society of London B: Biological Sciences **278**:3270-3276.

McIntosh, A. R., and B. L. Peckarsky. 1999. Criteria determining behavioural responses to multiple predators by a stream mayfly. Oikos **85**:554-564.

Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter Severity and Wolf Predation on a Formerly Wolf-Free Elk Herd. The Journal of Wildlife Management **65**:998-1003.

Mills, M. 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. Koedoe **27**:281-294.

Mills, M., and T. Shenk. 1992. Predator--prey relationships: The impact of lion predation on wildebeest and zebra populations. Journal of Animal Ecology **61**:693-702.

Moll, R. J., A. K. Killion, R. A. Montgomery, C. J. Tambling, and M. W. Hayward. 2016. Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. Ecology **97**:1123-1134.

Monterroso, P., P. C. Alves, and P. Ferreras. 2013. Catch me if you can: diel activity patterns of mammalian prey and predators. Ethology **119**:1044-1056.

Moreno, S., M. Delibes, and R. Villafuerte. 1996. Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Canadian Journal of Zoology **74**:1656-1660.

Muro, C., R. Escobedo, L. Spector, and R. Coppinger. 2011. Wolf-pack (Canis lupus) hunting strategies emerge from simple rules in computational simulations. Behavioural Processes **88**:192-197.

Murray, D. L., S. Boutin, M. O'Donoghue, and V. O. Nams. 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. Animal Behaviour **50**:1203-1210.

Ndaimani, H., P. Tagwireyi, L. Sebele, and H. Madzikanda. 2016. An Ecological Paradox: The African Wild Dog (Lycaon Pictus) Is Not Attracted to Water Points When Water Is Scarce in Hwange National Park, Zimbabwe. PLoS ONE **11**:e0146263.

Nicholson, K. L., C. Milleret, J. Månsson, and H. Sand. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. Oecologia **176**:69-80.

Nilsen, E. B., E. Milner-Gulland, L. Schofield, A. Mysterud, N. C. Stenseth, and T. Coulson. 2007. Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. Proceedings of the Royal Society of London B: Biological Sciences **274**:995-1003.

Ogutu, J. O., R. S. Reid, H.-P. Piepho, N. T. Hobbs, M. E. Rainy, R. L. Kruska, J. S. Worden, and M. Nyabenge. 2014. Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. Biodiversity and Conservation **23**:573-596.

Owen-Smith, N., and J. W. Cain. 2007. Indicators of adaptive responses in home range utilization and movement patterns by a large mammalian herbivore. Israel Journal of Ecology & Evolution **53**:423-438.

Owen-Smith, N., and M. G. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. Journal of Animal Ecology **77**:173-183.

Owen-Smith, N. 2014. Spatial ecology of large herbivore populations. Ecography **37**:416-430.

Padié, S., N. Morellet, A. Hewison, J. L. Martin, N. Bonnot, B. Cargnelutti, and S. Chamaillé-Jammes. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos **124**:1536-1546.

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

Périquet, S., L. Todd-Jones, M. Valeix, B. Stapelkamp, N. Elliot, M. Wijers, O. Pays, D. Fortin, H. Madzikanda, and H. Fritz. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behavioral Ecology:ars060.

Périquet, S., M. Valeix, A. J. Loveridge, H. Madzikanda, D. W. Macdonald, and H. Fritz. 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. Animal Behaviour **79**:665-671.

Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. Annual Review of Ecology, Evolution, and Systematics **45**:325-345.

Pomilia, M. A., J. W. McNutt, and N. R. Jordan. 2015. Ecological predictors of African wild dog ranging patterns in northern Botswana. Journal of Mammalogy:1-10.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology **88**:2744-2751.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. The Journal of Wildlife Management **73**:345-356.

Rahel, F. J., and R. A. Stein. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. Oecologia **75**:94-98.

Rainey, H. J., K. Zuberbühler, and P. J. Slater. 2004. The responses of black-casqued hornbills to predator vocalisations and primate alarm calls. Behaviour **141**:1263-1277.

