Mammalian herbivore resting behaviour under varying degrees of predation risk

by

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ABSTRACT

MAMMALIAN HERBIVORE RESTING BEHAVIOUR UNDER VARYING DEGREES OF PREDATION RISK

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Rest forms a crucial part of mammalian activity budgets and health. Yet, little research has been done on resting behaviour and the drivers behind resting behaviour. It has been suggested that predation risk, in particular, affects prey activity budgets and behaviour, and could potentially affect prey resting behaviour. Furthermore, factors such as weather, habitat, herd size, and position in the herd may also affect prey behaviour, but the effect of these factors on resting behaviour is still unknown. Thus, the purpose of this study was to explore these factors and how they may affect the resting behaviour of impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchelli*).

In my first data chapter, I collected observational data during the day from five study sites in KwaZulu-Natal that varied with regards to predator composition, and thus predation risk. I found that predation risk affected zebra resting probabilities, but not the likelihood of impala or wildebeest resting. Furthermore, I found that herd size, the interaction between predation risk and vegetation cover, position in the herd, and time of day affected the probability of zebra resting. However, only herd size affected impala rest. Surprisingly, none of the factors considered affected the probability of wildebeest resting. I suggest that

wildebeest and impala could rest more at night than during the day, and that when rest occurs during the day, it is relatively random. Ultimately, the findings from my first data chapter highlight the species-specific differences in resting behaviour and that predation risk does affect resting behaviour, but not as universally as expected.

The results from my first data chapter led me to further investigate wildebeest resting behaviour in my second data chapter. I used GPS data collected from collared wildebeest within Hluhluwe-iMfolozi Park in KwaZulu-Natal, and previously analysed lion habitat use and vegetation data. I found that wildebeest were much more likely to rest at night than during the day. However, when they did rest during the day, both vegetation cover and lion density had negligible effects. By contrast, at night the probability of a wildebeest resting was highest in areas with low lion densities, irrespective of vegetation cover. However, as predation risk increased, the probability of wildebeest resting decreased, specifically in more densely vegetated areas. These findings highlight that wildebeest resting probabilities are affected more by the long- and short-term habitat use by lions, than indirect proxies of predation risk (like vegetation cover). Ultimately, the results from both data chapters imply that predation risk plays a key role in determining prey resting probabilities, but other social, spatial, and temporal factors are also involved.

DISSERTATION LAYOUT

This dissertation consists of four chapters. Due to the overlap between the data chapters, some repetition is unavoidable. The first chapter is a literature review discussing rest and why it is a crucial part of animal activity budgets, which in turn explains why it is crucial for us to understand its drivers. Furthermore, I discuss the factors affecting resting behaviour in detail, with a specific focus on predation risk.

In the second chapter (first data chapter) I investigate the daytime resting behaviours of zebra, impala, and wildebeest under varying degrees of predation risk. Prey behaviour is affected by age, sex, body size, breeding phase, and predation risk (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009). This leads to individual and species-specific differences in behaviour, and causes individuals and species to adjust their behaviours differently in reaction to weather, diet quality, habitat characteristics, predation risk at the current site (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009), herd size, and position in the herd (Creel & Winnie, 2005; Lingle, 2001; Quinn & Cresswell, 2006; Valeix et al., 2009a). Specifically, I investigate the social (herd size and position in the herd), spatial (vegetation cover), and temporal (time of day) aspects of rest.

In the third chapter (second data chapter) I focused on wildebeest resting behaviour throughout the diel cycle. It has been suggested that wildebeest mostly feed at night and rest during the day as driven by predation risk and temperature (Maloney et al., 2005). However, prey behaviour changes with predation risk, which varies across the landscape and the diel cycle (Makin et al., 2017). Yet, predator preferences in terms of landscape and timing of activities do not guarantee that predators always abide by those preferences (Broekhuis et al., 2014). As such, in this chapter I focused on whether the long-term presence of lion and the vegetation density affect wildebeest resting probabilities throughout the diel cycle. Both data chapters are written in the format of scientific papers.

In chapter 4, I make connections between the results from my two data chapters to what is already known about resting behaviour. In addition, I explore how these results expand our understanding of the influence of predation risk on prey behaviour, specifically resting behaviour. Lastly, I make suggestions for future research into prey resting behaviour. This thesis is concluded with a single separate reference list formatted according to the journal for Animal Behaviour.

LIST OF ABBREVIATIONS

AWD	African Wild Dog
DL	Duiker Lodge
GPS	Global Positioning System
HiP	Hluhluwe-iMfolozi Park
KZN	KwaZulu-Natal
SP	Sunset Plains

DECLARATION

I, Biance Teseling, declare that the dissertation/thesis, which I hereby submit for the degree MSc Zoology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

ETHICS STATEMENT

The author, whose name appears on the title page of this dissertation/thesis, has obtained, for the research described in this work, the applicable research ethics approval (NAS333/2021).

The author declares that s/he has observed the ethical standards required in terms of the University of Pretoria's Code of Ethics for Researchers and the Policy guidelines for responsible research.

Signature:

Student name: Biance Teseling

Date: 13 December 2023

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CHAPTER 1   GENERAL INTRODUCTION

1.1   BACKGROUND AND SCOPE

Animals have limited time each day to engage in different essential behaviours (Dunbar et al., 2009). Thus, the partitioning of time between behaviours has a significant impact on the survival of a species due to the benefits and costs related to each behaviour (Nakayama et al., 1999; Watts, 1988). These behaviours include feeding, mating, ruminating (not applicable to non-ruminants), moving between resources, escaping from predators, vigilance, grooming, and resting (Jaman & Huffman, 2008; Jarman & Jarman, 1973).

The proportion of time different animal species spend on essential behaviours depends on their body size, age, sex, metabolic requirements, thermoregulatory methods, social structure, season, and predation pressure (Herbers, 1981). Additionally, in the short term, the need for an activity can be influenced by preceding active behaviours. For example, if there is increased energy expenditure due to escaping from predators, an individual would have to recover from muscle fatigue and thermal stresses (Janczarek et al., 2022) as well as replace energy spent (Portugal et al., 2016). Furthermore, due to limited time each day, time spent on one behaviour limits the time an individual can spend on other behaviours (Dunbar et al., 2009). For example, under high predation pressure animals will, on average, spend more time escaping from predators and being vigilant and likely less time grooming, mating, or resting. Yet, due to the importance of rest with regards to crucial restorative processes in the body (e.g., maintenance of the immune system, synaptic plasticity; Imeri & Opp, 2009; Mignot, 2008) the proportion of time spent foraging and territorial behaviours are more likely to change than the proportion of time spent resting (Herbers, 1981; Post, 1974; Stiles, 1971; Wolf & Hainsworth, 1971).

Resting, although crucial, makes an individual more vulnerable to predation and reduces opportunities for foraging and reproducing, thus the circumstances surrounding resting should be chosen wisely as to minimize costs (Brown, 1988). Thus, understanding

the circumstances surrounding rest is crucial for conservation. Yet, this part of research has been neglected, and research has primarily focused on the active portion of animals' time budgets (Shukla et al., 2021). Furthermore, when resting is researched, it is generally done in laboratories where ecological drivers such as predation risk, light, food availability, vegetation cover, temperature, and wind are neglected (Acerbi et al., 2008; Rattenborg et al., 2017; Voirin et al., 2014). Of the ecological drivers of rest neglected in laboratories, predation risk in particular could have a large impact on rest, leading to changes in resting location, the timing of rest, the sociality of rest, or a combination of strategies (Shukla et al., 2021). For example, horses (*Equus caballus*; Ruckebusch, 1972) and donkeys (*E. asinus*; Ruckebusch, 1963) slept for approximately 3 hours per 24 hrs, all of which were at night, when no predators were present, while under the same circumstances, cattle slept for 4 hours per 24 hrs, almost all of which was at night (Ruckebusch et al., 1974). Yet, when predation risk was increased by moving cows to a pasture, their total sleep duration decreased to ~2 hours per 24 hrs (Ruckebusch et al., 1974). To expand our understanding of rest in free-ranging herbivores, I explored the spatial, temporal, and social aspects of rest by focusing on the passive portion of zebra, impala, and wildebeests' time budgets in the wild under the influence of varying predation pressures.

My study focused on the influence of predation risk on prey resting behaviours during the transitional period between the dry and wet seasons (April and May 2022). I collected observational data on zebra, wildebeest, and impala from five study sites in KwaZulu-Natal, with varying predator compositions. This data was then used to determine the effect of different factors influencing prey behaviours, with a specific focus on predation risk, on the probability of an individual resting. The factors studied were predation risk (determined by predator composition at the study site), vegetation cover, herd size, time of day, and position in the herd. Additionally, I used previously collected GPS collar data from wildebeest within Hluhluwe-iMfolozi Park (HiP) in KZN to determine the influence of location specific lion activity, vegetation cover, and whether it was day or night on the probability of wildebeest resting.

1.2   WHAT IS REST?

There is no workable definition of rest in mammals. Siegel (2008), while focusing on neuroscience, described rest for animals as a rapidly reversible dormant state of relatively

short duration (<24 hours) within which the animal shows lowered sensory responsiveness and activity. Another important criterion for the definition of resting, but sleep specifically, is that a loss of sleep is followed by an increased need for rest (Lima et al., 2005). Lastly, some form of resting is universal across all taxa (Joiner, 2016; Siegel, 2009). This broad definition includes sleeping and being inactive (i.e., quiet wakefulness or laziness), but excludes torpor and hibernation which have distinct physiological correlates.

Different mammalian activity budget studies have used different species-specific definitions for resting. For example, a study on Japanese macaques described resting as a state where no other behaviours occur, regardless of posture (Jaman & Huffman, 2008). For mountain gorilla, rest was defined as a stationary behaviour during which the animal was not feeding nor engaging in social interactions, which specifically included sleeping (eyes closed) and autogrooming (Watts, 1988). For giraffe, the specific posture of lying down was used to identify rest (Burger et al., 2020). A study on steenbok, impala, kudu, and giraffe activity budgets used the definition of standing or lying down without ruminating, being vigilant, or grooming (Du Toit & Yetman, 2005). In a study on impala, resting was defined specifically as standing or sleeping without showing active behaviours such as feeding, vigilance, or grooming (Kurauwone et al., 2013). All these studies seem to have one thing in common, the definition of resting comes down to inactivity, as also suggested as a definition for rest by Pollard and Blumstein (2008).

1.3   WHY REST?

Mammals spend large portions of their day resting (Du Toit & Yetman, 2005; Kurauwone et al., 2013; Siegel, 2008), which suggests rest serves a crucial function for survival. By being inactive during the hottest parts of the day, resting can aid with thermoregulation (Korstjens et al., 2006). Furthermore, rest can help to deal with digestive constraints such as when high-quality resources are limited, and an individual's energy levels are low. Moreover, resting provides crypsis when predation risk is high, and allows bodily repair after strenuous activity (Korstjens et al., 2006; Pollard & Blumstein, 2008; Williamson & Dunbar, 1999). Sleep, specifically, has crucial functions ranging from maintaining synaptic plasticity, memory consolidation, and maintenance of immune function (Imeri & Opp, 2009; Mignot, 2008; Schmidt et al., 2017). It has been suggested that, due to its low energetic costs, rest can serve as a default behaviour when there is no need to engage in active behaviours such as feeding, mating, or being vigilant (Herbers, 1981; Iwamoto & Dunbar, 1983;

Korstjens et al., 2006). However, we know that when animals suffer chronic sleep deprivation, they show symptoms of lapses in attention, increased pain sensitivity, metabolic and cardiovascular disorders, decreased immunity, and rarely, death (Basner et al., 2013; Gottlieb et al., 2005; Gujar et al., 2011; Irwin & Opp, 2017; Schuh-hofer et al., 2017). Thus, some rest can be converted into active behaviours when needed, but time spent resting is not entirely made up of spare time capital and does serve crucial physiological functions (Dunbar, 1992).

