FUNCTIONAL SIGNIFICANCE OF MIXED-SPECIES GROUPS FOR ZEBRA (*EQUUS QUAGGA*) IN SAVANNA HABITATS

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ABSTRACT

Globally, herbivore populations are facing decline, which threatens their crucial role within the ecosystems they inhabit. Herbivores are essential to ecosystem structure and function because they act as prey for higher trophic levels, cycle soil nutrients, and alter vegetation structure. Understanding the drivers that shape herbivore habitat use and selection are therefore critical for making informed conservation and management decisions. Like all prey species, herbivores must balance a trade-off between acquiring resources and avoiding predation which is influenced by a number of species-specific intrinsic traits and various ecological drivers. Herbivores can also track risk over space and time, and certain habitat structures and landscape features can influence risk perception; this is termed the landscape of fear. To mitigate the risk-reward trade-off, herbivores employ a suite of behavioural responses. Group formation is likely the most well-documented of these responses. However, grouping results in the information-competition trade-off, wherein group members may obtain valuable information regarding the location of resources and/or the risk of predation, but may suffer from increased competition, especially among larger group sizes. Mixed-species groups—an assemblage of two or more species in close spatial association—have the potential to mitigate some of the competitive costs of larger conspecific groups and enhance the anti-predator and/or foraging benefits of grouping. African savannas provide a particularly useful natural laboratory to study mixed-species groups, due to the high diversity of prey species and habitat heterogeneity present. Previous studies have investigated the mixed-species effect within these systems, but have yet to quantify some of the identity-dependent costs and benefits associated with mixed-species herding. Thus, the overall aim of my study was to quantify the functional significance of mixed-species groups for zebra (*Equus quagga*) herding with two of their most common herding partners, impala (*Aepyceros* *melampus*) and wildebeest (*Connochaetes taurinus*). My study was conducted at multiple spatial scales in the southern portion of the Kruger National Park, South Africa between 2021 and 2022. I found that mixed-species herding altered zebra landscape use, resulting in a quantifiable intensification of habitat use compared to when they herd with conspecifics. I did not observe significant habitat expansion for zebra in mixed-species herds compared to single-species herds, likely because the anti-predator benefits of mixed-species herding convey enhanced foraging opportunities in already-safe habitats. Zebra foraging with impala achieved greater foraging success and experienced lower levels of competition, compared to zebra foraging with wildebeest. However, compared to foraging with conspecifics, the levelled landscape of fear zebra experienced when foraging with wildebeest resulted in increased foraging success across the landscape. My findings highlight the context-dependency of the costs and benefits associated with different herding partners for zebra, and suggest that in mixed-species herds with wildebeest, zebra experience increased potential fitness benefits compared to herding with impala or conspecifics. Overall, the findings of my study suggest that mixed-species herding is an important tool in the suite of anti-predator behaviours employed by prey species, and one with significant implications for survivorship, habitat use, and ultimately, community level interactions.

PREFACE

Each chapter in this thesis is prepared as a stand-alone manuscript. A study site description is included in each data chapter. As such, some repetition is present because the broader topics discussed in each data chapter overlap as do some of the methodologies. The thesis is structured as follows:

CHAPTER 1: General introduction that reviews the existing literature and describes the rationale for my study.

CHAPTER 2: Data chapter that explores the drivers of single- and mixed-species herding for zebra, as well as potential spatial benefits of such behaviour.

CHAPTER 3: Data chapter that assesses the context dependency of the risk-reward trade-off associated with different herding partners for zebra in terms of their foraging and anti-predator behaviour.

CHAPTER 4: Synthesis chapter that ties together the findings and significance of the preceding data chapters and situates the contribution of my study within the current scientific perspectives of my research themes.

REFERENCES: An inclusive reference list for all chapters.

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CHAPTER 1: General Introduction

Herbivores play an essential role in ecosystem structure and function, by acting as prey for higher trophic levels and influencing the herbaceous layer by altering vegetation structure and cycling nutrients (Balfour et al., 2021; Pringle et al., 2011; Schmitz, 2008). However, their population sizes have been severely declining, placing their ecological roles in jeopardy (Dirzo et al., 2014; Ripple et al., 2017a). Approximately 60% of large terrestrial herbivores are listed as threatened, and 58% are experiencing population declines (Ripple et al., 2015; Ripple et al., 2017a). The decline in global herbivore numbers undoubtedly has far reaching ecosystem-level impacts, such as shifts in plant community structure and species abundance following a depression or extirpation of the native herbivore population (Dirzo et al., 2014; Young et al., 2013). Consequently, understanding the drivers shaping herbivore habitat selection and use are required to facilitate management interventions and inform conservation decisions over time (Doser et al., 2022; Palmer & Gross, 2018; Ripple et al., 2017b). Specifically, herbivores are impacted by various ecological drivers, including forage quantity and quality, water availability, predation risk, and landscape characteristics (Anderson et al., 2010; Cain et al., 2012; Dwinnell et al., 2019; Fryxell, 1991; Fryxell et al., 2005; Gaylard et al., 2003; Owen-Smith & Mills, 2006; Preisser et al., 2005; Senft et al., 1987; van Beest et al., 2010; Young et al., 2020). Optimal foraging theory, habitat selection theory, and the marginal value theorem suggest frameworks to understand the relative influence of different factors informing an animal's risk-reward trade-off (Bailey et al., 1996; Charnov, 1976; MacArthur & Pianka, 1966; Owen-Smith et al., 2010; Rosenzweig, 1981; Stephens & Krebs, 1986).

Group formation is one of the most commonly observed responses to the trade-off prey species face between meeting nutritional requirements and avoiding predation (Clark & Mangel, 1986; Krause & Ruxton, 2002). While there are anti-predator benefits associated with forming groups, group members further incur costs and benefits linked to the information-competition trade-off, with resultant potential impacts for fitness and survivorship (Ale & Brown, 2007; Caraco, 1979; Fryxell et al., 2007; Lima, 1987; Sansom et al., 2008; Watts, 1985). Frameworks investigating the drivers of animal community structure increasingly include one particular assemblage: the mixed-species group (Gil et al., 2017; Gil et al., 2018; Graves &

Gotelli, 1993; Harrison & Whitehouse, 2011); wherein a moving group of animals forms through interspecific attraction (Goodale et al., 2020). Mixed-species groups are one such assemblage that has been found to influence the behaviour of herd members, including anti-predator behaviours (Beaudrot et al., 2020; Kiffner et al., 2022; Schmitt et al., 2014), resource acquisition (Fryxell et al., 2005; Stears et al., 2020), and competition, with subsequent impacts for species survivorship (Goodale et al., 2020). Hence, the conservation of mixed-species groups can be considered crucial for biodiversity protection (Veit & Harrison, 2017; Zou et al., 2018) and wildlife management (Goodale et al., 2020; Odadi et al., 2009).

Foraging ecology

From a foraging perspective, herbivores must choose resources that vary in quantity and quality across the landscape (Marshal et al., 2011; Merkle et al., 2016; Senft et al., 1987). As a result, the choice of where herbivores decide to feed influences their nutritional intake (Ungar & Noy-Meir, 1988). Moreover, where a herbivore decides to feed will have implications for time budgets and nutrient gains (Langvatn & Hanley, 1993; Long et al., 2016). The marginal value theorem states that an optimally foraging individual is influenced by resources that are unevenly distributed in the landscape: concentrated in some areas and sparce in others (Charnov, 1976). Herbivores will further face energetic costs travelling to find resources (Charnov, 1976). Within the landscape, herbivores therefore make foraging decisions at different scales (Bailey et al., 1996; Senft et al., 1987). Across their home range, herbivores choose habitats to use for foraging, and within those areas, patches to utilise. Finally, a herbivore will select a feeding station from within its selected patch (Charnov, 1976; Fryxell et al., 2004). Foraging behaviour is further influenced by species-specific traits that impact energetic requirements (Fryxell, 1991). In an effort to meet such requirements, resultant herbivore behaviour is therefore influenced by a number of factors including feeding guild, gut and mouth morphology, body size, and competition (Ben-Shahar & Coe, 1992; Charnov, 1976; Owen-Smith et al., 2010).

Feeding guild and gut morphology

The feeding guild and gut morphology of herbivore species both play a role in dictating the type and quality of vegetation that different species require (Burkepile et al., 2013; Cromsigt et al., 2009; Makin et al., 2018). These two traits will further influence the diversity of habitats herbivore species use for foraging, which promotes resource partitioning and coexistence (Illius, 1997; McNaughton & Georgiadis, 2003). Burkepile et al. (2013) found grazing species to prefer habitats with a higher grass:woody cover ratio, while browsing species prefer the opposite. For instance, bulk grazing zebra (*Equus quagga*) and buffalo (*Syncerus caffer*) prefer habitats with high availability of long grass, and species such as wildebeest (*Connochaetes taurinus*) prefer habitats with short grass. Conversely, browsers such as kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis giraffa*) have been observed to select for areas with significantly higher woody vegetation cover (Burkepile et al., 2013). However, the nutritional content of grass and browse forage often varies seasonally, and thus, mixed-feeders are able to alter their intake of respective vegetation types accordingly (Codron et al., 2007; Codron et al., 2006; Van der Merwe & Marshal, 2012). As such, mixed-feeders are mostly grazers in the wet season, but switch their diet to a larger proportion of browse in the dry season, because this vegetation type retains more nutrients throughout the dry period (Abraham et al., 2019; Codron et al., 2007). Within a feeding guild, it is likely that coexisting species do not compete with one another because digestive physiology, mouth morphology, and/or body size influence preference for forage and diet quality (Arsenault & Owen-Smith, 2011; Bell, 1970; Demment & Van Soest, 1985; Hopcraft et al., 2012; Prins et al., 2006).

Dietary preferences based on feeding guilds are further modified by digestive physiology (Clauss et al., 2013; Illius, 1997). Ruminant species retain forage for an extended period to maximise nutrient extraction, and therefore often rely on higher quality forage (Illius, 1997; Mandinyenya et al., 2020). For instance, pelleted forage for domestic cattle (*Bos taurus*) resulted in decreased nutrient uptake, likely because the rate of passage of particles was too rapid to allow for the absorption of fibre (Martz & Belyea, 1986). Conversely, the digestive tract of hind-gut fermenters have a faster rate of passage for ingested material, allowing these species to sustain their nutritional intake requirements on larger quantities of lower quality forage (Steuer et al., 2011; Steuer et al., 2013). Mouth morphology further dictates dietary preferences (Arsenault & Owen-Smith, 2011; Pérez-Barbería & Gordon, 2001; Shipley, 2007). For instance, Arsenault and Owen-Smith (2008) found that mouth width, rather than body size alone, plays a key role in grass height selection among grazers in Hluhluwe-iMfolozi Park, South Africa. They found that the wide mouth and lip plucking technique of white rhinoceros

(*Ceratotherium simum*) allowed them to feed effectively from short grass (Arsenault & Owen-Smith, 2008). Conversely, they found that the narrow mouth of impala (*Aepyceros melampus*) allowed them to selectively forage from a range of grass heights (Arsenault & Owen-Smith, 2008).

Body size

Herbivore body size also plays a role in influencing both nutritional requirements and predation risk, with resultant impacts for herbivore behaviour (Demment & Van Soest, 1985; du Toit & Owen-Smith, 1989). Jarman and Sinclair (1979) observed a negative relationship between herbivore body size and diet selectivity, wherein larger bodied herbivores were able to subsist on larger proportions of lower quality forage in their diet. Conversely, small-bodied herbivores required high quality vegetation to meet their metabolic requirements (Jarman & Sinclair, 1979). This relationship has been linked to the increased metabolic rate of smaller bodied herbivores and the lack of large quantities of high quality vegetation for larger species (Clauss et al., 2013; du Toit & Owen-Smith, 1989; Illius & Gordon, 1987). Furthermore, body size has implications for predation risk, including susceptibility to different species of predators and escape tactics (Owen-Smith & Mills, 2008). Recent work suggests that predation can have a greater impact on small-bodied herbivores than larger ones (Radloff & du Toit, 2004). Similarly, among birds, Beauchamp (2023) observed a negative relationship between adult body mass and susceptibility to predation. As a result, body size, with its implications for predation risk, further influences prey species' foraging decisions across the landscape (Houston et al., 1993; Périquet et al., 2012; Radloff & du Toit, 2004).

Competition

Competition is one of the most significant costs of group living in animals and plays an influential role in herbivore foraging behaviour (Krause & Ruxton, 2002). The threat of competition among group-living animals can induce avoidance behaviour, social monitoring, and have resultant implications for survivorship (Beauchamp, 2008; Berger & Gese, 2007; Broekhuis et al., 2013; Ferry et al., 2016; Giraldeau & Beauchamp, 1999). Competition can be influenced by group size, potentially constraining the anti-predator benefits of larger groups (Appleby, 1980; Caraco, 1979; Clark & Mangel, 1986; Shi & Dunbar, 2006; Watts, 1985). For instance, Shi et al. (2010) demonstrated that movement rate, an indicator of foraging competition (Minderman et al., 2006; Sansom et al., 2008), increased with group size among feral goats (*Capra hircus*) on the Isle of Rùm, Scotland. Similarly, Watts (1985) observed a positive relationship between group size and competitive interactions among mountain gorillas (*Gorilla gorilla beringei*), particularly for females.

Competition between individuals can take the form of interference competition–whereby one species reduces the ability of another to make use of shared resources–either through its presence or agonistic interactions (Amarasekare, 2002; Cresswell, 1994; Ferry et al., 2016). For instance, Colman et al. (2012) observed that behavioural interference between reindeer (*Rangifer tarandus tarandus*) and sheep (*Ovis aries*) increased when the two species foraged in closer proximity to one another, resulting in displacement for foraging individuals. Alternatively, scramble competition occurs when a group of animals collectively deplete a shared resource, negatively influencing the foraging efficiency for the entire group (Beauchamp & Ruxton, 2003; Snaith & Chapman, 2008). For example, Lima et al. (1999) observed a negative relationship between ingestion and net intake under scramble competition, due to poor digestion of hastily eaten foods.

Individuals foraging in both single- and mixed-species herds may also participate in social monitoring, which is the act of watching herd mates to gain information about the location of resources, or to mitigate potential competition (Favreau et al., 2010; Giraldeau & Beauchamp, 1999; Kotier et al., 2010; Shrader et al., 2007). For example, Shrader et al. (2007) observed group-feeding goats balancing a trade-off between proactively maximising their intake rate to offset potential competition, and gleaning social information from their herd mates about the location of high-quality foraging patches. Overall, competition is likely to be greatest among single-species herds, because these groups lack the niche partitioning that is often present among mixed-species groups (Hopcraft et al., 2012; Kartzinel et al., 2015). For example, Sinclair (1985) found that Thompson's gazelle (*Eudorcas thomsonii*), topi (*Damaliscus lunatus jimela*), waterbuck (*Kobus ellipsiprymnus*), and warthog (*Phacochoerus africanus*) increased their spatial overlap with wildebeest habitat during the dry season, suggesting the lack of interspecific competition was driving these species to expand their use of vegetation types.

Predation

Predators alter the demography (van Buskirk & Yurewicz, 1998), population density (Sheriff et al., 2020), space-use (Zalewska et al., 2021), habitat selection (Creel & Christianson, 2008), and activity patterns (Lima & Bednekoff, 1999) of prey through lethal (i.e., consumptive) and non-lethal effects (i.e., perceived predation risk, landscape of fear; Brown, 1999; Gaynor et al., 2019; Laundré et al., 2001; Wirsing et al., 2021). Mortality of adults among a prey species can have cascading impacts on the population dynamics of large-bodied, long-lived mammals (Gaillard et al., 2003). However, ecosystem productivity, landscape characteristics, and the predator community itself can influence the strength of consumptive effects on the prey community within an ecosystem (Chamaillé-Jammes et al., 2019; Owen-Smith, 2019). Because terrain and habitat types vary across a landscape, the hunting success of different predators with disparate species-specific behavioural and morphological adaptations is also expected to differ (Laundré et al., 2010; Longland & Price, 1991). For example, lions (*Panthera leo*) have been shown to exhibit greater hunting success in areas with thicker woody vegetation, due to increased cover facilitating their ambush hunting techniques (Hopcraft et al., 2005; Schaller, 1972). This finding highlights the important role that habitat features (e.g., vegetation structure) play in structuring the relative strength of consumptive predation. In contrast, cursorial predators, such as spotted hyaena (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*), roam over large areas seeking out prey, and thus, the encounter risk for prey species remains fairly unpredictable (Makin et al., 2017). As a result, prey species-specific assessments of the proportion of safe and risky habitats likely further demonstrates why the relative strengths of predation and resources are variable in different ecosystems (Chamaillé-Jammes et al., 2019).

Even when predators are not in the immediate vicinity, the threat of predation induces fear in prey species (Brown et al., 1999). These impacts can be considered non-lethal (i.e., non-consumptive) effects of predation, which have far reaching consequences for herbivore resource acquisition, space use, and even fitness (Barry, 1994; Beaudrot et al., 2020; Brown, 1988, 1999; Burkepile et al., 2013; Creel et al., 2005; Gil et al., 2017; Preisser et al., 2005). The non-lethal, perceived effects of predation risk can have stronger effects on herbivore population dynamics than the consumptive effects of direct predation (Gaynor et al., 2019; Winnie & Creel, 2017), influencing species' behaviour, habitat selection, and diet (Creel & Christianson, 2008; Creel et al., 2017; Hopcraft et al., 2010; Lima & Dill, 1990). Even in the absence of an immediate threat, prey species maintain a baseline level of apprehension due to the constant possibility or risk of predation (Brown et al., 1999) and further modify their habitat use and behaviour in selected habitats as a result (Lima & Dill, 1990). For example, zebra in the Laikipia Plateau, Kenya were reported to spend less time on grazing and other activities in response to increased perceived predation risk associated with denser habitats (Chen et al., 2021).

The spatial variation in perceived predation risk has been classified as the "landscape of fear," which relates to certain habitat structures and landscape features that influence perceived risk (Laundré et al., 2001; Laundré et al., 2010; Laundré et al., 2014). The landscape of fear each species experiences is unique to their specific behavioural modes and susceptibility to predation (Gaynor et al., 2019; Hernández & Laundré, 2005; Stears et al., 2020). For instance, roe deer (*Capreolus capreolus*) often prefer open habitats because they offer increased escape opportunities from wolves (*Canis lupus*), while moose (*Alces alces*) typically occupy habitats with increased woody cover because these habitats likely reduce detection by predators (Gervasi et al., 2013). The landscape of fear represents the relative levels of perceived predation risk for prey across their home range or foraging grounds and influences prey species' habitat selection (i.e., when and where to feed) and their ability to meet their nutritional requirements (i.e., foraging selectivity, how to handle food, and the distance they are willing to travel to a feeding site; Lima & Dill, 1990). For example, while increased woody vegetation offers browse and can also influence the quality and quantity of the herbaceous layer available to grazing species (Treydte et al., 2007), Pays et al. (2012) observed elevated vigilance behaviour among impala foraging in denser vegetation compared to open habitats. The change in vigilance behaviour was found to be in response to increased perceived predation risk, which is likely associated with greater ambush opportunities for predators and decreased visibility for the impala (Pays et al., 2012; Riginos & Grace, 2008; Underwood, 1982).

Landscape features beyond vegetation structure can also influence the landscape of fear and resultant herbivore habitat selection (Hopcraft et al., 2005; Thaker et al., 2011; Valeix et al., 2010). At a broader scale, proximity to water sources and terrain characteristics further impact herbivore behaviour in response to perceived predation risk (Burger & Gochfeld, 1992; Crosmary et al., 2012; Dellinger et al., 2019; Valeix et al., 2008; Valeix et al., 2009a). For example, Valeix et al. (2009b) found that herbivores in Hwange National Park, Zimbabwe exhibited higher vigilance levels when drinking at waterholes. Vigilance levels of prey species seeking water was further elevated when the long-term risk of encountering lions was high, illustrating how the perceived risks associated with drinking are context dependent (Burger & Gochfeld, 1992; Burger, 2001; Périquet et al., 2012; Valeix et al., 2008). Responding to these areas with increased vigilance is likely a response that is not only associated with the fear of attack—because some predators, like lions, are known to ambush their prey at waterholes (Hopcraft et al., 2005; Schaller, 1972)—but is also associated with the limited options to avoid a potential attack at such sites (Périquet et al., 2010; Valeix et al., 2008). However, additional studies have found that vigilance at water sources decreases with increased group size, highlighting how behavioural adjustments can be made to mitigate the landscape of fear (Périquet et al., 2010).

Terrain characteristics can also increase the perceived risk of predation within an area. For example, Lingle (1993) found that mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*), while morphologically similar, have distinct running gaits suited to escaping pursuing predators in different types of terrain. Dellinger et al. (2019) found that the presence of wolves elicited increased use of sloped terrain by mule deer, presumably because mule deer's stotting gait was advantageous to avoiding predation over uneven ground. Similarly, Beaudrot et al. (2020) found that mixed-species herds were more likely to occur in areas near kopjies (e.g., a small, rocky outcrop), which can provide vantage points for potential predators (Hopcraft et al., 2005), highlighting an anti-predator response induced by landscape characteristics. Findings from these studies further suggest a landscape of fear, cued by physical characteristics of the landscape which results in spatial variation in anti-predator responses (Gaynor et al., 2019). Thus, herbivore species face trade-offs between acquiring resources and avoiding predation risks. These trade-offs reflect in their landscape and habitat use, as well as in their individual behaviour and social dynamics.

Prey response to predation risk

The effects of predation risk are dynamic and can be further modulated by anti-predator behaviour adopted by prey species (Anderson et al., 2010; Bednekoff & Lima, 1998; Brown, 1999; Caro, 2005; Creel et al., 2005; Fitzgibbon, 1990). When presented with the risk of predation, herbivores are known to participate in behaviours that can reduce their perceived or actual predation risk (Brown & Kotler, 2004; Illius & Fitzgibbon, 1994). Anti-predator behaviours include selection of specific habitat structure (Creel et al., 2005; Wirsing et al., 2007), increased vigilance (Makin et al., 2018; Périquet et al., 2012), decreased foraging time (Fortin et al., 2004a), changes in group size (Ale & Brown, 2007; Beauchamp, 2017), and changes in group composition (i.e., mixed-species groups; Stears et al., 2020). Together, these behaviours influence the ability of prey species to navigate multiple threats while fulfilling nutritional requirements (Hebblewhite & Merrill, 2009; Sih, 1992).

Habitat Selection

By selecting certain habitats, prey species are able to mitigate predation risk. For instance, Hebblewhite and Merrill (2009) found that non-migrant, resident elk (*Cervus elaphus*) populations in Banff National Park, Canada mediated wolf predation risk by using habitats closer to human activity, which were habitats that wolves avoided. Prey species are able to track and respond to long-term risk levels and can adjust their landscape use as risk levels vary across time and space (Chamaillé-Jammes et al., 2019; Courbin et al., 2019; Creel et al., 2005; Laundré et al., 2001). Zebra in Hwange National Park have been found to forage near waterholes during the day, but move away from these areas at sunset when the risk of encountering lions increases (Courbin et al., 2019). Similarly, roe deer change the way they use the landscape when the hunting season starts and they become more vulnerable to humans, by reducing their use of risky habitats and decreasing their distance to refuge habitat (Padié et al., 2015). Furthermore, some prey species increase their use of refuge habitats (i.e., areas that predators cannot easily access) when predators are nearby (Kauffman et al., 2007; Matter & Mannan, 2005). For example, Creel et al. (2005) demonstrated how elk in Yellowstone National Park, USA were able to manage their risk of predation by shifting to protective cover when wolves were in the vicinity.

By shifting habitat selection to areas deemed safer, herbivores may decrease their vulnerability to predation but could then suffer from reduced feeding efficiency (Barnier et al., 2014; Hebblewhite et al., 2005; van Beest et al., 2010). For example, Dwinnell et al. (2019) found that when mule deer attempted to avoid perceived risk by selecting safer habitats, they limited their use of the foodscape and reduced the total amount of forage available to them. Similarly, Wirsing et al. (2007) found that dugongs (*Dugong dugong*) allocate more time to safer habitats, with lower quality forage, when the likelihood of encountering predators is elevated. When wolves were reintroduced to Yellowstone National Park in 1995, after over 50 years of absence, elk altered their habitat use away from their preferred open habitats, which they likely assessed to be more dangerous, to more wooded habitats with protective cover (Creel et al., 2005). This switch resulted in a decrease in diet quality, along with a suspected decrease in survival rates during times of resource stress, highlighting the potential cascading effect that the landscape of fear can have on the nutritional status of herbivores (Creel et al., 2005). Furthermore, decreased browsing pressure from elk resulted in increased growth of cotton wood (*Populus deltoides*) trees, further emphasizing the cascading effects of predation risk at the community level (Hernández & Laundré, 2005).

Vigilance

Changes in vigilance behaviour can act as a metric of perceived risk and also as an anti-predator response (Chen et al., 2021; Creel et al., 2017; Hochman & Kotler, 2007; Lima, 1987; Makin et al., 2012; Valeix et al., 2009b). Previous studies have shown that when prey species are using riskier habitats, they respond with increased vigilance, altering the trade-off between foraging and safety (Creel et al., 2014; Smith & Cain, 2008). For instance, Hochman and Kotler (2007) found that Nubian ibex (*Capra nubiana*) switched from apprehension to vigilance as the distance to their refuge habitat increased. Heightened vigilance can limit foraging success and consequently impact species survival, population growth, and reproduction (Creel et al., 2007; Gaynor et al., 2019). For example, Creel et al. (2007) found that the costs of anti-predator behaviour indirectly have a negative impact on the reproductive physiology and demography of elk. Together, these findings suggest that prey species are likely behaviourally complex, and many rely heavily upon vigilance and gleaned social cues and signals to inform decisions regarding perceived predation risk (Dall et al., 2005;

Danchin et al., 2004). Further behavioural responses to predation risk, such as altering group size or group composition, can potentially enhance the effectiveness of vigilance as an anti-predator behaviour (i.e., increased detection) and/or mitigate possible costs of vigilance on other processes, including foraging (Cowlishaw et al., 2004; Dehn, 1990; Fortin et al., 2004a; Schmitt et al., 2014; Vine, 1971).

Group size

Changes in group size can allow herbivores to glean increased social information from their herding partners (Gil et al., 2017; Gil et al., 2018; Seppänen et al., 2007; Shrader et al., 2007). A common pattern that has been observed across taxa is that group size is negatively correlated with individual vigilance (Ale & Brown, 2007; Beauchamp & Ruxton, 2003; Creel et al., 2014; Lima, 1995). For example, Shi et al. (2010) found that feral goats were able to decrease their individual vigilance as group size increased. The decrease in individual vigilance associated with larger group sizes is a result of either (1) dilution of risk (Hamilton, 1971; Vine, 1971) or (2) greater rate of predator detection (Fairbanks & Dobson, 2007; Pulliam, 1973; Stensland et al., 2003). Reduced risk resulting from the mechanism of dilution occurs when a predator can only attack one individual in a herd at a time, thus, the probability of any given individual being selected decreases as the total number of available prey increases (Foster & Treherne, 1981). Dehn (1990) found that for elk, dilution was the main benefit associated with larger group sizes, illustrating that an individual can enhance its chance of survival merely by being part of a group.

Reduced risk from the mechanism of detection, which can also be referred to as “the many eyes effect,” occurs because an increase in herd size corresponds to an increased number of individuals seeking out potential threats (Lazarus, 1979; Lima, 1995). Specifically, animals in a group engaging in low levels of vigilance can have the same probability of detecting a threat as a highly vigilant lone animal (Kenward, 1978; Pulliam, 1973). For example, Kenward (1978) and Lazarus (1979) demonstrated that larger groups of birds detected attacks from predators sooner than smaller groups, supporting the assumption that as long as one member detects an attack, all group members will benefit. However, despite the potential safety benefits of grouping, multiple studies have shown that larger group sizes can lead to increased competition among group members (Beauchamp, 2001; Beauchamp & Ruxton, 2003; Rind & Phillips, 1999; Snaith & Chapman, 2008; Watts, 1985). Bednekoff and Lima (2004) demonstrated in their models of competition that as group size increases, intake rate decreased, even if feeding effort increased. Thus, there is likely a threshold at which the competitive costs among a larger group of foragers outweigh any anti-predator benefit. As such, prey species may need to utilize alternate behavioural adjustments to mitigate the perceived risk of predation.

Group composition

While group size, dilution, and detection benefits of a single-species herd have been demonstrated in the literature (Bednekoff & Lima, 1998; Hebblewhite & Pletscher, 2002; Pays et al., 2012; Pulliam, 1973), an advantage of the diverse herbivore guild found in African savanna habitats is the potential to form mixed-species groups. Mixed-species groups are an additional anti-predator defence used commonly in a variety of taxa, including birds (e.g., Darrah & Smith, 2013; Farine et al., 2014; Gentry et al., 2019; Graves & Gotelli, 1993; Harrison & Whitehouse, 2011; Zou et al., 2018) and mammals (e.g., Beaudrot et al., 2020; Fitzgibbon, 1990; Gil et al., 2017; Kiffner et al., 2014; Pays et al., 2014; Schmitt et al., 2016; Stears et al., 2020). Because species can vary in their ability to detect and process information from their environment, the potential benefits of dilution and detection could be magnified in a mixed-species herd (Goodale et al., 2019; Scheel, 1993; Underwood, 1982). Heterospecific herd mates can either act as diluting partners (i.e., sharing a common predator) or as low-diluting partners, wherein heterospecific herd mates may not share common predators (Leuthold, 1977; Metcalfe, 1984; Schmitt et al., 2014).