Randler, C. 2006. Disturbances by dog barking increase vigilance in coots Fulica atra. European Journal of Wildlife Research **52**:265-270.

Relyea, R. A. 2003. How prey respond to combined predators: a review and an empirical test. Ecology **84**:1827-1839.

Remage-Healey, L., D. P. Nowacek, and A. H. Bass. 2006. Dolphin foraging sounds suppress calling and elevate stress hormone levels in a prey species, the Gulf toadfish. Journal of Experimental Biology **209**:4444-4451.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management **184**:299-313.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? Bioscience **54**:755-766.

Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management **230**:96-106.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, and M. P. Nelson. 2014. Status and ecological effects of the world’s largest carnivores. Science **343**:1241484.

Roberts, G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour **51**:1077-1086.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist:209-223.

Ross, J., A. Hearn, P. Johnson, and D. Macdonald. 2013. Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. Journal of zoology **290**:96-106.

Rovero, F., T. Jones, and J. Sanderson. 2005. Notes on Abbott's duiker (Cephalophus spadix True 1890) and other forest antelopes of Mwanihana Forest, Udzungwa Mountains, Tanzania, as revealed by camera-trapping and direct observations. Tropical Zoology **18**:13-23.

Roxburgh, D. J. 2008. Prey and range use of lions on Tswalu Kalahari Reserve. University of Pretoria.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? Proceedings of the Royal Society of London B: Biological Sciences **273**:1421-1427.

Schadt, S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Červený, P. Koubek, and T. Huber. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology **39**:189-203.

Schaller, G. B. 2009. The Serengeti lion: a study of predator-prey relations. University of Chicago Press.

Scheel, D., and C. Packer. 1991. Group hunting behaviour of lions: a search for cooperation. Animal Behaviour **41**:697-709.

Schmidt, K., and D. P. Kuijper. 2015. A “death trap” in the landscape of fear. Mammal Research **60**:275-284.

Schmidt, K. A., J. S. Brown, and R. A. Morgan. 1998. Plant defenses as complementary resources: a test with squirrels. Oikos **81**:130-142.

Schmidt, K. A., E. Lee, R. S. Ostfeld, and K. Sieving. 2008. Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. Behavioral Ecology **19**:759-763.

Schmitt, M. H., K. Stears, C. C. Wilmers, and A. M. Shrader. 2014. Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. Animal Behaviour **96**:151-158.

Schmitz, and Oswald. 2005. Behavior of Predators and Prey and Links with Population-Level Processes. Ecology of Predator-Prey Interactions:256.

Seyfarth, R. M., and D. L. Cheney. 2003. Signalers and receivers in animal communication. Annual Review of Psychology **54**:145-173.

Shrader, A. M., J. S. Brown, G. I. H. Kerley, and B. P. Kotler. 2008. Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. Journal of Arid Environments **72**:1811-1819.

Shrader, A. M., G. I. Kerley, J. S. Brown, and B. P. Kotler. 2012. Patch Use in Free-Ranging Goats: Does a Large Mammalian Herbivore Forage like Other Central Place Foragers? Ethology **118**:967-974.

Shriner, W. M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour **55**:529-536.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos **119**:610-621.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution **13**:350-355.

Sinclair, A., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator–prey system. Nature **425**:288-290.

Sinclair, A. R. 1985. Does interspecific competition or predation shape the African ungulate community? The Journal of Animal Ecology:899-918.

Skinner, J. D., and C. T. Chimimba. 2005. The mammals of the southern African sub-region. Cambridge University Press.

Smit, I. P., C. C. Grant, and B. J. Devereux. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. Biological Conservation **136**:85-99.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. The American Naturalist **140**:325-348.

Stahl, P., J. Vandel, V. Herrenschmidt, and P. Migot. 2001. Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. Journal of Applied Ecology **38**:674-687.

Stankowich, T., and R. G. Coss. 2007. The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. Proceedings of the Royal Society of London B: Biological Sciences **274**:175-182.

Stears, K., and A. M. Shrader. 2015. Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales. Animal Behaviour **108**:155-164.