1.4   FACTORS AFFECTING RESTING BEHAVIOUR

Rest forms an important part of mammalian time budgets, with REM sleep occurring in all studied terrestrial mammals (Siegel, 2008) and with various negative consequences related to not reaching a species or population specific 'target' of time spent resting (Joiner, 2016; Rattenborg et al., 2004). Furthermore, we can expect the characteristics of rest to differ between species and individuals due to differences in age, sex, body size, breeding phase, and predation risk (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009). Elephants, for example, spend more than a fifth of their time budget resting (Gravett et al., 2017; Guy, 1976; Owen-Smith & Goodall, 2014). Zebra spend ~40% of their time at rest, and buffalo and sable antelope ~50% of their time (Owen-Smith & Goodall, 2014). In a study on steenbok, impala, kudu, and giraffe, larger species suffered a greater loss of feeding time and spent more time resting on hotter days compared to smaller species (Du Toit & Yetman, 2005). As such, caution should be taken when suggesting universal drivers of resting behaviour.

However, apart from the need to rest, there are also costs related to resting. For example, resting limits the time an individual can spend foraging and mating. In addition, due to lower levels of responsiveness individuals are more vulnerable to predation while resting (Burger et al., 2020; Joiner, 2016; Lima, 1998; Lima et al., 2005). Due to these costs, and selection favouring behaviours with the lowest costs, we can expect the characteristics of rest (temporal, spatial, and social) to vary with external factors, such as weather, diet quality, habitat characteristics, and predation risk at the resting site (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009). For example, zebra, buffalo, and sable antelope rest is decreased during the dry season, when vegetation quality and quantity decreases, compared to the wet season, with higher vegetation quality as these herbivores need to spend more time searching for food during the dry season (Owen-Smith & Goodall,

2014). Furthermore, both rainfall and temperature affect predation risk (Owen-Smith, 2008) and thermoregulation in mammals (Hanya et al., 2018; Lopes & Bicca-Marques, 2017), which could in turn affect resting behaviour. Specifically, during the hottest parts of the day animals can become inactive to avoid overheating (Dunbar, 1992).

Predation Risk

The impact of predation risk is highlighted in the majority of studies on animal activity budgets, and in itself, varies with prey species, habitat, and prey activity patterns (time of day; Creel et al., 2014; Preisser et al., 2007; Valeix et al., 2009a). As such, predator composition and prey preference influence predation risk, which could in turn affect the social, temporal, and spatial aspects of prey behaviour. Increased perceived predation risk might lead to a decrease in time spent resting, increased arousal frequencies, and sleeping at different times of the day (Lima et al., 2005). Smaller mammalian prey species tend to adapt resting behaviour spatially and socially according to predation risk, while larger mammalian prey species exhibit more temporal changes in resting strategies (Shukla et al., 2021).

Predation risk is species specific as certain predators prefer certain prey, usually within specific body size ranges, due to predator energy requirements (Clements et al., 2014; Hayward, 2006; Hayward et al., 2011). Lion (*Panthera leo*) prefer larger prey, like wildebeest and zebra, while leopard (*Panthera pardus*), African wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*) and spotted hyaena (*Crocuta crocuta*) prefer smaller prey, like impala (Owen-Smith & Mills, 2008; Thaker et al., 2011). Smaller ungulates in the Serengeti suffer greater predation rates and experience stronger predation risk than larger ungulates primarily due to the fact that they have more predators (Sinclair et al., 2003). As such, smaller ungulates might exhibit stronger antipredator behaviour than larger ungulates. For example, smaller species (impala, warthog, waterbuck, kudu) utilised areas with lower predator activity than wildebeest, zebra, and giraffe (Thaker et al. 2011). Thus, one could observe species specific changes in resting behaviour according to the prey preferences and characteristics of the predators present.

Predation risk is not constant over time or space as predators have specific activity patterns and hunting strategies (Hayward & Slotow, 2009; Makin et al., 2017). This allows prey species to adjust their behaviour both temporally and spatially to reduce predation risk (Havmøller et al., 2020). Considering South Africa's large predator guild, leopards and spotted hyaena are nocturnal, while lions are both nocturnal and crepuscular (Hayward &

Slotow, 2009). African wild dogs are mainly crepuscular, whereas cheetahs are both crepuscular and diurnal (Hayward & Slotow, 2009). This suggests that the preferred prey of each of these species could experience increased predation risk during abovementioned times and in response they could temporally adjust their activity budgets accordingly.

Leopards (Hayward et al., 2006) and lions (Burkepile et al., 2013; Funston et al., 2001; Loarie et al., 2013) are both ambush predators, making closed habitats and areas often visited (like waterholes) by prey species unsafe (Makin et al., 2017). Cursorial predators, on the other hand, roam the landscape, which makes their distribution in the landscape relatively unpredictable, yet they are predominantly found in more open habitats (Preisser et al., 2007). African wild dogs, cheetah, and spotted hyaena are cursorial predators (Makin et al., 2017). Thus, the preferred prey species of predators could adjust the spatial aspect of resting behaviour to minimize predation risk.

Usually, prey species utilise a combination of both temporal and spatial adjustments to minimize predation risk. For example, zebra in Kruger National Park favoured open areas with little dense woody vegetation at night when their main predators (lion) were active, but, during the day when lions generally rested, zebra utilized both open and closed habitats (Burkepile et al., 2013). However, from the prey's perspective, a trade-off exists between food availability, food quality, and predation risk (Lima et al., 1985; Urban, 2007). For example, impala utilised riskier, more densely vegetated habitats with higher quality forage options during the day, and less risky habitats but with lower vegetation quality at night (Burkepile et al., 2013). It has been suggested that impala are more agile than zebra, allowing them to escape predators more successfully in more densely vegetated habitats (Burkepile et al., 2013). As such, the trade-off between foraging-efficiency and predation-risk is species specific according to body size, nutritional requirements, and escape or defence tactics (Creel et al., 2005; Riginos & Grace, 2008; Wirsing et al., 2007). If such a trade-off exists for foraging efficiency, it is possible that a similar trade-off exists for resting-efficiency and predation-risk.

Social adaptations in response to increased predation risk include changes in herd size. For example, wildebeest and zebra in Hwange National Park aggregate in larger herds as predator encounter risk increases (Valeix et al., 2009a) due to the anti-predatory advantages of dilution, collective detection, reduced individual risks, and confusion of predators (Creel & Winnie, 2005). However, as zebra in larger herds in Hwange National Park did not show increased survival, the fitness benefits from aggregation should not always

be assumed (Vitet et al., 2020). There are also costs related to aggregation, such as being more visible to predators (Wittenburger & Hunt, 1985) and increased aggression from other herd members, specifically during the breeding season (Body et al., 2014; Holand et al., 2006; Uccheddu et al., 2015). Due to abovementioned benefits and costs, individuals in a herd can change their activity budgets. For example, in larger groups, a decrease in vigilance has been observed (van Deventer & Shrader, 2021), which could suggest that individuals can spend more time on other activities, such as resting (Bednekoff & Lima, 1998; Dehn, 1990; Roberts, 1996; Treves, 2000).

Where an individual is positioned in the herd also affects behaviour, as edge individuals are usually targeted by predators (Lingle, 2001; Quinn & Cresswell, 2006). As such, edge individuals show high levels of antipredator vigilance (Blanchard et al., 2008; Favreau et al., 2010; van Deventer & Shrader, 2021), which could result in lower degrees of resting behaviour. Similar suggestions were made for mallard ducks, where edge individuals showed a high degree of unihemispheric slow wave sleep (a lighter degree of rest), whilst individuals at the centre of the group tended to enter deeper rest (Rattenborg et al., 1999). Yet, impala in the centre of the herd showed higher proportional use of social vigilance whereas individuals at the edge of herds showed antipredator vigilance under intermediate and high predation risk (van Deventer & Shrader, 2021). As such, centre individuals might not enter a deep degree of rest when under higher predation risk, due to high predation risk enforcing vigilance behaviour even in prey situated at the centre of a herd.

An important factor to keep in mind for resting efficiency and when choosing a resting spot is temperature, as mammals are unable to thermoregulate during deep sleep (Parmeggiani, 2003). Animals have the option to rest in thermodynamically favourable places (e.g. in the shade of a tree), however, these places might increase predation risk (Krause & Ruxton, 2002; Lima et al., 2005). As such, animals might rather rest in exposed spots where predators can be spotted easily (Say-Sallaz et al., 2019), however, animals might then reflect a bias towards more shallow resting states in exposed areas (Krause & Ruxton, 2002; Lima et al., 2005). For example, in the presence of multiple predators with multiple hunting strategies, impala in Kenya showed no difference in vigilance between open and closed habitats as all habitats were considered as risky (Shorrocks & Cokayne, 2005). In such cases, it is possible that prey may choose the most thermodynamically suitable sites to rest. Yet, the effect of temperature on behaviour is species specific due to differences in body size, thermoregulatory adaptations, and thermoregulatory constraints (Bonebrake et al.,

2020; Rezende & Bacigalupe, 2015). Wildebeest, for example, mostly feed at night and spend their days being inactive, lying down in cooler weather and standing as temperature increases (Maloney et al., 2005). Impala, on the other hand, are more active during the day than at night (Shrestha et al., 2013).

1.5   PROJECT RATIONALE

Resting behaviour forms a crucial part of animal health (Korstjens et al., 2006; Pollard & Blumstein, 2008; Williamson & Dunbar, 1999) and activity budgets (Du Toit & Yetman, 2005; Kurauwone et al., 2013; Siegel, 2008). Yet, little research has been done on mammalian resting behaviour, specifically on the impact of predation risk on prey resting behaviour (Rattenborg et al., 2017; Tougeron & Abram, 2017). Animal behaviour varies between individuals, species (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009), across the landscape, with weather (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009), and with social structures (Creel & Winnie, 2005; Lingle, 2001; Quinn & Cresswell, 2006; Valeix et al., 2009a). Due to the complexity of animal behaviour and our rudimentary understanding of resting behaviour, I focussed on three common and widespread species (i.e. impala, wildebeest, zebra). A wide variety of research has been done on the behaviour of all three species (Dröge et al., 2019; Kurauwone et al., 2013; Maloney et al., 2005; Matson et al., 2005; Mills & Shenk, 1992; Shorrocks & Cokayne, 2005), which can be used to aid in understanding the species and the potential drivers of their resting behaviour which could then be used to better our understanding of other species' resting behaviour and finally aid in conservation.

1.6   PROJECT AIM AND OBJECTIVES

The aim of this study was to investigate the social, spatial, and temporal aspects of resting behaviour, and specifically, the impact of predation risk.

Objectives

1.) Investigate how predation risk affects the diurnal resting probabilities of wildebeest, zebra, and impala according to vegetation cover, position in the herd, herd size, and time of day.

2.) Investigate how lion spatial use and vegetation cover affect wildebeest resting probabilities throughout the diel cycle.

CHAPTER 2

The probability of zebra, wildebeest, and impala resting under varying degrees of predation risk.