Moreover, certain species may receive heightened benefits from the quality of social information offered by their heterospecific herd mate, rather than solely relying on the quantity of heterospecific herd mates as an anti-predator benefit (Gil et al., 2017; Seppänen et al., 2007; Stears et al., 2020). For example, Schmitt et al. (2014) found that zebra herding with wildebeest in smaller herds were half as vigilant compared to those in single-species herds of the same size. However, zebra herding with impala needed to be in a herd made up of at least 75% impala before they received the same benefit (Schmitt et al., 2014). These findings suggests that zebra receive benefits of dissimilar quality from different species of heterospecific herd mate, likely because lions are a common predator for both zebra and wildebeest, and therefore, wildebeest act as both a diluting partner and threat detector. Conversely, impala are not a common prey item for lions, but do have a number of other predators (Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006). Additionally, previous studies have shown that zebra, among other ungulates, respond to impala alarm calls with less intensity than the alarms of other species, most likely because they do not share a common predator (Meise et al., 2020; Palmer & Gross, 2018). Thus, impala likely benefit zebra with some amount of detection, but are less likely to offer the benefit of dilution. Regardless of the specific driver of decreased individual vigilance in mixed-species groups, individuals are likely able to devote more time to other activities, potentially allowing them to intensify their use of a specific area (Fitzgibbon, 1990; Goodale et al., 2020; Kluever et al., 2009; Rodewald & Brittingham, 2002; Stears et al., 2020; Stensland et al., 2003). For example, Stears et al. (2020) demonstrated that zebra foraging in mixed-species herds under low levels of predation risk decreased their investment in costly vigilance (i.e., ears focused, ceased chewing, interrupting the ingestion process) by 60%, thus allowing greater time allocation for foraging. Similarly, Rodewald and Brittingham (2002) suggest that joining mixed-species flocks allows migrant bird species to decrease their predation risk and simultaneously increase their foraging efficiency in habitats with high vegetation heterogeneity.

An increase in threat detection and/or dilution offered by mixed-species groups has the potential to also allow individual species access to parts of the landscape previously deemed to be too risky (Darrah & Smith, 2013; Gentry et al., 2019; Zou et al., 2011). Risky habitats can be valuable for foraging species because these areas generally have higher food availability due to lower overall use, compared to safer habitats (Riginos & Grace, 2008; Thaker et al., 2011; Treydte et al., 2007; Valeix et al., 2009a). Furthermore, because different species of herbivores may exhibit niche partitioning, herding with heterospecifics can mitigate some of the potential competition costs associated with herding with larger groups of conspecifics (Beaudrot et al., 2020; Gwynne & Bell, 1968), and could offer opportunities for increased foraging success (Ale & Brown, 2007; Pays et al., 2007). For example, Beaudrot et al. (2020) observed an increased likelihood of mixed-species herds, including zebra and wildebeest herds, occurring in habitats with increased perceived predation risk. Furthermore, Stears et al. (2020) observed that compared to single-species herds, zebra in mixed-species herds were able to decrease their vigilance and therefore invest more time towards foraging. Thus, the combined findings of these two studies highlight the anti-predator benefits of forming mixed-species groups, while also suggesting the formation of these groups increases members' ability to access risky, yet potentially valuable areas in the landscape (Ludwig et al., 2004; Riginos & Grace, 2008; Treydte et al., 2007). However, because of the range of anti-predator behaviour prey species can take advantage of, individual species responses to risk are not uniform and vary intrinsically, based on interspecific disparities in body size, gut morphology, feeling guild, and the threat of potential competition.

Foraging under predation risk: the risk-reward trade-off

Herbivores occupy heterogenous habitat types with spatiotemporal variations in food availability and predation risk (Gallagher et al., 2017; Riginos & Grace, 2008). Optimal foraging theory provides a theoretical framework to understand foraging behaviour among herbivores, suggesting that they should forage in areas that maximise their energy gain per unit time (Bailey et al., 1998; Brown et al., 1999; Charnov, 1976; MacArthur & Pianka, 1966; Stephens & Krebs, 1986). Additionally, habitat selection theory assumes that herbivore habitat selection is driven by forage quality and availability, along with water availability (Rosenzweig, 1981). Increasingly, prey avoidance behaviours—and their resultant impact on foraging behaviour and habitat selection—have been recognized to be context-dependent (Riginos, 2015; Ripple & Beschta, 2006). Consequently, herbivores face trade-offs between forage acquisition and minimizing the risk of predation (Hebblewhite et al., 2005; Makin et al., 2012; Moe et al., 2007; Riginos, 2015).

Several recent studies have shown that herbivores spatially avoid habitats where the likelihood of encountering a predator is high (Thaker et al., 2011; Valeix et al., 2009a). To maintain their energetic requirements, herbivores are impacted by their environment, as well as the lethal and non-lethal effects of predation (Brown, 1988; Brown et al., 1999; Brown, 1999; Brown & Kotler, 2004; Gaynor et al., 2019; McArthur et al., 2012; Wirsing et al., 2021). Anti-predator behaviours are innate and likely impact where, and with what intensity, herbivores forage (Caro, 2005). Optimal foraging (MacArthur & Pianka, 1966; Owen-Smith et al., 2010) and habitat selection (Rosenzweig, 1981) theories dictate that to maximise their energetic demands, herbivores face constant trade-offs between acquiring resources and avoiding risks attributed to predators (Mitchell & Powell, 2012). Apart from risks which impact the survival of herbivores through direct and indirect predation (Gaynor et al., 2019), forage quantity and quality, and water availability regulate herbivores through resource restrictions from lower trophic levels (Turkington, 2009). For example, Sitati et al. (2014) observed significant decreases in forage and water availability, attributed to prolonged drought, driving substantial declines in the wildebeest population in Kenya and Tanzania.

At the landscape scale, the safest habitats may provide the greatest resource quality and availability. However, this is unlikely because forage in safe areas is likely to be depleted first, driving herbivores to trade-off safety to meet their nutritional requirements (Chamaillé-Jammes et al., 2019). Stears and Shrader (2015) observed that oribi (*Ourebia ourebi*) increased their risk-taking behaviour to access habitats with increased food availability. According to the ‘leap-frogging’ predator strategy, predators are more likely to occupy habitats with a higher abundance of resources because these are likely to attract a greater number of potential prey species (Sih, 2005). Because habitats with higher resource availability are often associated with a greater risk of predation (i.e., perceived or actual), foraging in these habitat types likely impacts prey responses as a result (Riginos & Grace, 2008). At the individual level, the decision to engage in anti-predator behaviour (e.g., vigilance) in areas associated with a greater risk of predation has further implications for foraging success (Brown, 1999; Fortin et al., 2004a; Laundré et al., 2001). For example, Creel et al. (2014) found a 38% reduction in foraging success for impala foraging in the presence of a predator. Optimal foraging theory further predicts that herbivores will sacrifice feeding behaviour in response to increased perceived predation risk (Bailey et al., 1998; Charnov, 1976; MacArthur & Pianka, 1966; Stephens & Krebs, 1986). They do so by either (a) reducing their time dedicated to foraging, or (b) increasing their level of vigilance (Brown et al., 1999); however, the strength of this response is also dependent on the quality or quantity of food (Le Saout et al., 2015).

The availability and quality of food, as well as differences in perceived predation risk result in non-uniform habitat use for herbivores foraging in the landscape, with certain areas being preferred over others (Butler et al., 2005; Hannon et al., 2006). Whether a herbivore forages in a certain patch is ultimately determined by its potential foraging efficiency in that area (Langvatn & Hanley, 1993; Morrison et al., 2021), in addition to the perceived predation risk (Creel et al., 2005). For example, Pays et al. (2012) observed an interaction between grass height and foraging patch enrichment affecting vigilance among impala in Hwange National Park, suggesting that forage quality was the main driver in habitats with improved visibility, and risk of predation was the main driver in dense habitats with lower visibility. Furthermore, Martin and Owen-Smith (2016) observed that unlike zebra, wildebeest were less likely to flee an open, resource-rich patch after an encounter with lions, likely owing to their restricted habitat preferences compared to zebra. Thus, herbivore foraging behaviour and habitat selection have critical implications within a foraging system because they play a role in both determining the nutrient intake of herbivores (Prache et al., 1998), and because they can have implications for energy transfer in the food chain (Fortin et al., 2004a).

Motivation and aims

Focal species

My study focussed on zebra, impala, and wildebeest herding patterns and the resultant foraging and anti-predator behaviours of zebra during the dry season within Kruger National Park (KNP), South Africa in the Skukuza and Pretoriuskop sections. Zebra are a medium-sized ungulate common throughout the savanna regions of southern and east Africa (Estes, 2012). Zebra are non-territorial, gregarious herbivores with a nonruminant (i.e., hind-gut fermenter) digestive physiology (Estes, 2012; Illius, 1997). Like all prey species, zebra face a trade-off between maximising resource acquisition and minimizing predation risk, resulting in a landscape of fear influencing their habitat use, foraging behaviour, and anti-predator responses (Courbin et al., 2016; Groom & Harris, 2010; Mandinyenya et al., 2020; Rubenstein, 2010; Stears et al., 2020; Thaker et al., 2011; Valeix et al., 2009b). Behavioural time allocation for zebra has been found to be the result of both intrinsic and extrinsic factors (Seeber et al., 2019). Zebra have been shown to increase their vigilance in response to increased woody cover (Chen et al., 2021), as well as temporally avoid habitats with heightened risk (Courbin et al., 2019). Thaker et al. (2010) demonstrated that female zebra avoided resource-rich open scrub habitat in Karongwe Game Reserve, adjacent to the KNP, which could result in significant energetic costs in areas where resources are limited. Zebra frequently form mixed-species herds to gain increased information regarding potential predation (Kiffner et al., 2014; Schmitt et al., 2014; Schmitt et al., 2016). For example, Schmitt et al. (2016) found that zebra were able to decrease their perceived predation risk when herding with giraffe by gleaning social cues.

Previous studies have often found zebra in mixed-species herds and have noted that zebra may form the nucleus of such a group, possibly because their phenotypic appearance might visually cue other herbivores to facilitate a mixed-species group (Ireland & Ruxton, 2017; Kiffner et al., 2014). Zebra are often found grazing in association with the ruminant wildebeest (Bodenstein et al., 2000). van Hoven (1996) classified wildebeest as a short grass feeder and zebra as a tall grass feeder, however, because both are grazing species, the potential for competition remains, most notably because zebra and wildebeest have been found to utilize several of the same grass species (Ben-Shahar & Coe, 1992; Bodenstein et al., 2000). Zebra and wildebeest share lions as a common predator, indicating that associations of these species would benefit both herd mates with increased dilution and detection (Dehn, 1990; Hayward & Kerley, 2005; Schmitt et al., 2014). Alternatively, the ruminant impala is another species zebra with which are frequently associated (Pays et al., 2014; Schmitt et al., 2014). Impala are mixed-feeders and switch between graze and browse vegetation seasonally, suggesting that competition should be limited between these two species (Demment & Van Soest, 1985; Hopcraft et al., 2010; Skinner & Chimimba, 2005). However, unlike zebra and wildebeest, impala are not a preferred prey item for lions, thus impala likely act only as a low-diluting partner for zebra (Hayward & Kerley, 2005; Schmitt et al., 2014). As such, it is likely that zebra are subject to differing degrees of costs and benefits in mixed-species herds, depending upon the identity of their herd mate.

Motivation for this study

Previous studies have tested the mixed-species effect in herbivores and have illustrated that the formation of mixed-species groups can alter their space use (Fitzgibbon, 1990; Kiffner et al., 2014; Pays et al., 2012; Pays et al., 2014). However, the spatial benefit, as well as the source of the benefit (i.e., intensification of use of a certain area, or expansion into previously unused habitat), has yet to be quantified. Furthermore, numerous investigations have sought to disentangle the influence of social information, competition, and predation risk on perceived risk, grouping behaviour, and foraging behaviour, as well as how these behaviours play a role in the larger trade-off that exists between resource acquisition and perceived predation risk (e.g., Abramsky et al., 2001; Amarasekare, 2002; Beauchamp & Ruxton, 2003; Beaudrot et al., 2020; Bednekoff & Lima, 2004; Favreau et al., 2010; Ferry et al., 2016; Gil et al., 2017; Hopcraft et al., 2014; Minderman et al., 2006; Pays et al., 2007; Schmitt et al., 2014; Stears et al., 2020). However, there remains a gap in the literature examining how the influence of mixed-species herds on zebra anti-predator behaviour, and resultant foraging behaviour, might differ between the individual and landscape scale. Acknowledging the drivers of mixed-species herding and how these factors impact herbivore foraging and anti-predator behaviours, as well as understanding their resultant influence on species distributions and habitat selection, is of critical importance to understand how the formation of mixed-species groups could benefit herding species. Furthermore, because herbivores possess species-specific traits that influence their perception of the landscape of fear, resultant behaviours, and habitat use (Gaynor et al., 2019; Laundré et al., 2010; Riginos, 2015; Stears et al., 2020), it is plausible that the benefits of forming mixed-species herds may vary with different herding partners.

Overall, my study sought to understand the functional significance of mixed-species herding using zebra as a focal species. I aimed to disentangle the relative importance of various drivers on the occurrence of zebra in single- and mixed-species herds across the landscape. Additionally, I sought to quantify potential spatial benefits for zebra herding in mixed-species groups. Moreover, I aimed to examine potential differences in foraging and anti-predator behaviour among zebra in single-species herds and with either of their to common heterospecific herd mates—wildebeest and impala. I further sought to quantify anti-predator behaviour and foraging success among zebra foraging in these herd types across varying degrees of perceived predation risk present in the landscape.

CHAPTER 2: Environmental and behavioural drivers of single- and mixed-species herding of zebra and the spatial benefits of different herding partners

INTRODUCTION

Animals spend their lives navigating landscapes with heterogenous habitat types and variable levels of predation risk and food availability (Gallagher et al., 2017; Martin et al., 2015; Owen-Smith, 2019; Riginos & Grace, 2008). In general, herbivores choose patches that will allow them to meet their daily energy intake requirements while minimizing the risk of predation, thereby striking a balance between resource (i.e., forage and water) acquisition and perceived predation risk (Hebblewhite et al., 2005; Makin et al., 2012; Riginos, 2015). The landscape of fear therefore represents the relative levels of predation risk perceived by prey across their foraging grounds or home range (Laundré et al., 2001). By gleaning information from their environment, as well as social information about the presence or location of predators from herd mates—whether it be from conspecifics or heterospecifics—prey species can mitigate their perception of risk, thus influencing their landscape of fear (Goodale et al., 2019; Stears et al., 2020). Understanding the relationship between herbivore habitat use and the landscape of fear is of critical importance due to the cascading effect of predator-prey relationships within ecosystems and the resultant impact of this relationship on biodiversity and species coexistence (Paulo Breviglieri et al., 2017; Pringle et al., 2019).

As terrain and habitat type vary across a landscape, so does the hunting success of predators, based on their different adaptations (Laundré et al., 2010; Longland & Price, 1991). For example, Schmitt et al. (2022) illustrated that increased woody cover is positively correlated with increased perceived predation risk, likely due to greater ambush opportunities for predators and decreased visibility for prey species (Underwood, 1982). In addition to providing browse, woody vegetation cover also influences the quality and quantity of the herbaceous layer available to grazing species (Treydte et al., 2007). Proximity to water and the act of drinking further influences the landscape of fear (Crosmary et al., 2012; Périquet et al., 2010; Valeix et al., 2009a). Valeix et al. (2009b) found that herbivores exhibited higher vigilance levels at waterholes and spent more time assessing water to drink when the long-term risk of encountering lions (*Panthera leo*) was high.

Common herbivores in African savannas not only vary with respect to body size, but also with respect to their digestive physiology (i.e., ruminants and hind-gut fermenters) and the feeding guild to which they belong (i.e., grazers, browsers, and mixed-feeders). While body size plays a role in dictating predation risk, both gut morphology and feeding guild influence the type and quality of vegetation each species requires, as well as the diversity of habitats they use (Burkepile et al., 2013; Burkepile et al., 2016; Cromsigt et al., 2009; du Toit & Owen-Smith, 1989; Isaacs et al., 2013; Makin et al., 2018). Moreover, perceived predation risk can have stronger impacts on herbivore population dynamics than actual predation risks, further influencing species' behaviour and habitat selection (Creel et al., 2007; Gaynor et al., 2019; Winnie & Creel, 2017). Thus, because of the diversity of traits associated with species that typically occupy an African savanna system, the risk-reward trade off within the landscape of fear is likely to be species specific (Burkepile et al., 2016; Cromsigt et al., 2009).

The landscape of fear is dynamic and can be further modulated by anti-predator behaviour adopted by prey species. When presented with the risk of predation, many herbivores will participate in behaviour to reduce their perceived or actual risk (i.e., anti-predator behaviours; Brown & Kotler, 2004; Illius & Fitzgibbon, 1994). Anti-predator behaviours include selection of specific habitat structure (Creel & Winnie, 2005; Wirsing et al., 2007), increased vigilance (Makin et al., 2018; Périquet et al., 2012), decreased foraging time (Fortin et al., 2004a), changes in group size (Ale & Brown, 2007; Beauchamp, 2017), and changes in group composition (i.e., mixed-species groups; Stears et al., 2020). By selecting certain habitats, herbivores can lower their perceived risk but may also decrease the forage available to them, as forage quality and forage quantity are often inversely correlated (Hebblewhite et al., 2002; Riginos & Grace, 2008; van Beest et al., 2010). Increased vigilance can also limit foraging success and consequently impact species survival, population growth, and reproduction (Creel et al., 2007; Gaynor et al., 2019). Group size influences both dilution and detection, potentially allowing herbivores to navigate the landscape of fear by increasing the social information available to the herd (Fairbanks & Dobson, 2007; Gil et al., 2017; Hamilton, 1971; Pulliam, 1973; Stensland et al., 2003; Vine, 1971).

While group size could be increased by herding with a larger number of conspecifics, an advantage of the diverse herbivore guild found in savanna habitats is the potential to form mixed-species groups. Mixed-species groups are an additional anti-predator defence used commonly in a variety of taxa (e.g., Carlson et al., 2023; Darrah & Smith, 2013; Fitzgibbon, 1990; Pays et al., 2014; Schmitt et al., 2014; Schmitt et al., 2016; Stears et al., 2020). While mixed-species groups comprising species of the same trophic level can be associated with similar costs and benefits as that of a single-species group (Kiffner et al., 2014; Pays et al., 2014), they can potentially offer benefits beyond those of a single-species group in two ways (Kiffner et al., 2014). First, because different species of herbivores may exhibit niche partitioning, herding with heterospecifics can mitigate some of the potential competition costs associated with herding with larger groups of conspecifics (Beaudrot et al., 2020; Gwynne & Bell, 1968). Second, because species could vary in their ability to detect predators and process information from their environment, mixed-species groups might facilitate increased predator detection and ultimately, provide opportunities for increased foraging success (Beaudrot et al., 2020; Fitzgibbon, 1990; Schmitt et al., 2016).

An increase in threat detection offered by mixed-species groups has the potential to allow individual species access to parts of the landscape previously deemed to be too risky (Cords, 1987; Darrah & Smith, 2013; Zou et al., 2011). Areas associated with higher risk can often have greater resource availability due to lower overall use (Riginos & Grace, 2008; Thaker et al., 2011; Treydte et al., 2007). Thus, expansion into riskier habitats can be a valuable opportunity for herbivores during the dry season when resources are limited. Habitat expansion as a benefit of forming mixed-species groups has been documented among birds (e.g., Darrah & Smith, 2013; Hogstad, 1978; Zou et al., 2011) and primates (e.g., Cords, 1987; Heymann & Buchanan-Smith, 2000), however, it has yet to be quantified among savanna herbivores. Alternatively, if the formation of mixed-species groups allows individuals to decrease their investment in vigilance, group members can devote more time to other activities, such as foraging (Pays et al., 2014; Stears et al., 2020), potentially allowing them to intensify their use of a specific area. For instance, the habitat intensification advantages of mixed-species groups for zebra (*Equus quagga*) have been evidenced by the work of Stears et al. (2020), who studied zebra occurring in game reserves of either high- or low-risk (i.e., dependent upon the predator guild). Their findings demonstrate that by forming mixed-species groups, zebra in high-risk landscapes were able to achieve vigilance levels equivalent to zebra living in single-species herds in low-risk landscapes. Stears et al. (2020) then modelled the foraging implications of this lowered level of vigilance using average zebra intake rates published in the literature. Their model suggested that zebra in mixed-species herds were able to forage more intensely: in high-risk habitats, zebra in mixed-species herds could achieve the same number of bites 51 minutes faster than zebra in single-species herds (Stears et al., 2020). Thus, the levelling of the landscape of fear zebra experienced by forming mixed-species groups suggests that they could potentially take advantage of riskier areas in a landscape and even expand into previously unused habitats.

It is further possible that the spatial benefits of mixed-species herding might be dependent upon the identity of the heterospecific herd mate. Zebra frequently herd with both impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) in African savannas (Bodenstein et al., 2000; Pays et al., 2014; Schmitt et al., 2014). Wildebeest and zebra are common prey species for lions (Hayward & Kerley, 2005), resulting in anti-predator benefits to both species when herding together (Schmitt et al., 2014). Schmitt et al. (2014) found that while zebra in mixed-species herds overall exhibited lower vigilance than zebra herding with conspecifics, zebra herding with wildebeest had significantly lower vigilance levels than their counterparts herding with impala. Their findings suggest that impala may not offer the same anti-predator benefits to zebra as wildebeest could, potentially because impala are not a common prey item for lions (Hayward & Kerley, 2005). Further, because impala are vulnerable to a larger proportion of the predator community, their alarm calls induced a weaker response among zebra than the alarm calls of wildebeest, suggesting that their potential benefit to zebra as a herd mate in terms of predator detection was less than that of wildebeest (Palmer & Gross, 2018). As a result, herding with wildebeest, rather than impala, might offer zebra a greater opportunity to intensify their habitat use, due to their shared predator. However, because wildebeest generally prefer more open habitats, zebra forming mixed-species herds with wildebeest may be unlikely to achieve the benefit of habitat expansion (Owen-Smith & Martin, 2015; Owen-Smith et al., 2015; Yoganand & Owen-Smith, 2014). Because impala are mixed-feeders, they often increase their browse intake in the dry season, making them potentially less likely to be a source of forage competition for zebra (Codron et al., 2007; Codron et al., 2006; Gwynne & Bell, 1968). Thus, impalas' preference for browse during this period (Abraham et al., 2019; Codron et al., 2007) might also enable zebra to access areas of the landscape in greater food quality and availability, associated with increased woody cover

(Ludwig et al., 2004; Riginos & Grace, 2008; Treydte et al., 2007). As a result, herding with impala, rather than wildebeest, could provide zebra with the benefit of habitat expansion.

A number of previous studies have sought to understand the mixed-species effect and illustrate that the formation of mixed-species groups can alter prey species space use (e.g., Beaudrot et al., 2020; Darrah & Smith, 2013; Farine et al., 2014; Fitzgibbon, 1990; Kiffner et al., 2014; Pays et al., 2014; Schmitt et al., 2014; Schmitt et al., 2016; Stears et al., 2020; Zou et al., 2011). However, the spatial benefit (i.e., potential increase in useable habitat) associated with forming mixed-species groups has yet to be quantified among mammalian herbivores. Furthermore, previous studies do not differentiate between whether the spatial benefit is a result of either increased use of existing habitats (i.e., intensification) or expansion into previously unused areas, when compared with herbivores in single-species herds. Acknowledging the distinction between intensification and expansion as a spatial benefit of mixed-species herding is critical to understanding how mixed-species groups can benefit herding species, as well as influence their distributions and habitat selection. Furthermore, because different herbivore species each possess species-specific traits that influence their habitat use (e.g., Hochman & Kotler, 2007; Martin & Owen-Smith, 2016), foraging behaviour (e.g., Pays et al., 2012; Senft et al., 1987; Smith & Cain, 2008), and susceptibility to predation (e.g., Owen-Smith & Mills, 2008; Radloff & du Toit, 2004), the spatial benefits of forming mixed-species groups has the potential to vary with different herding partners.

The aim of this chapter was to disentangle the relative importance of various drivers for the occurrence of zebra in single- and mixed-species herds, as well as to examine the potential spatial benefits for zebra herding with heterospecifics. To address this, I used two vegetation variables; normalised difference vegetation index (NDVI) and percent woody cover; and two topographical variables; distance to rivers and distance to drainage lines; along with perceived predation risk of zebra. These variables have been hypothesized to influence species' resource acquisition, perceived predation risk, and resultant spatial distribution (Burkepile et al., 2013; Chen et al., 2021; Courbin et al., 2019; Groom & Harris, 2010; Owen-Smith & Traill, 2017; Owen-Smith, 2019; Valeix et al., 2009a). Using the aforementioned variables as covariates, I used maximum entropy models (Maxent) to predict zebra occurrence with the following herd mates: (1) conspecifics, (2) impala, and (3) wildebeest.

Further, I used the resultant predictions for each herd type to determine the spatial benefit for zebra in mixed-species herds and quantified this benefit as either an intensification of use or expansion into previously unused habitats. I hypothesized that (1) the predicted occurrence of zebra in single-species herds would be highest in the safest environments (i.e., areas with low perceived risk). Additionally, I hypothesized that (2) the predicted occurrence for zebra in mixed-species herds would be higher than that of zebra in single-species herds in riskier areas (i.e., areas with high perceived risk). Finally, I predicted that (3) forming mixed-species herds would offer a spatial benefit to zebra, because heterospecifics may allow access into previously unused parts of the landscape, due to increased threat detection offered by mixed-species herds. Linked to this final prediction, I also predicted that (3a) impala would provide zebra the greatest opportunity of expansion into unused habitats because they are mixed-feeders and occupy a range of habitats (Bonyongo, 2005; Codron et al., 2007; Demment & Van Soest, 1985; Moe et al., 2014). Alternatively, (3b) because impala are consumed by a larger range of predators and do not share a primary predator with zebra (Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006), they might not provide much opportunity for zebra to decrease their vigilance, thus, herding with impala may provide no spatial benefit to zebra. Additionally, I predicted that (3c) wildebeest would likely provide the best intensification benefit to zebra in shared habitats because zebra have been shown to reduce vigilance in the presence of wildebeest (Schmitt et al., 2014; Stears et al., 2020). However, as a herding partner, (3d) wildebeest likely would not provide a large expansion benefit to zebra because they prefer more open habitats (Owen-Smith & Martin, 2015; Owen-Smith et al., 2015; Yoganand & Owen-Smith, 2014).

METHODS

Study site

The Kruger National Park (KNP) covers approximately 20000km^2 in the north-eastern corner of South Africa, bordering both Zimbabwe to the north and Mozambique to the east. The park is home to more than 1900 species of trees, shrubs, forbs, and grasses, and supports 147 mammal species (SANParks, 2019a, 2019b). Data were collected in the low-lying savanna regions of the Skukuza and Pretoriuskop sections of southern KNP (centred at 25˚3’27” S, 31˚25’8” E; Figure 2.1) from a study area covering approximately 50km^2.

The climate of this area is classified as semi-arid subtropical and receives 500-700 mm p.a. of rainfall. Climatic conditions vary from warm, dry winters (i.e., May to September) and hot, wet summers (i.e., October to April), with most of the rainfall occurring in January (Kruger et al., 2002; Scholes et al., 2001). Data were collected during the winter months (i.e., June to August 2021, July to September 2022) due to increased visibility to accurately observe the focal species (Scholtz et al., 2014). The dry season has an average maximum temperature of 26˚ Celsius (i.e., June) and an average minimum temperature of 17˚ Celsius (i.e., August; Kruger et al., 2002).

The vegetation of this region of KNP is classified as a mixed *Combretum* savanna woodland, with the dominant trees in the deep, sandy soils of the region being *Combretum sericea* and species belonging to the *Terminalia* genera. The more shallow-soiled, steeper slopes are dominated by *Sclerocarya birrea* and species belonging to the *Albizia* and *Vachellia* genera (Gertenbach, 1983).

The geology underlying the site is Archaean granite and gneiss of the Nelspruit suite (Barton et al., 1986). These features give rise to a characteristically undulating landscape, with drainage lines approximately 3 kilometres apart (Scholes et al., 2001). Soils in this region are dominated by Hutton and Clovelly forms, with Glenrosa forms on the steeper slopes (Gertenbach, 1983).