Stensland, E., A. Angerbjörn, and P. Berggren. 2003. Mixed species groups in mammals. Mammal Review **33**:205-223.

Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. Nature communications **7**:1-7.

Tambling, C. J., D. J. Druce, M. W. Hayward, J. G. Castley, J. Adendorff, and G. I. Kerley. 2012. Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. Ecology **93**:1297-1304.

Tambling, C. J., L. Minnie, J. Meyer, E. W. Freeman, R. M. Santymire, J. Adendorff, and G. I. Kerley. 2015. Temporal shifts in activity of prey following large predator reintroductions. Behavioral Ecology and Sociobiology **69**:1153-1161.

Team, R. C. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013. ISBN 3-900051-07-0.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology **92**:398-407.

Theuerkauf, J., and S. Rouys. 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. Forest Ecology and Management **256**:1325-1332.

Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Canadian Journal of Zoology **87**:1129-1137.

Traill, L., J. Martin, and N. Owen-Smith. 2016. Lion proximity, not moon phase, affects the nocturnal movement behaviour of zebra and wildebeest. Journal of zoology **299**:1-7.

Valeix, M., H. Fritz, A. J. Loveridge, Z. Davidson, J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2009a. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral Ecology and Sociobiology **63**:1483-1494.

Valeix, M., G. Hemson, A. J. Loveridge, G. Mills, and D. W. Macdonald. 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. Journal of Applied Ecology **49**:73-81.

Valeix, M., A. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. Macdonald. 2009b. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology **90**:23-30.

Valeix, M., A. J. Loveridge, Z. Davidson, H. Madzikanda, H. Fritz, and D. W. Macdonald. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology **25**:337-351.

Van Beest, F. M., A. Mysterud, L. E. Loe, and J. M. Milner. 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. Journal of Animal Ecology **79**:910-922.

van der Meer, E., H. Fritz, and O. Pays. 2015. Anti-predator behaviour of kudu and impala in response to mimicked African wild dog presence: do age and sex matter? Behaviour **152**:1209-1228.

van der Veen, I. T. 2002. Seeing is believing: information about predators influences yellowhammer behavior. Behavioral Ecology and Sociobiology **51**:466-471.

Venables, W. N., and B. D. Ripley. 2002. Random and mixed effects. Pages 271-300 Modern Applied Statistics with S. Springer.

Webster, H., J. W. McNutt, and K. McComb. 2012. African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. Ethology **118**:147-156.

West, P., C. Packer, J. Kingdon, and M. Hoffmann. 2013. Panthera leo Lion. Mammals of Africa Volume V: Carnivores, pangolins, equids and rhinoceroses:149-159.

Woodroffe, R., P. A. Lindsey, S. S. Romañach, and S. M. ole Ranah. 2007. African wild dogs (Lycaon pictus) can subsist on small prey: implications for conservation. Journal of Mammalogy **88**:181-193.

Zuberbühler, K., D. Jenny, and R. Bshary. 1999. The predator deterrence function of primate alarm calls. Ethology **105**:477-490.

Zuberbühler, K., R. Noë, and R. M. Seyfarth. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Animal Behaviour **53**:589-604.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects modelling for nested data. Pages 101-142 Mixed effects models and extensions in ecology with R. Springer.

APPENDIX 1

Table 1. List of mammal species found within Tswalu Kalahari Reserve.