2.1   ABSTRACT

Predation-risk affects prey behaviours. Yet, the impact on rest remains unclear. When resting, animals are specifically vulnerable due to lowered responsiveness to predator cues. Thus, animals could vary the location, timing, and sociality of rest to increase survival. To explore this, I observed zebra, wildebeest, and impala during the day at five sites in KwaZulu-Natal with different predator compositions (i.e. an index of risk). I explored how predation risk, time of day, herd size, herd position, and vegetation cover affected resting probability. I found that zebras were more likely to rest during the day at sites with greater predation risk, where rest could be lost at night due to predator activity, than under low and moderate predation risk, where zebra could rest more at night. Furthermore, zebra resting probability increased with time of day, which could be linked with increasing daytime temperatures. Zebra preferred to rest in the centre of the herd, compared to the more dangerous edge, but the probability of rest decreased with herd size. Lastly, I found that under moderate and high predation risk, the probability of zebra resting was greater in open areas, where predators could be spotted, compared to more densely vegetated areas, which could be more thermodynamically suitable. Yet, under low predation risk, zebra utilized more densely vegetated and thermodynamically suitable areas to rest. Impala resting probabilities was higher within small (<20 individuals) and large herds (>40 individuals) than within medium herds (20 to 40 individuals). None of the factors considered affected wildebeest resting behaviour, which may be due to them primarily resting at night. Overall, I found that resting behaviours and the drivers there-off is highly species-specific. Furthermore, I found that predation risk does affect resting behaviour, but not as much as expected, other social, spatial, and temporal factors should also be considered.

Key words: Diurnal, predation risk, resting, thermoregulatory, trade-offs, vegetation cover, vigilance

2.2   INTRODUCTION

Predator-prey interactions are crucial in shaping communities (Lima, 1998; Paine, 1992). Predation risk drives adaptations in prey morphology, physiology, and behaviour (Burger et al., 2020; Lima & Dill, 1990). In an attempt to minimize predation risk, prey animals can adjust their behaviours socially, temporally, and spatially (Shukla et al., 2021). Although the impact of predation risk on prey vigilance (Ndiweni et al., 2015; Pecorella et al., 2018; van

Deventer & Shrader, 2021) and foraging behaviour (Fortin et al., 2004; Lima & Dill, 1990; Nersesian et al., 2012) is relatively well understood, the potential impact on resting behaviour remains unclear (Rattenborg et al., 2017; Tougeron & Abram, 2017).

Resting is a broad term describing inactive states such as sleep, drowsiness, or quiet wakefulness (Siegel, 2009). Resting differs from other inactive states, such as hibernation and torpor, as 1) some form of resting is universal across all taxa, 2) it is rapidly reversible (within seconds), and 3) it is of relatively short duration (shorter than 24 hours; Joiner, 2016; Siegel, 2009). Rest could have evolved to help with restorative processes sustaining brain performance (Lesku et al., 2012), energy saving when activity is unproductive, thermoregulation, and even predator avoidance (Joiner, 2016; Lima, 1998; Siegel, 2009). Yet, there is no consensus on the specific function of rest (Joiner, 2016; Siegel, 2009). It, however, does serve a vital function, as there are various negative consequences related to not getting enough rest (Joiner, 2016; Rattenborg et al., 2004). Different species require varying amounts of rest to maintain health (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009). For example, despite needing little sleep, elephants (*Loxodonta Africana*), still spend more than a fifth of their time resting (Gravett et al., 2017; Guy, 1976; Owen-Smith & Goodall, 2014), while zebra spend ~40% of their time at rest, and cape buffalo (*Syncerus caffer*) and sable antelope (*Hippotragus niger*) ~50% (Owen-Smith & Goodall, 2014).

There are, however, some costs related to resting. For example, when resting, individuals are unable to forage or be reproductively active, and are ultimately more vulnerable to predation, due to lower responsiveness to predator cues (Burger et al., 2020; Joiner, 2016; Lima, 1998; Lima et al., 2005). Due to these costs, the characteristics of rest (temporal, spatial, and social) likely vary with external factors, such as weather, food availability and quality, habitat characteristics, and predation risk at the resting site (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009). For example, zebra, cape buffalo, and sable antelope in Kruger National Park spread their rest evenly throughout the day and night during the wet season (Owen-Smith & Goodall, 2014). Yet, during the dry season, when vegetation quality and quantity are low, they spend more time searching for limited high-quality food resulting in reduced time spent resting per day (Owen-Smith & Goodall, 2014).

One adaptation to increased predation risk is increasing herd size. Benefits of moving in larger herds include the anti-predatory advantages of dilution, collective detection, greater

defence, confusion of predators, and reduced domains of danger (Burger et al., 2000; Childress & Lung, 2003; Creel & Winnie, 2005; Hamilton, 1971). For example, wildebeest and zebra in Hwange National Park aggregate in larger herds as predator encounter risk increases (Valeix et al., 2009a). There are, however, costs related to larger groups including being more visible to predators (Wittenburger & Hunt, 1985) and increased competition and aggression between herd members (Body et al., 2014; Holand et al., 2006; Uccheddu et al., 2015). Due to abovementioned benefits and costs, individuals in a herd can change their activity budgets. For example, in larger groups individuals have lower levels of vigilance (Burger et al., 2000; Childress & Lung, 2003), which allows them to spend more time on other activities, whether resting or competing with other herd members for food or mates (Bednekoff & Lima, 1998; Dehn, 1990; Roberts, 1996; Treves, 2000).

Where an individual is positioned in the herd also affects behaviour, as edge individuals are usually targeted by predators (Lingle, 2001; Quinn & Cresswell, 2006). As such, edge individuals tend to show high levels of antipredator vigilance (Blanchard et al., 2008; Favreau et al., 2010; van Deventer & Shrader, 2021), which could reduce rest. Similar suggestions were made for mallard ducks (*Anas platyrhynchos*), where edge individuals showed a high degree of unihemispheric slow wave sleep (a lighter degree of rest), whilst individuals at the centre tended to enter deeper rest (Rattenborg et al., 1999).

Predation risk is not constant over time or space or species as predators have specific activity patterns, hunting strategies, and prey preferences (Hayward & Slotow, 2009; Makin et al., 2017). This, however, allows prey species to adjust their behaviour both temporally and spatially to reduce predation risk (Havmøller et al., 2020). Considering South Africa's large predator guild, leopards (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*) are nocturnal, while lions (*Panthera leo*) are both nocturnal and crepuscular (Hayward & Slotow, 2009). African wild dogs (*Lycaon pictus*) are mainly crepuscular, whereas cheetahs (*Acinonyx jubatus*) are both crepuscular and diurnal (Hayward & Slotow, 2009). Lastly, lion prefer larger prey, like wildebeest and zebra, while leopard, African wild dogs, cheetahs and spotted hyaena prefer smaller prey, like impala (Owen-Smith & Mills, 2008; Thaker et al., 2011). This indicates that different prey species likely experience different temporal peaks in predation risk. In response, they likely adjust their activity budgets to minimise this risk.

In addition, landscape features such as vegetation cover also influence predation risk. For example, dense vegetation favours ambush predators such as leopards (Hayward et al., 2006) and lion (Burkepile et al., 2013; Funston et al., 2001; Loarie et al., 2013), while more

open habitats favour cursorial predators such as African wild dogs, cheetah, and spotted hyaena (Makin et al., 2017). In response, prey species can reduce risk by adjusting their temporal and spatial use of the landscape.

Another factor that may influence deep rest, such as sleep is temperature, as mammals are unable to thermoregulate during deep sleep (Parmeggiani, 2003). Animals have the option to rest in thermodynamically favourable places (e.g. in the shade of a tree). However, these places might increase predation risk by reducing escape options and blocking sightlines (Krause & Ruxton, 2002; Lima et al., 2005). As such, animals might rather rest in exposed spots where predators can be spotted easily (Say-Sallaz et al., 2019), but not enter deep states of rest (Krause & Ruxton, 2002; Lima et al., 2005). Nevertheless, if predation risk is similar across the landscape (e.g. both ambush and cursorial predators present) prey species may choose to rest in thermodynamically suitable sites.

I explored how predation risk (i.e. predator composition), herd size, position in the herd, vegetation cover, and time of day influence the rest (e.g. quiet wakefulness to sleep; see detail below) of zebra, wildebeest, and impala. As all three of these herbivores are group-living, I predicted that the probability of resting would decrease as predation risk increased, as prey needed to engage in more anti-predator behaviours instead of resting. Alternatively, I predicted that rest would increase as predation risk increased, due to prey being silent (increasing the probability of hearing predators) and prey being cryptic (visually hiding from predators) while at rest. Furthermore, I predicted that the probability of rest would increase with herd size, due to the benefits of aggregation. Within these herds, individuals in the centre, where it is safer, would show higher probabilities of rest compared to edge individuals. In addition, in sites where ambush predators were common, I predicted that the probability of rest would be higher in more open habitats, as predators can be spotted from farther away, compared to densely vegetated areas. Alternatively, the probability of rest should be higher in more densely vegetated habitats compared to more open habitats in sites where ambush predators were absent and cursorial predators where present. However, if the herbivores selected heavy vegetated areas with ambush predators present then this could be due to the inability of these species to thermoregulate during deep rest, with vegetated areas offering thermodynamically suitable microhabitats. In addition, dense habitats likely creating visual obstructions of prey from predators and thus reduce predation risk. Lastly, I predicted that the probability of resting would increase around sunrise and sunset, as predators are most active and resting reduces surrounding sound and allows prey to be more

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cryptic. Alternatively, resting would increase around midday, when temperatures are highest and predators are less active (i.e. lower predation risk). The added benefit is that resting reduces prey activity and body temperatures during this physiologically stressful period.

2.3   METHODS

Study area

I conducted my study at five sites in KwaZulu-Natal, South Africa. Predator composition of Hluhluwe-iMfolozi Park (HiP; 28°13'12.1"S 31°57'07.2"E, 96 000 ha) comprised lion, hyaena, cheetah, leopard, and wild dogs. Phinda Private Game Reserve (Phinda; 27°48'31.2"S 32°20'45.7"E, 29 000 ha) had the same predators as HiP, but lacked wild dogs. Ithala Game Reserve (Ithala; 27°32'45.9"S 31°18'51.9"E, 30 000 ha) contained only leopard and hyaena, while Duiker Lodge (DL; 27°54'37.4"S 32°11'29.4"E, 400 ha) and Sunset Plains (SP; 27°55'01.7"S 32°18'37.6"E, 250 ha) only contained leopard but it was uncertain whether these individuals were resident or only stayed in the reserves for short periods.

Data collection

I collected data across the five sites during April and May 2022. I drove through the study sites each day for approximately five days. Drives started at different time intervals (i.e., sunrise around 6:00, 8:00, 11:00, 14:00, 16:00, stopping at sunset around 17:30). Intervals were extrapolated from previous temperature trends in the study area by identifying intervals with little (≤4°C) variation in temperature as to cover a range of temperatures. Average temperatures at sunrise was 20°C, 8:00 (20°C), 11:00 (24°C), 14:00 until 16:00 (25°C), and sunset (22°C; Wanderlog, 2023a). I drove continuously throughout the reserve during each interval, avoiding roads already driven during that interval. In the small reserves, where roads were limited, I would stop if I revisited a herd. At which point, I would drive 100 m away from the herd, as to avoid disturbance, and wait to resume data collection until the next time interval began.