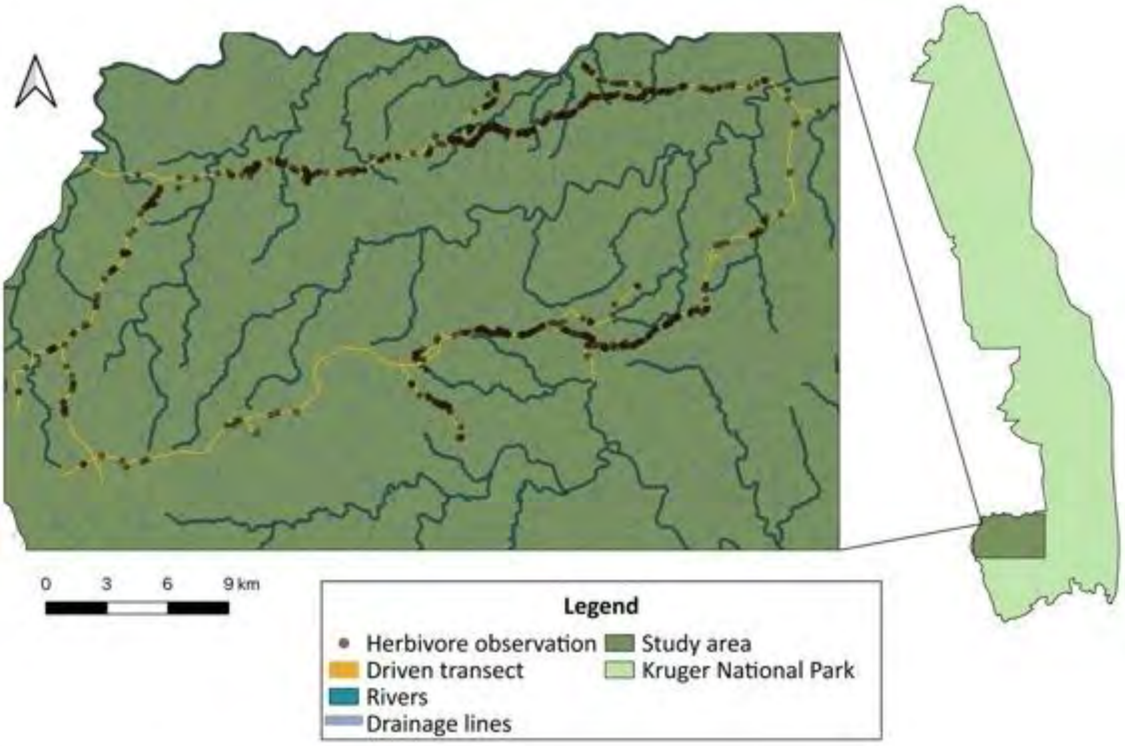

Figure 2.1: Map of Kruger National Park (KNP) and the study area, showing the driving transect route (yellow line) and herbivore observations (black dots).

Field Methods

Species herding observations

I selected impala and wildebeest as focal, herding partner species of zebra, based on their abundances in the landscape (Chirima et al., 2012; du Toit, 2003) and propensity to form mixed-species herds with one another (Schmitt et al., 2014; Schmitt et al., 2016). An approximately 50 kilometre driving transect was identified between the Skukuza and Pretoriuskop sections of KNP. For a three month period, covering the dry season from June-August 2021 and July- September 2022, the route was surveyed twice a day, in the morning and afternoon hours. Morning transects were driven between 8:00am and 11:00am, and afternoon transects between 3:00pm and 6:00pm. Different routes were driven in the morning and afternoon each day. Every second day, the driven direction of the transect was reversed (i.e., driven north to south, then south to north the following day) in an effort to sample different parts of the route at all times of day. All observations occurred from a stationary vehicle using binoculars (Carson 3D Series, TD-042ED, 10x42mm). Observations were within 150m of the road; greater distances increased the potential for inaccurate species counts due to decreased visibility.

Each encounter with any combination of the following herd types was recorded; zebra-only (n=188 herds), zebra-wildebeest (n=34 herds), and zebra-impala (n=70 herds). Single-species zebra herds were considered to be a group of individuals within six body lengths from the next nearest individual (Scheel, 1993; Schmitt et al., 2014). Animals were considered to be in mixed-species herds if they were found no more than 12 meters (determined using a range finder; Pro Range Quad) from each other, which allows them to benefit from the dilution and detection of their herd mates (Scheel, 1993; Schmitt et al., 2014).

For each observation, the species, herd size (i.e., number of conspecifics), and global positioning system (GPS) location were recorded. In addition to GPS locations, the distance and cardinal direction from the road was recorded using the range finder, to correct the coordinates during data analysis. Coordinates were converted to UTM and were corrected by adding or subtracting the herds' distance from the road depending on the direction (i.e., for herds found 30m north of the road, 30 was added to the northing value). If a mixed-species herd was encountered, the identity and herd size of heterospecifics were also recorded.

Environmental variables

To model zebra occurrence at the landscape scale, I used four environmental variables as predictors of zebra occurrence in each herd type (i.e., zebra-only, zebra-wildebeest, and zebra-impala). I selected two vegetation variables and two topographical variables hypothesized to influence herbivores' resource acquisition and perceived predation risk, as well as their resultant distribution across the landscape (Bartlam-Brooks et al., 2013a; Bartlam-Brooks et al., 2013b; Groom & Harris, 2010).

I included NDVI derived from Sentinel-2A/ -2B imagery and a map of percent woody cover at a 10m resolution based on LiDAR data from Milan et al. (2018) as the vegetation variables for my study. The Sentinel-2A/ -2B data (Tile No: 36JUT) used for this study were obtained from Copernicus Open Access Hub (scihub.copernicus.eu). I processed the Sentinel-2A/ -2B data using QGIS (Qgis.org, 2022) to create a mean NDVI layer using six satellite images from cloudless days during the study period (i.e., June, July, August 2021 and July, August, September 2022; Urban et al., 2018). NDVI was used as a measure of productivity to provide an assessment of herbivore food quality and availability within the study area (Box et al., 1989; Pettorelli et al., 2011).

Two topographical variables were also assessed; distance to rivers (m) and distance to drainage lines (m), due to their importance in structuring patterns of herbivore habitat use (Anderson et al., 2016; Hopcraft et al., 2005). I originally included distance to dams (i.e., artificial waterholes) as an additional topographical variable, however, all observations occurred over two kilometres from them. Such a large distance from water sources is unlikely to influence risk (Courbin et al., 2019; Valeix et al., 2010), thus, after initial data exploration, this variable was removed. A distance layer for drainage lines and rivers in the study area was calculated using the *gDistance* function from the *rgeos* package in R (Bivand et al., 2023). *gDistance* calculates the distance between given geometries in the function. For my study, each cell of a raster layer within the extent of the study area was assigned a distance from the nearest feature of interest (i.e., rivers or drainage lines), at a resolution of 10m (Bivand et al., 2023).

Perceived predation risk

To understand the impact of perceived predation risk on zebra occurrence, I collected vigilance data for zebra in single-species herds within the study area. I used vigilance as a measurable variable to understand perceived predation risk driven by landscape features (i.e., vegetation and topographic variables) across the landscape. I collected data following the same transect route and observation protocol described above, including the location (i.e., GPS coordinates and correction) of the herd (Schmitt et al., 2014; Stears et al., 2020). Additionally, the vehicle was switched off to avoid disturbing the animals' behaviour when conducting observations (as per: Schmitt et al., 2016; Stears et al., 2020).

To quantify vigilance behaviour in zebra-only herds (herds: n=58; focal individuals: n=182), a single adult zebra was randomly selected within a herd and observed for a total of three minutes (as per: Schmitt et al., 2014; Schmitt et al., 2016). Using audio recordings during this observation period, I recorded the total time spent vigilant in seconds. Vigilance occurred when the individual lifted their head above grazing height and scanned the surroundings without moving its feet (Pays et al., 2014; Schmitt et al., 2014); I timed each event to calculate the total time spent vigilant per observation. I repeated the recordings with a different focal adult zebra within the herd until at least 50% of the herd had been observed (as per: Stears et al., 2020). To avoid pseudoreplication when working with data collected from the same herd during the same period, I used the herd as the unit of replication, rather than the individual and, thus, created a herd average to calculate proportion of time spent vigilant (as per: Stears et al., 2020).

Data Analysis

Modelling perceived risk across the landscape

To predict the landscape of fear across the study region, I used the proportion of time zebra spent vigilant as a metric for perceived risk. I used a Generalized additive modelling (GAM) approach to model the proportion of time zebra spent vigilant across the study area, based on average herd vigilance for zebra when they herded with conspecifics. I used the above-mentioned raster layers of environmental variables to extract the value for each variable at the GPS location where I collected vigilance for zebra in single-species herds. Prior to data analysis, I tested for collinearity. I deemed data to be colinear if the correlation between two variables was greater than 0.6 or below -0.6 (Martínez-Abraín, 2008). I found that there was no collinearity between variables. Thus, I included the following variables: distance to rivers, distance to drainage lines, and percent woody cover. NDVI was not included as an independent variable in this model. The average herd vigilance data were collected over the course of two years and, thus, the amalgamated annual differences in NDVI would have been inappropriate to include in the model.

I then modelled how the proportion of time spent vigilant varied as a function of the environmental covariates (i.e., distance to rivers, distance to drainage lines, and percent woody cover). Because herd size significantly influences perceived risk, I included herd size in my model as a covariate in the GAM to account for the influence that differences in herd size may have on vigilance behaviour (Testa et al., 2017). The GAM was developed using smoothed terms for all variables, penalized splines for the environmental variables, and a ridge penalty for herd size (i.e., equivalent to an assumption that the covariate is a normal random effect) to prevent overfitting the model. Moreover, for each variable in the model, I tested whether a smoothed term was more appropriate than a linear term to further prevent overfitting (Fisher et al., 2018). Because vigilance data are proportional, I used a binomial distribution and a logit link function. I used a restricted maximum likelihood to make the estimates for the variance parameters of the model independent from those of the fixed effects. I fitted the model using the *mgcv* package in R (Wood, 2017). To evaluate my model, I used the *caret* package in R (Kuhn, 2011) to conduct cross validation. To do this, I divided the data into a training dataset (70%) for model fitting with the remainder of the data (30%) used as an independent test set for model validation (Swanepoel et al., 2013).

To create a perceived predation risk map for zebra across my study area, I projected the predictions of the above GAM model onto a raster brick of my environmental variables. For this map, each pixel represented the proportion of time zebra spent being vigilant. Because I did not have a spatial layer representing zebra herd size, I set a constant of eight individuals for the raster projection, which is the average herd size for zebra (Rubenstein, 2010; Stears et al., 2020). I combined this perceived risk layer (i.e., a representation of the landscape of fear) with my aforementioned environmental variables raster layers to create a raster brick, which I used to predict zebra occurrence at the landscape scale.

Modelling zebra occurrence across the landscape

To understand if mixed-species herding influenced zebra occurrence across the landscape, I modelled zebra occurrence in single- and mixed-species herds. To produce a model of zebra occurrence for each focal herd type (i.e., zebra-only, zebra-wildebeest, and zebra-impala) for my study area, I used Maxent, which has been shown to outperform many other methods of species distribution modelling (Merow et al., 2013). Maxent takes into account presence only species or herd records along with associated environmental factors and finds the least-constrained distribution of species or herd type (Dai et al., 2022; Elith et al., 2011; Phillips et al., 2006). This method of species distribution modelling also allows for the inclusion of test data, which can improve the predictive quality of the output (Elith et al., 2006). By making use of presence-only data, Maxent can mitigate potential bias created by false absences that occur when species or herd detectability is variable (Elith et al., 2011). I ran all species distribution models using the *dismo* package in R (Hijmans et al., 2022).

To fit the Maxent model, I combined the layers of environmental and topographical variables, along with the layer of perceived risk to create a single raster brick. I used the presence points (i.e., GPS coordinates) for each herd that I collected during direct observations to extract the associated values for each variable from the raster brick. I used this method for each of the three herd types to create a separate model for each. For these models, the data for each herd type was spatially thinned to leave only one data point per cell in the study area. Further, 70% of the occurrence data were randomly selected for each model's training and the remaining 30% used for model testing (Swanepoel et al., 2013). To test the accuracy of the models, 100 background points per each occurrence point for each herd type were randomly generated within the study area and evaluated within each of the three models. Phillips and Dudík (2008) suggest using the area under the curve (AUC) of the Receiver Operating Curve as a measure of model performance, which was generated for each model. AUC scores of greater than 0.9 indicate high accuracy and scores between 0.7 and 0.9 are useful, while scores below 0.7 are considered to be poor (Boyce et al., 2002). I projected the Maxent model outputs for each herd type to create a visual representation of predicted zebra occurrence. I used the response curves generated from the Maxent models, as well as the map layers, to understand the relationship between zebra occurrence and the associated environmental variables and to visualize how this relationship varied across the landscape.

Spatial benefit of mixed-species herding

To quantify if mixed-species herding allowed zebra to use previously avoided areas or use specific areas more intensely (i.e., quantifying the spatial benefit), I calculated the percent change in zebra occurrence for each pixel generated in the above landscape projections of the Maxent models for each herd type. The areas where zebra predicted occurrence increased between single- and mixed-species herds were split into areas of expansion and intensification for both herd types. Because the results yielded no absolute zeroes for probability of zebra occurrence in any herd type, I set a threshold of 5% or lower as a proxy for zero occurrence in the area (McCain et al., 2021).

An expansion was defined as any area where the initial probability of zebra occurrence for zebra in single-species herds was less than or equal to 5%, and the probability of zebra occurrence in a mixed-species herd was above 5%. Conversely, an intensification was defined as any area where the initial probability of zebra occurrence for zebra in single-species herds was above 5% and the probability of zebra occurrence in mixed-species herds was greater than that of a single-species herd. This approach allowed for an approximation of areas in the study area where the formation of mixed-species herds increased the predicted zebra occurrence, despite environmental variables remaining the same.

RESULTS

Drivers of perceived risk for zebra across the landscape

The best fit model suggested that all of the environmental covariates, as well as herd size, predict zebra perceived predation risk in the landscape. I found that perceived predation risk for zebra was significantly influenced by distance to rivers (χ^2=144.86, *edf*=5.94, $p< 0.001$) distance to drainage lines (χ^2=91.67, *edf*=3.91, $p< 0.001$), percent woody cover (χ^2=87.77, *edf*=5.74, $p< 0.001$), and number of zebra in the herd (χ^2=101.36, *edf*=0.99 $p< 0.001$). Cross-validation of the GAM model of perceived risk revealed an R^2 value of 0.37 and a mean absolute error (MAE) of 33.25.

Drivers of zebra occurrence in single- and mixed-species herds

Each model of predicted zebra occurrence by herd type across the landscape had similar AUC values. All values were greater than 0.7, which suggests that all models have good predictive abilities (Boyce et al., 2002). The model for zebra only herds had an AUC value of 0.74, zebra-wildebeest herds was 0.76, and zebra-impala herds was 0.78.

Proportion of time zebra spent vigilant was used as a measurable variable to understand perceived risk and was the most important predictor of zebra occurrence in each herd type (zebra-only: 33% contribution to the model; zebra-impala: 36% contribution to the model; zebra-wildebeest: 56% contribution to the model; Figure 2.2). However, subsequent variable contribution differed for each herd type. Following perceived risk, the most important predictor of occurrence for zebra herding with conspecifics was NDVI (30% contribution to the model) and distance to drainage lines (29% contribution to the model; Figure 2.2). Further, for zebra herding with wildebeest, perceived risk was followed by percent woody cover (23% contribution to the model) and distance to rivers (12% contribution to the model; Figure 2.2). Distance to drainage lines (23% contribution to the model) and percent woody cover (19% contribution to the model), respectively, were the second and third greatest contributors to the model for zebra herding with impala (Figure 2.2).

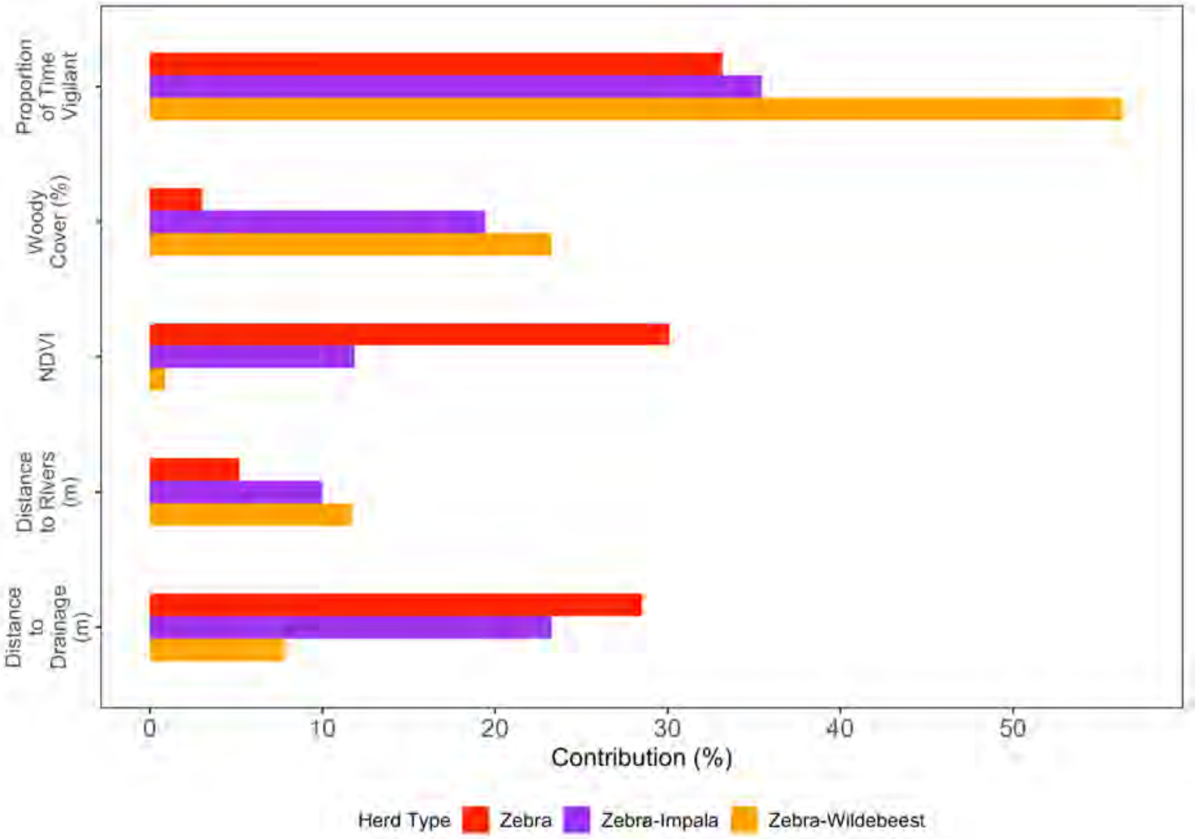

Figure 2.2: The ranked contribution of each predictor variable (environmental and behavioural) to the final predicted zebra occurrence model for each herd type (zebra-only, zebra-wildebeest, zebra-impala).

All three zebra herd types showed a similar response to perceived predation risk, with the highest predicted occurrences being in areas of low vigilance (i.e., safe areas). Predicted occurrence peaks for zebra herding with conspecifics at approximately 0.20 proportion of time spent vigilant and sharply declines thereafter (Figure 2.3A). Conversely, the predicted occurrence for zebra herding with wildebeest or impala peaks at an even lower proportion of time spent vigilant, approximately 0.10 (Figure 2.3A). Zebra experienced an increase in predicted occurrence in areas with a greater percentage of woody cover (i.e., potentially risky areas) when they formed mixed-species herds, compared to when they formed herds with conspecifics. In areas where the percent woody cover was between 45–80%, the predicted occurrence for zebra herding with conspecifics decreased sharply, however, predicted occurrence for zebra herding with wildebeest remained stable, and predicted occurrence increased for zebra herding with impala (Figure 2.3B). All three zebra herd types exhibited the greatest predicted occurrence in areas with low NDVI (i.e., likely safe areas). When zebra herd with conspecifics, they exhibited greater predicted occurrence than either of the mixed-species herd types in low NDVI areas (0–0.20; Figure 2.3C). Predicted occurrence for zebra herding with conspecifics sharply declined as NDVI increased (0.20–0.50; Figure 2.3C). By contrast, when zebra herded with impala and wildebeest, they had lower predicted occurrence in low NDVI areas, but similar predicted occurrence to zebra herding with conspecifics in higher NDVI areas (0.25–0.50; Figure 2.3C). Zebra occurrence in mixed-species herds was greater than that of zebra herding with conspecifics in areas both closer to rivers and to drainage lines (i.e., potentially risky areas). Zebra herding with either wildebeest or impala exhibited greater predicted occurrence, less than one kilometre from rivers and less than 250m from drainage lines, than zebra herding with conspecifics (Figure 2.3D, 2.3E). Conversely, the predicted occurrence for zebra herding with conspecifics increased sharply with greater distance from these topographical features (Figure 2.3D, 2.3E).

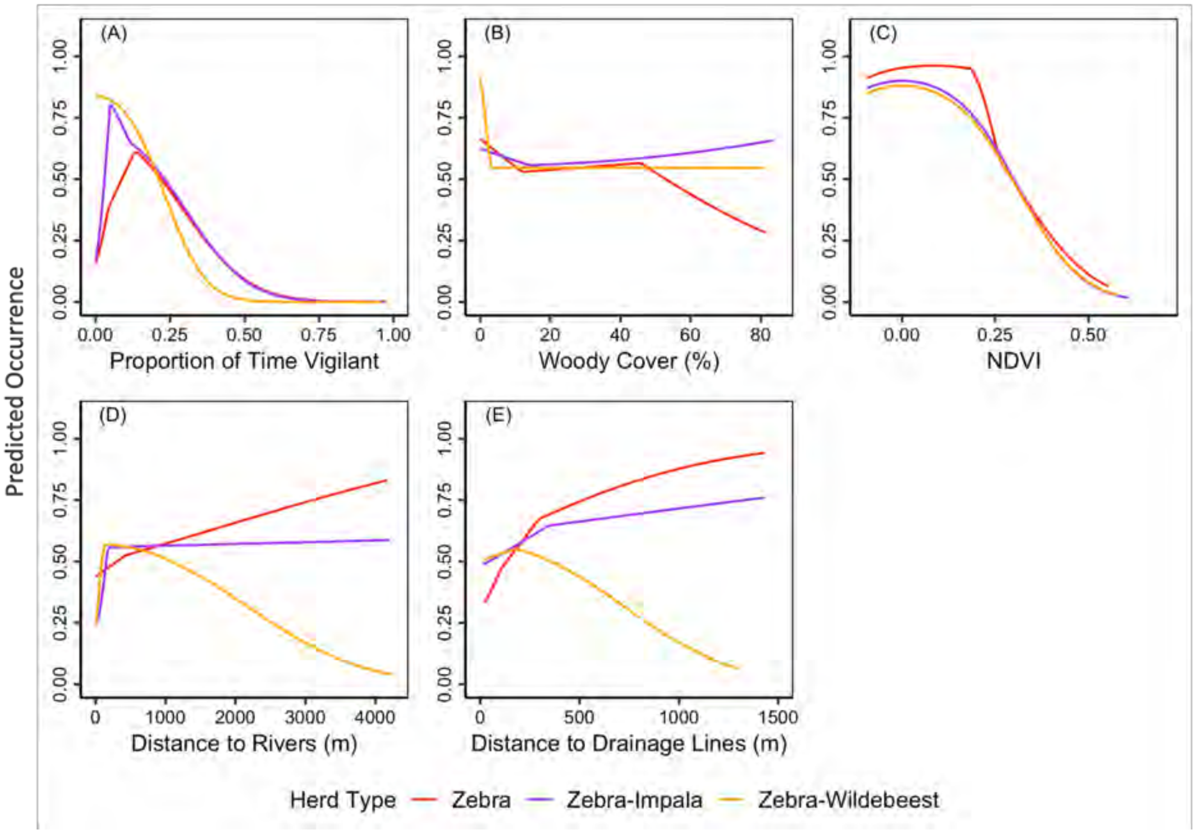

Figure 2.3: The effect of each variable on the Maxent models in determining predicted occurrence for zebra in single- and mixed-species herds. The response curves show how the model prediction changes in response to the variable of interest, while keeping all other variables constant at their average value.

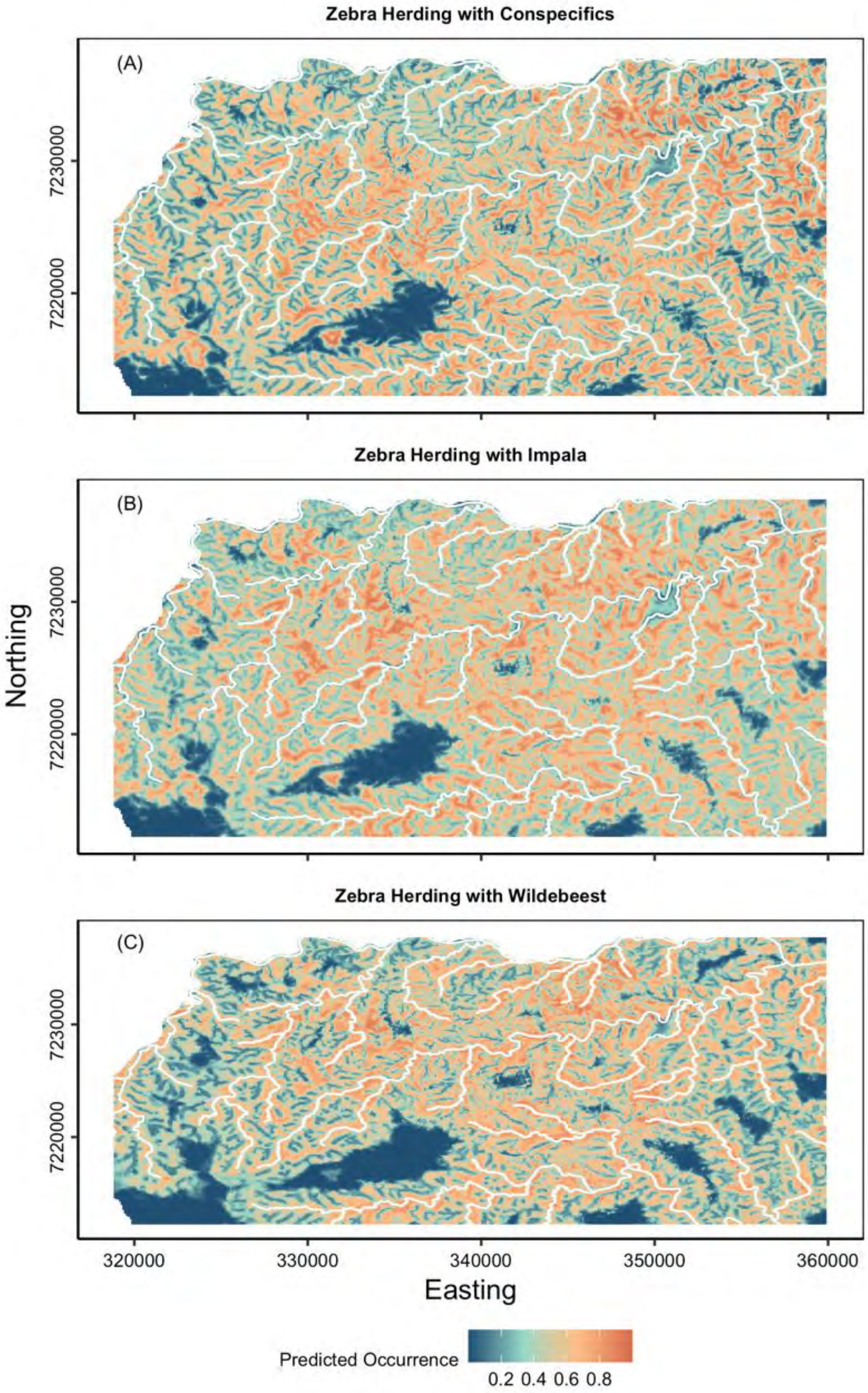

Figure 2.4: Maxent output maps of models restricted to the study area for each herd type; zebra-only, zebra-wildebeest, and zebra-impala. Two years of presence data were used to illustrate predicted occurrence for (A) zebra in single-species herds (n=188), (B) zebra in mixed-species herds with wildebeest (n=34), and (C) zebra in mixed-species herds with impala (n=70). Rivers are shown in white on each map.

Spatial benefit of mixed-species herding

There was a spatial increase in predicted zebra occurrence for both mixed-species herd types (Figure 2.5). Zebra herding with wildebeest experienced an overall spatial increase in predicted occurrence across 36586ha, or 37% of the total study area, and zebra herding with impala experienced an increase across 54203ha, or 55% of the total study area. Spatial benefits for both mixed-species herd types were dominated by intensification benefits. Intensification for zebra herding with impala was observed over 52894ha (Figure 2.5), approximately 54% of the total study area. For zebra herding with wildebeest, there was an intensification across 36553ha, approximately 37% of the total study area (Figure 2.5). Zebra herding with impala experienced an expansion across 1309ha (Figure 2.5), accounting for approximately 1% of the total study area. However, expansion occurred for zebra herding with wildebeest across only 33ha of the study area, which is almost negligible.

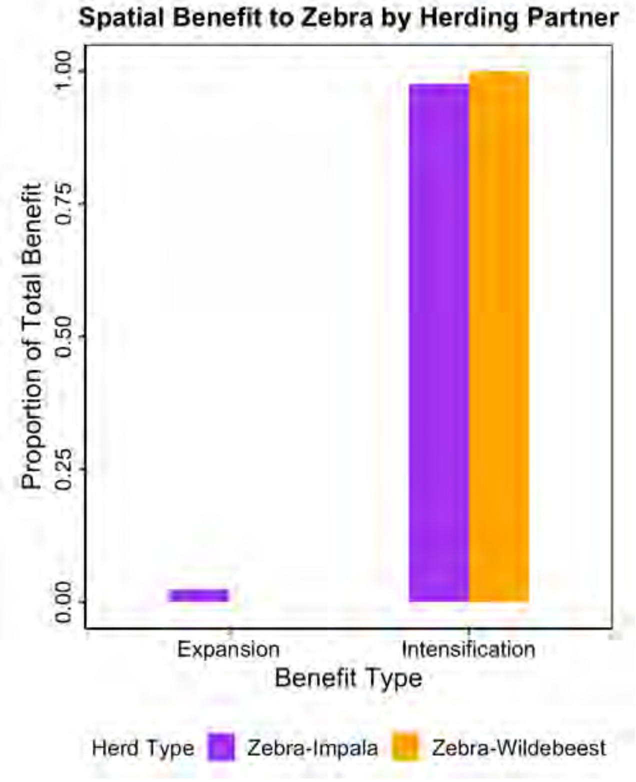

Figure 2.5: A comparison of the proportion of total spatial benefit attributed to expansion or intensification to zebra by forming mixed-species herds with either impala or wildebeest.