Common Name	Species	Common Name	Species
Aardvark	*Orycteropus afer*	Klipspringer	*Oreotragus oreotragus*
Aardwolf	*Proteles cristatus*	Kudu	*Tragelaphus strepsiceros*
African wild cat	*Felis lybica*	Leopard	*Panthera pardus*
Bat-eared fox	*Octocyon megalotis*	Lion	*Panthera leo*
Black wildebeest	*Connochaetes gnou*	Mountain redbuck	*Redunca fulvorfula*
Black-backed jackal	*Canis mesomelas*	Nyala	*Tragelaphus angasii*
Blesbok	*Damaliscus pygargus phillipsi*	Plains zebra	*Equus burchelli*
Blue Wildebeest	*Connochaetes taurinus*	Porcupine	*Hystrix africaeaustralis*
Brown hyena	*Hyaena brunnea*	Red hartebeest	*Alcelaphus buselaphus*
Buffalo	*Syncerus caffer*	Roan	*Hippotragus equinus*
Caracal	*Caracal caracal*	Rock hyrax	*Procavia capensis*
Chacma baboon	*Papio ursinus*	Sable	*Hippotragus niger*
Cheetah	*Acinonyx jubatus*	Small spotted cat	*Felis nigripes*
Common duiker	*Sylvicapra grimmia*	Springbok	*Antidorcas marsupialis*
Eland	*Tragelaphus oryx*	Steenbok	*Raphicerus campestrus*
Gemsbok	*Oryx gazella*	Tsessebe	*Damaliscus lunatus*
Giraffe	*Giraffa camelopardalis*	Warthog	*Phacochoerus africanus*
Hartmann's Mountain Zebra	*Equus zebra ssp. Hartmannae*	Waterbuck	*Kobus ellipsiprymnus*
Honey badger	*Mellivora capensis*	Wild dog	*Lycaon pictus*
Impala	*Aepyceros melampus*		