I focused my data collection on impala, wildebeest, and zebra as they were common across all the study sites. To ensure herds were not disturbed by the vehicle, I only sampled herds more than 50 m away from the road. I used a scan sampling method to record the activity of each individual in the herd. For each herd, I did a single scan across the entire herd and recorded the behaviours of each individual. I classified behaviours as resting, foraging, vigilant, grooming, moving, and socializing. Resting was defined as an individual

either standing or lying down, with a neutral head position, relaxed body posture, ruminating or not ruminating (in the case of impala and wildebeest), with eyes either open or closed (Mortola & Lanthier, 2005; Olsson et al., 2007; Rook & Penning, 1991). Foraging was defined as an individual taking bites of vegetation. I considered an animal as vigilant if its ears were in an upright position and its head raised above chest height (Schmitt et al., 2014; van Deventer & Shrader, 2021). Individuals biting and scratching themselves in a relaxed state was identified as grooming (Hart & Hart, 1992). Lastly, individuals interacting with one another, such as chasing or allogrooming, were identified as socializing. In addition, I recorded the species, herd size, time of day, ambient temperature (thermometer held outside the car window), and vegetation cover (low to none, or moderate to dense). Ambient temperature was, however, not used in the analysis as it was moderately correlated with time of day (0.51). Time of day was the preferred variable as it accounted for changes in temperature and the time since sunrise and until sunset, which was expected to have an effect because of how predation risk changes predator activity patterns throughout the day.

Vegetation cover was classified as low to none if the individual was in a patch with only grass and sparse trees, and the individual's vision of the surrounding area was not obscured by vegetation for at least 100 m. I determined the distance between an individual and vegetation using a rangefinder. If a small number of trees surrounded the individual and vision was slightly obstructed in some directions, but the individual could likely see up to 50 m through the trees, vegetation cover was classified as moderate. Vegetation cover was classified as dense if the individual was located in between many trees and vision of the surrounding environment was severely obstructed, with an individual not being able to see more than 20 m in any direction. Within the study sites, shifts between vegetation cover was sudden, with clear differences between low, moderate, and high vegetation covers. Position in the herd was either on the edge or in the centre of the herd. Central individuals were defined as those individuals where I could draw a line between two edge individuals, and it passed through the focal individual.

1.1.1   Classification of Predation Risk

Predation risk was defined at a reserve level, based on the predator composition. When all five of Africa's large predator guild were present (i.e. lion, wild dog, cheetah, spotted hyaena, leopard), or the predators were active throughout the 24-hour period (i.e.

diurnal/nocturnal/crepuscular), or utilised both ambush and cursorial hunting strategies, a reserve was classified as high predation risk. Reserves classified as high predation risk were HiP and Phinda Private Game Reserve. When not all the predators were present, or when one of the activity patterns were not utilised (i.e. diurnal/nocturnal/crepuscular), or the predators within the reserve utilised only one of the hunting strategies (i.e. ambush or cursorial), a reserve was classified as intermediate predation risk. Of the five sites, only Ithala Game Reserve was classified as having intermediate predation risk. Finally, when predators were rarely present (i.e. Duiker Lodge and Sunset Plains), the reserve was classified as having low predation risk.

Data analysis

1.1.2 Models

I used generalized linear mixed models (Brook et al., 2017) to quantify how a variety of predictor variables affected the probability of an individual being observed resting, for each of the study species (impala, wildebeest, zebra). The probability of an individual resting is calculated by the glmmTMB function in R and is dependent on the independent variables (i.e., predation risk, time of day, herd size, vegetation cover, and position in the herd) in the model. The models were set up identically for all species. I used a binomial family for the distribution of errors, as the response variable only had two possible outcomes: whether an individual was resting or not. The predictor variables comprised predation risk, time of day, herd size (as 2nd-order polynomial to allow a non-linear relationship), vegetation cover, and position in the herd. Additionally, interactions between predation risk and vegetation cover, herd size, time of day, and position in the herd were also included. I added herd ID as a random effect variable.

Figures 1 and 3 were generated in R from the full original model. However, as the figures generated in R include the output from full model, I used stepwise variable selection to generate figures 2 and 4 to limit the figure to the significant 2-way interaction being discussed. Thus, to generate figure 2, from the zebra model, the non-significant interaction between herd size and predation risk was removed. To generate figure 4, for impala, the non-significant interaction between herd size and predation risk was removed.

2.4   RESULTS

Zebra

Zebra rested for 58% of observations. Predation risk affected the probability of an individual zebra resting (χ2=9.08, df=2, p=0.01), with a lower probability of rest at moderate predation risk than at low and high predation risk (Figure 1). Time of day also affected zebra rest (χ2=16.28, df=1, p<0.005) with a steady increase in the probability of an individual zebra resting later in the day (Figure 2). However, the interaction between time of day and predation risk was not significant (χ2=0.59, df=2, p=0.74).
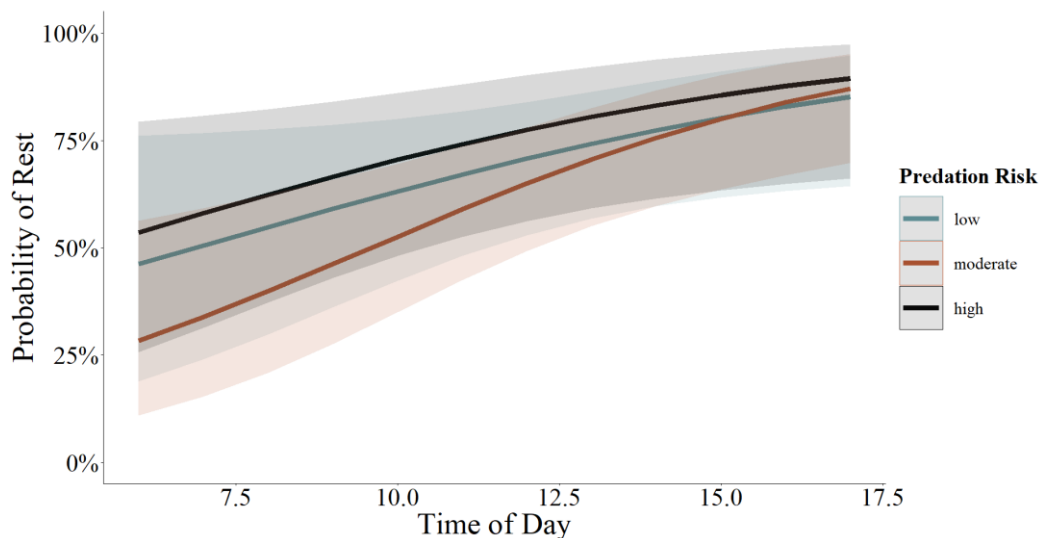

Figure 1: Predictions of the expected probability (%) of an individual zebra resting and its 95% confidence limits according to the time of day and predation risk (low, moderate, and high).

The mean size of the zebra herds was 8 individuals (range 1-21). The probability of an individual zebra resting was influenced by herd size (χ2=6.60, df=2, p=0.04), with a decrease in the probability of rest as herd size increased (Figure 2). However, the interaction between herd size and predation risk was not significant (χ2=6.60, df=4, p=0.15).
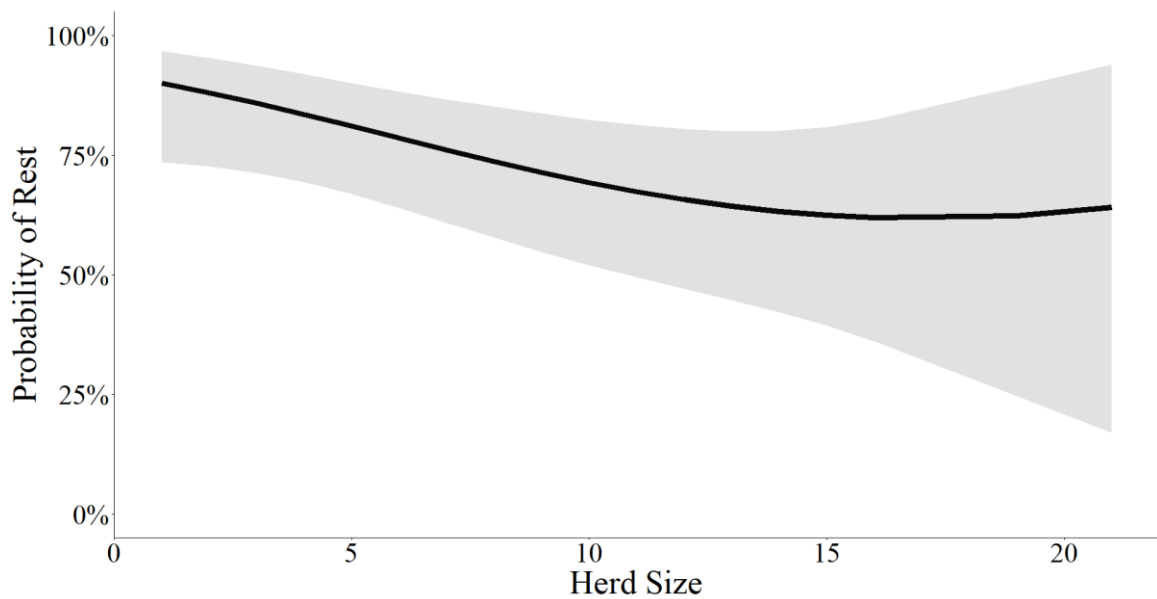
Figure 2: Predictions of the expected probability (%) of an individual zebra resting and its 95% confidence limits according to the size of the herd.

Vegetation cover on its own did not affect the probability of an individual zebra resting (Figure 3, $\chi2=2.17$, df=1, p=0.14). However, the interaction of vegetation cover and predation risk did influence rest ($\chi2=9.88$, df=2, p=0.007). Under moderate and high predation risk, zebra showed higher probabilities of rest in more open areas compared to more densely vegetated areas. However, under low predation risk, zebras showed a higher probability of rest in more densely vegetated areas compared to more open areas. In addition, where a zebra was positioned in the herd significantly affected its resting (Figure 3, $\chi2=18.16$, df=1, p<0.005), with the probability of individuals resting in the centre of the herd being higher than at the edge. However, the interaction between predation risk and position in the herd was not significant ($\chi2=0.72$, df=2, p=0.70).
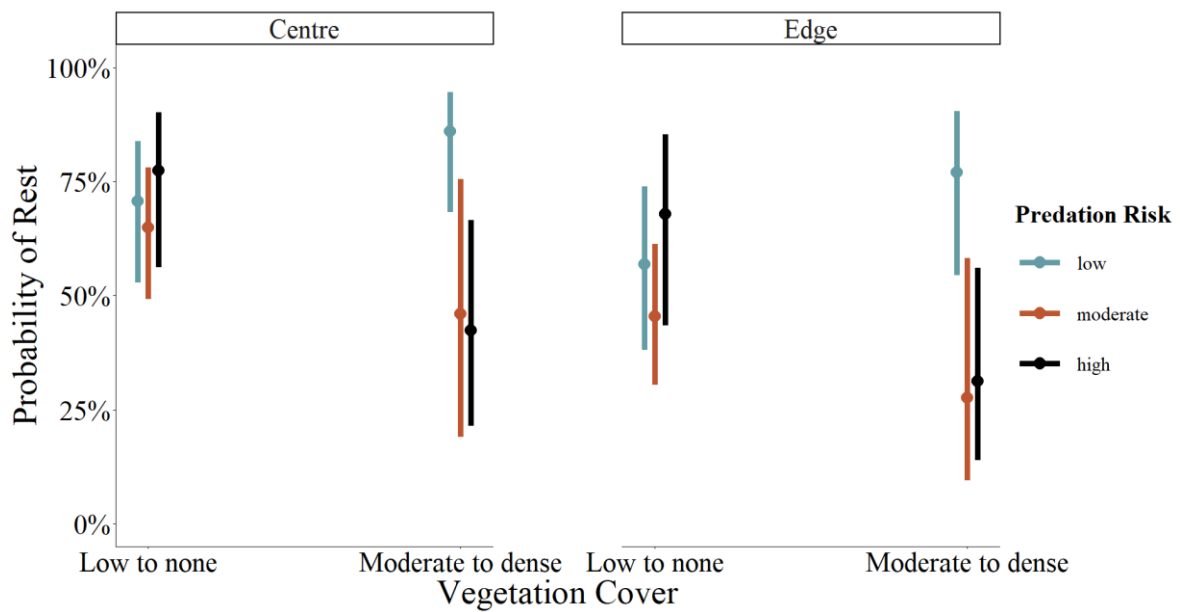
Figure 3: The marginal means (+/- 95% confidence intervals) of the probability (%) of an individual zebra resting in the centre and on the edge of the herd under varying predation risk (low, moderate, and high) and in different vegetation covers (low to none, and moderate to dense).