DISCUSSION

Animals exist in a landscape that varies not only in resource availability, but also in predation risk (Gallagher et al., 2017; Martin et al., 2015; Riginos & Grace, 2008). To balance these risks and rewards, herbivores can alter their grouping behaviour (Ale & Brown, 2007; Creel et al., 2014; Fitzgibbon, 1990; Schmitt et al., 2016; Stears et al., 2020). Thus, I aimed to disentangle the relative importance of vegetation, topographical, and behavioural drivers of single- and mixed-species herding of zebra with two of their most common herding partners—impala and wildebeest. I also wanted to assess the spatial benefits for zebra when herding with each species. I found that for zebra, mixed-species herding results in altered landscape use. Risk was always the most important predictor of zebra occurrence across herd types, however, the relative importance of the other variables differed among herd types. These differences in the relative importance of drivers likely represent the trait-based differences among herding species (Burkepile et al., 2013; Gwynne & Bell, 1968; Hopcraft et al., 2010). Despite the anti-predator benefits of mixed-species herding, zebra did not exhibit a higher probability of occurrence in riskier habitats when herding in mixed-species herds with impala or wildebeest. Instead, they increased their use of safer habitats in mixed-species herds. This finding illustrates the importance of the potential fitness benefits offered by mixed-species herds—by forming mixed-species groups, zebra are able to use areas across the landscape more intensely, which is likely because mixed-species herding reduces the perceived risk for zebra (Goodale et al., 2019; Pays et al., 2014; Stears et al., 2020). Irrespective of herding partner, the most significant benefit of mixed-species herding was not an expansion into previously avoided habitats, but rather an intensification of use in safer habitats.

Perceived predation risk influences the way herbivores use a landscape, while they balance the need to meet nutritional requirements and avoid predation (Davies et al., 2021; Houston et al., 1993; Lima, 1987; Sinclair & Arcese, 1995). For each herd type, I found that perceived risk was the most important factor in determining probability of zebra occurrence. In contrast to previous studies' findings that mixed-species groups were more likely to occur in risky areas (Beaudrot et al., 2020; Kiffner et al., 2022), zebra exhibited greater predicted occurrence in zebra-wildebeest and zebra-impala herds in areas where perceived risk was low (i.e., 0–0.2 proportion of time spent vigilant; Figure 2.3A). This finding suggests that mixed-species herds take advantage of safer habitats with greater intensity than risky habitats. It is possible that by doing this, zebra are able to capitalize on foraging opportunities in these already-safe areas, meaning that they can maximise foraging benefits. This finding aligns with that of Stears et al. (2020), who found that zebra in mixed-species herds reduced vigilance by 60% in safe habitats, allowing increased time for activities besides costly anti-predator behaviour. When zebra herd with wildebeest, they displayed the lowest predicted occurrence in areas where perceived predation risk was above 0.25 proportion of time spent vigilant (Figure 2.3A). This is likely because zebra join wildebeest in their preferred habitats, which are typically more open, grass-dominated habitats (Martin & Owen-Smith, 2016; Sinclair & Arcese, 1995), and which also have potentially lower perceived predation risk than more wooded habitats (Chen et al., 2021; Hopcraft et al., 2005; Owen-Smith & Mills, 2008). Another explanation for my observed pattern revolves around the number of opportunities zebra and wildebeest have to co-herd. Owen-Smith and Mills (2006') study on ungulate assemblages in KNP found that the population of wildebeest in the southern part of the park is just under half that of the zebra population. Thus, the observed patterns may reflect limited encounters between the two species due to the smaller population of wildebeest in southern KNP. Despite this, I expected to observe greater predicted occurrence for zebra in all herds types in habitats with lower perceived risk, because it is well documented that herbivores reduce their probability of being killed by avoiding risky habitats in favour of safer ones (Creel & Winnie, 2005; Kittle et al., 2008; Orrock et al., 2004; Thaker et al., 2011; Winnie & Creel, 2017). However, my findings were contrary to my prediction (i.e., Prediction 2) that the formation of mixed-species herds would occur in areas of high perceived risk. Although, similar to the findings of Stears et al. (2020), it is plausible that anti-predator behaviour, such as the avoidance of habitats over a certain threshold of perceived risk, is innate and cannot be overcome even by the addition of a heterospecific herd mate.

Another important feature that is well-known to shape patterns of herbivore habitat use is woody plant cover (Burkepile et al., 2013; Butler et al., 2005; Riginos & Grace, 2008; Riginos, 2015). Woody cover is a key component in the distribution of herbivores across a landscape because it simultaneously influences food availability and quality, as well as predation risk (Riginos, 2015; Schmitt & Shrader, 2019; Smit & Prins, 2015). I found that percent woody cover was the second and third most important contributor to models of predicted occurrence for zebra when they herd with wildebeest and with impala, respectively (Figure 2.2). Interestingly, when zebra herd with either wildebeest or impala, they were at least twice as likely to be found in areas of higher woody cover (i.e., over 40% woody cover), compared to when zebra herd with conspecifics, where they were most likely to be found in areas with less than 10% woody cover (Figure 2.3B). Zebra herding with impala experienced the greatest and most sustained increase in predicted occurrence as the percent woody cover increased (Figure 2.3B). As a mixed-feeder, impala likely spend time foraging in areas of higher woody cover because they seek to increase their browse intake in the dry season to maximize forage quality (Demment & Van Soest, 1985; Hopcraft et al., 2010; Moe et al., 2014; O'Kane et al., 2014). Thus, because zebra in single-species herds exhibit lower predicted occurrence in areas with a greater percentage of woody cover, it is possible that impala may offer a benefit to zebra herding with them in areas with decreased visibility (Figure 2.3B). Previous studies have found that lions experience greater hunting success in areas with more complex vegetation, including denser vegetation and higher woody cover, which gives them increased opportunities for ambushing prey (Burkepile et al., 2013; Funston & Mills, 2006; Loarie et al., 2013). Further, because lions have a strong influence on the foraging and vigilance behaviour of herbivores of a range of body sizes (Périquet et al., 2012; Valeix et al., 2009a), it is possible that the presence of a heterospecific herd mate in areas with higher woody cover, and lower visibility, allows zebra to use habitats which likely fall on the higher end of their range of preferred perceived risk, with greater intensity (Fitzgibbon, 1990; Stears et al., 2020).

Beyond vegetation structure, there are other aspects of vegetation that can drive patterns of herbivore habitat use across the landscape. For example, NDVI is an accepted indicator of forage productivity and quality, which is also tied to species distribution and movement patterns (Groom & Harris, 2010; Ryan et al., 2007). I found that NDVI was the second most important contributor in determining predicted occurrence for zebra in single-species herds (Figure 2.2). While zebra in all herd types exhibited the highest probability of occurrence in areas of lower NDVI, zebra in single-species herds had a higher probability of occurrence in low NDVI areas compared to zebra in mixed-species herd types (Figure 2.3C). Previous studies have found that zebra have a wider range of acceptance for forage quality, likely due to their gut morphology and bulk grazing strategy (Ben‐Shahar, 1991; Bodenstein et al., 2000;

Macandza, 2010). As hind-gut fermenters, zebra are able to process food at relatively faster rates, requiring lower forage protein content than foregut ruminants (Bell, 1971) and have been shown to exhibit lower levels of forage selectivity compared to ruminant wildebeest and impala (Bailey et al., 1996; Ben-Shahar, 1991; Hack et al., 2002). For example, Davies et al. (2021) found that wildebeest tolerated greater predator encounter risk in exchange for preferred forage. The lack of increase in predicted occurrence for zebra in all herd types in areas of higher NDVI suggests that, if increased NDVI is linked to perceived risk (Smith et al., 2019), zebra accept lower quality forage compared with the forage requirements of their potential herd mates.

Other aspects of the landscape, such as topographical features, including distance to rivers and drainage lines, play an important role in shaping the landscape of fear and, ultimately, herbivore distributions. My findings for both distance to rivers and drainage lines show that, compared to zebra in single-species herds, zebra herding with heterospecifics had an increase in probability of occurrence in the immediate vicinity (i.e., less than 1km to rivers and within 250m of drainage lines; Figure 2.3D, 2.3E) of these features. These results likely support the findings of Thaker et al. (2011), who demonstrated that zebra avoided habitats in closed riverine and woodland areas, which is possibly due to the perception of these areas as being higher risk because they are preferred hunting ground for lions (Hayward & Kerley, 2005). However, zebra are considered a water dependent species (Hayward & Hayward, 2012) and typically visit a water source every one to two days (Cain et al., 2012). Based on the increased predicted occurrence for zebra in mixed-species herds near rivers (Figure 2.3D), it is possible that the presence of a heterospecific herd mate may facilitate drinking opportunities or the ability to access higher quality riverine vegetation.

The driver-specific results for zebra in single- and mixed-species herds can be contextualized with the inclusion of a spatial benefit analysis. Taking all potential drivers of mixed-species herding (i.e., NDVI, percent woody cover, distance to rivers and drainage lines, and perceived risk) into account at the landscape scale, the results show clear differences in the predicted occurrence of zebra across the different herd types (i.e., zebra-only, zebra-impala, and zebra-wildebeest; Figure 2.4). Because the results show that the probability of zebra occurrence was higher in mixed-species herds than in single-species herds in areas that could be considered more risky (Figure 2.3B, 2.3D, 2.3E), it is plausible that the formation of these herd types would increase the proportion of useable landscape for herd members. However, I found that mixed-species herding does not allow zebra to expand into previously avoided habitats, despite these results having been observed in previous studies of birds, in both temperate and deciduous forests (Darrah & Smith, 2013; Gentry et al., 2019), and primates in forest habitats (Cords, 1987; Heymann & Buchanan-Smith, 2000). Alternatively, the benefits of mixed-species herding may arise from the intensification of habitat use for zebra herding with both wildebeest and impala (Figure 2.5). Risky, previously unused habitats likely have greater food quality, because grass growth can potentially be facilitated by soil nutrient availability as a result of increased tree cover (Ludwig et al., 2004), and could have increased food availability, due to lower overall herbivore use (Schmitt et al., 2022; Winnie & Creel, 2017). Furthermore, when resources are limited, zebra have been shown to use riskier areas (Riginos, 2015). However, Stears et al. (2020) illustrated that zebra in risky habitats are more likely to have increased vigilance compared with zebra in safe habitats. Increased vigilance often translates to less time available for foraging, implying that intake rates in risky habitats may be lower than those in safe habitats (Brown & Kotler, 2004; Fortin et al., 2004a). By forming mixed-species herds in habitats with already low perceived risk, zebra in mixed-species herds can potentially take advantage of both the baseline safety of the areas, as well as the enhanced safety associated with mixed-species herding to further increase their time dedicated to foraging (see Chapter 3: Context dependency of herd mate identity in the competition-information trade-off).

Ultimately, my results suggest that both single- and mixed-species herding is driven largely by perceived predation risk, and while the formation of mixed-species herds does appear to offer anti-predator benefits with regard to certain landscape features (e.g., woody cover, distance to rivers, and distance to drainage lines), these outcomes do not offer the resultant benefit of expansion into previously avoided habitats. Instead, mixed-species herds allowed for the intensification of use in habitats with lower perceived risk, which may convey an enhanced foraging benefit in safe habitats. Thus, the following chapter aims to quantify potential differences in anti-predator and foraging benefits to zebra when co-herding with impala and wildebeest.

CHAPTER 3: Context dependency of herd mate identity in the competition-information trade-off: Impacts of herding partner on zebra foraging and anti-predator behaviour

INTRODUCTION

Prey species are subject to an intricate network of factors that influence their ability to balance the trade-off that exists between the risk of predation and food quality and availability (Burkepile et al., 2013; Laundré et al., 2001; Owen-Smith, 2019; Stears & Shrader, 2015; Stears et al., 2020). This trade-off shapes herbivore behaviour across scales, influencing decisions made from the landscape (e.g., habitat use and selection) to individual scale (e.g., anti-predator and foraging behaviour). Previous studies from several terrestrial ecosystems have found evidence that prey species avoid areas commonly used by predators or that have a higher perceived risk of predation (Creel & Winnie, 2005; Hebblewhite et al., 2002; Riginos & Grace, 2008; Ripple & Beschta, 2006; Valeix et al., 2009a). As a result, varying degrees of predation risk across the landscape may shape the decisions that a herbivore makes regarding foraging in resource-rich habitats (Burkepile et al., 2013).

African savannas provide a particularly interesting example of the food and safety trade-off for herbivores, not only because savannas host a high diversity of predator and prey species (De Visser et al., 2011; du Toit & Cumming, 1999; Thaker et al., 2011), but also because these landscapes are characterized by high vegetation heterogeneity (Gaylard et al., 2003; Venter et al., 2003), which influences both risk and reward. Species-specific traits such as feeding guild (i.e., grazers, browsers, and mixed-feeders) and digestive physiology (i.e., ruminants and hind-gut fermenters) influence foraging behaviour, while body size impacts susceptibility to predation (Davies et al., 2021; Gil et al., 2017; Makin et al., 2018). Therefore, the grass:woody cover ratio within a savanna can impact both the quantity of high-quality forage available to herbivores, as well as the predation risk for herbivores occupying a given savanna (Isaacs et al., 2013; O'Connor et al., 2014; Schmitt et al., 2014). Predation risk (i.e., perceived and actual) has been demonstrated to influence individuals' behaviour, with significant consequences for resource acquisition (Beaudrot et al., 2020; Périquet et al., 2010; Stears et al., 2020; Valeix et al., 2009b).

Because predation is a selective force, behavioural decisions made by prey species to avoid predation have consequences for their probability of survival (DeCesare et al., 2014; Owen-Smith & Mills, 2008; Stears et al., 2020). Herbivores can behaviourally mitigate perceived predation risk through a number of responses, including the selection of specific habitat structure (Creel et al., 2005; Wirsing et al., 2007), increased vigilance (Makin et al., 2018; Périquet et al., 2012), decreased foraging time (Fortin et al., 2004a), changes in group size (Ale & Brown, 2007; Beauchamp, 2017; Hebblewhite & Pletscher, 2002), and changes in group composition (i.e., mixed-species groups; see Chapter 2: Environmental and behavioural drivers of single- and mixed-species herding of zebra and the spatial benefits of different herding partners; Stears et al., 2020). Across a gradient of habitat structure with varying degrees of perceived predation risk (Gaynor et al., 2019; Laundré et al., 2010), changes in group size and group composition can allow herbivores to glean increased social information from their herding partners, which can illicit collective behaviour such as grouping and group vigilance (Gil et al., 2017; Krause & Ruxton, 2002; Shrader et al., 2007).

Vigilance behaviour is central to the trade-off between foraging and safety, influencing how herbivores balance resource acquisition and gain social information (Brown, 1999). It is well documented that as group size increases—be it with con- or heterospecifics—individual vigilance decreases (Dehn, 1990; Makin et al., 2012; Stears et al., 2020; Underwood, 1982), as a result of either (1) dilution of risk (Hamilton, 1971; Vine, 1971) or (2) greater rate of predator detection (Fairbanks & Dobson, 2007; Pulliam, 1973; Stensland et al., 2003). In the case of dilution, increased herd size is beneficial because a predator can only attack one individual in a herd at a time, thus, the probability of any given individual being selected decreases as the total number of available prey increases (Foster & Treherne, 1981). Detection, on the other hand, can be referred to as "the many eyes effect," because an increase in herd size corresponds to an increased number of individuals searching for potential threats at any given time (Lazarus, 1979; Lima, 1995).

While an increase in group size can magnify the benefits of dilution and detection, one of the most significant costs of larger group size among animals is increased competition for resources (Krause & Ruxton, 2002). Group members may participate in social monitoring, which is the act of watching herd mates (i.e., potential competitors) to obtain social information on rich foraging patches (Beauchamp, 2008; Favreau et al., 2010; Giraldeau & Beauchamp, 1999; Kotier et al., 2010). However, time spent scanning to glean social information between bites can increase the search time for the next bite and consequently decrease intake rates (Fortin et al., 2004b). Given that vigilance—whether for the purpose of threat detection or to mediate competition—can conflict with food searching (Illius & Fitzgibbon, 1994), increased time spent scanning the environment can decrease the intake rate of foraging herbivores (Fortin et al., 2004a). Furthermore, some species can anticipate and actively reduce encounters with competitors (Berger & Gese, 2007; Broekhuis et al., 2013; Ferry et al., 2016). Avoidance behaviours, at both spatial and temporal scales, can impact species distributions, and while they could decrease competitive interactions, such behaviour can also have negative implications for intake rates (Abramsky et al., 2001; Cresswell, 1994; Ferry et al., 2016). In groupings of herbivores, interference competition can occur when a species reduces the ability of another to make use of shared resources, either by agnostic interactions or by its mere presence (Amarasekare, 2002; Minderman et al., 2006). Additionally, scramble competition may occur when a group collectively depletes a limited resource, which results in reduced foraging efficiency for the entire group (Beauchamp & Ruxton, 2003; Janson & Van Schaik, 1988; Nicholson, 1954). Scramble competition is most intense in larger group sizes, and as such, there is likely a size threshold that conspecific groupings will not surpass because the reduction in foraging efficiency past this limit cannot be tolerated (Cresswell & Quinn, 2011; Snaith & Chapman, 2008). Conversely, competition is likely to be lessened in mixed-species herds, due to the niche partitioning that exists between heterospecifics (Hopcraft et al., 2012; Kartzinel et al., 2015).

An example of niche partitioning among herbivore species is the feeding guild to which they belong, which influences the type and quality of vegetation each species requires, as well as the diversity of habitats each species will use (Burkepile et al., 2013; Burkepile et al., 2016; Cromsigt et al., 2009; Isaacs et al., 2013; Makin et al., 2018). Feeding guilds influence the habitats herbivores use because they seek to meet the nutritional requirements of their respective diet (Illius, 1997). Grazers often prefer foraging in areas with a higher grass:woody cover ratio, while browsers typically prefer the opposite (Burkepile et al., 2013; Schmitt & Shrader, 2019). Mixed-feeders can take advantage of the variations in nutrient content of different vegetation types, which differ in their quality and availability across seasons, by adjusting the ratio of their grass:woody vegetation intake (Codron et al., 2006; Van der Merwe & Marshal, 2012). Body size also plays a role in both influencing the nutritional requirements of herbivores and dictating predation risk. Studies have highlighted a negative relationship between body size, for both grazers and browsers, and diet selectivity (Clauss et al., 2013; Jarman & Sinclair, 1979), meaning that as herbivore body size increases, diet selectivity tends to decrease. This relationship is mainly due to the higher relative metabolic rates of smaller ungulates (du Toit & Owen-Smith, 1989) and the scarcity of large quantities of high-quality food available for larger animals (Clauss et al., 2013; Illius & Gordon, 1987). Body size dictates prey species' susceptibility to specific predators (Owen-Smith & Mills, 2008; Radloff & du Toit, 2004), and also influences escape tactics used to avoid predators (Lima, 1992; Wirsing et al., 2010). More agile species may be willing to risk foraging in areas with denser woody vegetation where they can outmanoeuvre potential predators (Burkepile et al., 2013). For example, Lima (1990), found that the cover-dependent escape tactic of the White-crowned Sparrow (*Zonotrichia leucophrys*) allowed the species to feed in cover while under predation risk, whereas Lark Buntings (*Calamospiza melanocorys*) fed in the open while under predation risk, due to their cover-independent escape strategy. Therefore, in a landscape with high levels of vegetation heterogeneity, in addition to varying degrees of perceived predation risk (Gaylard et al., 2003; Martin et al., 2015; Thaker et al., 2011; Venter et al., 2003), the potential advantages of heterospecific group members with unique diet requirements and habitat preferences may be able to mediate some of the vigilance and foraging costs associated with the competition-information trade-off (Krause & Ruxton, 2002; Seppänen et al., 2007).

Hopcraft et al. (2014) found that zebra (*Equus quagga*) are willing to sacrifice safety to access habitats with higher vegetation biomass availability during the dry season. Zebra often form mixed-species herds with wildebeest (*Connochaetes taurinus*) and impala (*Aepyceros melampus*) in African savannas (Bodenstein et al., 2000; Chirima et al., 2012; Skinner & Chimimba, 2005), and Beaudrot et al. (2020) observed a greater occurrence of mixed-species groups in risky areas. Because herbivores often avoid areas with dense woody vegetation due to increased predation risk (Hayward & Kerley, 2005; Riginos & Grace, 2008), the finding of Beaudrot et al. (2020) suggests that herding with heterospecifics could allow herbivores to alter their foraging behaviour. Furthermore, the increased likelihood of mixed-species herds occurring in densely vegetated areas could indicate that group members are able to mitigate potential interspecific competition by foraging in areas associated with increased forage quality and availability (Ludwig et al., 2004; Sinclair, 1985; Treydte et al., 2007).

Mixed-species herding has the potential to further magnify the benefits of dilution and detection (Scheel, 1993; Underwood, 1982). Different herbivore species often have distinct sensory modalities, and therefore differ in their ability to detect potential threats (Meise et al., 2020). As a result, social cues and signals gleaned from alarm calls and body posture can provide valuable information (Beaudrot et al., 2020; Meise et al., 2020). However, due to species-specific traits, including susceptibility to predation and feeding guild, it is likely that not all species of heterospecific herd mates will offer the same benefits (Beaudrot et al., 2020; Goodale et al., 2010; Schmitt et al., 2016). Heterospecific herd mates can either act as diluting partners (i.e., sharing a common predator) or as low-diluting partners (i.e., different common predator; Schmitt et al., 2014). For example, because lions (*Panthera leo*) are a common predator for zebra and wildebeest (Hayward & Kerley, 2005), wildebeest can offer both threat detection and act as a diluting partner when they form mixed-species herds with zebra. Conversely, impala are not a preferred prey item for lions (Hayward & Kerley, 2005), but are preferred prey for a number of other predators (Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006). As such, impala can offer heightened detection for zebra, but are less likely to benefit zebra as a diluting partner (Schmitt et al., 2014). Thus, while different species may offer distinct benefits as a herd partner, in general, forming mixed-species herds has the potential to offer a more comprehensive threat assessment and potentially reduce predation risk (Beaudrot et al., 2020; Dehn, 1990; Fitzgibbon, 1990; Goodale et al., 2020; van Langevelde et al., 2022). Anti-predator benefits associated with mixed-species herding can further allow for a reduction in individual vigilance and a resultant increase in time available for other activities, such as foraging (Makin et al., 2012; Schmitt et al., 2016; Stears et al., 2020; Underwood, 1982). However, it is important to consider that in terms of the competition-information trade-off, individual species may present varying levels of suitability as a heterospecific herd mate.

Previous studies have sought to disentangle the relative importance of social information, competition, and predation risk on vigilance, grouping behaviour, and foraging behaviour (e.g., Beauchamp, 2019; Favreau et al., 2010; Gil et al., 2017; Hebblewhite et al., 2002; Owen-Smith, 2019; Pays et al., 2007; Ripple & Beschta, 2006; Seppänen et al., 2007; Shrader et al., 2007; Stutz et al., 2018). Additionally, there are also studies examining the impact of vegetation biomass and nutritional quality on vigilance and foraging behaviours, elucidating the trade-off that exists between resource acquisition and perceived predation risk amongst single-species herds (e.g., Fortin et al., 2004a; Pays et al., 2012). Furthermore, recent studies have demonstrated the benefits of mixed-species herding in levelling the landscape of fear for various savanna herbivores (e.g., Beaudrot et al., 2020; Pays et al., 2014; Schmitt et al., 2014; Schmitt et al., 2016; Stears et al., 2020; van Langevelde et al., 2022). However, there remains a gap in the literature quantifying the influence of mixed-species herding—and the identity of herd mates—on the interplay between foraging behaviour (i.e., competition, foraging efficiency and success) and anti-predator behaviour (i.e., vigilance) from the individual to the landscape scale. Acknowledging how these factors may contribute to foraging behaviour is of critical importance to understanding how mixed-species groups may benefit herding species, as well as influence herd members' potential fitness across varying degrees of perceived predation risk present in the landscape. Behavioural interactions between species can shape herbivore habitat selection in both positive and negative ways, potentially by enabling resource acquisition (Goodale et al., 2010; Goodale et al., 2020; Schmitt et al., 2016) or hindering it due to interspecific competition (Brown, 1988; Hopcraft et al., 2014; O'Kane et al., 2014; Pringle et al., 2019). Furthermore, because different herbivore species each possess species-specific traits that influence their habitat use, foraging behaviour, and susceptibility to predation, the foraging and anti-predator behaviour associated with forming mixed-species groups also has the potential to vary with different herding partners.

The aim of this chapter was to examine the differences in foraging and anti-predator behaviours for zebra in single-species herds and in mixed-species herds with either wildebeest or with impala, to determine which herding partner might be the most beneficial to zebra. I aimed to quantify the differences in anti-predator behaviours (i.e., vigilance) across these herd types (i.e., zebra-only, zebra-wildebeest, and zebra-impala). I also examined metrics for competition (i.e., step rate), foraging efficiency (i.e., bites per step), and foraging success (i.e., intake rate) across these herd types. Additionally, I assessed how anti-predator behaviour and foraging success changed between areas of high and low perceived risk across the landscape, to explore how risk influenced the foraging and anti-predator behaviour patterns of zebra observed across herd types. I predicted that (1) zebra in single-species herds would exhibit the highest amount of anti-predator behaviour and have the lowest foraging success across both perceived risk categories, and (2) zebra in mixed-species herds would exhibit lower levels of anti-predator behaviour and higher foraging success than zebra herding with conspecifics. I also predicted that (2a) zebra herding with impala would have lower levels of anti-predator behaviour and experience greater foraging success than zebra herding with conspecifics or with wildebeest in low-risk areas. As a mixed-feeder, impala might not compete with zebra in the same way as wildebeest. Furthermore, even though impala are a low-diluting partner for zebra (Schmitt et al., 2014), in low-risk areas, the potential foraging benefits of herding with impala might outweigh the lack of threat-related social information they offer. Finally, I predicted that (2b) in high-risk areas, zebra herding with wildebeest would exhibit the lowest level of anti-predator behaviour and greatest foraging success of all herd types because wildebeest share a common predator with zebra (Hayward & Kerley, 2005). However, because wildebeest are grazers (Bodenstein et al., 2000; Codron et al., 2007), they might present a greater source of competition for zebra, thus reducing their foraging efficiency and foraging success.

METHODS

Study site

The Kruger National Park (KNP) covers approximately 20000km^2 in the north-eastern corner of South Africa, bordering both Zimbabwe to the north and Mozambique to the east. The park is home to more than 1900 species of trees, shrubs, forbs, and grasses, and supports 147 mammal species (SANParks, 2019a, 2019b). Data were collected in the low-lying savanna regions of the Skukuza and Pretoriuskop sections of southern KNP (centred at 25˚3’27” S, 31˚25’8” E; Figure 3.1) from a study area covering approximately 50km^2.

The climate of this area is classified as semi-arid subtropical and receives 500-700 mm p.a. of rainfall. Climatic conditions vary from warm, dry winters (i.e., May to September) and hot, wet summers (i.e., October to April), with most of the rainfall occurring in January (Kruger et al., 2002; Scholes et al., 2001). Data were collected during the winter months (ie., June to August 2021, July to September 2022) due to increased visibility to accurately observe the focal species (Scholtz et al., 2014). The dry season has an average maximum temperature of 26˚ Celsius (i.e., June) and an average minimum temperature of 17˚ Celsius (i.e., August; Kruger et al., 2002).

The vegetation of this region of KNP is classified as a mixed *Combretum* savanna woodland, with the dominant trees in the deep, sandy soils of the region being *Combretum sericea* and species belonging to the *Terminalia* genera. The more shallow-soiled, steeper slopes are dominated by *Sclerocarya birrea* and species belonging to the *Albizia* and *Vachellia* genera (Gertenbach, 1983). This area is considered to be relatively nutrient rich savanna (i.e., sweet veld) and dominant grass species are *Panicum maximum, Pogonarthria squarrosa, Digitaria eriantha,* and *Brachiaria nigropedata* (Davies et al., 2014).

The geology underlying the site is Archaean granite and gneiss of the Nelspruit suite (Barton et al., 1986). These features give rise to a characteristically undulating landscape, with drainage lines approximately 3 kilometres apart (Scholes et al., 2001). Soils in this region are dominated by Hutton and Clovelly forms, with Glenrosa forms on the steeper slopes (Gertenbach, 1983).