APPENDIX 2

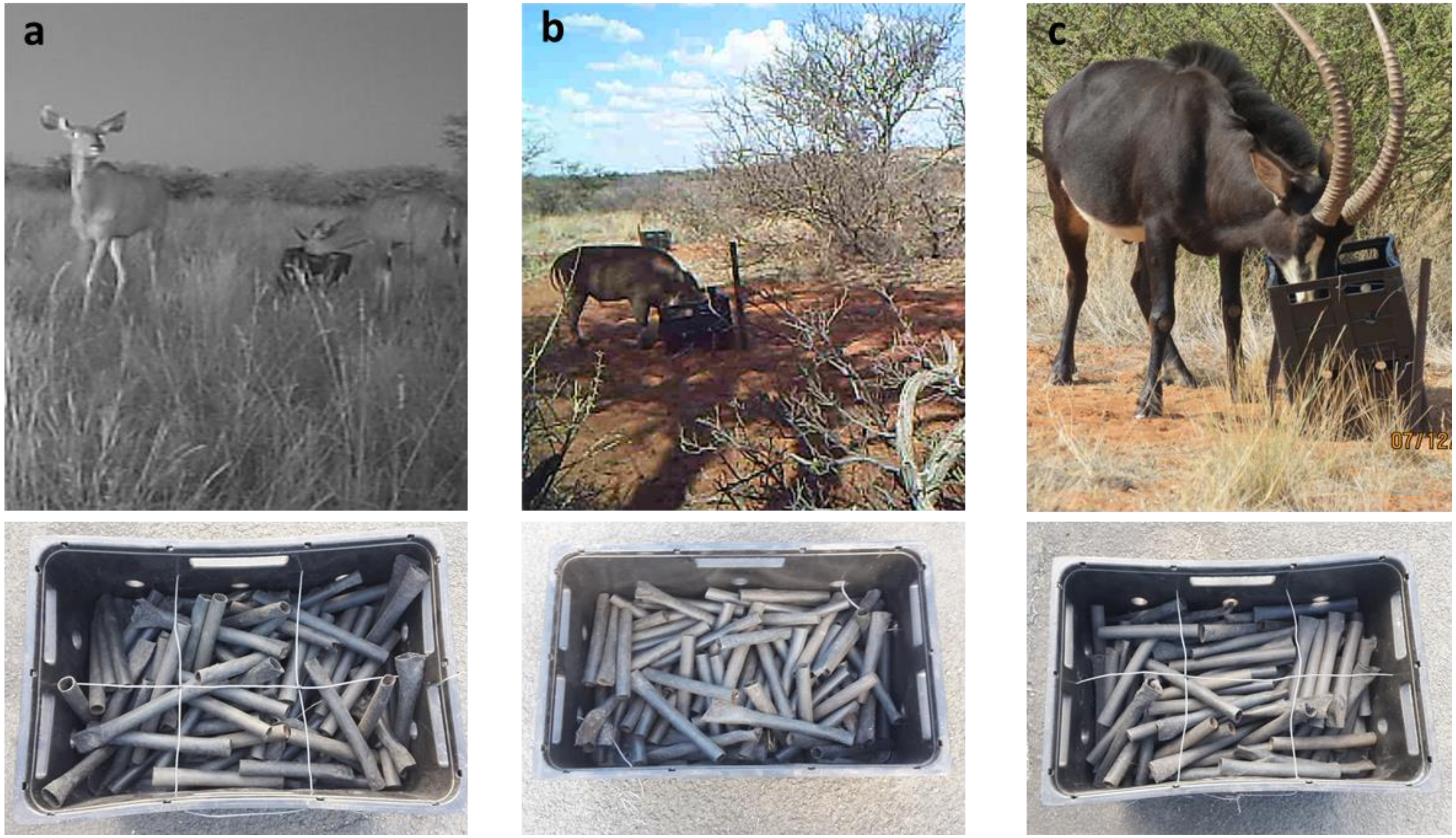
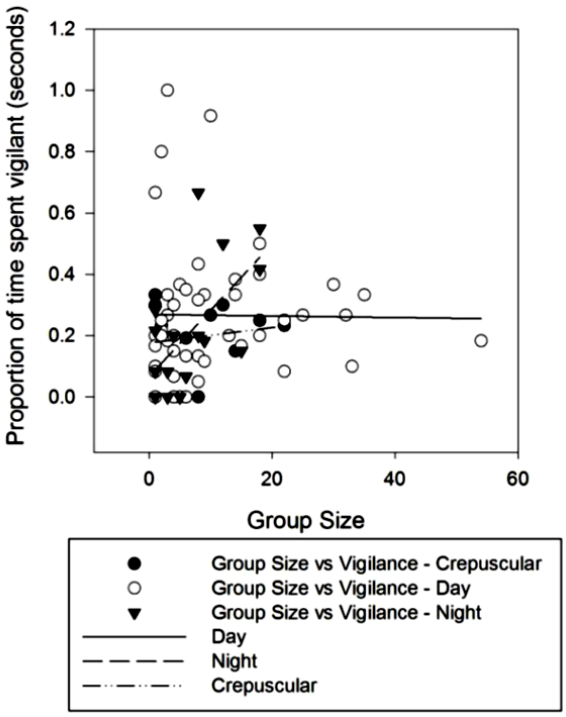
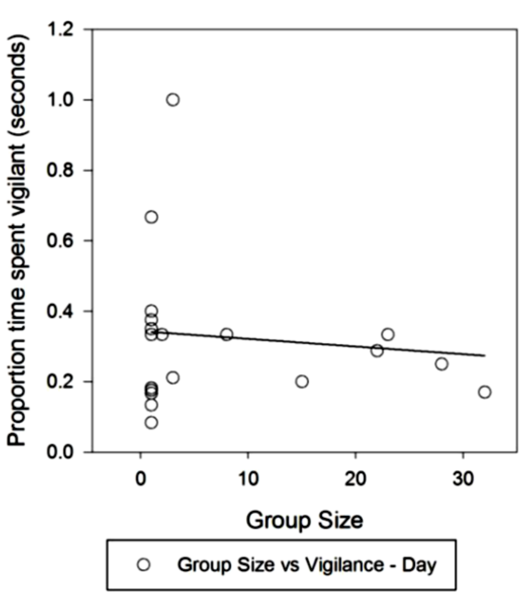
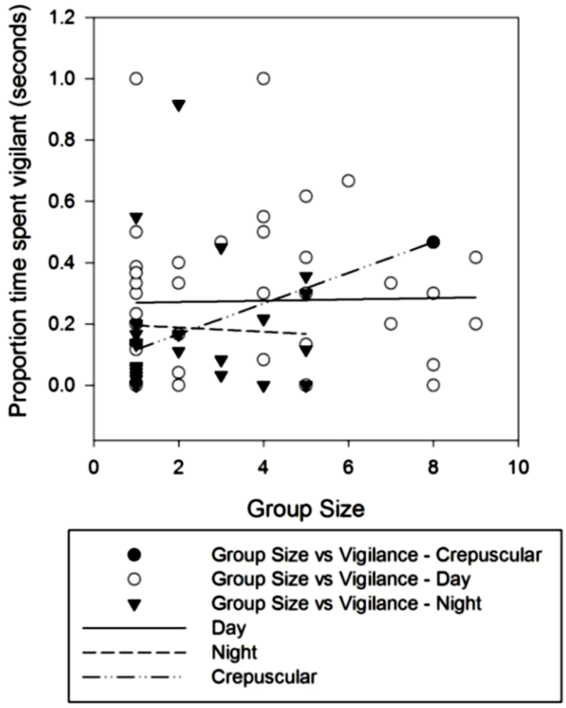