Impala

Rest occurred in 30% of the impala observations. Of all the variables I tested, only herd size affected the probability of an individual impala resting (Figure 4, $\chi2=21.54$, df=2, p<0.0005). The mean herd size for impalas was 23 individuals (range 1-55 individuals). Despite large confidence intervals, the probability of an individual impala resting in moderate sized herds (20 to 40 individuals) was lower than within small (<20 individuals) and large (>40 individuals) herds. Yet, the interaction between herd size and predation risk was not significant ($\chi2=1.50$, df=4, p=0.83).
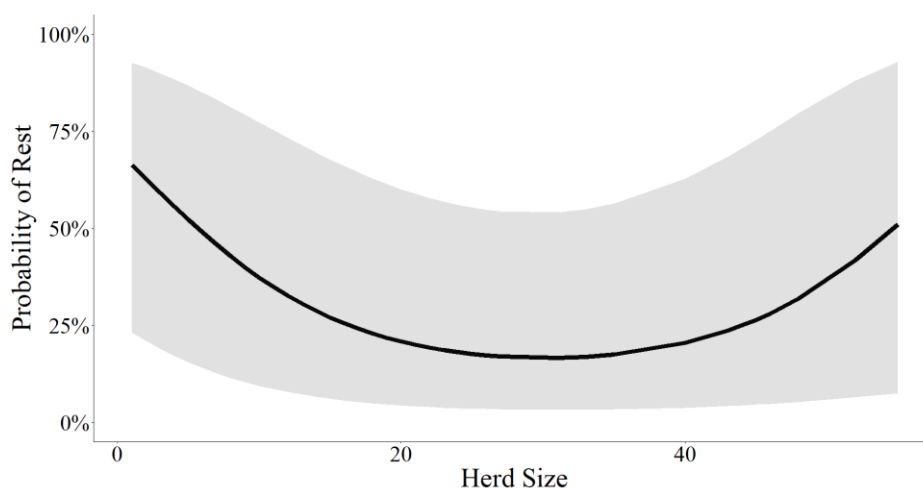
Figure 4: Predictions of the expected probability (%) of an individual impala resting and its 95% confidence limits according to the size of the herd.

Wildebeest

Wildebeest rested for 61.90% of observations. In contrast to zebra and impala, none of the variables measured affected the probability of a wildebeest resting (i.e., predation risk ($\chi2$=0.70, df=2, p=0.71), time of day ($\chi2$=0.30, df=1, p=0.59), herd size ($\chi2$=3.55, df=2, p=0.73), vegetation cover ($\chi2$=0.12, df=2, p=0.73); position in the herd ($\chi2$=2.62, df=1, p=0.11)). Moreover, the interactions of these variables were also non-significant (time of day and predation risk $\chi2$=2.42, df=2, p=0.30; herd size and predation risk $\chi2$=3.07, df=2, p=0.17; vegetation cover and predation risk $\chi2$=3.07, df=2, p=0.22; position in the herd and predation risk $\chi2$=3.71, df=2, p=0.15).

2.5   DISCUSSION

Predation risk is one of the key drivers affecting prey behaviour (Creel, 2018; Lima & Dill, 1990). Nevertheless, the impact on resting behaviour remains unclear (Lima et al., 2005). I found differences in resting behaviour between the three species I observed with the probability of zebra resting affected by predation risk, position in the herd, herd size, time of day, and the interaction between predation risk and vegetation cover. By contrast, the only factor that affected the probability of impala resting was herd size, while none of the factors affected the probability of wildebeest resting.

Zebra

During the day, zebras were more likely to rest in sites with high predation risk compared to low and moderate predation risk. A key factor that defined my high predation risk sites were lions. As they prefer larger prey like zebra (Owen-Smith & Mills, 2008; Thaker et al., 2011), it is possible that lion presence increased perceived risk by zebra, specifically at night when lions are more active (Fischhoff et al., 2007; Funston et al., 2001). In turn, this increase in nighttime predation risk could lead to increased zebra vigilance, reducing their foraging (Creel et al., 2017; Hunter & Skinner, 1998), and possibly reducing their rest at night. If this was the case, then zebra under high predation risk may have needed to rest more during the day, when data was gathered, compared to zebra under low and moderate predation risk. However, measures of nighttime rest would be needed to determine this. Furthermore,

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increased resting probabilities under high predation risk could suggest that, during the day, zebra utilise rest as an antipredator mechanism through crypsis, making zebra harder for predators to detect (Korstjens et al., 2006; Pollard & Blumstein, 2008; Williamson & Dunbar, 1999). Additionally, surrounding noise is kept to a minimum while resting. Prey can hear approaching predators and alarm calls more easily compared to during noisy behaviours such as feeding and grooming (Lima & Bednekoff, 1999; Quinn et al., 2006; Smith, 1986). Alternatively, predation risk may not be the only major determinant of resting during the day. Other unaccounted-for confounding factors such as conducting other crucial activities (e.g. feeding, escaping predators; Joiner, 2016; Lima, 1998; Siegel, 2009), wind speed (Maloney et al., 2005), age (Van Der Meer et al., 2015), breeding stage (Hunter & Skinner, 1998), and human activity (Makin et al., 2017; Wheat & Wilmers, 2016) may have played key roles in determining the extent to which zebra rest during the day.

My results indicate that zebra rest is not only determined by overall predation risk (i.e. predator composition). Rather, across all study sites, the probability of zebra resting increased as it became later in the day. These results contrast to some degree with those of Owen-Smith & Goodall (2014), who found that within Kruger National Park resting in zebra decreased around sunrise and sunset when zebra increased their foraging. In areas with high predation risk, zebra resting late in the afternoon, when lion are most active (Fischhoff et al., 2007), make zebra harder to spot, while allowing them to hear approaching predators and alarm calls (Korstjens et al., 2006; Pollard & Blumstein, 2008; Williamson & Dunbar, 1999). However, as some aspects of antipredator behaviour are innate (Baxter-Gilbert et al., 2018; Dalesman et al., 2006, 2007), the fact that I found zebra resting around sunset, irrespective of predation risk, suggests that there may be innate driver of the timing when zebra in my study rested.

Resting also allows mammals to thermoregulate, as metabolic heat production is minimized (Joiner, 2016; Lima, 1998; Siegel, 2009). During Autumn in Northern Kwazulu-Natal, average temperature around five in the afternoon was ~25° C, with a maximum temperature of 33° C recorded. Zebra can survive in much more extreme temperatures ranging from below freezing up to at least 40° C (Cobb & Cobb, 2019). As such, the average temperature of ~25° C might not be extreme enough for zebra to change their resting behaviour (see Shrestha et al., 2013). For example, zebra in Kruger National Park increased rest over the hottest parts of the day during the summer months (December and January; Owen-Smith & Goodall, 2014) when temperatures reached 34° C (Wanderlog, 2023b). Yet,

during the cooler months (June, July), zebra still rested during the hottest parts of the day when temperatures were only 27° C (Owen-Smith & Goodall, 2014; Wanderlog, 2023c), which suggests temperature may not be the main driver of zebra resting during the afternoon. For example, when vegetation quality and availability decreased in the late dry season, resting decreased and foraging increased, even during the hottest parts of the day (Owen-Smith & Goodall, 2014). As such, resting could occur when other essential behaviours (such as feeding and breeding) have been completed, which would allow zebra to conserve energy (Joiner, 2016; Lima, 1998; Siegel, 2009). Thus, the relationship between resting and time of day could be seasonal, with vegetation quality and availability important drivers during the dry cold seasons and temperature being important during the wet warm season.

Herd size affected zebra resting probability, but the relationship was not as I predicted. Rather, there was a decrease in the probability of a zebra resting with an increase in herd size. I had assumed that with increasing herd size there would be a decrease in individual vigilance, which would then allow individuals to increase the time they spent on other behaviours, such as resting (Hunter & Skinner, 1998; Schmitt et al., 2014; Shorrocks & Cokayne, 2005). Yet, my results suggest that an increase in herd size does not necessarily directly result in an increase in rest. This could be due to interactions and competition with other herd members interrupting activities and thus limiting resting opportunities (Body et al., 2014; Holand et al., 2006; Smith & Cain, 2009; Uccheddu et al., 2015).

Under moderate and high predation risk, the probability of zebra resting was greater in open areas compared to more densely vegetated areas. Resting in open areas likely allow zebras to spot predators from farther away, thus increasing the chance of escaping (Mysterud & Ostbye, 1999; Say-Sallaz et al., 2019). Furthermore, zebras' main predator, lion, prefer to hunt in and around densely vegetated habitats (Elliott et al., 1977), making these habitats more risky to rest in. Yet, under low predation risk, zebra preferred to rest in more densely vegetated areas compared to more open areas. This could suggest that given a choice, zebra prefer to rest in areas with more constant temperatures, sheltered from solar radiation and wind, which reduces the costs related to maintaining body temperature (Huot, 1974; Schmitz, 1991). It is possible that the combination of these results suggests that, as predation risk increased, the perceived costs of being attacked by ambush predators, such as lions, were greater than the thermoregulatory benefits, thus zebra rested in the more open safer areas with less cover. This, however, would require further study.

With regards to herd position, zebras showed a higher probability of rest in the centre of the herd compared to at the edge, irrespective of predation risk. The centre of the herd is generally perceived as being safer (Lingle, 2001; Quinn & Cresswell, 2006), which may allow individuals to reduce their vigilance levels (Blanchard et al., 2008; Favreau et al., 2010; van Deventer & Shrader, 2021) and increase rest. Similarly, springbok on the edge of the herd are almost twice as vigilant as individuals in the centre (Bednekoff & Ritter, 1994), thus allowing centre individuals to engage in other behaviours. One limiting factor of my study, however, is that I did not observe the herd location of individuals at the onset of rest. By studying herd position at the onset of rest and then how rest changes depending on how the individual's position in the herd changes would provide insight into the process of choosing a resting position within herds. Especially if individuals move to the centre of the herd for the purpose of resting, or exit a resting state if risk increases (e.g., if the herd moves and individual is no longer in the centre but rather at the edge). As such, future studies could consider herd position at onset of rest (i.e. whether an individual moved to a specific position before onset of rest) and then stopped resting if they were not in that position anymore.

Impala and Wildebeest

As expected, impala showed higher resting probabilities in large herds (>40 individuals), compared to moderate herd sizes (20 to 40 individuals), irrespective of predation risk. In large herds, individuals have the advantages of reduced individual risk, dilution, confusion, and collective detection (Burger et al., 2000; Childress & Lung, 2003; Creel & Winnie, 2005). As such, larger herds provide a safer opportunity to rest. Additionally, individuals within large herds can take turns being vigilant, leading to increased 'spare' time that can be spent resting.