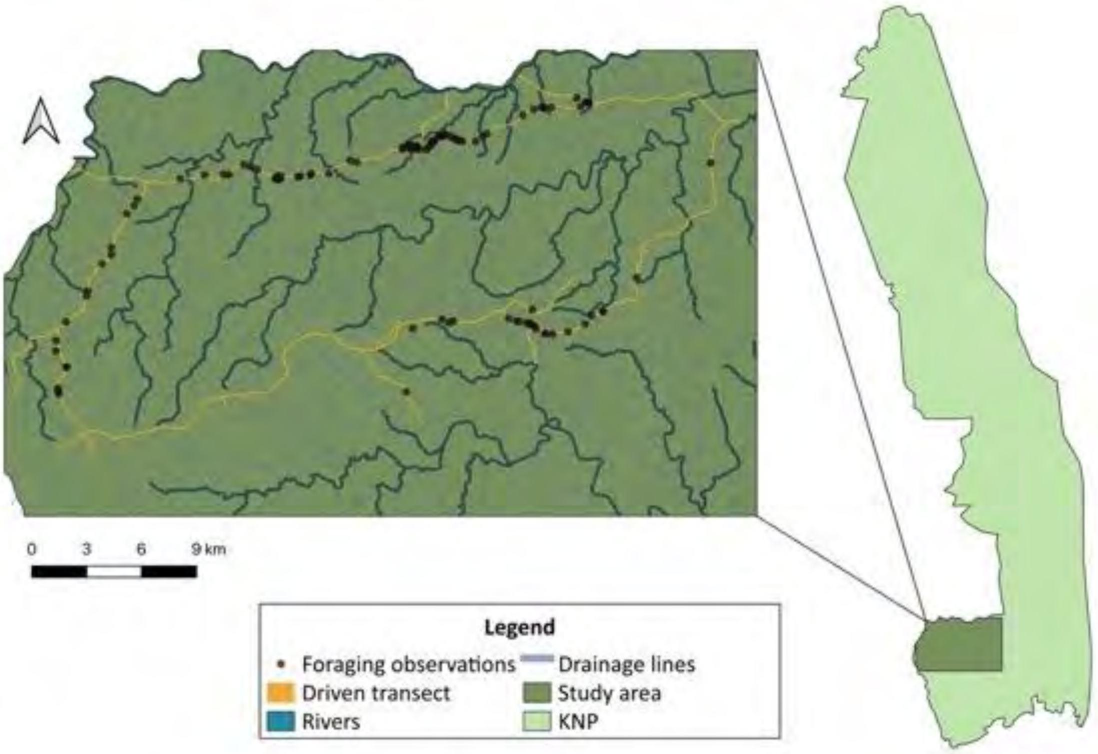

Figure 3.1: Map of Kruger National Park (KNP) and the study area, showing the driving transect route (yellow line) and foraging observations (black dots). Rivers and drainage lines are shown in blue.

Field Methods

Zebra foraging and vigilance observations

I selected impala and wildebeest as focal herding partner species of zebra based on their abundances in the landscape (Chirima et al., 2012) and propensity to form mixed-species herds with one another (Schmitt et al., 2014; Schmitt et al., 2016). To quantify zebra foraging (i.e., number of bites per step, bite rate, and intake rate) and anti-predator behaviour (i.e., vigilance) when herding with con- and heterospecifics, I observed zebra while they were actively foraging in three different group types: zebra-only (herds: n=59; focal individuals: n=187), zebra-wildebeest (herds: n=28; focal individuals: n=103), and zebra-impala (herds: n=34; focal individuals: n=116). To collect vigilance and foraging data for the mixed-species herd types, I used the same driving transects used to collect species location and zebra-only vigilance data (see Chapter 2 Methods: Species herding observations). All observations were made from a stationary vehicle using binoculars (Carson 3D Series, TD-042ED, 10x42mm), with the vehicle switched off to avoid disturbing the animals' behaviour (as per: Schmitt et al., 2016; Stears et al., 2020). Observations were within 150m of the road; greater distances increased the potential for inaccurate behavioural observations due to decreased visibility.

I recorded each encounter with the aforementioned herd combinations where adult zebra were engaged in foraging activity. The herd was considered to be foraging if a majority (i.e., at least 50% plus one) of the members were actively seeking out food, rather than resting, moving, or vigilant (as per: Burkepile et al., 2013). For each observation, the herd type (i.e., zebra-only, zebra-impala, and zebra-wildebeest), number of conspecifics, and number and identity of heterospecifics were recorded. Single-species (i.e., zebra-only) herds were defined as a group of individuals within six body lengths from the next nearest individual (Scheel, 1993; Schmitt et al., 2014) but further than 12 meters from other species. Herds were considered mixed-species (i.e., zebra-wildebeest and zebra-impala) if heterospecific herd mates were within no more than 12 meters from each other (determined using a range finder; Pro Range Quad; Scheel, 1993; Schmitt et al., 2014). The Global Positioning System (GPS) location of the herd was also recorded. In addition to GPS coordinates, the distance and cardinal direction of the herd from the road was recorded using the range finder, to correct the coordinates during data analysis. Coordinates were converted to UTM and were corrected by adding or subtracting the herds' distance from the road depending on the direction (i.e., for herds found 30m north of the road, 30 was added to the northing value).

I chose a focal, foraging adult zebra at random from the focal herd and observed their behaviour for a period of three minutes (as per: Schmitt et al., 2014; Schmitt et al., 2016). Using an audio recording during this observation period, each step, bite, and vigilance scan (i.e., time in seconds) was recorded. Through my observations, I identified two different sizes of bites based on the bite size in relation to the total height of the grass tuft. Bites were classified as short or long, depending on whether the animal bit from above or below half the height of the grass tuft being eaten, respectively. The total number of bites (i.e., both short and long) and the total number of steps were used to calculate a step rate (i.e., number of steps per minute) and the number of bites per step for each individual. These data were highly variable due to natural variations in individual foraging behaviour, so I calculated a herd median for both metrics (Potvin & Roff, 1993). Step rate was used as an index of potential competition between herd mates, because it has been shown to indicate interference competition (Minderman et al., 2006; Sansom et al., 2008; Shi et al., 2010). The number of bites zebra took per step can be used to understand foraging efficiency because it is indicative of movement between feeding stations within a patch (Odadi et al., 2009).

Vigilance scans occurred when an individual lifted its head above grazing height and scanned the surroundings without moving its feet (Pays et al., 2014; Schmitt et al., 2014). Each vigilance event was timed to calculate the total time spent vigilant during the observation period, which was used to calculate the average time spent vigilant for the herd. I repeated the audio recordings with a different focal adult zebra within the herd until at least 50% of the herd had been observed (Stears et al., 2020). To avoid pseudoreplication when working with data collected from the same herd during the same period, I used the herd as the unit of replication, rather than the individual and used a herd average for time spent vigilant (as per: Stears et al., 2020).

Quantifying zebra foraging success

To understand potential differences in foraging behaviour when zebra herd with con- and heterospecifics, I used intake rate (i.e., grams of forage consumed per minute) as an indicator of foraging success. To determine the intake rate of a foraging zebra, I used the bite count and hand-plucking method first described by Halls (1954). This method allows for the estimation of masses of single bites and causes minimal disturbance to the animals (Bonnet et al., 2015; Wallis De Vries, 1995). I estimated bite masses by collecting grass samples as a proxy for bites taken by zebra. Following the same driving transect and protocol described for the foraging observations, grazing zebra were observed at different foraging stations and the tufts of grass they fed from were identified. Through my observations, I identified two different sizes of bites: long bites and short bites, based on the bite size in relation to the total height of the grass tuft. When the animals finished foraging, I collected representative samples of the two bite sizes from the same tuft of grass, mimicking the bite that had been taken (long bites n=76; short bites n=79). To ensure accuracy when collecting sample bites, I located the exact bite taken by the foraging zebra. I then confirmed that the bite was fresh by examining bitten grass stalks to ensure the ends had not dried, and I measured the width of the bite to replicate it when cutting the sample bite. Each sample was stored in a brown paper bag before being dried in an oven at 60˚ Celsius for 48 hours and then weighed for a final dry mass to be recorded (Okello et al., 2002). The dry mass for each bite type was averaged to determine a mean bite mass for each bite type. Based on the total number of bites taken from each bite type during a foraging observation, the intake rate was calculated for each individual observation. To avoid pseudoreplication, I used the herd as the unit of replication and calculated a herd median for intake rate (as per: Stears et al., 2020). I used a median value, rather than an average, because these data were highly variable due to natural differences in individual feeding behaviour (Potvin & Roff, 1993).

Data Analysis

Modelling zebra foraging behaviour in single- and mixed-species herds

To determine the impact of mixed-species herding with different species of herd mates on the foraging behaviour of zebra, I focussed on three foraging metrics. The first was the number of steps zebra took per minute (i.e., step rate), which is a metric used to understand potential competition between herd mates (Rind & Phillips, 1999; Shi et al., 2010). The second was the number of bites zebra took per step, which can be used to understand foraging efficiency (Odadi et al., 2009). Finally, I assessed intake rate (i.e., grams of forage consumed per minute), which represents a measure of foraging success. These data were highly variable due to natural differences in individual feeding behaviour, thus, I used herd median values for all three sets of analyses (Potvin & Roff, 1993). Prior to data analysis, I found that the year of data collection (i.e., 2021 and 2022) did not influence zebra step rate, bites per step, or intake rates (step rate: χ^2=1.33, df=2, p=0.77; bites per step: χ^2=1.274, df=2, p=0.68; intake rate: χ^2=2.92, df=2, p=0.22). Therefore, I did not include the year of data collection as a variable in my subsequent analysis. To determine how zebra step rate, bites per step, and intake rates varied as a function of herd type, I used three separate Generalized Linear Models (GLM) using the *lme4* package in R (Bates et al., 2023). For each of these models, I controlled for the number of zebra and the number of heterospecifics in the herd by including these variables as covariates in the model. In addition, each model used a Gamma distribution and an inverse link function. Finally, I conducted a Tukey's post hoc analysis of the marginal means to determine differences between herd types for each analysis.

Modelling zebra anti-predator behaviour in single- and mixed-species herds

To understand whether zebra adjusted their anti-predator in response to the identity of their herd mates (i.e., the mixed-species effect), I examined the proportion of time zebra spent vigilant (i.e., a metric for anti-predator behaviour) across each herd type. To avoid pseudoreplication, I used herd averages for the proportion of time spent vigilant during the observation period (Schmitt et al., 2014). Prior to data analysis, I found that the year of data collection influenced zebra vigilance across different herd types (χ^2=1.35, *df*=2, *p*<0.001) and therefore included this in the subsequent model as a random effect. To address overdispersion, I included an observation level random effect (OLRE; subsequent overdispersion parameter: 1.006; Harrison, 2015). Adding an OLRE assigns a unique level of random effect to each observation, which helps absorb extra-parametric variation present in these data (Elston et al., 2001; Harrison, 2015). I used a Generalized Linear Mixed-effects Model from the *lme4* package in R (Bates et al., 2023) to model how the proportion of time zebra spent vigilant varied as a result of herd type. For this model, I controlled for the number of zebra and heterospecifics in the herd by adding these variables as additional fixed effects, and I used a binomial distribution with a logit link function. Finally, I conducted a Tukey's post hoc analysis of the marginal means to elucidate differences among herd types.

Modelling the effect of predation risk on zebra foraging and anti-predator behaviour

To examine how foraging success (i.e., intake rate) and anti-predator behaviour (i.e., proportion of time spent vigilant) in foraging zebra changed across herd types in different parts of the study area that have varying degrees of risk, I created a layer of perceived risk across the landscape for zebra, by accounting for the distance to drainage lines, distance to rivers, percent woody cover and the normalised difference vegetation index (NDVI; see Chapter 2 Methods: Modelling perceived risk across the landscape). Based on the GPS locations of each foraging herd, I extracted the associated value of perceived risk for their location. I then calculated a mean value for perceived risk across the landscape, and based upon whether the extracted values fell above or below the mean value, I categorized each herd observation as occurring in areas of either high or low perceived predation risk.

Foraging models

Because the year of data collection did not influence zebra bites rate, bites per step, or intake rates, I used a GLM approach to model changes in zebra foraging behaviour as a result of the interaction between herd type and perceived risk. I created three separate GLM models with median bite rate, bites per step, and intake rate as the dependent variable, using a Gamma distribution and inverse link function. For each of these models, I controlled for the number of con- and heterospecifics in the herd by including these variables as covariates. Finally, I conducted a Tukey's post hoc analyses of marginal means for each model to elucidate differences among zebra bite rates, bites per step, and intake rates in herd types foraging in each risk category.

Vigilance model

Prior to data analysis, I found that the year of data collection influenced the proportion of time zebra spent vigilant. Therefore, I included it as a random effect in the subsequent model. I used a GLMM approach to model how the proportion of time zebra spent vigilant varied as a result of the interaction between herd type and perceived risk, using a binomial distribution and logit link function. I controlled for the number of zebra and the number of heterospecifics in the herd by including these variables as covariates in the model. To address overdispersion found in the initial model, I added observation level random effects when I built the full model (subsequent overdispersion parameter: 1.007; Harrison, 2015). Finally, I used a Tukey's post hoc analysis of marginal means to determine differences among the proportion of time zebra spent vigilant in herd types in each risk category.

RESULTS

Foraging implications of mixed-species herding

I found that the competition (i.e., step rate, as measured by the number of steps per minute) zebra experienced was significantly influenced by herd type (χ^2=11.46, *df*=2, *p*=0.003). Neither the number of zebra nor the number of heterospecifics in a herd significantly influenced the competition zebra experienced while foraging (*p*=0.54 and *p*=0.41, respectively). The Tukey's post hoc analysis revealed that when zebra foraged with conspecifics, they experienced similar competition (mean ± SE: 4 ± 0.33 steps per minute; Figure 2A), compared to when they fed with impala (mean ± SE: 3 ± 0.37 steps per minute; *p*=0.72; Figure 2A) and wildebeest (mean ± SE: 5 ± 0.58 steps per minute; *p*=0.06; Figure 2A). However, when zebra foraged with wildebeest, zebra experienced significantly higher competition (mean ± SE: 5 ± 0.58 steps per minute; Figure 2A) compared to when they foraged with impala (mean ± SE: 3 ± 0.37 steps per minute; *p*=0.01; Figure 2A).

Further, herd type also significantly influenced zebra foraging efficiency (i.e., bites per step; χ^2=9.32, *df*=2, *p*=0.01). When zebra foraged in single-species herds, the Tukey's post hoc analysis revealed that their foraging efficiency (mean ± SE: 3 ± 0.31 bites per step; Figure 2B) was similar to that of both zebra foraging with wildebeest (mean ± SE: 2 ± 0.32 bites per step; *p*=0.29; Figure 2B) and with impala (mean ± SE: 4 ± 0.63 bites per step; *p*=0.24; Figure 2B). In contrast, zebra experienced significantly lower foraging efficiency in herds with wildebeest (mean ± SE: 2 ± 0.32 bites per step; Figure 2B) compared to when they foraged in mixed-species herds with impala (mean ± SE: 4 ± 0.63 bites per step; *p*=0.01; Figure 2B). As with the results of the competition model, the number of zebra and the number of heterospecific herd mates did not significantly impact zebra foraging efficiency (*p*= 0.06 and *p*=0.386, respectively).

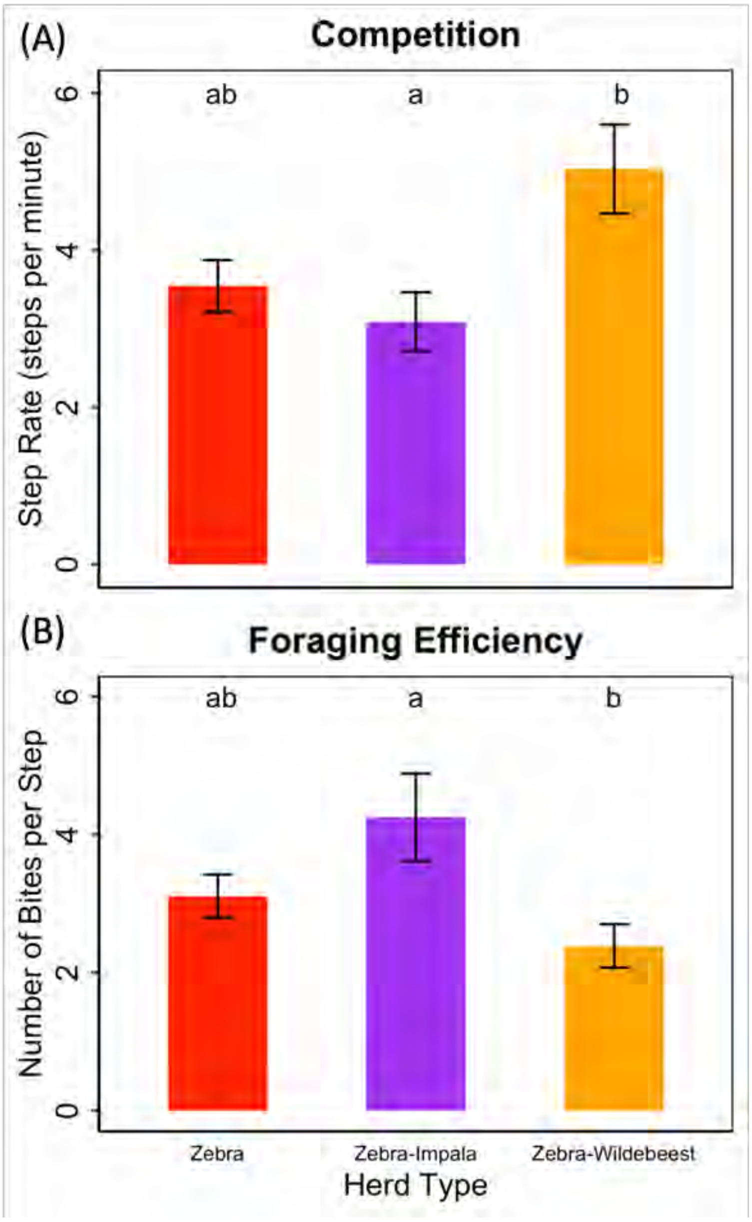

Figure 3.2: Differences in (A) the median step rate (± SE) for zebra in single- and mixed-species herds, and (B) the median number of bites per step (± SE) zebra took in single- and mixed-species herds. (A) Step rate is indicative of interference competition between herd mates. (B) Bites per step is indicative of foraging efficiency. Medians with no letter in common are significantly different ($\alpha = 0.05$).

I found that herd type significantly influenced the foraging success (i.e., intake rate; measured in grams of forage consumed per minute) of zebra (χ^2=6.52, *df*=2, *p*=0.04). The results of the Tukey's post hoc analysis revealed that when zebra foraged with impala, they achieved similar foraging success (mean ± SE: 12 ± 0.88 grams per minute; Figure 3A) to zebra in single-species herds (mean ± SE: 11 ± 0.60 grams per minute; *p*=0.93; Figure 3A) and zebra foraging with wildebeest (mean ± SE: 14 ± 0.93 grams per minute; *p*=0.22; Figure 3A). However, zebra herding with wildebeest achieved significantly higher foraging success (mean ± SE: 14 ± 0.93 grams per minute; Figure 3A) compared to zebra foraging with conspecifics (mean ± SE: 11 ± 0.60 grams per minute; *p*=0.05; Figure 3A). Zebra foraging success was not significantly influenced by either the number of zebra or the number of heterospecifics in the herd (*p*=0.92; and *p*=0.94, respectively).

The effect of herd type on zebra anti-predator behaviour

The results of the GLMM model for the effect of herd type on anti-predator behaviour (i.e., proportion of time spent vigilant) among zebra revealed that vigilance among foraging zebra was significantly influenced by herd type (χ^2=7.98, *df*=2, *p*=0.02). The proportion of time zebra spent vigilant while foraging was not significantly influenced by the number of zebra or the number of heterospecific herd mates (*p*=0.06 and *p*=0.09, respectively). The Tukey's post hoc analysis showed that zebra herding with impala devoted a similar proportion of time to vigilance (mean ± SE: 0.10 ± 0.02 proportion of time; Figure 3B) compared to when they foraged with wildebeest (mean ± SE: 0.08 ± 0.02 proportion of time; *p*=0.48; Figure 3b) and with conspecifics (mean ± SE: 0.13 ± 0.02 proportion of time; *p*=0.36; Figure 3b). However, when zebra foraged with wildebeest, they devoted a significantly lower proportion of time to vigilance (mean ± SE: 0.08 ± 0.02 proportion of time; Figure 3B) than zebra foraging in single-species herds (mean ± SE: 0.13 ± 0.02 proportion of time; *p*=0.02; Figure 3B).

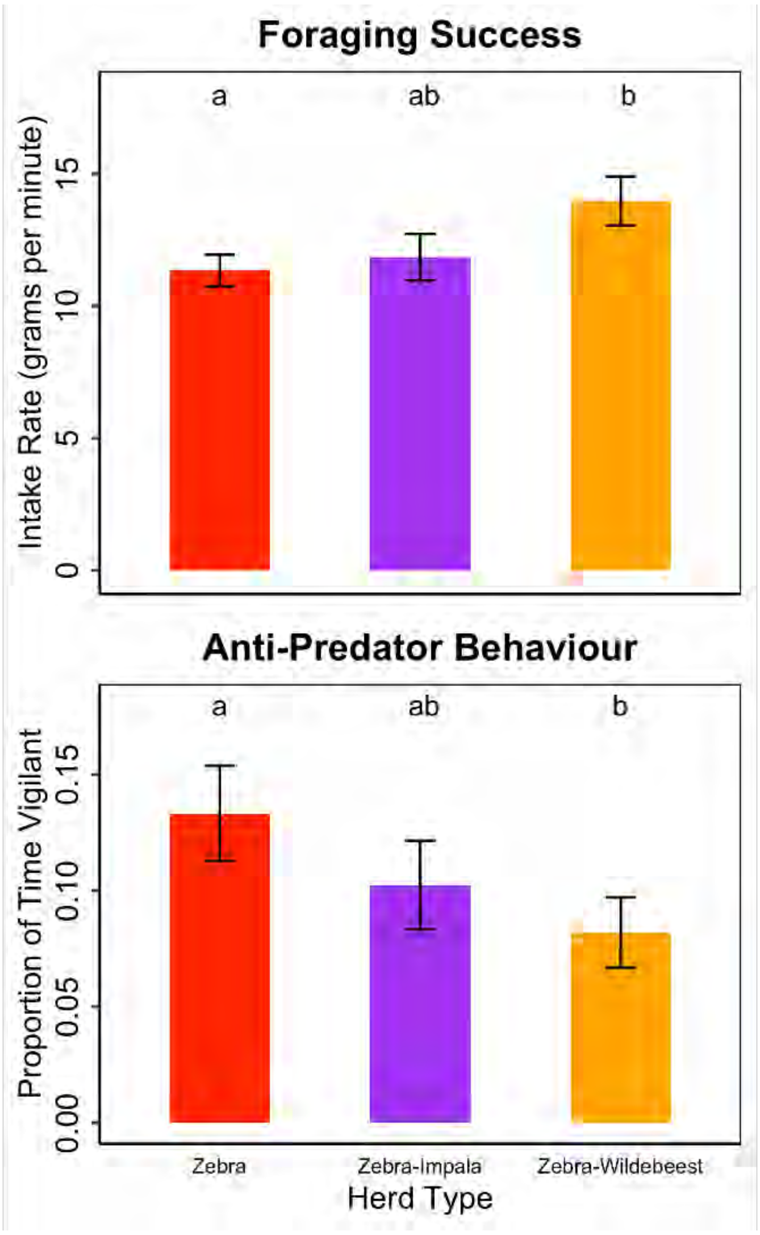

Figure 3.3: Differences in (A) herd mean proportion of time spent vigilant (± SE) for zebra in single- and mixed-species herd types, and (B) herd median intake rate (grams consumed per minute; ± SE) for zebra in single- and mixed-species herd types during the three minute observation period. Medians (intake rate) and Means (vigilance) with no letter in common are significantly different ($\alpha = 0.05$).

Comparing zebra foraging and anti-predator behaviour across the landscape of fear

Neither the competition (i.e., bite rate), nor the foraging efficiency (i.e., bites per step) that zebra experienced when foraging were significantly influenced by the interaction between herd type and perceived risk category (bite rate: χ^2=48.53, *df*=2, *p*=0.64; bites per step: χ^2=46.43, *df*=2, *p*=0.87). In contrast, zebra foraging success (i.e., intake rate, as measured by grams of forage consumed per minute) was significantly influenced by the interaction between herd type and perceived risk category (χ^2=7.74, *df*=2, *p*=0.02). Neither the number of heterospecifics, nor the number of conspecifics significantly influenced zebra intake rates in low- and high-risk habitats (*p*=0.70 and *p*=0.89, respectively). The intake rates zebra experienced with impala remained similar, regardless of the degree of perceived risk (low-risk mean ± SE: 12 ± 0.94 grams per minute; high-risk mean ± SE: 12 ± 1.39 grams per minute; *p*=1.00; Figure 4A). However, in high perceived risk habitats, the Tukey's post hoc analysis revealed that zebra herding with conspecifics achieved significantly lower intake rates (mean ± SE: 10 ± 0.91 grams per minute) than their counterparts in habitats with low perceived risk (mean ± SE: 12 ± 0.73 grams per minute; *p*=0.05; Figure 4A). In contrast, zebra foraging with wildebeest benefitted from significantly intake rates in high perceived risk habitats (mean ± SE: 19 ± 3.28 grams per minute) compared to low perceived risk habitats (mean ± SE: 13 ± 0.93 grams per minute; *p*=0.04; Figure 4A).

I found that the interaction between herd type and perceived risk category showed a trend that approached significance in influencing zebra anti-predator behaviour (i.e., proportion of time spent vigilant; χ^2=5.71, *df*=2, *p*=0.06). Moreover, the influence of the number of heterospecifics in a herd on the proportion of time zebra spent vigilant also showed a trend approaching significance (χ^2=3.55, *df*=1, *p*=0.06). Zebra vigilance was further significantly influenced by the number of zebra in the herd (χ^2=4.97, *df*=1, *p*=0.03). The Tukey's post hoc analysis revealed that zebra foraging with wildebeest exhibited a similar investment in vigilance behaviour in both low and high perceived risk habitats (low-risk mean ± SE: 0.08 ± 0.01 proportion of time; high-risk mean ± SE: 0.06 ± 0.02 proportion of time; *p*=0.97; Figure 4B). Similarly, when foraging in mixed-species herds with impala, zebra also devoted a similar amount of time to vigilance, regardless of the perceived risk associated with the habitat (low-risk mean ± SE: 0.10 ± 0.02 proportion of time; high-risk mean ± SE: 0.11 ± 0.03 proportion of time; *p*=0.99; Figure 4B). However, zebra in single-species herds foraging in habitats with high perceived risk spent a larger proportion of time vigilant (mean ± SE: 0.12 ± 0.02 proportion of time) than those in habitats with low perceived risk (mean ± SE: 0.20 ± 0.04 proportion of time; *p*=0.02; Figure 4B).

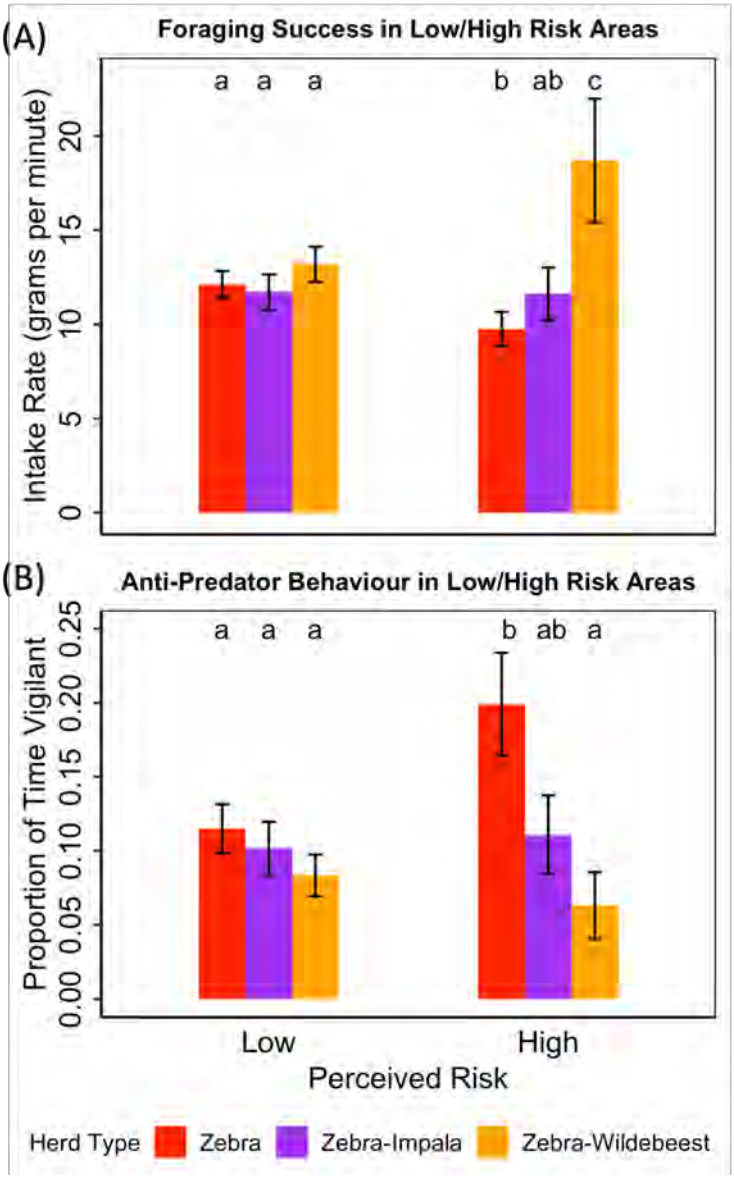

Figure 3.4: The differences in (A) herd median intake rate (grams of forage consumed per minute; ± SE) and (B) herd mean proportion of time spent vigilant (± SE) for zebra in single- and mixed-species herds in parts of the study area classified as high (above landscape mean) and low (below landscape mean) perceived risk. Medians (intake rate) and Means (vigilance) with no letter in common are significantly different (α = 0.05).