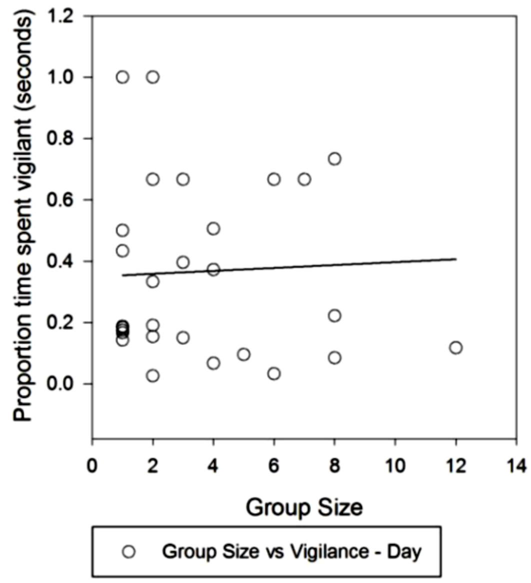
Figure 1. **a)** kudu, **b)** warthog and **c)** sable, feeding from giving-up-density (GUDs) trays comprised of black plastic trays, filled with 10 litres of pvc piping as an inedible substrate over which 200 g of sheep pellets were poured, with a wire grid across the top for kudu and sable.