It has been suggested that resting can be used as a way to pass time and conserve energy when all other crucial activities (feeding, breeding, and grooming) have been completed (Joiner, 2016; Lima, 1998; Siegel, 2009). Yet, large herds are more conspicuous (Piccolo et al., 2022) and there are many other individuals to interact and compete with (Body et al., 2014; Holand et al., 2006; Uccheddu et al., 2015). Thus, the costs associated with living in large and moderate sized herds may prevent individuals from resting. If this is the case, then it may explain the unexpected increase in resting behaviour in smaller herds (<20 individuals). Being in a small herd may allow the entire herd to be more cryptic and rest could be interrupted less by fellow herd members, compared to large herds. This would

in turn allow individuals in small herds to show increased resting probabilities. Nevertheless, rather unexpectedly, I recorded a lower probability of rest at moderate herd sizes, compared to small and large herds. Within moderate herd sizes the benefits of small and large herds might not be completely realised, and the costs (i.e. increased conspicuousness, interaction, competition) might be maximised. If so, then this might explain the low probability of individual impala resting in moderate sized herds.

Somewhat surprisingly, none of the variables I recorded affected the probability of rest in wildebeest. This may be the result of wildebeest resting randomly during the day as the majority of their rest occurred at night due to their visual acuity being decreased at that time (Broekhuis et al., 2014; Kronfeld-Schor & Dayan, 2003). Future studies can consider how predation risk affects resting probabilities at night. Lastly, species-specific differences that I recorded in the factors affecting diurnal resting behaviour could be due to species specific predators (Hayward & Slotow, 2009; Makin et al., 2017) anatomical differences affecting predation risk and the ability to evade predators (Beneski, 1989; Bosher et al., 2006), and differences in digestive physiology.

One potential factor that could lead to differences between the species with regards to rest could be that, as ruminants, impala and wildebeest had an extra rest category of rest (i.e. ruminating). However, the probability of impala resting was less (~30% of observations) than that of zebra (~55% of observations), while the probability of wildebeest resting was similar to zebra (~60%). Thus, there was not a consistent pattern shown by impala and wildebeest (e.g., greater rest than zebra) that could have been driven by the extra the resting while ruminating category.

Although predation is a major driver of natural selection and in turn evolution, predation risk only affected general resting probabilities of zebra and the vegetation cover they rested in during the day. However, other factors also affect zebra resting probabilities, such as position in the herd, herd size, and time of day. Furthermore, predation risk did not affect the resting behaviour of impala and wildebeest. Surprisingly, only herd size affected resting probability in impala during the day, and none of the factors considered affected wildebeest resting during the day. Ultimately, the results of my study provide greater insight into the drivers determining the social, temporal, and spatial characteristics of resting behaviour of mammalian herbivores, a field that we know little about. These insights allow us to better understand the daily activity patterns of prey species and how local factors can influence these patterns across a species range.

CHAPTER 3

Wildebeest resting behaviour within Hluhluwe-iMfolozi Park according to lion density patterns and vegetation cover.

3.1   ABSTRACT

Rest is crucial for animal well-being and survival. Yet, due to vulnerability while at rest, prey need to carefully consider where, when, and how to rest. Predation risk, determined by predator hunting strategies, activity patterns, and prey preference, could affect prey resting behaviour. In turn, mammals' inability to thermoregulate while at rest, might lead them to trade-off predation risk and thermodynamic characteristics with regards to the timing and habitat within which they rest. Using GPS data of wildebeest in Hluhluwe-iMfolozi Park (HIP) and vegetation cover and lion density maps, I calculated the probability of wildebeest resting. I found that wildebeest were more likely to rest at night (>40%) when their main predator (lions) were active, than during the day (<20%). When rest did occur during the day, predation risk and vegetation cover had negligible effects on wildebeest resting probabilities, suggesting that wildebeest did not trade-off between the thermodynamic advantages and predation risk when choosing a location to rest. When resting at night, wildebeest did not show a preference for habitat when lion density was low. Yet, as lion density increased, the probability of resting decreased to as little as ~40%. Wildebeest then rested more in open areas, where predators could be spotted and lions do not prefer to hunt, compared to closed areas. Ultimately, my results indicate that predation risk had the greatest impact on wildebeest resting strategies, determining when and where wildebeest rested.

Key Words: Activity patters, habitat, hunting strategies, predation risk, prey preference, rest, thermoregulate, trade-off

3.2   INTRODUCTION

Rest is a crucial part of animals' activity budgets (Siegel, 2008), with some mammals spending up to 75% of their diel cycle resting (Herbers, 1981; Schaller, 1972). Rest includes inactive states such as sleep, drowsiness, and quiet wakefulness, which are universal across taxa, reversible within seconds, and continue for less than 24 hours (Joiner, 2016; Siegel, 2009). Without rest, animals exhibit lapses in attention, metabolic and cardiovascular disorders, increased sensitivity to diseases, and in rare cases, death (Basner et al., 2013; Gottlieb et al., 2005; Gujar et al., 2011; Irwin & Opp, 2017; Schuh-hofer et al., 2017). In addition to these vital functions, rest is an effective way to deal with fluctuations in weather and predation risk (Siegel, 2009). For example, rest allows animals to be more cryptic to predators (Schmidt, 2014; Siegel, 2009). However, rest limits time available for other activities, and, due to lowered responsiveness to predator cues, increases vulnerability to

predation (Burger et al., 2020; Joiner, 2016; Lima, 1998; Lima et al., 2005). Due to these costs, it is likely that resting behaviour varies with external factors, such as weather, diet quality, habitat characteristics, and predation risk (Dewasmes et al., 2001; Ohayon et al., 2004; Rattenborg et al., 2017; Siegel, 2009).

Predation risk is determined by a predator's hunting strategy, its activity pattern, and its preferred prey (Makin et al., 2017). For example, lions are ambush predators (Burkepile et al., 2013; Funston et al., 2001; Loarie et al., 2013) that hunt large prey like zebra, buffalo, and wildebeest (Hayward et al., 2011; Hayward & Kerley, 2005; Somers et al., 2017) around water sources, and in more densely vegetated areas (Makin et al., 2017). Furthermore, they are nocturnal and crepuscular, mostly hunting at night and during sunrise and sunset (Hayward & Slotow, 2009). As such, large prey like wildebeest might adjust their resting behaviour both spatially and temporally to reduce predation risk from lions. Yet, the temporal and spatial preferences of a predator does not guarantee that they always show those preferences (Broekhuis et al., 2014). For example, just because lions prefer to hunt in closed environments, does not guarantee that they will always be there, or that they will never hunt in open environments. The actual presence of a predator (immediate / short-term risk), or its cues due to recent visitation or continuous use in an environment (long-term risk) could evoke different reactions than indirect proxies of predation risk, such as vegetation cover (Dröge et al., 2019; Gigliotti et al., 2021; Valeix et al., 2009b).

Other factors, such as thermoregulatory constraints, can also affect resting behaviour. For example, in summer, elephants seek out cool shady habitats during the hottest part of the day (Kinahan et al., 2007). In addition, wildebeest respond to heat stress in the summer months by resting (Ben-Shahar & Fairall, 1987; Berry et al., 1982). However, thermoregulatory drivers cannot be considered in isolation, especially in areas with high predation risk (Krause & Ruxton, 2002; Lima et al., 2005). Animals have the option to rest in thermodynamically favourable places (e.g. in the shade of a tree), yet, these places might increase predation risk (Krause & Ruxton, 2002; Lima et al., 2005). As such, animals might rather sleep in exposed spots where predators can be spotted easily (Say-Sallaz et al., 2019). Yet, these exposed areas will not allow for deep rest in endotherms due to the inability to thermoregulate during deep sleep (Parmeggiani, 2003), thus reflecting a bias towards more shallow sleep states in exposed areas (Krause & Ruxton, 2002; Lima et al., 2005).

To explore the influence of predation risk and habitat characteristics on resting behaviour, I used GPS collar data from 21 adult female wildebeest in Hluhluwe-iMfolozi

Park, South Africa. I predicted that wildebeest would rest more at night than during the day, since their main predator, lions, mainly hunt at night. Resting at night reduces surrounding noise, allowing wildebeest to detect predators more easily. Moreover, resting during this time would also allow wildebeest to be more cryptic. Alternatively, wildebeest may prefer to rest during the day when predation risk from lions is low. Additionally, I predicted that wildebeest would more likely rest in open areas, although less thermodynamically suitable and could lead to more shallow sleep states, as it is easier to spot approaching predators in open areas, and their main predator, lions, rarely hunt in these areas. Yet, if thermoregulatory costs were greater than the anti-predator benefits of resting in the open areas, then the wildebeest would prefer to rest in closed shady habitats. Lastly, I predicted that wildebeest resting probabilities would be lower in areas with higher lion densities, as predation risk is higher in these areas, compared to areas with lower lion densities.

3.3   METHODS

Data Collection

I used global positioning system (GPS) data from 21 adult female wildebeest representing 21 separate herds, at the time of collaring, within the Hluhluwe-iMfolozi Park (28°13'12.1"S 31°57'07.2"E, 96 000 ha) in KwaZulu-Natal, South Africa. The vegetation in the reserve is heterogeneous, comprising savannah, open grasslands, and patches of forest. In 2020, lion density within the park was estimated at 120 individuals in 11 prides at a density of ~12 lions/100 km^2 (Davies et al., 2021; Marneweck, 2020). Wildebeest were collared with Ecotone (Gdynia, Poland) or Vectronic (Berlin, Germany) collars from March 2019 until January 2021. However, not all the collars were active over the entire period, with collar duration ranging from two to 35 months. Inter-location intervals ranged from one location every 20 minutes, to one location every six hours. Wildebeest were captured and collared by a veterinary team from the park. For anaesthesia 3 mg etorphine, 40 mg stresnil, hyalase 4000 mg, and naltrexone 60 mg for reversal, was used to subdue the animals during the collaring process.

Fitting Hidden Markov Models

I used Hidden Markov Models (HMM) to classify the wildebeest movement behaviours from the GPS data into the most likely underlying behaviours (e.g. resting, foraging, moving). HMMs have recently become popular to analyse animal movements and behavioural states

using GPS data. They have been applied to a number of animal species including marine fish (Bacheler et al., 2019; Darby et al., 2021; Patterson et al., 2009; Phillips et al., 2015), muskoxen (Beumer et al., 2020), blue wildebeest, plains zebra, and eland (Linssen et al., 2022).

As HMMs require consistent time intervals, I regularised the trajectories to one fix every hour before analysing the data. If there was a missing GPS location for a fix, I used the crawlWrap function from the momentUHMM package (McClintock & Michelot, 2021) to predict coordinates for that fix. However, if there are many missing fixes in a data set, substantial uncertainty can arise from predicting locations. As such, if there were more than six successive missing fixes within an individual's dataset, that dataset was split into two to eliminate the missing fixes. I used the CrawlWrap function to calculate step length and turning angle at all the fixes. Step length indicates the distance moved between fixes, while turning angle indicates a change in the direction an individual is facing between fixes. As such, if an animal is moving in a straight line, the step length would be high and the turning angle close to zero. I used gamma distributions for step length and wrapped Cauchy distribution for turning angles (McClintock & Michelot, 2021).