DISCUSSION

The foraging behaviour of herbivores determines where they feed, their diet selection, and ultimately their foraging efficiency and success (i.e., bites per step and intake rate). However, their individual foraging behaviours can be influenced by anti-predator behaviour (i.e., vigilance) and potential competition with other herbivores. Further, group-forming species must balance the costs and benefits associated with group living, such as increased information about the predation risk or the of quality foraging patches versus potential competition from larger herd sizes or heterospecific herd mates (i.e., competition-information trade-off; Beauchamp, 2017; Gil et al., 2017; Goodale et al., 2010; Goodale et al., 2017; Krause & Ruxton, 2002; Shrader et al., 2007). To balance the risks and rewards associated with meeting their daily nutritional intake requirements and avoiding predation risk and potential competition, herbivores can alter their grouping behaviour while foraging. However, there has been little research comparing the foraging and anti-predator behaviours for wild herbivores herding with conspecifics and different species of heterospecifics. Studying these herding patterns can clarify the costs and benefits of various heterospecific herding partners in terms of perceived predation risk, competition, foraging efficiency and success. I found that herd type significantly influenced zebra foraging behaviours and perceived predation risk at both the individual and landscape scale. However, the benefits zebra received differed depending on the identity of their herding partner. In agreement with my predictions, zebra foraging with impala experienced less competition and greater foraging efficiency than those foraging with wildebeest. When foraging with wildebeest, zebra were able to significantly decrease their investment in anti-predator behaviour, resulting in increased foraging success. At the landscape scale, zebra in mixed-species herds were able to maintain similar anti-predator behaviour across habitats with low and high perceived risk, effectively levelling their landscape of fear. However, when zebra foraged with wildebeest, they were able to significantly increase their foraging success in habitats with high perceived risk, compared to habitats with low perceived risk.

A number of studies have shown a mixed-species effect where vigilance differed for herbivores in mixed-species herds compared with single-species herds (Beaudrot et al., 2020; Gil et al., 2017; Kiffner et al., 2022; Kluever et al., 2009; Périquet et al., 2010). For example, Schmitt et al. (2016) found that zebra significantly reduced vigilance behaviour when herding with giraffe (*Giraffa camelopardalis giraffa*). These findings are in line with those of my study, where I found that overall anti-predator behaviour for foraging zebra was significantly lower when they formed mixed-species groups with wildebeest (Figure 3.3B). However, this was not the case for zebra foraging in mixed-species herds with impala (Figure 3.3B), likely due to lessened dilution and detection benefits associated with impala life history traits (Hayward & Kerley, 2005; Okello et al., 2002; Pays et al., 2014; Smith & Cain, 2008; Van der Merwe & Marshal, 2012). Wildebeest are a known diluting partner for zebra, which means that aggregations of these two species result in a decreased chance that any one individual will be attacked, due to sharing the lion as a predator (Dehn, 1990; Hayward & Kerley, 2005; Schmitt et al., 2016). As a threat detector, wildebeest likely also possess complementary sensory abilities and/or behavioural modes, such as scanning rates and frequency (Scheel, 1993). Furthermore, Palmer and Gross (2018) found that zebra, along with wildebeest, did not respond to the alarm calls of impala with the same frequency as other herd mates (i.e., wildebeest or zebra), reflecting the overlap in predator guild predicted by the reliability hypothesis (Magrath et al., 2009; Magrath et al., 2015). Thus, it appears that zebra may find the social information gleaned from wildebeest regarding potential predation risk to be more valuable than that of impala.

Apart from altering anti-predator behaviour, additional benefits of mixed-species herding include the potential to increase foraging efficiency. Interestingly, I found that zebra experienced significantly lower foraging efficiency (i.e., bites per step) when they foraged with wildebeest, compared to zebra foraging with impala (Figure 3.2B; Odadi et al., 2009). The increased foraging efficiency zebra experience when herding with impala is likely linked to the habitats where zebra and impala form mixed-species herds. In areas of increased percent woody cover, I found that zebra are more likely to form mixed-species herds with impala than with wildebeest (see Chapter 2 Results: Drivers of zebra occurrence in single- and mixed-species herds). Habitats with increased woody cover have been associated with increased perceived predation risk (Riginos, 2015) and even increased hunting success for lions (Burkepile et al., 2013; Funston & Mills, 2006; Loarie et al., 2013). When hunting, lions employ an ambush (i.e., sit and wait) strategy, as opposed to cursorial hunting tactics, and therefore rely more heavily on prey movements to initiate encounters (Greene, 1986). Thus, it is plausible that while foraging with impala in areas associated with a higher risk of predation from ambush predators, zebra simply do not roam as much, therefore leading to increased foraging efficiency. Alternatively, habitats with higher woody cover can be associated with increased nutrient content in the available graze (Ludwig et al., 2004). It is therefore possible that zebra foraging with impala achieved increased foraging efficiency in these areas because they did not need to utilize as many feeding stations within the patch (Odadi et al., 2009; Okello et al., 2002).

Competition between herd mates, whether con- or heterospecific, is one of the most significant costs of group living (Krause & Ruxton, 2002). Interestingly, when examining the step rates of zebra foraging in different herd types, I found that wildebeest were a significantly greater source of competition than impala (Figure 3.2A). This result could be because both zebra and wildebeest are grazers, and zebra may view wildebeest as competitors for forage (Ben-Shahar & Coe, 1992; Bodenstein et al., 2000). Conversely, zebra herding with impala experienced decreased levels of competition (Figure 3.2A), likely because impala have a higher browse intake in the dry season than in the wet season (Demment & Van Soest, 1985; Moe et al., 2014; O'Kane et al., 2014). Alternatively, it is possible that using bites per step and step rate as metrics are limited in their ability to accurately explain foraging efficiency and competition among herd types. Because my data were collected in the dry season, it is plausible that zebra and their herd mates experience greater habitat utilization (i.e., increased movement within foraging patches) to reach their required nutritional intake in a season of increased resource stress (Beauchamp & Ruxton, 2003; Gordon, 1989). Future studies could investigate foraging efficiency and competition across both wet and dry seasons to elucidate potential shortfalls in these metrics for single-season data.

Overall, I found that foraging efficiency was maximised and competition minimised for zebra foraging with impala compared to wildebeest (Figure 3.2). Furthermore, while I did observe a decrease in anti-predator behaviour among zebra when they foraged with wildebeest (Figure 3.3B), Beauchamp and Ruxton (2003) suggest that with limited resources, foragers may decrease their vigilance to take advantage of resources, but this does not necessarily result in increased intake rates. Thus, it is reasonable to expect that the results examining foraging success would reflect the same benefits of impala as a herding partner. However, I found that zebra herding with wildebeest achieved significantly greater foraging success, while zebra foraging with impala maintained similar foraging success, compared to zebra in single-species herds (Figure 3.3A). Despite wildebeest being a greater source of competition for zebra than impala, the foraging success and anti-predator behaviour of zebra herding with wildebeest do not reflect the same cost. In fact, these findings suggest the opposite; that foraging with wildebeest potentially facilitates the greatest foraging and anti-predator benefits. This dichotomy could plausibly be explained by the dilution and detection benefits wildebeest offer to zebra (Schmitt et al., 2014). The same does not appear to be true for zebra herding with impala. While I found that zebra herding with impala did not experience the same level of competition for forage acquisition as those herding with wildebeest, zebra foraging with impala lacked the additional benefits of decreased anti-predator behaviour and increased foraging success (Figure 3.3). Thus, despite being a source of forage competition for zebra, herding with wildebeest may allow zebra to decrease their anti-predator behaviour to such an extent that they are able to nullify any competitive costs and, as a result, increase their foraging success compared to zebra foraging with conspecifics. By foraging with wildebeest, it appears zebra are able to rely on the combined dilution and detection abilities of their herd mates, increasing their time available to devote to foraging, resulting in increased foraging success. This finding further supports the conclusion that while mixed-species herding overall is beneficial to zebra foraging behaviour, certain heterospecific herd mates offer more substantial benefits than others.

The patterns I observed at the herd level for zebra foraging and anti-predator behaviour were largely reflected at the landscape scale when examining these behaviours between low and high perceived risk habitats (Figure 3.4). Zebra foraging in single-species herds devoted significantly more time to anti-predator behaviour in high perceived risk areas than they did in low-risk areas (Figure 3.4B). This finding supports that of Chen et al. (2021), who observed zebra increase their vigilance in areas with higher woody cover, reflecting the heightened risk associated with these habitats. Importantly though, in habitats with high perceived risk, zebra foraging in either mixed-species herd type were able to maintain a similar investment in anti-predator behaviour as they did in habitats with low perceived risk (Figure 3.4B). In agreement with Stears et al. (2020), who previously quantified the degree to which mixed-species herding can reduce perceived predation risk across different levels of risk, it appears that by herding with heterospecifics, zebra may be able to level their landscape of fear. However, future studies should investigate the potential impacts that herd composition (i.e., proportion of heterospecifics vs. proportion of conspecifics) may have on anti-predator behaviour in areas with varying degrees of perceived predation risk.

My study controlled for the number of zebra and number of heterospecifics in the herd as covariates, but because these data were not a representative sample of variation in herd compositions, I could not test the direct effects of herd composition on zebra foraging and anti-predator behaviour. The relative influence of herd composition on anti-predator behaviour has been demonstrated by Schmitt et al. (2014), who found that zebra experienced only a slight reduction in vigilance when they formed mixed-species with impala, until impala made up 75% of the total herd size, but these findings were not examined across varying degrees of predation risk. Zebra and impala do not share a common predator (Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006), suggesting that the anti-predator benefits impala offer are mainly a reflection of increased detection, rather than dilution (Schmitt et al., 2014). Furthermore, impala often form larger aggregations (Jarman & Jarman, 1973; Pays et al., 2012; Pays et al., 2021). Thus, it is possible that the similar investment in anti-predator behaviour that I observed among zebra foraging with impala across the landscape was a reflection of the herd composition being made up largely by impala and not a benefit related solely to the presence of a heterospecific herd mate. In contrast, zebra and wildebeest share a common predator (Hayward & Kerley, 2005), suggesting that the anti-predator benefits zebra experienced foraging with wildebeest in habitats with high-risk are a function of both detection and dilution benefits, as evidenced by Schmitt et al. (2014).

Zebra were able to capitalize upon a levelled landscape of fear when foraging in mixed-species herds by maintaining their foraging success when they formed herds with impala in both low- and high-risk habitats (Figure 3.4A). Furthermore, the combination of dilution and detection benefits offered to zebra herding with wildebeest was reflected in the zebra’s foraging success across the landscape. When foraging with wildebeest, zebra achieved significantly greater foraging success in habitats with high perceived risk, compared to when they foraged in habitats with low perceived risk (Figure 3.4A). The impacts of this finding are two-fold. First, the significant increase in foraging success for zebra herding with wildebeest in high-risk habitats suggests that zebra are able to take advantage of increased resource availability potentially present in riskier habitats. Second, this result illustrates the potential of wildebeest as a herding partner to mitigate the detrimental impacts of perceived risk on zebra foraging behaviour. In contrast, zebra foraging with conspecifics experienced significantly lower foraging success in high perceived risk habitats, compared to low perceived risk habitats (Figure 3.4A). This finding supports the foraging costs of vigilance highlighted by previous studies (Cowlishaw et al., 2004; Creel et al., 2014; Fortin et al., 2004a; Pays et al., 2021). For instance, Pays et al. (2021), found that foraging in areas with higher perceived predation risk led to increased vigilance and a resultant decrease in intake rates for impala. Thus, benefits for zebra foraging success and anti-predator behaviour when they formed mixed-species herds with wildebeest suggest increased foraging opportunities in riskier habitats for group-forming herbivores, potentially explaining why strong cascading effects caused by predators are not often observed in complex savanna ecosystems (Ford et al., 2015). The results of this chapter build upon these findings by investigating the changes in zebra foraging behaviour resulting from altered risk perception in mixed-species herds.

The results of this chapter support previous investigations of the mixed-species effect (e.g., Fitzgibbon, 1990; Goodale et al., 2017; Kluever et al., 2009; Scheel, 1993; Stears et al., 2020; Van der Meer et al., 2012; van Langevelde et al., 2022). My findings are also consistent with those of Gil et al. (2017), who found that social information and mixed-species herding were not detrimental for individual fitness because the fitness benefits always outweighed the potential competition costs. Furthermore, Kiffner et al. (2014) observed zebra as the nucleus of mixed-species herds, so while the aim of this chapter was to understand the foraging and vigilance benefits of mixed-species herding for zebra, it is likely that these benefits would extend their heterospecific herd mates (i.e., impala and wildebeest; Meise et al., 2020). Future investigations should seek to ascertain the presence and significance of the benefits of mixed-species herding with different herbivores as a focal species. These studies have the potential to elucidate a broader understanding of the trade-off that exists between competition and social information, as well as risk and reward, which herbivores face living under predation risk.

Ultimately, my results quantify the benefit of mixed-species herding in reshaping the trade-off between food and fear from the herd to the landscape scale. Furthermore, my findings support a levelled landscape of fear for zebra foraging in mixed-species herds. However, the foraging benefits of mixed-species herding were context dependent and varied based on the identity of their herd mate. By forming mixed-species herds with wildebeest, zebra were able to take advantage of anti-predator benefits, resulting in greater foraging benefits compared to forming mixed-species herds with impala. My findings not only illustrate the importance of potential fitness benefits offered by forming mixed-species herds across scales, but also the context-dependency of benefits associated with specific heterospecific herd mates. Zebra were able to devote more time to foraging when they formed mixed-species herds with wildebeest, regardless of the perceived risk of the habitat where they foraged. Thus, zebra appear to balance not only the competition-information trade-off but also, by potentially selecting for the quality of herd mates, they maximize the benefits of group living (Gil et al., 2017; Schmitt et al., 2014; Seppänen et al., 2007). Overall, the findings of my study suggest that mixed-species herding in foraging zebra is an important tool in the suite of anti-predator behaviours employed by prey species, and one with significant implications for survivorship, habitat use, and ultimately, community level interactions.

CHAPTER 4: Synthesis

Herbivores face a trade-off that exists between meeting their energetic requirements and avoiding predation (Brown et al., 1999; Brown, 1999; Laundré et al., 2001; Owen-Smith et al., 2010). This trade-off can impact their habitat use and selection, foraging behaviour, and anti-predator behaviour (Burkepile et al., 2013; Creel et al., 2005; Cromsigt et al., 2009; Hebblewhite & Merrill, 2009; Muposhi et al., 2016; Van der Merwe & Marshal, 2012). Herbivores attempt to mediate this trade-off by accessing the anti-predator benefits associated with group size (Ale & Brown, 2007; Burger & Gochfeld, 1992; Clark & Mangel, 1986; Fairbanks & Dobson, 2007; Lima, 1995) and group composition (Beaudrot et al., 2020; Fitzgibbon, 1990; Gentry et al., 2019; Goodale et al., 2017; Goodale et al., 2020; Kiffner et al., 2014), while balancing the costs of potential competition between group members (Abramsky et al., 2001; Amarasekare, 2002; Bednekoff & Lima, 2004; Brown, 1988; Palmer et al., 2003). Mixed-species grouping is one such strategy that has been studied in depth among prey species, from birds (e.g., Gentry et al., 2019; Graves & Gotelli, 1993; Harrison & Whitehouse, 2011; Rodewald & Brittingham, 2002; Zou et al., 2018), to fish (e.g., Allan, 1986; Paijmans et al., 2019; Theo & Shanker, 2023; Ward et al., 2002), to mammals (e.g., Fitzgibbon, 1990; Kiffner et al., 2014; Kiffner et al., 2022; Pays et al., 2014; Stears et al., 2020; Stensland et al., 2003). Groupings of heterospecifics have the potential to mitigate some of the competitive costs associated with larger groups of conspecifics and magnify foraging and anti-predator benefits (Kartzinel et al., 2015; Scheel, 1993; Schmitt et al., 2014; Underwood, 1982). Moreover, for mixed-species herds, the costs and benefits linked with different species of herding partners across a landscape with a high degree of vegetation heterogeneity and varying degrees of perceived risk has hardly been explored.

My study aimed to build upon the existing knowledge regarding the functional significance of mixed-species herding for zebra (*Equus quagga*) when they herd with different heterospecific herd mates. I examined the environmental drivers of single- and mixed-species herding for zebra across the landscape, as well as assessed the costs and benefits for zebra when they foraged in single- and mixed-species herds with two different herding partners (i.e., wildebeest, *Connochaetes taurinus*, or impala, *Aepyceros melampus*), at the individual and landscape scale. Overall, I found that for zebra, forming a mixed-species herds with either impala or wildebeest alters their landscape use by allowing for the intensification of habitat use. However, when I focussed on finer-scale behaviours of foraging zebra, I found that the identity of their herding partner significantly influenced the magnitude of potential benefits to foraging and anti-predator behaviour at both the individual and landscape scale.

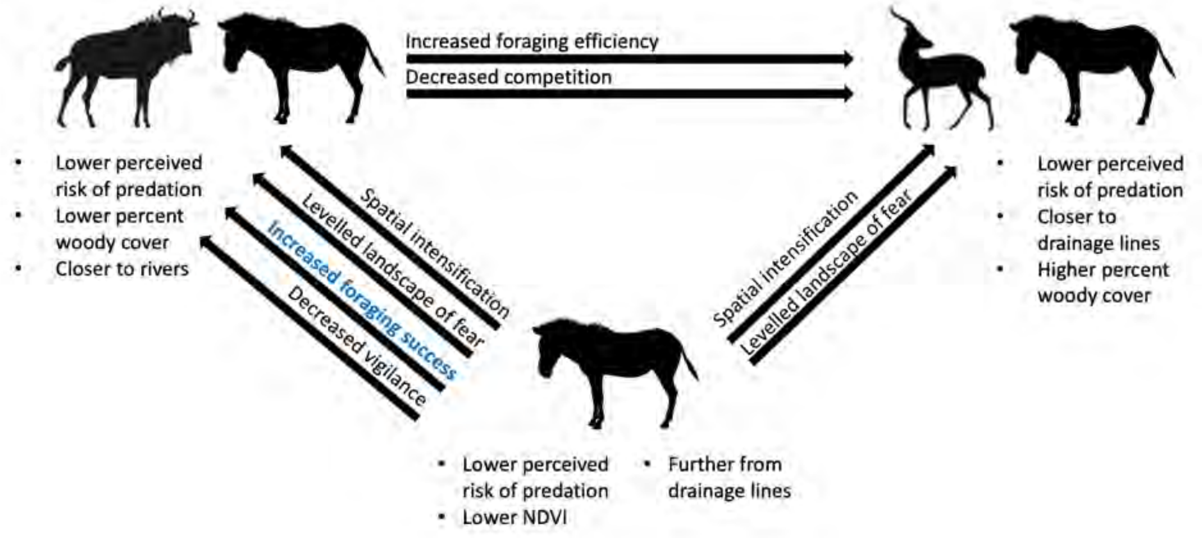

Figure 4.1: The three environmental drivers with the most important contribution to predicted occurrence for zebra in each herd type. Between each herd type, arrows point in the direction of the herding partner that offers the listed benefit (benefits for zebra at both the individual and landscape scale shown in blue).

Behavioural and landscape patterns of zebra in conspecific herds

Similar to the findings for all the herd types (i.e., zebra-only, zebra-impala, zebra-wildebeest), I found that the predicted occurrence for zebra in single-species herds across the landscape was driven largely by perceived risk (Figure 4.1). This result supports the findings of Owen-Smith (2019), Dwinnell et al. (2019), Thaker et al. (2011), and Wirsing et al. (2007), who demonstrated that prey species avoid habitats with increased perceived risk of predation. Zebra have also been shown to respond to long-term risk associated with certain habitats, influencing their landscape use (Courbin et al., 2019; Thaker et al., 2010; Valeix et al., 2009a). Distance to drainage lines was another important driver of predicted occurrence for zebra in single-species herds, and they were more likely to occur further from this landscape feature. Because zebra's main predator, the lion (*Panthera leo*), has been found to preferentially hunt in habitats with higher vegetation complexity to suit their ambush hunting strategy (Funston

& Mills, 2006; Hayward & Kerley, 2005; Loarie et al., 2013). Additionally, Lehmann et al. (2008) demonstrated that the core home range of lions in Karongwe Game Reserve, South Africa were along drainage lines, and 74% of territorial scent marks were also in these areas. As such, it is likely that zebra's avoidance of drainage lines reflects the increased perceived risk associated therein. Moreover, predicted occurrence for zebra was highest in areas with a low normalised difference vegetation index (NDVI; Figure 4.1). It is plausible that zebra select habitats with low NDVI because doing so might offer them better visibility, and therefore increased potential to detect possible threats (Burger, 2001; Chen et al., 2021; Smith et al., 2019). Previous studies have also found that hind-gut fermenters, like zebra, can maintain their nutritional requirements on lower quality vegetation (Bailey et al., 1998; Ben‐Shahar, 1991; Bodenstein et al., 2000). However, while zebra have a wider range of acceptance for forage quality, it is likely that my findings regarding increased predicted occurrence for zebra in areas with lower NDVI are intertwined with their avoidance of drainage lines and increased perceived predation risk. Thus, these findings may further clarify how the non-lethal effects of predation significantly impact herbivore behaviour and habitat use (Beauchamp, 2023; Brown, 1988, 1999; Burkepile et al., 2013; Creel et al., 2005; Gil et al., 2017; Wirsing et al., 2021).

When foraging, zebra in single-species herds experienced similar levels of competition and foraging to their counterparts in mixed-species herds with impala or wildebeest. However, zebra's foraging success and anti-predator behaviour when they herded with conspecifics differed significantly from when they formed mixed-species herds with wildebeest (Figure 4.1). The foraging success and anti-predator behaviour of zebra foraging in single-species herds were reflected at the landscape scale as well. In areas with high perceived risk, zebra foraging in single-species herds engaged in significantly higher vigilance than their counterparts in habitats with low perceived risk. Because vigilance can interfere with food searching (Illius & Fitzgibbon, 1994), it appears that the increased vigilance levels I observed for zebra in high-risk habitats resulted in significantly lower foraging success compared to zebra in low perceived risk habitats. My findings illustrate how, though zebra take increased risks to access higher vegetation biomass when resources are scarce (Hopcraft et al., 2014), the increase in anti-predator behaviour associated with these areas does not result in better foraging success.

Behavioural and landscape patterns of zebra herding with impala

Zebra in mixed-species herds with impala intensified their habitat use over the majority of the study area (Figure 4.1). Across 55% of the landscape, zebra were more likely to occur in mixed-species herds with impala than they were in single-species herds. This finding highlights the spatial benefit and altered landscape use linked with forming mixed-species herds, likely in terms of decreased risk associated with heterospecific herd mates (Beaudrot et al., 2020; Fitzgibbon, 1990; Goodale et al., 2019; Schmitt et al., 2016).

Across the landscape, zebra in mixed-species herds with impala were largely driven by the perceived risk of predation in the habitats they utilized (Figure 4.1). As Caro (2005) illustrates, anti-predator behaviour is innate, and my findings further highlight how it is possible that risk assessments likely cannot be fully overcome by the addition of a heterospecific herd mate (Stears et al., 2020), particularly if herd members do not share a common predator (Dehn, 1990; Goodale et al., 2017; Magrath et al., 2015; Seppänen et al., 2007). Zebra-impala herds were further driven by percent woody cover and distance to drainage lines; the predicted occurrence for these herd types increased in habitats with higher percent woody cover and in habitats closer to drainage lines, compared to zebra in single-species herds (Figure 4.1). As mixed-feeders, impala shift their diet selection to include a larger proportion of browse in the dry season, and therefore plausibly use habitats with greater percent woody cover as a result, which can also be associated with drainage line habitats (Demment & Van Soest, 1985; Hopcraft et al., 2010; Moe et al., 2014; O'Kane et al., 2014). During a period of diminished resource availability, habitats with increased woody cover may also offer graze in higher quantities and/or with greater nutritional quality, which could be valuable for zebra (Ludwig et al., 2004; Riginos & Grace, 2008; Treydte et al., 2007). When I examined zebra foraging behaviour with impala, I found that they experienced greater foraging efficiency and significantly less competition compared to foraging herds of zebra and wildebeest (Figure 4.1). This finding is likely because impala do not present the same competitive risk for zebra, due to their increased browse intake in the dry season (Abraham et al., 2019; Codron et al., 2007).

Moreover, in habitats where forage availability is more concentrated or nutritional quality is higher, it is possible that species utilize a smaller proportion of the habitats, likely leading to the increased foraging efficiency that I observed for zebra herding with impala, compared to wildebeest (Odadi et al., 2009; Pays et al., 2012; Pays et al., 2021; Smith et al., 2006; Smith & Cain, 2008). However, I found that zebra foraging success and anti-predator behaviour with impala remained similar to those of zebra in a single-species herd.

When I enlarged the scope of my analysis to examine anti-predator behaviour at the landscape scale, I found that zebra levelled their landscape of fear and maintained their foraging success when herding with impala in high-risk habitats (Figure 4.1). However, zebra herding with impala did not increase their foraging success in high-risk habitats compared to low-risk habitats, as they did with wildebeest. These findings highlight two, likely intertwined, potential explanations for zebra's lack of increased foraging success and stable anti-predator behaviour with impala, despite the foraging efficiency and competition benefits they experienced. First, Chen et al. (2021) showed a positive correlation between woody cover and zebra vigilance. Thus, while zebra appear to be more likely to use habitats with increased percent woody cover and/or nearer to drainage lines when they herd with impala, it is plausible that their vigilance therefore remains stable due to the increased perceived predation risk of these areas (Funston & Mills, 2006; Hayward & Kerley, 2005; Loarie et al., 2013). Second, it is likely that zebra receive very little dilution benefits when herding with impala, due to divergent common predators (Dehn, 1990; Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006). Furthermore, previous studies have shown that savanna mammals, including zebra, do not react to impala alarm calls with great intensity, suggesting they do not offer heightened detection benefits compared to other species (Meise et al., 2020; Palmer & Gross, 2018). This is likely because of the larger number of predators that pose a threat to impala, as opposed to zebra (Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006). Similarly, Schmitt et al. (2014) showed that a herd needed to be made up of at least 75% impala before zebra decreased their investment in vigilance. While I did not assess herd composition in terms of the proportion of con- and heterospecifics, it is plausible that the zebra in my study did not decrease their vigilance when foraging with impala because they do not share lions as a common predator, thus minimizing the anti-predator benefits associated therein (Dehn, 1990; Fitzgibbon, 1990; Goodale et al., 2020).

Kiffner et al. (2014) observed zebra as the nucleus of many mixed-species herds, and Pays et al. (2014) found that impala were able to adjust their vigilance behaviour when they formed mixed-species herds with zebra. As such, while zebra may not receive a quantifiable benefit to anti-predator behaviour or foraging success when foraging with impala, it is possible that the foraging behaviour of impala may benefit and/or they may experience diminished perceived predation risk with zebra and thus seek out zebra as valuable heterospecific herd mates. Future investigations should seek to assess this possibility and quantify the foraging and anti-predator behaviours of impala in mixed-species herds in the context of Kruger National Park (KNP).

Behavioural and landscape patterns of zebra herding with wildebeest

Mirroring my findings of the spatial benefit for zebra herding with impala, zebra herding with wildebeest benefitted with an intensification in predicted occurrence across 37% of the study area (Figure 4.1). As with zebra-impala herds, this finding highlights how the formation of mixed-species herds can enable herd members to alter their landscape use (Beaudrot et al., 2020; Schmitt et al., 2016; Stears et al., 2020). The greatest driver of predicted occurrence for zebra-wildebeest herds was low perceived predation risk, further supporting previous findings that certain anti-predator behaviours are innate and cannot be overcome by the addition of a heterospecific herd mate (Figure 4.1; Berger et al., 2001; Caro, 2005; Stears et al., 2020).

Predicted occurrence for zebra-wildebeest herds was also driven by percent woody cover, and they were most likely to occur in areas with lower percent woody cover (Figure 4.1). As selective grazers, this finding likely reflects wildebeests' narrow range of habitat selection, and thus zebra joining them in these areas (Martin et al., 2015; Martin & Owen-Smith, 2016; Owen-Smith & Martin, 2015; Owen-Smith et al., 2015; Yoganand & Owen-Smith, 2014). When zebra foraged with wildebeest, they experienced increased competition and lower foraging efficiency compared to zebra foraging with impala. Hansen et al. (1985) found that zebra and wildebeest in the Serengeti have a near complete dietary overlap in the dry season, possibly accounting for the increased competition and diminished foraging efficiency I observed between these species foraging together, compared to zebra foraging with impala. However, despite the costs zebra incurred while foraging with wildebeest, they also experienced significant benefits. Zebra foraging in mixed-species herds with wildebeest were able to significantly increase their foraging success compared to zebra in single-species herds (Figure 4.1). This result is likely because when zebra foraged with wildebeest, they were also able to significantly decrease their investment in vigilance, which allowed them to mitigate the foraging efficiency and competitive costs associated with wildebeest (Figure 4.1; Bodenstein et al., 2000; Hansen et al., 1985). Zebra and wildebeest share lions as a common predator (Hayward & Kerley, 2005; Owen-Smith & Mills, 2008), and the decreased vigilance that zebra were able to achieve with this herding partner further supports previous investigations into the benefits of dilution and detection in a mixed-species herd (Dehn, 1990; Goodale et al., 2020; Pays et al., 2014; Périquet et al., 2010; Schmitt et al., 2016; Stears et al., 2020). In line with my findings, Schmitt et al. (2014) observed that when zebra formed mixed-species herds with wildebeest, they were able to substantially decrease their vigilance compared to those herding with conspecifics or impala. My results further suggest that zebra take advantage of the combined dilution and detection benefits afforded to them by herding with wildebeest beyond just when they are foraging. I observed an increase in predicted occurrence for zebra-wildebeest herds in habitats closer to rivers, which can be associated with higher perceived predation risk from lions (Figure 4.1; Hopcraft et al., 2005; Schaller, 1972). During the dry season, greater vegetation biomass can be found near water sources, and the depletion of surface-water often forces in congregations of water-dependent herbivores closer to remaining water (Cain et al., 2012; Hayward & Hayward, 2012; Young et al., 2020). As with foraging behaviour, it is possible that forming mixed-species herds with wildebeest allows zebra to decrease their perceived predation risk in habitats near rivers, thus resulting in increased predicted occurrence.