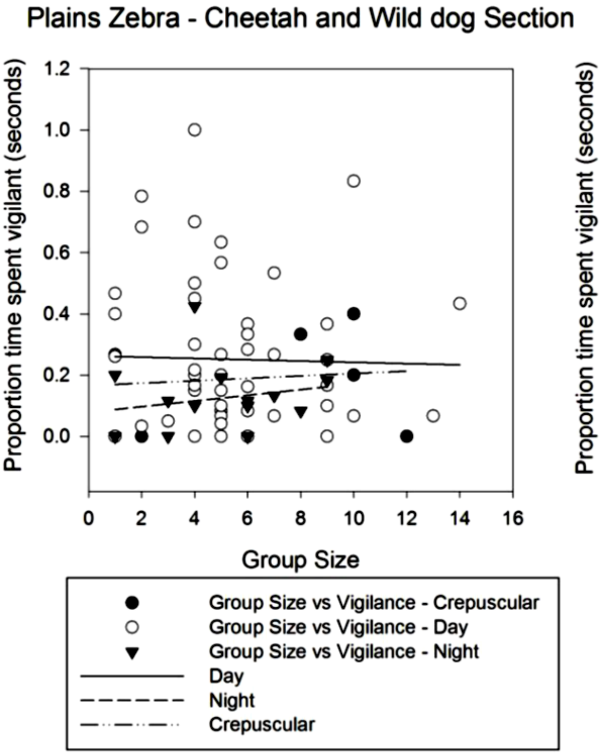
APPENDIX 3


Eland- Cheetah and Wild dog Section

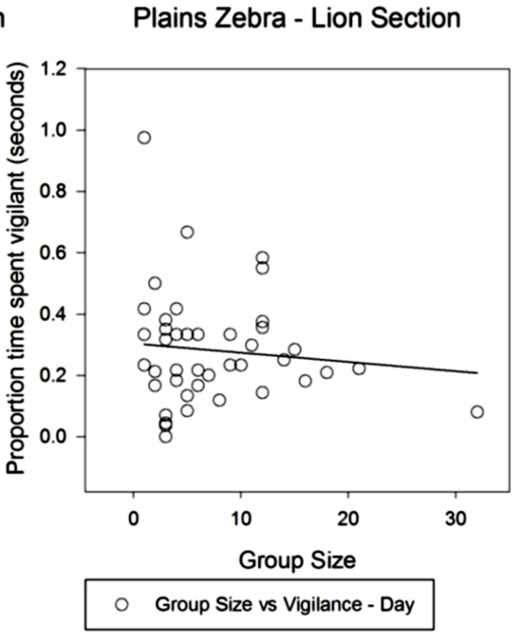

Eland - Lions Section


Gemsbok- Cheetah and Wild dog Section

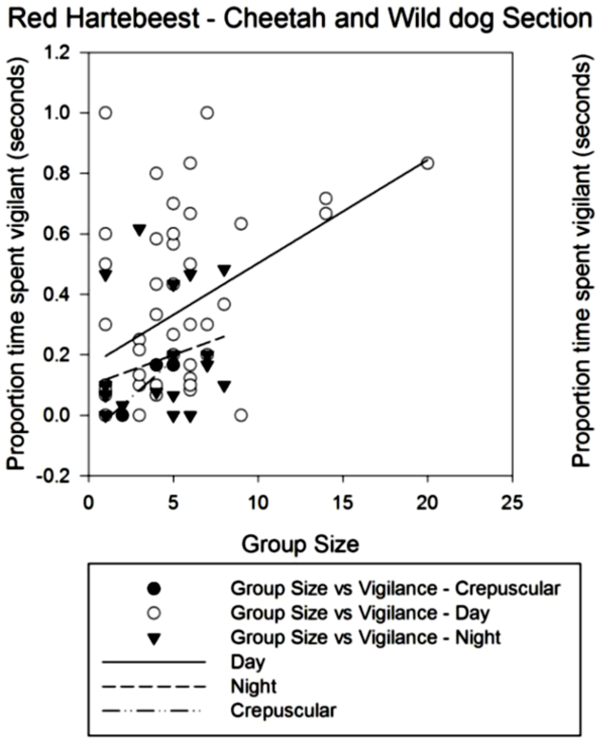

Gemsbok-Lion Section



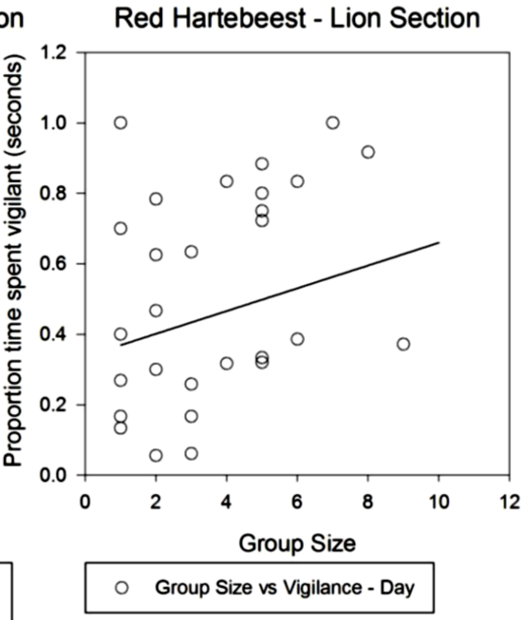
Plains Zebra - Cheetah and Wild dog Section