Step length and turning angle is then used to fit HMMs to the data. The number of states to be identified requires a combination of statistical and biological inferences. I chose to fit a three-state HMM, the most common in movement ecology, as it does not overcomplicate the model, which would lead to higher uncertainty (Bacheler et al., 2019; Beumer et al., 2020; Darby et al., 2021; McClintock & Michelot, 2021). The three states used in HMMs usually match the resting, foraging and moving phases. Initial parameters were provided to begin optimization, but if poorly chosen the function can be highly inaccurate (McClintock & Michelot, 2021). To ensure convergence and minimize the negative log-likelihood, I set the retryFits argument within the fitHMM function in the momentUHMM package to 5. The retryFits argument causes the function to run the first time on the initial parameters set, and rerun the function based on random perturbations of the new parameter estimates created by the function.

Position data

For each GPS position, I determined whether it was taken during the day or night. In addition, I determined the vegetation cover and lion landscape use for each position by using intensity maps created from previously collected data. The woody vegetation cover map

(Figure 1a) was created by Gustave Fradin (unpublished data) using Pleiade satellite images of the park with a resolution of 2 m. The images were taken in February and August 2016. Supervised classification of the habitat types according to the presence and absence of woody cover (trees and shrubs) was carried out by using the Semi-Automatic Classification Plugin (version 6.2.9) from QGIS. A binary raster coding was obtained for the presence or absence of woody cover (resolution of 2 m). To account for pixel-level errors, keeping in consideration that GPS data usually come with a measurement error greater than 2 m, the map resolution was downscaled to a 20 m resolution. Each 20 m-wide pixel was assigned the mean value of the original 2 m pixels to indicate the relative vegetation cover. This resulted in a vegetation cover value between 0 (no cover) and 1 (complete cover).

To determine predation risk, I overlaid the wildebeest positions on a lion landscape use map (Figure 1b). This map was created using GPS data collected from 2013 until 2021 from 23 collared lions within Hluhluwe-iMfolozi Park (Dejeante, 2021). Six of these lions were monitored between March 2019 and January 2021, which coincided with the wildebeest monitoring. By using the adehabitatHR package (Calenge, 2006), a map of landscape use was created, giving the density probability of lions (between 0 and 1) with a resolution of 100 m. Season was not taken into account for the sake of simplicity, and because an analysis based on the Bhattacharyya affinity index (Fieberg & Kochanny, 2005) comparing the overlap of landscape use between seasons showed a significant overlap indicating that the lions did not adjust their landscape use seasonally.
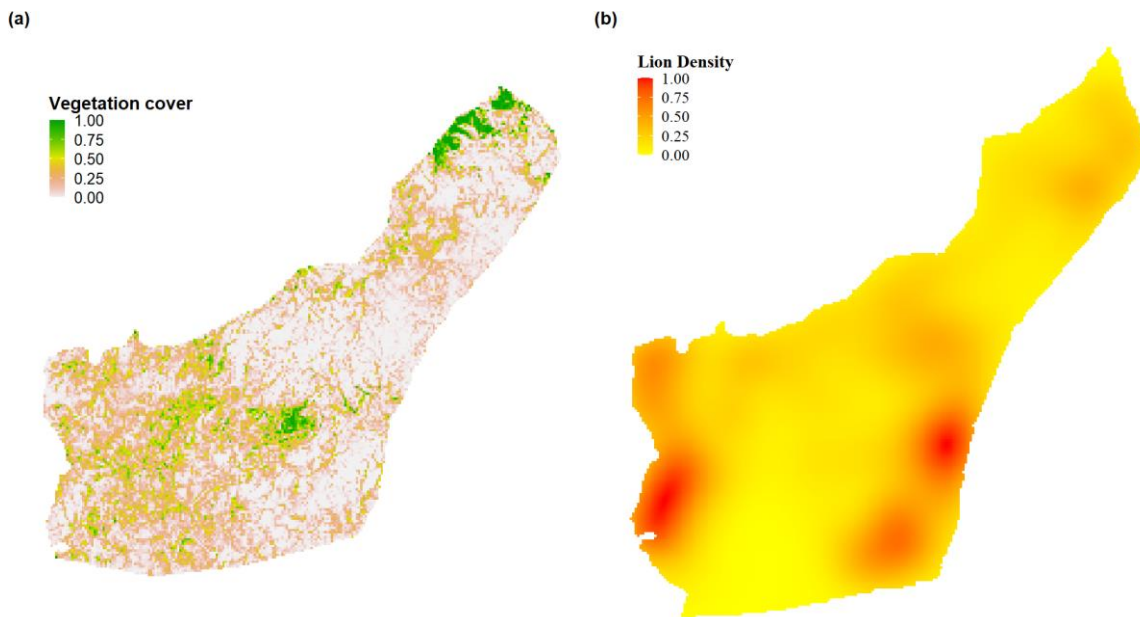
Figure 1: Vegetation cover map according to woody plant cover (a; Fradin unpublished data) and lion density map according to lion habitat use (b; Dejeante 2021).

Models

The independent variables included in the HMM function were woody vegetation cover, lion density, time of day (i.e. day or night), and interactions between woody cover and time of day, cover and lion density and time of day and lion density. I ran a model with ID as a random effect variable. However, the results showed that there was not a significant difference between the model with or without ID. McClintock (2021) suggested that including ID in HMMs does not generally improve the majority of models. Therefore, to simplify the model, I removed ID. Additionally, I tried to fit the most complete model with a three-way interaction between cover, time of day, and lion density, but the model was not converging. As such, I decided to not use the three-way interaction model. The FitHMM function estimated the probability of being in a behavioural state as well as the probabilities of transitioning from one state to another depending on the covariates.

3.4 RESULTS

During the day, the probability of a wildebeest resting was low (<20%), irrespective of vegetation cover or risk of encountering lions (Figure 2). Wildebeest were mostly found foraging, but as predation risk and vegetation cover increased, they shifted from foraging to moving.

At night, the probability of wildebeest resting was higher compared to during the day. The highest probability of rest (~70%) occurred in areas where lions were not present, irrespective of vegetation cover (Figure 2). Under these same circumstances, wildebeest showed a low probability of moving (~5%), and a low probability of foraging (~30%). However, as lion density and vegetation cover increased, the probability of resting decreased to as low as ~40%. Moreover, the probability of foraging decreased from ~45% to ~20% and the probability of moving increased from ~5% to ~40% (Figure 2).
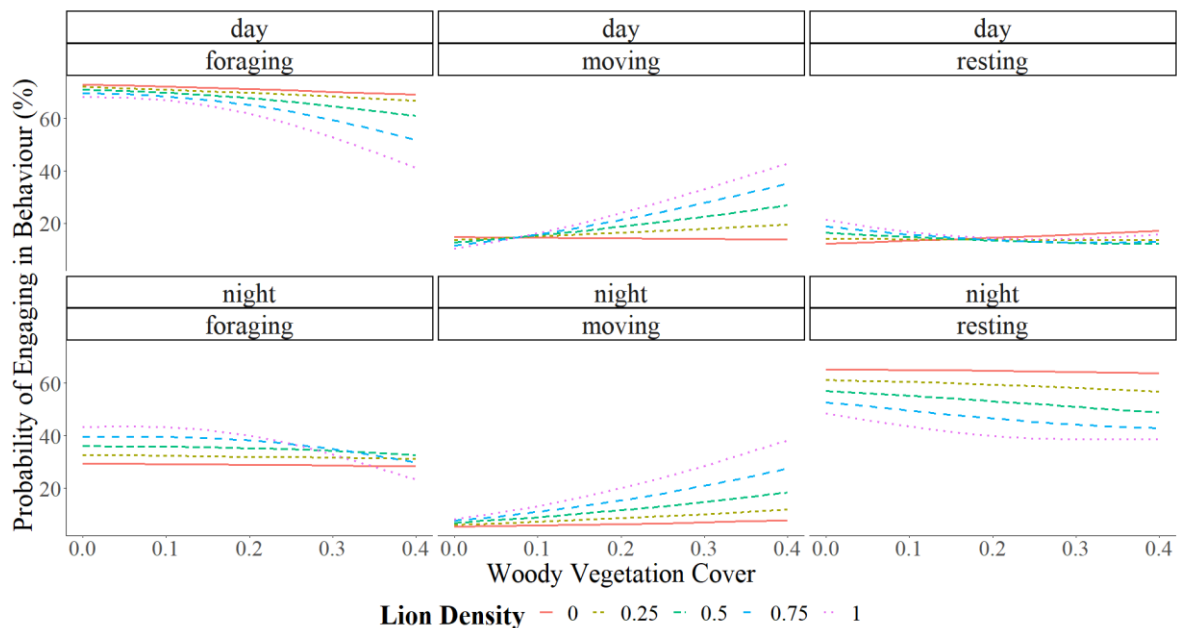

Figure 2: The probability (%) of a wildebeest engaging in foraging, moving, or resting, depending on whether it is day or night and according to the vegetation cover (%), and lion density.

3.5   DISCUSSION

When resting, animals must weigh up the thermoregulatory benefits of habitats and the costs of predation risk associated with those habitats (Krause & Ruxton, 2002; Lima et al., 2005). These trade-offs between benefits and costs determine when and for which activities animals utilise specific habitats (Owen-Smith, 2015). Overall, wildebeest were much more likely to rest at night than during the day. Furthermore, diurnal resting probabilities did not vary greatly with predation risk or vegetation cover. At night, and where lion densities were low, wildebeest were likely to be found resting (70%), and this did not vary with vegetation cover. However, as lion densities increased, the likelihood of finding wildebeest at rest decreased dramatically, and this effect was slightly stronger where vegetation cover was higher, further reducing the likelihood of wildebeest resting.

Wildebeest did rest occasionally during the day, with resting probabilities below 20%, but predation risk and vegetation cover had negligible effects. Dealing with thermal stress could explain the rare occurrences of diurnal resting (also see Siegel, 2009). For example, wildebeest in the Kalahari sought out cool microclimates when ambient temperatures exceeded 27° C (Boyers et al., 2019). Other studies also suggested that wildebeest need to rest to maintain normal body temperatures (Jarman & Jarman, 1973; Leuthold, 1977). Furthermore, some rare bouts of diurnal rest could be compensatory due to sudden increases in energy expenditure from escaping from predators (Campbell & Tobler, 1984; Joiner, 2016). However, I do not have any data to explore this possibility.

The increased probability of foraging and moving during the day suggests that wildebeest felt safer than they did at night (due to decreased lion activity during the day; Hayward & Slotow, 2009) to engage in active, but crucial, activities. Furthermore, during the day, wildebeest could rely on other antipredator adaptations when lion encounters did occur. During the day, wildebeest show increased predator detection due to increased visual acuity (Broekhuis et al., 2014; Kronfeld-Schor & Dayan, 2003) and the increased ability to navigate the landscape and evade predators during a chase (Burkepile et al., 2013). As such, wildebeest likely did not utilise the antipredator advantages of resting (i.e. decreased noise and increased crypticity; Schmidt, 2014; Siegel, 2009) during the day.