At the landscape scale, zebra were further able to take advantage of the anti-predator benefits offered by forming mixed-species herds with wildebeest. In habitats with high perceived risk, zebra herding with wildebeest were able to maintain anti-predator behaviour similar to those in low perceived risk habitats. This finding supports those of Stears et al.

(2020), that by forming mixed-species herds, zebra are able to effectively level their landscape of fear. Moreover, in high perceived risk habitats, zebra were able to further take advantage of the altered landscape of fear while herding with wildebeest by achieving foraging success that was significantly greater than in habitats with low perceived risk (Figure 4.1). Because zebra have been shown to take greater risks in the dry season (Hopcraft et al., 2014), it appears that by foraging with wildebeest, zebra are able to not only take advantage of the possibly higher quantity and/or quality of forage available in risky habitats, but that they further benefit from the increased dilution and detection benefits associated with wildebeest by achieving significantly higher foraging efficiency.

It is further possible that the benefits of mixed-species herding, which zebra experienced, could be mutual for wildebeest, due to the species' similarities in terms of feeding guild, body size, and susceptibility to predation (Burkepile et al., 2013; Jarman & Sinclair, 1979; Martin & Owen-Smith, 2016; Owen-Smith & Mills, 2008). As with impala, future investigation could therefore seek to quantify potential costs and benefits for wildebeest in mixed-species herds.

Future directions

Beaudrot et al. (2020) found that mixed-species herds were more likely to occur in risky areas during a time when resources are more plentiful. The data for my study were collected during the dry season, which could therefore potentially overlook a seasonal shift in mixed-species herding behaviour. Future studies should investigate whether the drivers and context dependent benefits of mixed-species herding, which I observed among zebra during the dry season, align with those of the wet season. Resources are not as limited during the wet period (Yoganand & Owen-Smith, 2014), potentially altering the drivers of mixed-species herding and decreasing competition between foraging species (i.e., zebra and wildebeest, compared to zebra and impala), which has the potential to further magnify the benefits to foraging success that I found wildebeest offer to zebra. Alternatively, vegetation biomass is higher in the wet season, potentially limiting visibility, which could alter herbivore perception of risk, anti-predator behaviour, and landscape use, with negative potential impacts on foraging efficiency and foraging success (Chen et al., 2021; Riginos & Grace, 2008; Schmitt & Shrader, 2019; Smit & Prins, 2015; Yoganand & Owen-Smith, 2014).

Schmitt et al. (2014) found that in smaller herds, zebra were half as vigilant when they formed mixed-species herds with wildebeest, compared to zebra herding with conspecifics. In contrast, in mixed-species herds with impala, zebra only decreased their investment in vigilance when impala made up 75% of the herd (Schmitt et al., 2014). The proportion of con- and heterospecifics within a herd was not a variable my study was able to account for, due to limited sample sizes of very large and very small herds. However, my analysis of the influence that the interaction between herd type and perceived predation risk has on anti-predator behaviour suggests that herd composition (i.e., number of con- vs. heterospecifics) may clarify the patterns I observed. As such, it is possible that while zebra were able to level their landscape of fear by herding with impala, they did not increase their foraging efficiency because impala cannot offer the same dilution benefits as wildebeest (Hayward & Kerley, 2005; Hayward et al., 2006a; Hayward et al., 2006b; Hayward et al., 2006c; Hayward, 2006). Future studies could investigate the role that herd composition plays for herbivores foraging under predation risk across the landscape to further elucidate the identity-dependent costs and benefits associated with mixed-species herding for zebra.

My findings illustrate the benefits for zebra foraging in mixed-species herds with either impala or wildebeest, in terms of predicted occurrence and foraging and anti-predator behaviours. While these findings are valuable to advance the understanding of how zebra can take advantage of the intrinsic traits of their heterospecific herd mates, it is possible that that wildebeest and impala receive similar, if not greater benefits by herding with zebra. For instance, Palmer and Gross (2018) found that both impala and wildebeest responded strongly to zebra alarm calls, suggesting that in mixed-species herds, group members rely on the vigilance behaviour of zebra to inform their perception of risk. Similarly, Pays et al. (2014) observed impala decreasing their investment in vigilance behaviour when they formed mixed-species groups with zebra and/or wildebeest compared to impala-only groups. Furthermore, Ireland and Ruxton (2017) propose that zebra stripes might have evolved to act as a cue to induce mixed-species herding. Thus, future investigations could consider the overall functional significance of zebra as a herd mate for other common savanna herbivores.

CONCLUSION

The results of my study support previous investigations of the mixed-species effect, while building on the understanding of how benefits to individual anti-predator and foraging behaviour impact zebra fitness at the landscape scale. Overall, my study highlights both the innate anti-predator behaviours associated with living under the risk of predation, as well as elucidates the costs and benefits to zebra forming mixed-species herds. Thus, while zebra were able to alter their landscape use and received benefits to foraging efficiency with reduced competition in mixed-species herds with impala compared to wildebeest, these foraging benefits were not significantly different to zebra in single-species herds. However, at the landscape scale, mixed-species herding enabled zebra to level their landscape of fear, supporting the findings of a previous investigation (Stears et al., 2020). Furthermore, by forming mixed-species herds with wildebeest, zebra not only altered their landscape use, but also experienced resultant benefits to their foraging success, highlighting a more substantial influence on their risk-reward trade-off (Hebblewhite & Merrill, 2009; Houston et al., 1993; Pays et al., 2021; Stears et al., 2020). This illustrates a crucial distinction in the context-dependency associated with mixed-species herding for zebra, which likely has implications for fitness and survivorship (Ale & Brown, 2007; Fryxell et al., 2007; Hebblewhite & Merrill, 2009; Lima & Dill, 1990). It is likely that the context-dependent benefits, which I observed for zebra in mixed-species herds, are not exclusive to savanna herbivores and also play a role in shaping the risk-reward trade-off associated with mixed-species groupings among other taxa (Allan, 1986; Freeberg et al., 2017; Hogstad, 1978). Furthermore, by illustrating the identity-dependent costs and benefits for zebra foraging in mixed-species herds, my findings suggest zebra might select for the quality of social information gleaned from a heterospecific herd mate. In a changing world, it is essential for practitioners and stakeholders alike to be able to understand the processes driving herbivore community structure, to make adaptive management decisions towards successful ecosystem management and wildlife conservation.

REFERENCES

Abraham, J. O., Hempson, G. P., & Staver, A. C. (2019). Drought-response strategies of savanna herbivores. *Ecology and Evolution*, *9*(12), 7047-7056.

Abramsky, Z., Rosenzweig, M. L., & Subach, A. (2001). The cost of interspecific competition in two gerbil species. *Journal of Animal Ecology*, *70*(4), 561-567.

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

Allan, J. R. (1986). The influence of species composition on behaviour in mixed-species cyprinid shoals. *Journal of Fish Biology*, *29*, 97-106.

Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings of the Royal Society B: Biological Sciences*, *269*(1509), 2541-2550.

Anderson, T. M., Hopcraft, J. G. C., Eby, S., Ritchie, M., Grace, J., & Olff, H. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, *91*(5), 1519-1529.

Anderson, T. M., White, S., Davis, B., Erhardt, R., Palmer, M., Swanson, A., Kosmala, M., & Packer, C. (2016). The spatial distribution of african savannah herbivores: Species associations and habitat occupancy in a landscape context. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1703), 20150314.

Appleby, M. C. (1980). Social rank and food access in red deer stags. *Behaviour*, *74*(3-4), 294-309.

Arsenault, R., & Owen-Smith, N. (2008). Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, *117*(11), 1711-1717.

Arsenault, R., & Owen-Smith, N. (2011). Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa. *Canadian Journal of Zoology*, *89*(10), 900-907.

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, *49*(5), 386-400.

Bailey, D. W., Dumont, B., & WallisDeVries, M. F. (1998). Utilization of heterogeneous grasslands by domestic herbivores: Theory to management. *Animal Research*, *47*(5-6), 321-333.

Balfour, N. J., Durrant, R., Ely, A., & Sandom, C. J. (2021). People, nature and large herbivores in a shared landscape: A mixed-method study of the ecological and social outcomes from agriculture and conservation. *People and Nature*, *3*(2), 418-430.

Barnier, F., Valeix, M., Duncan, P., Chamaillé-Jammes, S., Barre, P., Loveridge, A. J., Macdonald, D. W., & Fritz, H. (2014). Diet quality in a wild grazer declines under the threat of an ambush predator. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1785), 20140446.

Barry, M. J. (1994). The costs of crest induction for Daphnia carinata. *Oecologia*, *97*(2), 278-288.

Bartlam-Brooks, H. L. A., Bonyongo, M. C., & Harris, S. (2013a). How landscape scale changes affect ecological processes in conservation areas: external factors influence land use by zebra (*Equus burchelli*) in the Okavango Delta. *Ecology and Evolution*, *3*(9), 2795-2805.

Bartlam-Brooks, H. L. A., Beck, P. S. A., Bohrer, G., & Harris, S. (2013b). In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, *118*(4), 1427-1437.

Barton, J. M., Bristow, J. W., & Venter, F. J. (1986). A summary of the precambrian granitoid rocks of the Kruger National Park. *Koedoe*, *29*(1), 39-44.

Bates, D., Mæchler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Schiepl, F., & Grothendieck, G. (2023). *Linear mixed-effects models using 'Eigen' and S4*. In *R Studio*

Beauchamp, G. (2001). Should vigilance always decrease with group size? *Behavioral Ecology and Sociobiology*, *51*(1), 47-52.

Beauchamp, G., & Ruxton, G. D. (2003). Changes in vigilance with group size under scramble competition. *The American Naturalist*, *161*(4), 672-675.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, *76*(6), 1935-1942.

Beauchamp, G. (2017). Disentangling the various mechanisms that account for the decline in vigilance with group size. *Behavioural Processes*, *136*, 59-63.

Beauchamp, G. (2019). On how risk and group size interact to influence vigilance. *Biological Reviews*, *94*(6), 1918-1934.

Beauchamp, G. (2023). Susceptibility to predation varies with body mass, foraging niche, and anti-predator responses among bird species. *Birds*, *4*(1), 73-84.

Beaudrot, L., Palmer, M. S., Anderson, T. M., & Packer, C. (2020). Mixed-species groups of Serengeti grazers: A test of the stress gradient hypothesis. *Ecology*, *101*(11).

Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology and Evolution*, *13*(7), 284-287.

Bednekoff, P. A., & Lima, S. L. (2004). Risk allocation and competition in foraging groups: Reversed effects of competition if group size varies under risk of predation. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1547), 1491-1496.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In A. Watson (Ed.), *Animal Populations in Relation to Their Food Resources* (pp. 111-124). Blackwell Scientific.

Bell, R. H. V. (1971). A grazing ecosystem in the serengeti. *Scientific American*, *225*(1), 86-93.

Ben-Shahar, R., & Coe, M. J. (1992). The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia*, *90*(3), 422-428.

Ben-Shahar, R. (1991). Selectivity in large generalist herbivores: Feeding patterns of African ungulates in a semi-arid habitat. *African Journal of Ecology*, *29*(4), 302-315.

Berger, J., Swenson, J. E., & Persson, I. L. (2001). Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science (New York, N.Y.)*, *291*(5506), 1036-1039.

Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, *76*(6), 1075-1085.

Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K. O., Giraudoux, P., Davis, M., & Santilli, S. (2023). *Interface to geometry engine- Open Source ('GEOS')*. In *R Studio* Open Source Geospatial Foundation. **https://libgeos.org/**

Bodenstein, V., Meissner, H. H., & van Hoven, W. (2000). Food selection by Burchell's zebra and blue wildebeest in the Timbavati area of the Northern Province Lowveld. *South African Journal of Wildlife Research*, *30*(2), 63-72.

Bonnet, O. J. F., Meuret, M., Tischler, M. R., Cezimbra, I. M., Azambuja, J. C. R., & Carvalho, P. C. F. (2015). Continuous bite monitoring: A method to assess the foraging dynamics of herbivores in natural grazing conditions. *Animal Production Science*, *55*(3), 339-349.

Bonyongo, M. C. (2005). Habitat utilization by impala (*Aepyceros melampus*) in the Okavango Delta. *Botswana Notes and Records*, *37*, 227-235.

Box, E. O., Holben, B. N., & Kalb, V. (1989). Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO2 flux. *Vegetatio*, *80*(2), 71-89.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*(2-3), 281-300.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology*, *82*(5), 1098-1105.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*(1), 37-47.

Brown, J. S., Laundre, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic ineractions. *Journal of Mammology*, *80*(2), 385-399.

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

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999-1014.

Burger, J., & Gochfeld, M. (1992). Effect of group size on vigilance while drinking in the coati, *Nasua narica* in Costa Rica. *Animal Behaviour*, *44*(6), 1053-1057.

Burger, J. (2001). Visibility, group size, vigilance, and drinking behavior in coati (*Nasua narica*) and white-faced capuchins (*Cebus capucinus*): Experimental evidence. *Acta Ethologica*, *3*(2), 111-119.

Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G. M., Govender, N., Nelson, V., Thompson, D. I., Zinn, A. D., & Smith, M. D. (2013). Habitat selection by large herbivores in a southern African savanna: The relative roles of bottom-up and top-down forces. *Ecosphere*, *4*(11), 1-19.

Burkepile, D. E., Thompson, D. I., Fynn, R. W. S., Koerner, S. E., Eby, S., Govender, N., Hagenah, N., Lemoine, N. P., Matchett, K. J., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K., & Smith, M. D. (2016). Fire frequency drives habitat selection by a diverse herbivore guild impacting top–down control of plant communities in an African savanna. *Oikos*, *125*(11), 1636-1646.

Butler, S. J., Whittingham, M. J., Quinn, J. L., & Cresswell, W. (2005). Quantifying the interaction between food density and habitat structure in determining patch selection. *Animal Behaviour*, *69*(2), 337-343.

Cain, J. W., Owen-Smith, N., & Macandza, V. A. (2012). The costs of drinking: Comparative water dependency of sable antelope and zebra. *Journal of Zoology*, *286*(1), 58-67.

Caraco, T. (1979). Time budgeting and group size: A test of theory. *Ecology*, *60*(3), 618-627.

Carlson, N. V., Freeberg, T. M., Goodale, E., & Theo, A. H. (2023). Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *378*(1878), 20220093.

Caro, T. M. (2005). *Antipredator Defense in Birds and Mammals*. University of Chicago Press.

Chamaillé-Jammes, S., Valeix, M., & Cromsigt, J. (2019). Predator effects on herbivore dynamics and behavior: What mechanisms lead to trophic cascades in savannas? In *Savanna Woody Plants and Large Herbivores* (pp. 279-308).

Charnov, E. (1976). Optimal foraging: The marginal value theorem. *Theoretical Population Biology*, *9*(2), 129-136.

Chen, A., Reperant, L., Fischhoff, I. R., & Rubenstein, D. I. (2021). Increased vigilance of plains zebras (*Equus quagga*) in response to more bush coverage in a Kenyan savanna. *Climate Change Ecology*, *1*(100001).

Chirima, G. J., Owen-Smith, N., & Erasmus, B. F. N. (2012). Changing distributions of larger ungulates in the Kruger National Park from ecological aerial survey data. *Koedoe*, *54*(1), 1009.

Clark, C. W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology*, *30*(1), 45-75.

Clauss, M., Steuer, P., Müller, D. W. H., Codron, D., & Hummel, J. (2013). Herbivory and body size: Allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PLOS ONE*, *8*(10), e68714.

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R., & Fourie, N. (2007). Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, *273*(1), 21-29.

Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C., & De Ruiter, D. J. (2006). Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: Spatial and landscape differences. *Journal of Mammalogy*, *87*(1), 27-34.

Colman, J. E., Tsegaye, D., Pedersen, C., Eidesen, R., Arntsen, H., Holand, O., Mann, A., Reimers, E., & Moe, S. R. (2012). Behavioral interference between sympatric reindeer and domesticated sheep in Norway. *Rangeland Ecology and Management*, *65*(3), 299-308.

Cords, M. (1987). *Mixed-species association of Cercopithecus monkeys in a Kakamega Forest, Kenya* (Vol. 117). University of California Publications in Zoology.

Courbin, N., Loveridge, A. J., Macdonald, D. W., Fritz, H., Makuwe, E. T., & Chamaillé-Jammes, S. (2016). Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, *125*(6), 829-836.

Courbin, N., Loveridge, A. J., Fritz, H., Macdonald, D. W., Valeix, M., & Chamaillé-Jammes, S. (2019). Zebra diel migrations reduce encounter risk with lions over selection for safe habitats. *Journal of Animal Ecology*, *88*(1), 92-101.

Cowlishaw, G., Lawes, M. J., Lightbody, M., Martin, A., Pettifor, R., & Rowcliffe, J. M. (2004). A simple rule for the costs of vigilance: Empirical evidence from a social forager. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1534), 27-33.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, *86*(12), 3387-3397.

Creel, S., & Winnie, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, *69*(5), 1181-1189.

Creel, S., Christianson, D., Liley, S., & Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science*, *315*(5814), 960-960.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, *23*(4), 194-201.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, *25*(4), 773-784.

Creel, S., Dröge, E., M'Soka, J., Smit, D., Becker, M., Christianson, D., & Schuette, P. (2017). The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. *Ecology*, *98*(8), 2081-2092.

Cresswell, W. (1994). Age-dependent choice of Redshank (*Tringa totanus*) feeding location: Profitability or risk? *The Journal of Animal Ecology*, *63*(3), 589-589.

Cresswell, W., & Quinn, J. L. (2011). Predicting the optimal prey group size from predator hunting behaviour. *Journal of Animal Ecology*, *80*(2), 310-319.

Cromsigt, J. P. G. M., Prins, H. H. T., & Olff, H. (2009). Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: Interaction of body mass and digestive strategy. *Diversity and Distributions*, *15*(3), 513-522.

Crosmary, W. G., Makumbe, P., Côté, S. D., & Fritz, H. (2012). Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. *Animal Behaviour*, *83*(6), 1367-1376.

Dai, X., Wu, W., Ji, L., Tian, S., Yang, B., Guan, B., & Wu, D. (2022). MaxEnt model-based prediction of potential distributions of Parnassia wightiana (Celastraceae) in China. *Biodiversity Data Journal*, *10*, e81073.

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, *20*(4), 187-193.

Danchin, É., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, *305*(5683), 487-491.

Darrah, A. J., & Smith, K. G. (2013). Comparison of foraging behaviors and movement patterns of the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) traveling alone and in mixed-species flocks in Amazonian Ecuador. *The Auk*, *130*(4), 629-636.

Davies, A. B., Robertson, M. P., Levick, S. R., Asner, G. P., Van Rensburg, B. J., Davies, C. L. P., Robertson, M. P., & Rensburg, V. (2014). Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. *Journal of Vegetation Science*, *25*(6), 1405-1416.

Davies, A. B., Cromsigt, J. P. G. M., Tambling, C. J., le Roux, E., Vaughn, N., Druce, D. J., Marneweck, D. G., & Asner, G. P. (2021). Environmental controls on African herbivore responses to landscapes of fear. *Oikos*, *130*(2), 171-186.

De Visser, S. N., Freymann, B. P., & Olff, H. (2011). The Serengeti food web: Empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology*, *80*(2), 484-494.

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., & Musiani, M. (2014). Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, *83*(2), 343-352.

Dehn, M. M. (1990). Vigilance for predators: Detection and dilution effects. *Behavioral Ecology and Sociobiology*, *26*(5), 337-342.

Dellinger, J. A., Shores, C. R., Craig, A., Heithaus, M. R., Ripple, W. J., & Wirsing, A. J. (2019). Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia*, *189*(2), 487-500.

Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*(5), 641-672.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401-406.

Doser, J. W., Leuenberger, W., Sillett, T. S., Hallworth, M. T., & Zipkin, E. F. (2022). Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources. *Methods in Ecology and Evolution*, *13*(4), 919-932.

du Toit, J. T., & Owen-Smith, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. *The American Naturalist*, *133*(5), 736-740.

du Toit, J. T., & Cumming, D. H. M. (1999). Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, *8*(12), 1643-1661.

du Toit, J. T. (2003). Large herbivores and savnna heterogeneity. In J. T. du Toit, K. H. Rogers, & H. C. Biggs (Eds.), *The Kruger Experience: Ecology and Management of Savanna Hetergeneity*. Island Press.

Dwinnell, S. P. H., Sawyer, H., Randall, J. E., Beck, J. L., Forbey, J. S., Fralick, G. L., & Monteith, K. L. (2019). Where to forage when afraid: Does perceived risk impair use of the foodscape? *Ecological Applications*, *29*(7), e01972.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend

Peterson, A., . . . E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129-151.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43-57.

Elston, D. A., Moss, R., Boulinier, C., Arrowsmith, C., & Lambim, X. (2001). Analysis of aggregation, a worked example: Number of ticks on red grouse. *Parasitology*, *122*, 563-569.

Estes, R. D. (2012). *The Behavior Guide to African Mammals - Including Hoofed Animals, Carnivores, Primates*. Berkley & Los Angeles, University of California Press.

Fairbanks, B., & Dobson, F. S. (2007). Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: Dilution versus detection. *Animal Behaviour*, *73*(1), 115-123.

Farine, D. R., Downing, C. P., & Downing, P. A. (2014). Mixed-species associations can arise without heterospecific attraction. *Behavioral Ecology*, *25*(3), 574-581.

Favreau, F. R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1690), 2089-2089.

Ferry, N., Dray, S., Fritz, H., & Valeix, M. (2016). Interspecific interference competition at the resource patch scale: Do large herbivores spatially avoid elephants while accessing water? *Journal of Animal Ecology*, *85*(6), 1574-1585.

Fisher, R., Wilson, S. K., Sin, T. M., Lee, A. C., & Langlois, T. J. (2018). A simple function for full-subsets multiple regression in ecology with R. *Ecology and Evolution*, *8*(12), 6104-6113.

Fitzgibbon, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: The antipredator benefits. *Animal Behaviour*, *39*(6), 1116-1126.

Ford, A. T., Goheen, J. R., Augustine, D. J., Kinnaird, M. F., O'Brien, T. G., Palmer, T. M., Pringle, R. M., & Woodroffe, R. (2015). Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology*, *96*(10), 2705-2714.

Fortin, D., Boyce, M. S., Merrill, E. H., & Fryxell, J. M. (2004a). Foraging costs of vigilance in large mammalian herbivores. *Oikos*, *107*(1), 172-180.

Fortin, D., Boyce, M. S., & Merrill, E. H. (2004b). Multi-tasking by mammalian herbivores: Overlapping processes during foraging. *Ecology*, *85*(8), 2312-2322.

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, *293*(5832), 466-467.

Freeberg, T. M., Eppert, S. K., Sieving, K. E., & Lucas, J. R. (2017). Diversity in mixed species groups improves success in a novel feeder test in a wild songbird community. *Scientific Reports*, *7*, 43014.

Fryxell, J. M. (1991). Forage quality and aggregation by large herbivores. *The American Naturalist*, *138*(2), 478-498.

Fryxell, J. M., Wilmshurst, J. F., & Sinclair, A. R. E. (2004). Predictive models of movement by serengeti grazers. *Ecology*, *85*(9), 2429-2435.

Fryxell, J. M., Wilmshurst, J. F., Sinclair, A. R. E., Haydon, D. T., Holt, R. D., & Abrams, P. A. (2005). Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*, *8*(3), 328-335.

Fryxell, J. M., Mosser, A., Sinclair, A. R. E., & Packer, C. (2007). Group formation stabilizes predator-prey dynamics. *Nature*, *449*(7165), 1041-1043.

Funston, P. J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *South African Journal of Wildlife Research*, *36*(1), 9-22.

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. (2003). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*, 367-393.

Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology and Evolution*, *32*(2), 88-96.

Gaylard, A., Owen-Smith, N., & Redfern, J. (2003). Surface water availability: Implications for heterogeneity and ecosystem processes. In J. T. du Toit, K. H. Rogers, & H. C. Biggs (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (pp. 171-188). Island Press.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology and Evolution*, *34*(4), 355-368.

Gentry, K. E., Roche, D. P., Mugel, S. G., Lancaster, N. D., Sieving, K. E., Freeberg, T. M., & Lucas, J. R. (2019). Flocking propensity by satellites, but not core members of mixed-species flocks, increases when individuals experience energetic deficits in a poor-quality foraging habitat. *PLOS ONE*, *14*(1), e0209680.

Gertenbach, W. P. D. (1983). Landscapes of the Kruger National Park. *Koedoe*, *26*, 9-121.

Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P., & Linnell, J. D. C. (2013). Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, *23*(7), 1722-1734.

Gil, M. A., Emberts, Z., Jones, H., & St. Mary, C. M. (2017). Social information on fear and food drives animal grouping and fitness. *The American Naturalist*, *189*(3), 227-241.

Gil, M. A., Hein, A. M., Spiegel, O., Baskett, M. L., & Sih, A. (2018). Social information links individual behavior to population and community dynamics. *Trends in Ecology and Evolution*, *33*(7), 535-548.

Giraldeau, L. A., & Beauchamp, G. (1999). Food exploitation: Searching for the optimal joining policy. *Trends in Ecology and Evolution*, *14*(3), 102-106.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution*, *25*(6), 354-361.

Goodale, E., Beauchamp, G., & Ruxton, G. D. (2017). *Mixed-Species Groups of Animals: Behavior, Community Structure, and Conservation*. Academic Press.

Goodale, E., Ruxton, G. D., & Beauchamp, G. (2019). Predator eavesdropping in a mixed-species environment: How prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. *Frontiers in Ecology and Evolution*, *7*, 431708.

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z, G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, *95*(4), 889-910.

Gordon, I. J. (1989). Vegetation community selection by ungulates on the Isle of Rhum. I. Food supply. *Journal of Applied Ecology*, *26*, 35-51.

Graves, G. R., & Gotelli, N. J. (1993). Assembly of avian mixed-species flocks in Amazonia. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(4), 1388-1391.

Greene, C. H. (1986). Patterns of prey selection: Implications of predator foraging tactics. *The American Naturalist*, *128*(6), 824-839.

Groom, R., & Harris, S. (2010). Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment. *African Journal of Ecology*, *48*(1), 159-168.

Gwynne, M. D., & Bell, R. H. V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature*, *220*(5165), 390-393.

Hack, M. A., East, R., & Rubenstein, D. I. (2002). Status and action plan for the Plains zebra (*Equus burchellii*). *Equids: zebras, asses, and horses. Status survey and conservation plan*, 43-60.

Halls, L. K. (1954). The approximation of cattle diet through herbage sampling. *Journal of Range Management*, *7*(6), 269-269.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295-311.

Hannon, M. J., Jenkins, S. H., Crabtree, R. L., & Swanson, A. K. (2006). Visibility and vigilance: Behavior and population ecology of uinta ground squirrels (*Spermophilus armatus*) in different habitats. *Journal of Mammalogy*, *87*(2), 287-295.

Hansen, R. M., Mugambi, M. M., & Bauni, S. M. (1985). Diets and trophic ranking of ungulates of the northern Serengeti. *The Journal of Wildlife Management*, *49*(3), 823-829.

Harrison, N. M., & Whitehouse, M. J. (2011). Mixed-species flocks: an example of niche construction? *Animal Behaviour*, *81*(4), 675-682.

Harrison, X. A. (2015). A comparison of observation-level randomeffect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ*, *3*, e1114.

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, *267*(3), 309-322.

Hayward, M. W., O'Brien, J., Hofmeyr, M., & Kerley, G. I. H. (2006a). Prey preferences of the African wild dog (*Lycaon pictus)* (Canidae: Carnivora): Ecological requirements for conservation. *Journal of Mammalogy*, *87*(6), 1122-1131.

Hayward, M. W., Hofmeyr, M., O'Brien, J., & Kerley, G. I. H. (2006b). 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*(4), 615-627.

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006c). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, *270*(2), 298-313.

Hayward, M. W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology*, *270*(4), 606-614.

Hayward, M. W., & Hayward, M. D. (2012). Waterhole use by African fauna. *African Journal of Wildlife Research*, *42*(2), 117-127.

Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, *80*(5), 800-809.

Hebblewhite, M., Pletscher, D. H., & Paquet, P. C. (2002). Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, *80*(5), 789-799.

Hebblewhite, M., Merrill, E. H., & McDonald, T. L. (2005). Spatial decomposition of predation risk using resource selection functions: An example in a wolf-elk predator-prey system. *Oikos*, *111*(1), 101-111.

Hebblewhite, M., & Merrill, E. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*(12), 3445-3454.

Hernández, L., & Laundré, J. W. (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk, *Cervus elaphus*, and bison, *Bison bison*. *Wildlife Biology*, *11*(3), 215-220.

Heymann, E. W., & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews*, *75*, 169-190.

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2022). *dismo: Species Distribution Modeling*. In *R package version 1.3-9* **https://CRAN.R-project.org/package=dismo**>

Hochman, V., & Kotler, B. P. (2007). Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. *Behavioral Ecology*, *18*(2), 368-374.