Plains Zebra - Lion Section



Red Hartebeest - Cheetah and Wild dog Section



Red Hartebeest - Lion Section

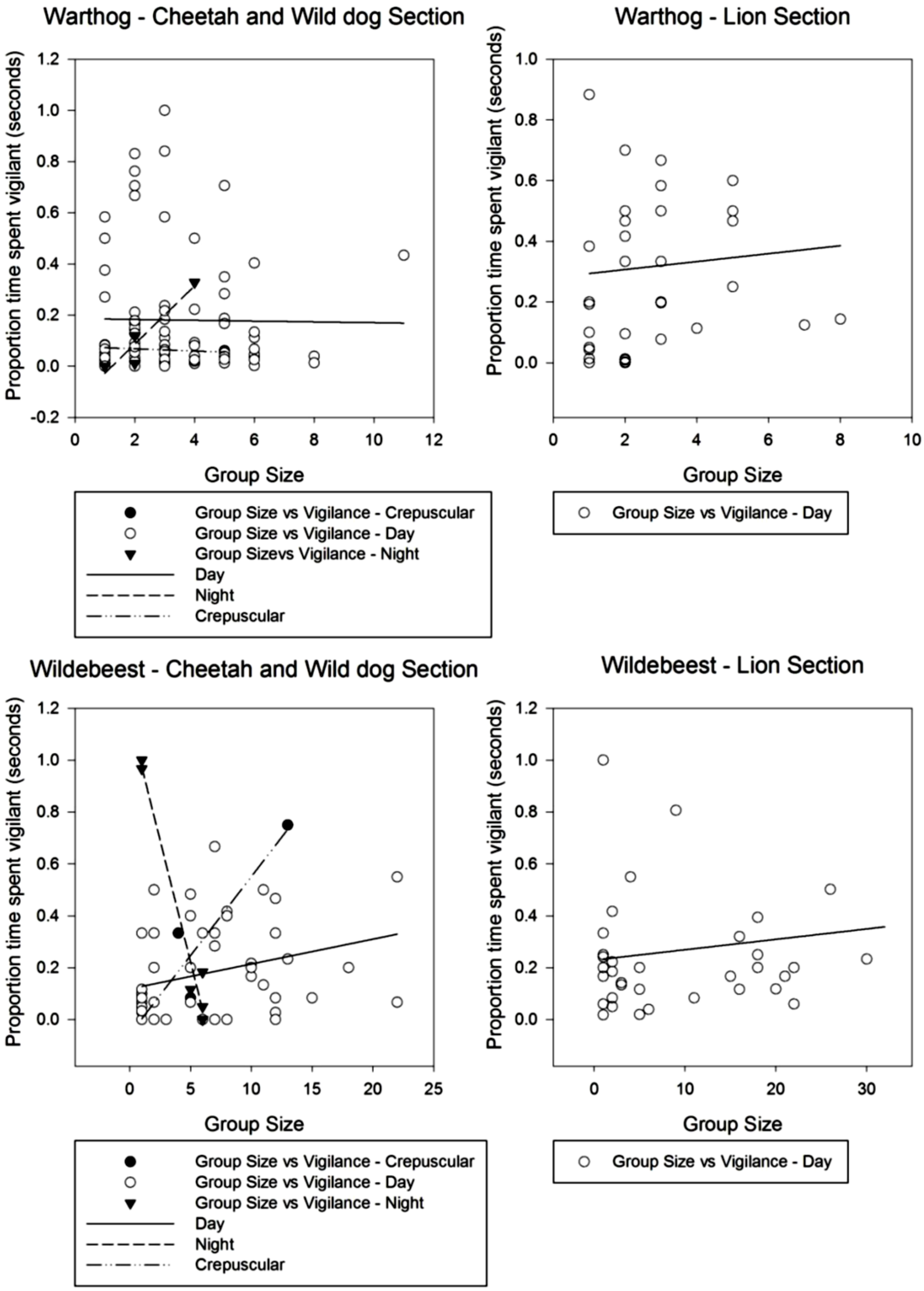


Figure 1. Mean proportion time herbivore groups spent vigilant at waterholes comparing the different predator sections (lions vs cheetah and wild dogs) and time periods (Day, Crepuscular, Night).