Hogstad, O. (1978). Differentiation of foraging niche among tits, *Paurus spp.*, in Norway during winter. *Ibis*, *120*(2), 139-146.

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*(3), 559-566.

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution*, *25*(2), 119-128.

Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E., & Olff, H. (2012). Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, *81*(1), 201-213.

Hopcraft, J. G. C., Morales, J. M., Beyer, H. L., Borner, M., Mwangomo, E., Sinclair, A. R. E., Olff, H., & Haydon, D. T. (2014). Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs*, *84*(3), 355-372.

Houston, A. I., McNamara, J. M., & Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *341*(1298), 375-397.

Illius, A., & Gordon, I. (1987). The allometry of food intake in grazing ruminants. *Journal of Animal Ecology*, *56*(3), 989-989.

Illius, A., & Fitzgibbon, C. (1994). Costs of vigilance in foraging ungulates. *Animal Behaviour*, *47*(2), 481-484.

Illius, A. (1997). Physiological adaptation in savanna ungulates. *Proceedings of the Nutrition Society*, *56*(3), 1041-1048.

Ireland, H. M., & Ruxton, G. D. (2017). Zebra stripes: an interspecies signal to facilitate mixed-species herding? *Biological Journal of the Linnean Society*, *121*(4), 947-952.

Isaacs, L., Somers, M. J., & Dalerum, F. (2013). Effects of prescribed burning and mechanical bush clearing on ungulate space use in an African savannah. *Restoration Ecology*, *21*(2), 260-266.

Janson, C. H., & Van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour*, *105*(1-2), 165-186.

Jarman, M. V., & Jarman, P. J. (1973). Daily activity of impala. *African Journal of Ecology*, *11*(1), 75-92.

Jarman, P. J., & Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In A. R. E. Sinclair & M. Norton-Griffiths (Eds.), *Serengeti: Dynamics of an Ecosystem* (pp. 130-163). University of Chicago Press.

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., Rubenstein, D. I., Wang, W., & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(26), 8019-8024.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, *10*(8), 690-700.

Kenward, R. E. (1978). Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology*, *47*(2), 449-460.

Kiffner, C., Kioko, J., Leweri, C., & Krause, S. (2014). Seasonal patterns of mixed species groups in large East African mammals. *PLOS ONE*, *9*(12), e113446.

Kiffner, C., Boyle, D. M., Denninger-Snyder, K., Kissui, B. M., Waltert, M., & Krause, S. (2022). Refining the stress gradient hypothesis for mixed species groups of African mammals. *Scientific Reports*, *12*(1), 17715.

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, *157*(1), 163-175.

Kluever, B. M., Howery, L. D., Breck, S. W., & Bergman, D. L. (2009). Predator and heterospecific stimuli alter behaviour in cattle. *Behavioural Processes*, *81*(1), 85-91.

Kotier, B. P., Brown, J., Mukherjee, S., Berger-Tal, O., & Bouskila, A. (2010). Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1687), 1469-1469.

Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford University Press.

Kruger, A. C., Makamo, L. B., & Shongwe, S. (2002). An analysis of Skukuza climate data. *Koedoe*, *45*(1), 1-7.

Kuhn, M. (2011). *The caret Package*. In *R Studio*

Langvatn, R., & Hanley, T. A. (1993). Feeding-patch choice by red deer in relation to foraging efficiency: An experiment. *Oecologia*, *95*(2), 164-170.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401-1409.

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

Laundré, J. W., Hernández, L., López Medina, P., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P., & Browning, D. M. (2014). The landscape of fear: The missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, *95*(5), 1141-1152.

Lazarus, J. (1979). The early warning function of flocking in birds: An experimental study with captive Quelea. *Animal Behaviour*, *27*(3), 855-865.

Le Saout, S., Martin, J. L., Blanchard, P., Cebe, N., Hewison, A. J. M., Rames, J. L., & Chamaillé-Jammes, S. (2015). Seeing a ghost? Vigilance and its drivers in a predator-free world. *Ethology*, *121*(7), 651-660.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008). Home range utilisation and territorial behaviour of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PLOS ONE*, *3*(12).

Leuthold, W. (1977). *African Ungulates: A Comparative Review of Their Ethology and Behavioral Ecology*. Springer Berlin Heidelberg.

Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology*, *124*(3), 303-316.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619-640.

Lima, S. L. (1990). Protective cover and the use of space: Different strategies in finches. *Oikos*, *58*(2), 151-151.

Lima, S. L. (1992). Strong preferences for apparently different habitats? A consequence of differential escape from predators. *Oikos*, *64*(3), 597-600.

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11-20.

Lima, S. L., Zollner, P. A., & Bednekoff, P. A. (1999). Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology*, *46*(2), 110-116.

Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, *153*(6), 649-659.

Lingle, S. (1993). Escape gaits of white-tailed deer, mule deer, and their hybrids: Body configuration, biomechanics, and function. *Canadian Journal of Zoology*, *71*(4), 708-724.

Loarie, S. R., Tambling, C. J., & Asner, G. P. (2013). Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour*, *85*(5), 899-906.

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., Findholt, S. L., Dick, B. L., & Kie, J. G. (2016). Linking habitat selection to fitness-related traits in herbivores: The role of the energy landscape. *Oecologia*, *181*(3), 709-720.

Longland, W. S., & Price, M. V. (1991). Direct observations of owls and heteromyid rodents: Can predation risk explain microhabitat use? *Ecology*, *72*(6), 2261-2273.

Ludwig, F., De Kroon, H., Berendse, F., & Prins, H. H. T. (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, *170*, 93-105.

Macandza, V. A. (2010). *Resource partitioning between low-density and high-density grazers : sable antelope, zebra and buffalo* University of Witwatersrand]. **http://hdl.handle.net/10539/7640**

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603-609.

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behavioral Ecology*, *20*(4), 745-752.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560-586.

Makin, D. F., Payne, H. F. P., Kerley, G. I. H., & Shrader, A. M. (2012). Foraging in a 3-D world: How does predation risk affect space use of vervet monkeys? *Journal of Mammalogy*, *93*(2), 422-428.

Makin, D. F., Chamaillé-Jammes, S., & Shrader, A. M. (2017). Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal Behaviour*, *127*, 225-231.

Makin, D. F., Chamaillé-Jammes, S., & Shrader, A. M. (2018). Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. *Journal of Mammalogy*, *99*(2), 341-350.

Mandinyenya, B., Monks, N., Mundy, P. J., Sebata, A., & Chirima, A. (2020). Habitat choices of African buffalo (*Syncerus caffer*) and plains zebra (*Equus quagga*) in a heterogeneous protected area. *Wildlife Research*, *47*(2), 137-145.

Marshal, J. P., Rajah, A., Parrini, F., Henley, M., Henley, S. R., & Erasmus, B. F. N. (2011). Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. *European Journal of Wildlife Research*, *57*(3), 537-548.

Martin, J., Benhamou, S., Yoganand, K., & Owen-Smith, N. (2015). Coping with spatial heterogeneity and temporal variability in resources and risks: Adaptive movement behaviour by a large grazing herbivore. *PLOS ONE*, *10*(2), e0118461.

Martin, J., & Owen-Smith, N. (2016). Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour*, *116*, 163-170.

Martínez-Abraín, A. (2008). Statistical significance and biological relevance: A call for a more cautious interpretation of results in ecology. *Acta Oecologica*, *34*(1), 9-11.

Martz, F. A., & Belyea, R. L. (1986). Role of particle size and forage quality in digestion and passage by cattle and sheep. *Journal of Dairy Science*, *69*(7), 1996-2008.

Matter, W. J., & Mannan, W. R. (2005). How do prey persist? *Journal of Wildlife Management*, *69*(4), 1315-1320.

McArthur, C., Orlando, P., Banks, P. B., & Brown, J. S. (2012). The foraging tightrope between predation risk and plant toxins: A matter of concentration. *Functional Ecology*, *26*(1), 74-83.

McCain, C. M., King, S. R. B., & Szewczyk, T. M. (2021). Unusually large upward shifts in cold-adapted, montane mammals as temperature warms. *Ecology*, *102*(4), e03300.

McNaughton, S. J., & Georgiadis, N. J. (2003). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, *17*(1), 39-66.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2020). Alarm communication networks as a driver of community structure in African savannah herbivores. *Ecology Letters*, *23*(2), 293-304.

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1833), 20160456.

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36*(10), 1058-1069.

Metcalfe, N. B. (1984). The effects of habitat on the vigilance of shorebirds: Is visibility important? *Animal Behaviour*, *32*(4), 981-985.

Milan, D., Heritage, G., & Tooth, S. (2018). *Dataset record: Kruger National Park rivers LiDAR data*.

Minderman, J., Lind, J., & Cresswell, W. (2006). Behaviourally mediated indirect effects: Interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology*, *75*(3), 713-723.

Mitchell, M. S., & Powell, R. A. (2012). Foraging optimally for home ranges. *Journal of Mammalogy*, *93*(4), 917-928.

Moe, S. R., Rutina, L. P., & du Toit, J. T. (2007). Trade-off between resource seasonality and predation risk explains reproductive chronology in impala. *Journal of Zoology*, *273*(3), 237-243.

Moe, S. R., Rutina, L., Hytteborn, H., & Du Toit, J. T. (2014). Impala as controllers of elephant-driven change within a savanna ecosystem. In C. Skarpe, J. T. du Toit, & S. R. Moe (Eds.), *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National Park, Botswana* (pp. 154-171). John Wiley & Sons, Ltd.

Morrison, T. A., Merkle, J. A., Hopcraft, J. G. C., Aikens, E. O., Beck, J. L., Boone, R. B., Courtemanch, A. B., Dwinnell, S. P., Fairbanks, W. S., Griffith, B., Middleton, A. D., Monteith, K. L., Oates, B., Riotte-Lambert, L., Sawyer, H., Smith, K. T., Stabach, J. A., Taylor, K. L., & Kauffman, M. J. (2021). Drivers of site fidelity in ungulates. *Journal of Animal Ecology*, *90*(4), 955-966.

Muposhi, V. K., Gandiwa, E., Chemura, A., Bartels, P., Makuza, S. M., & Madiri, T. H. (2016). Habitat heterogeneity variably influences habitat selection by wild herbivores in a semi-arid tropical savanna ecosystem. *PLOS ONE*, *11*(9), e0163084.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian Journal of Zoology*, *2*(1), 9-65.

O'Connor, T. G., Puttick, J. R., & Hoffman, M. T. (2014). Bush encroachment in southern Africa: Changes and causes. *African Journal of Range and Forage Science*, *31*(2), 67-88.

O'Kane, C. A. J., Page, B. R., & Macdonald, D. W. (2014). Differing influences of resource availability on the demographics and habitat selection of wildebeest compared with impala. *Journal of Tropical Ecology*, *30*(3), 189-198.

Odadi, W. O., Okeyo-Owuor, J. B., & Young, T. P. (2009). Behavioural responses of cattle to shared foraging with wild herbivores in an East African rangeland. *Applied Animal Behaviour Science*, *116*(2-4), 120-125.

Okello, M. M., Wishitemi, R. E. L., & Muhoro, F. (2002). Forage intake rates and foraging efficiency of free-ranging zebra and impala. *South African Journal of Wildlife Research*, *32*(2), 93-100.

Orrock, J. L., Danielson, B. J., & Brinkerhoff, R. J. (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology*, *15*(3), 433-437.

Owen-Smith, N., & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs*, *76*(1), 73-92.

Owen-Smith, N., & Mills, M. G. L. (2008). Predator-prey size relationships in an African large-mammal food web. *Animal Ecology*, *77*(1), 173-183.

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2267-2278.

Owen-Smith, N., & Martin, J. (2015). Identifying space use at foraging arena scale within the home ranges of large herbivores. *PLOS ONE*, *10*(6), e0128821.

Owen-Smith, N., Martin, J., & Yoganand, K. (2015). Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere*, *6*(9), 1-17.

Owen-Smith, N., & Traill, L. W. (2017). Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food? *Journal of Zoology*, *303*(4), 281-290.

Owen-Smith, N. (2019). Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological Conservation*, *232*, 51-58.

Padié, S., Morellet, N., Hewison, A. J. M., Martin, J. L., Bonnot, N., Cargnelutti, B., & Chamaillé-Jammes, S. (2015). Roe deer at risk: Teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos*, *124*(11), 1536-1546.

Paijmans, K. C., Booth, D. J., & Wong, M. Y. L. (2019). Towards an ultimate explanation for mixed-species shoaling. *Fish and Fisheries*, *20*(5), 921-933.

Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: Antipredator responses vary according to signaller reliability. *Animal Behaviour*, *137*, 1-9.

Palmer, T. M., Stanton, M. L., & Young, T. P. (2003). Competition and coexistence: Exploring mechanisms that restrict and maintain diversity within mutualist guilds. *The American Naturalist*, *162*(S4), S63-S79.

Paulo Breviglieri, C. B., Oliveira, P. S., & Romero, G. Q. (2017). Fear mediates trophic cascades: Nonconsumptive effects of predators drive aquatic ecosystem function. *The American Naturalist*, *189*(5), 490-500.

Pays, O., Renaud, P. C., Loisel, P., Petit, M., Gerard, J. F., & Jarman, P. J. (2007). Prey synchronize their vigilant behaviour with other group members. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1615), 1287-1291.

Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. (2012). Detecting predators and locating competitors while foraging: An experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, *169*(2), 419-430.

Pays, O., Ekori, A., & Fritz, H. (2014). On the advantages of mixed-species groups: Impalas adjust their vigilance when associated with larger prey herbivores. *Ethology*, *120*(12), 1207-1216.

Pays, O., Blanchard, P., Chamaillé-Jammes, S., Valeix, M., Loveridge, A. J., Macdonald, D. W., Périquet, S., Van der Meer, E., Duncan, P., Mtare, G., & Fritz, H. (2021). Disentangling the roles of bottom-up and top-down drivers in the trade-off between food acquisition and safety in prey with multiple predators. *Functional Ecology*, *35*(2), 435-449.

Pérez-Barbería, F. J., & Gordon, I. J. (2001). Relationships between oral morphology and feeding style in the ungulata: A phylogenetically controlled evaluation. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1471), 1023-1032.

Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W., & Fritz, H. (2010). Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour*, *79*(3), 665-671.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., MacDonald, D. W., & Loveridge, A. J. (2012). Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, *23*(5), 970-976.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15-27.

Phillips, S. B., Aneja, V. P., Kang, D., & Arya, S. P. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3-4), 231-259.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161-175.

Potvin, C., & Roff, D. A. (1993). Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology*, *74*(6), 1617-1628.

Prache, S., Gordon, I. J., & Rook, A. J. (1998). Foraging behaviour and diet selection in domestic herbivores. *Animal Research*, *47*(5-6), 335-345.

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, *86*(2), 501-509.

Pringle, R. M., Palmer, T. M., Goheen, J. R., McCauley, D. J., & Keesing, F. (2011). Ecological importance of large herbivores in the Ewaso ecosystem. *Smithsonian Contributions to Zoology*, *632*(632), 43-53.

Pringle, R. M., Kartzinel, T. R., Palmer, T. M., Thurman, T. J., Fox-Dobbs, K., Xu, C. C. Y., Hutchinson, M. C., Coverdale, T. C., Daskin, J. H., Evangelista, D. A., Gotanda, K. M., A. Man in ’t Veld, N., Wegener, J. E., Kolbe, J. J., Schoener, T. W., Spiller, D. A., Losos, J. B., & Barrett, R. D. H. (2019). Predator-induced collapse of niche structure and species coexistence. *Nature*, *570*(7759), 58-64.

Prins, H. H. T., De Boer, W. F., Van Oeveren, H., Correia, A., Mafuca, J., & Olff, H. (2006). Co-existence and niche segregation of three small bovid species in southern Mozambique. *African Journal of Ecology*, *44*(2), 186-198.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, *38*(2), 419-422.

Qgis.org. (2022). *QGIS Geographic Information System*. In *Open Source Geospatial Foundation Project* **http://www.qgis.org**

Radloff, F. G. T., & du Toit, J. T. (2004). Large predators and their prey in a southern African savanna: A predator's size determines its prey size range. *Journal of Animal Ecology*, *73*(3), 410-423.

Riginos, C., & Grace, J. B. (2008). Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology*, *89*(8), 2228-2238.

Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, *84*(1), 124-133.

Rind, M. I., & Phillips, C. J. C. (1999). The effects of group size on the ingestive and social behaviour of grazing dairy cows. *Animal Science*, *68*(4), 589-596.

Ripple, W. J., & Beschta, R. L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management*, *230*(1-3), 96-106.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science advances*, *1*(4), e1400103.

Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., Bennett, E. L., Beschta, R. L., Bruskotter, J. T., Campos-Arceiz, A., Corlett, R. T., Darimont, C. T., Dickman, A. J., Dirzo, R., Dublin, H. T., Estes, J. A., Everatt, K. T., Galetti, M., Goswami, V. R., . . . Zhang, L. (2017a). Conserving the world's megafauna and biodiversity: The fierce urgency of now. *BioScience*, *67*(3), 197-200.

Ripple, W. J., Wolf, C., Newsome, T. M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I., & Laurence, W. F. (2017b). World scientists' warning to humanity: A second notice. *BioScience*, *67*(12), 1026-1028.

Rodewald, P. G., & Brittingham, M. C. (2002). Habitat use and behavior of mixed species landbird flocks during fall migration. *Wilson Bulletin*, *114*(1), 87-98.

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, *62*(2), 327-335.

Rubenstein, D. I. (2010). Ecology, social behavior, and conservation in zebras. *Advances in the Study of Behavior*, *42*, 231-258.

Ryan, S. J., Knechtel, C. U., & Getz, W. M. (2007). Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*). *Behavioral Ecology*, *18*(4), 635-644.

SANParks. (2019a). *Kruger National Parks biodiversity statistics*. **https://www.sanparks.org/parks/kruger/conservation/scientific/ff/biodiversity_statistics.php**

SANParks. (2019b). *Kruger National Parks conservation scientific maps*. **https://www.sanparks.org/parks/kruger/conservation/scientific/maps/maps_environment.php**

Sansom, A., Cresswell, W., Minderman, J., & Lind, J. (2008). Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Animal Behaviour*, *75*(6), 1869-1875.

Schaller, G. B. (1972). *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press.

Scheel, D. (1993). Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Animal Behaviour*, *46*(4), 695-704.

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

Schmitt, M. H., Stears, K., & Shrader, A. M. (2016). Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral Ecology*, *27*(4), 1073-1077.

Schmitt, M. H., & Shrader, A. M. (2019). Browser population–woody vegetation relationships in savannas. In *Savanna Woody Plants and Large Herbivores* (pp. 245-278). John Wiley & Sons, Ltd.

Schmitt, M. H., Stears, K., Donovan, M. K., Burkepile, D. E., & Thompson, D. I. (2022). Integrating herbivore assemblages and woody plant cover in an African savanna to reveal how herbivores respond to ecosystem management. *PLOS ONE*, *17*(8), e0273917.

Schmitz, O. J. (2008). Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 133-152.

Scholes, R. J., Gureja, N., Giannecchinni, M., Dovie, D., Wilson, B., Davidson, N., Piggott, K., McLoughlin, K., van der Velde, K., Freeman, A., Bradley, S., Smart, R., & Ndala, S. (2001). The environment and vegetation of the flux measurement site near Skukuza, Kruger National Park. *Koedoe*, *44*(1), a187.

Scholtz, R., Kiker, G. A., Smit, I. P. J., & Venter, F. J. (2014). Identifying drivers that influence the spatial distribution of woody vegetation in Kruger National Park, South Africa. *Ecosphere*, *5*(6), 1-12.

Seeber, P. A., Franz, M., Greenwood, A. D., & East, M. L. (2019). Life history stage and extrinsic factors affect behavioural time allocation in plains zebras (*Equus quagga*) in the Serengeti ecosystem. *Behavioral Ecology and Sociobiology*, *73*, 126.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies: Landscape ecology can enhance traditional foraging theory. *BioScience*, *37*(11), 789-799.

Seppänen, J. T., Forsman, J. T., Monkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, *88*(7), 1622-1633.

Sheriff, M. J., Peacor, S. D., Hawlena, D., & Thaker, M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology*, *89*(6), 1302-1316.

Shi, J., & Dunbar, R. I. M. (2006). Feeding competition within a feral goat population on the Isle of Rùm, NW Scotland. *Journal of Ethology*, *24*(2), 117-124.

Shi, J., Beauchamp, G., & Dunbar, R. I. M. (2010). Group-size effect on vigilance and foraging in a predator-free population of feral goats (*Capra hircus*) on the Isle of Rùm, NW Scotland. *Ethology*, *116*(4), 329-337.

Shipley, L. A. (2007). The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, *116*(12), 1964-1974.

Shrader, A. M., Kerley, G. I. H., Kotler, B. P., & Brown, J. S. (2007). Social information, social feeding, and competition in group-living goats (*Capra hircus*). *Behavioral Ecology*, *18*(1), 103-107.

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *The American Naturalist*, *139*(5), 1052-1069.

Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. In P. Barbarosa & I. Castellanos (Eds.), *Ecology Of Predator-Prey Interactions* (pp. 240-255). Oxford University PressNew York, NY.

Sinclair, A. R., & Arcese, P. (1995). Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology*, *76*(3), 882-891.

Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology*, *54*(3), 899-918.

Sitati, N., Lekishon, K., Bakari, S., Warinwa, F., Mwiu, S. N., Gichohi, N., Bitok, E., Mwita, M., Ija, H. K., Mukeka, J., Sitati, N., Lekishon, K., Bakari, S., Warinwa, F., Mwiu, S. N., Gichohi, N., Bitok, E., Mwita, M., Ija, H. K., & Mukeka, J. (2014). Wildebeest (*Connochaetes taurinus*) population densities and distribution in dry and wet season in the Kilimanjaro Landscape. *Natural Resources*, *5*(13), 810-821.

Skinner, J. D., & Chimimba, C. T. (2005). *The Mammals of the Southern African Sub-Region*. Cambridge University Press.

Smit, I. P. J., & Prins, H. H. T. (2015). Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. *PLOS ONE*, *10*(9), e0137857.

Smith, D. G., Cuddeford, D., & Pearson, R. A. (2006). The effect of extended grazing time and supplementary forage on the dry matter intake and foraging behaviour of cattle kept under traditional African grazing systems. *Tropical Animal Health and Production*, *38*(1), 75-84.

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019). Integrating temporal refugia into landscapes of fear: Prey exploit predator downtimes to forage in risky places. *Oecologia*.

Smith, S. M., & Cain, J. W. (2008). Foraging efficiency and vigilance behaviour of impala: The influence of herd size and neighbour density. *African Journal of Ecology*, *47*(1), 109-118.

Snaith, T. V., & Chapman, C. A. (2008). Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behavioral Ecology*, *19*(6), 1289-1296.

Stears, K., & Shrader, A. M. (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.

Stears, K., Schmitt, M. H., Wilmers, C. C., & Shrader, A. M. (2020). Mixed-species herding levels the landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1922), 20192555.

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. *Mammal Review*, *33*(3-4), 205-223.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Steuer, P., Südekum, K. H., Müller, D. W. H., Franz, R., Kaandorp, J., Clauss, M., & Hummel, J. (2011). Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *160*(3), 355-364.

Steuer, P., Südekum, K. H., Müller, D. W. H., Kaandorp, J., Clauss, M., & Hummel, J. (2013). Fibre digestibility in large herbivores as related to digestion type and body mass - An in vitro approach. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *164*(2), 319-326.

Stutz, R. S., Bergvall, U. A., Leimar, O., Tuomi, J., & Rautio, P. (2018). Cohesiveness reduces foraging efficiency in a social herbivore. *Animal Behaviour*, *135*, 57-68.

Swanepoel, L. H., Lindsey, P., Somers, M. J., van Hoven, W., & Dalerum, F. (2013). Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation*, *16*(1), 41-50.

Testa, F., Marano, G., Ambrogi, F., Boracchi, P., Casula, A., Biganzoli, E., & Moroni, P. (2017). Study of the association of atmospheric temperature and relative humidity with bulk tank milk somatic cell count in dairy herds using Generalized additive mixed models. *Research in Veterinary Science*, *114*, 511-517.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., & Slotow, R. (2010). Group dynamics of zebra and wildebeest in a woodland savanna: Effects of predation risk and habitat density. *PLOS ONE*, *5*(9), 1-6.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, *92*(2), 398-407.

Theo, A. H., & Shanker, K. (2023). Mixed-species groups of herbivorous reef fishes show variable responses to ecosystem perturbations in the Lakshadweep Islands, India. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878).

Treydte, A. C., Heitkönig, I. M. A., Prins, H. H. T., & Ludwig, F. (2007). Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*(4), 197-205.

Turkington, R. (2009). Top-down and bottom-up forces in mammalian herbivore – vegetation systems: An essay review. *Botany*, *87*(8), 723-739.

Underwood, R. (1982). Vigilance Behaviour in Grazing African Antelopes. *Behaviour*, *79*(2/4), 81-107.

Ungar, E. D., & Noy-Meir, I. (1988). Herbage intake in relation to availability and sward structure: Grazing processes and optimal foraging. *Journal of Applied Ecology*, *25*(3), 1045-1045.

Urban, M., Berger, C., Mudau, T. E., Heckel, K., Truckenbrodt, J., Odipo, V. O., Smit, I. P. J., & Schmullius, C. (2018). Surface moisture and vegetation cover analysis for drought monitoring in the southern Kruger National Park using Sentinel-1, Sentinel-2, and Landsat-8. *Remote Sensing*, *10*(9), 1482.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F., & Madzikanda, H. (2008). The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, *46*(3), 402-410.

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

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2009b). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, *63*(10), 1483-1494.

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

van Beest, F. M., Mysterud, A., Loe, L. E., & Milner, J. M. (2010). Forage quantity, quality and depletion as scaledependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology*, *79*(4), 910-922.

van Buskirk, J., & Yurewicz, K. L. (1998). Effects of predators on prey growth rate: Relative contributions of thinning and reduced activity. *Oikos*, *82*(1), 20-20.

Van der Meer, E., Pays, O., & Fritz, H. (2012). The effect of simulated African wild dog presence on anti-predator behaviour of kudu and impala. *Ethology*, *118*(10), 1018-1027.

Van der Merwe, J., & Marshal, J. P. (2012). Hierarchical resource selection by impala in a savanna environment. *Austral Ecology*, *37*(3), 401-412.

van Hoven, W. (1996). The natural diet of game. In J. L. van Schaik (Ed.), *Game Ranch Management* (pp. 176-191).

van Langevelde, F., Suselbeek, L., & Brown, J. S. (2022). Modeling vigilance in mixed-species groups. *Natural Resource Modeling*, *35*(2), e12340.

Veit, R. R., & Harrison, N. M. (2017). Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. *Frontiers in Ecology and Evolution*, *5*, 291697.

Venter, F. J., Scholes, R. J., & Eckhardt, H. C. (2003). The abiotic template and its associated vegetation pattern. In J. T. du Toit, K. H. Rogers, & H. C. Biggs (Eds.), *The Kruger*

Experience: Ecology and Management of Savanna Heterogeneity (pp. 83-129). Island Press.

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, *30*(2), 405-422.

Wallis De Vries, M. F. (1995). Estimating forage intake and quality in grazing cattle: A reconsideration of the hand-plucking method. *Journal of Range Management*, *48*, 370-375.

Ward, A. J. W., Axford, S., & Krause, J. (2002). Mixed-species shoaling in fish: The sensory mechanisms and costs of shoal choice. *Behavioral Ecology and Sociobiology*, *52*(3), 182-187.

Watts, D. P. (1985). Relations between group size and composition and feeding competition in mountain gorilla groups. *Animal Behaviour*, *33*(1), 72-85.

Winnie, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, *12*, 88-94.

Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007). Living on the edge: Dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour*, *74*(1), 93-101.

Wirsing, A. J., Cameron, K. E., & Heithaus, M. R. (2010). Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, *79*(3), 531-537.

Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., & Schmitz, O. J. (2021). The context dependence of non-consumptive predator effects. *Ecology Letters*, *24*(1), 113-129.

Wood, S. (2017). *Generalized Additive Models: An Introduction with R* (2 ed.). Chapman & Hall.

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography*, *37*(10), 969-982.

Young, C., Fritz, H., Smithwick, E. A. H., & Venter, J. A. (2020). The landscape-scale drivers of herbivore assemblage distribution on the central basalt plains of Kruger National Park. *Journal of Tropical Ecology*, *36*(1), 13-28.

Young, H. S., McCauley, D. J., Helgen, K. M., Goheen, J. R., Otárola-Castillo, E., Palmer, T. M., Pringle, R. M., Young, T. P., & Dirzo, R. (2013). Effects of mammalian herbivore declines on plant communities: Observations and experiments in an African savanna. *Journal of Ecology*, *101*(4), 1030-1041.

Zalewska, K., Waggershauser, C. N., Kortland, K., & Lambin, X. (2021). The best defence is not being there: avoidance of larger carnivores is not driven by risk intensity. *Journal of Zoology*, *315*(2), 110-122.

Zou, F., Chen, G., Yang, Q., & Fellowes, J. R. (2011). Composition of mixed-species flocks and shifts in foraging location of flocking species on Hainan Island, China. *Ibis*, *153*(2), 269-278.

Zou, F., Jones, H., Colorado Z, G. J., Jiang, D., Lee, T. M., Martínez, A., Sieving, K., Zhang, M., Zhang, Q., & Goodale, E. (2018). The conservation implications of mixed-species flocking in terrestrial birds, a globally-distributed species interaction network. *Biological Conservation*, *224*, 267-276.