Overall, wildebeest were more likely to rest at night, when lions are active, than during the day. Resting has been suggested as a way of dealing with increases in predation risk, as resting allows an animal to be cryptic, and the act of resting is quiet and allows prey to hear potential threats (Schmidt, 2014; Siegel, 2009). Hearing threats is specifically important at night, as wildebeest vision is impaired, which reduces the ability to visually detect predators (Broekhuis et al., 2014; Kronfeld-Schor & Dayan, 2003), resulting in the need for other behavioural adaptations. In areas with low lion densities, the probability of wildebeest resting was ~70%, irrespective of vegetation cover. This suggests that wildebeest prefer to rest in safe areas with low lion densities, potentially due to reduced responsiveness during rest (Burger et al., 2020; Joiner, 2016; Lima, 1998; Lima et al., 2005). However, as vegetation cover did not affect resting probabilities at low lion densities, it seems that in the absence of lion, wildebeest did not cue off of indirect proxies of predation risk (such as vegetation cover). Yet, as lion density increased, resting probability decreased, with resting probabilities at its lowest in more vegetated areas. This suggests that when predators are present in a habitat, wildebeest do rely on indirect proxies of predation risk (i.e. vegetation

cover) when determining a safe resting site. Due to lion being ambush predators (Burkepile et al., 2013; Funston et al., 2001; Loarie et al., 2013), closed areas tend to be linked with greater predation risk. Yet, wildebeest still rested (~40% probability) in areas with high lion densities and increased vegetation cover. This suggests that resting is still utilised as an antipredator behaviour in areas with high predation risk, but to a lesser extent.

As lions were already present in the area, the advantages of being cryptic would be limited due to the scent cues given off by prey (Carthey et al., 2011). As such, lying in wait could be riskier under specific circumstances (e.g. if lions were particularly close) than moving around in the environment and being unpredictable in space (Traill et al., 2016). Which could explain the increase in movement observed as lion density increased (Traill et al., 2016). Similar increases in movement with predator proximity have been observed in boreal caribou (Basille et al., 2015). Furthermore, zebra in Hwange National Park moved away from risky areas at night as to reduce predation risk (Courbin et al., 2019).

In conclusion, I demonstrated that wildebeest primarily take predation risk into consideration when choosing when and where to rest. Wildebeest were more likely to rest at night when predation risk was higher, than during the day. At night, wildebeest preferred to rest in areas with low lion densities, irrespective of vegetation cover. Yet, in areas with higher lion densities, vegetation cover was taken into account when choosing where to rest, as it likely affected the probability of detecting a predator. During the day, wildebeest resting behaviour was not driven by predation risk or vegetation cover, but sparce resting bouts could occur as to deal with thermoregulatory pressure. This study provides valuable insight into the drivers behind wildebeest resting behaviour, a rather neglected field up until now. Specifically, we now have a better understanding of the impact of predation risk on the temporal and spatial aspects of wildebeest resting behaviour.

CHAPTER 4 GENERAL DISCUSSION AND CONCLUSIONS

4.1 CONCLUSION AND IMPLICATIONS

Resting is crucial for animal health and survival (Basner et al., 2013; Gottlieb et al., 2005; Gujar et al., 2011; Irwin & Opp, 2017; Schuh-hofer et al., 2017). Yet the drivers there-off are still poorly understood (Rattenborg et al., 2017; Tougeron & Abram, 2017). The aim of my study was to explore the social, spatial, and temporal aspects of resting behaviour, with a special focus on the impact of predation risk. To do so, I observed zebra, wildebeest, and impala behaviour under different degrees of predation risk to test whether predation risk affected the probability of these herbivores resting under different social (herd size, herd position), spatial (vegetation cover), and temporal (time of day) circumstances. Furthermore, I used GPS data to investigate the differences in diurnal and nocturnal wildebeest resting behaviour in different lion densities (i.e., predation risk) and vegetation covers (spatial aspects).

The results of my experiments show that predation risk affects the resting behaviour of large mammalian herbivores to some extent. It is even possible that direct predation risk (i.e., the presence of predators and/or their cues) outweighs the effect of indirect proxies of predation risk (i.e., riskier, densely vegetated, environments) on resting behaviour (Dröge et al., 2019; Gigliotti et al., 2021; Valeix et al., 2009b). This was seen in Chapter 3, where wildebeest showed no preference for resting in certain vegetation covers when lions were not present, but as lion density increased, the likelihood of wildebeest resting decreased.

However, a crucial trade-off exists between thermodynamically favourable resting spots (Krause & Ruxton, 2002; Lima et al., 2005) and spots safer from predators (Say-Sallaz et al., 2019). When resting, mammalian bodies generate and dissipate heat to maintain thermal stability (Mota-Rojas et al., 2021), but to a limited extent (Parmeggiani, 2003).

When changes in environmental temperatures or within the organisms itself occur, the speed of heat generation or dissipation is altered, which could lead to hyperthermia or hypothermia (Lendez et al., 2021; Reyes-Sotelo et al., 2021; Villanueva-García et al., 2021). The drive to choose for thermodynamically favourable spots was observed in Chapter 2 where zebra, under no predation risk, were more likely to rest in densely vegetated areas, that would aid with thermoregulation, but would be riskier in areas with higher predation risk, as predators cannot be spotted. However, as predation risk decreased, the probability of zebra resting in open habitats, where predators could be spotted, exceeded the probability of resting in closed habitats, that would aid with thermoregulation. Surprisingly, no such preference for thermoregulatory favourable spots or areas with lower predation risk was observed for impala (Chapter 2) or wildebeest (Chapter 2 and 3) that were resting during the day. It is possible that impala and wildebeest rest during the day could be relatively random, maybe driven by daily variability in how long it takes individuals to locate food, or that they rest primarily at night. For example, I found in chapter three that wildebeest, rested mainly at night, which is in contrast to a previous study that suggested that wildebeest in Benfontein Game Farm mainly feed at night and rest during the day (Maloney et al., 2005). This difference could be due to higher average temperatures in Benfontein game farm than in HiP, thus thermoregulatory constraints may have resulted in an increased need for rest and a decreased ability to forage during the day (Maloney et al., 2005). Moreover, a previous study on impala, also suggested that they are more active during the day and rest more at night (Shrestha et al., 2013). This may also be the case in my study, but unfortunately, I was not able to record the extent to which impala rested at night.

Another way to reduce the impact of heat is to partition activity (Cotton & Parker, 2000; Murray & Smith, 2012). This was observed in Chapter 2 when zebra showed an increase in resting probability as it became later in the day, irrespective of predation risk. Resting probability was at its highest around sunset when lions were active. This could be due to thermoregulatory constraints (Joiner, 2016; Lima, 1998; Siegel, 2009), as temperature rises as it becomes later in the day, or due to innate behaviours driving the timing of rest even in the absence of predators (Baxter-Gilbert et al., 2018; Dalesman et al., 2006, 2007).

Another contributing factor that may help explain this pattern could be that as the day progressed, the zebra became satiated as they foraged. As a result, late in the day they no longer needed to feed and thus provided time for them to rest. However, determining this

would require detailed monitoring of individuals' foraging, which is beyond the scope of my study.

The results of my study also provide greater understanding of the social aspects of zebra resting behaviour. As predicted, individuals in the centre of the herd were more likely to rest, as the centre of the herd is considered safer than at the edge (Rattenborg et al., 1999). Surprisingly, however, prey resting probabilities did not increase with herd size. Previous studies suggested that a decrease in individual vigilance with increasing group size allows individuals more time for other activities such as foraging (Burger et al., 2000; Childress & Lung, 2003). Thus, it is possible that they may use some of this extra time for resting. Yet, for zebra, resting probability decreased as herd size increased, and impala at moderate herd sizes were less likely to rest than those in small and large herds. This suggests that the relationship between herd size and predation risk is more complex than expected (Vitet et al., 2020), possibly due to interference of resting bouts by other herd members. Further research would have to be done on wildebeest and impala, specifically at night (Maloney et al., 2005; Shrestha et al., 2013), to better understand how herd size and position in the herd affects the probability of rest as I did not find significant differences during the day.

Ultimately, the results from my two data chapters suggest that predation risk does affect prey resting probabilities. However, my results also indicated that there are a multitude of other important variables to keep in mind, specifically the trade-off between thermoregulation and predation risk. Although this study showed that prey can mitigate this trade-off by either changing resting sites or by changing the timing of activity, further research is needed into how these changes differ between seasons and ambient temperatures. Understanding the effect of temperature on resting behaviour could be particularly interesting as thermoregulation in mammals is limited during deep sleep (Parmeggiani, 2003). As such, animals could shift between resting states as to maintain thermal equilibrium, apart from alternating between resting sites. Furthermore, prey resting behaviours change according to their social, spatial, and temporal circumstances, but the changes are species specific, and it is crucial to consider the diel cycle in its entirety to fully comprehend these changes.

4.2   FUTURE RESEARCH

My study has provided a foundation for future research on prey resting behaviour and specifically for studies on mammalian herbivore resting behaviour. To date, there has been

little research on resting behaviour. As such, future studies could investigate the trade-off between vigilance and rest, specifically whether vigilance and certain degrees of rest (e.g. deep sleep) could be considered as opposites such that an increase in vigilance results in a decrease in rest. In addition, one could explore how animals trade off different types of rest throughout the 24-hour cycle and how different factors influence the use of different types of rest. Finally, as human presence (e.g. habitat destruction, noise, and light pollution) is expanding into a number of habitats, it will be important to explore how these impacts may affect animal rest. It is important that behavioural studies focusing on resting take place under natural circumstances and not only in laboratories. Moreover, as observed in Chapter 3, it is imperative to look at the full picture (i.e., the entire diel cycle), as diurnal and nocturnal resting behaviours can differ along with the drivers of these behaviours. New tracking and GPS technology and ground-breaking analytical methods can aid in researching animals in their natural environment.

Vigilance vs. Rest

Previous studies have investigated the factors that influence vigilance behaviour (Ndiweni et al., 2015; Pecorella et al., 2018; van Deventer & Shrader, 2021). Furthermore, there is a lot of literature on the trade-off between vigilance and foraging (Blanchard et al., 2008; Childress & Lung, 2003; Creel et al., 2014, 2017; Fortin et al., 2004; Smith & Cain, 2009). Yet, little research exists on the trade-off between vigilance and resting. It is possible that vigilance behaviour and resting behaviour are mutually exclusive, such that a decrease in one could mean an increase in the other. Yet, we do not know the extent to which time not spent on vigilance behaviour is spent resting. Vigilance could be considered as quiet wakefulness (i.e. resting) as some postures related to vigilance is relaxed (Das, 2001; Henson et al., 2004; Herbers, 1981) and less energy is spent than on active behaviours (e.g. grooming, foraging). Furthermore, we have not studied how different factors (i.e. position in the herd, vegetation cover, herd size) affect vigilance and resting behaviour at the same time. For example, edge individuals are generally more vigilant than those at the centres of herds (Blanchard et al., 2008; Favreau et al., 2010; Matson et al., 2005; van Deventer & Shrader, 2021), which could suggest that edge individuals are likely to spend less time on other activities, such as rest. In this study we saw that zebras on the edge of a herd are in fact less likely to rest than those in the centre. However, as individuals adjust their position within a herd throughout the day, it may be that all individuals obtain adequate amounts of rest.

However, in species with a social hierarchy, subordinate individuals may have less time per day to rest.

However, it is possible that there is not really a trade-off between vigilance behaviour and resting. Each species has a critical minimum time they need to spend resting to perform crucial restorative processes in the body (Joiner, 2016; Rattenborg et al., 2004). As such, time spent on other activities could be more likely to change, as time spent being vigilant changes, than time spent resting (Herbers, 1981; Post, 1974; Stiles, 1971; Wolf & Hainsworth, 1971).

To investigate the potential trade-off between vigilance and resting behaviour, foraging and rest, and even rumination and rest, I would suggest collaring herbivore species with accelerometers, GPS, and possibly cameras or audio loggers as to identify the activities prey are engaging in across the landscape and diel cycle. I would look specifically at the probabilities of prey engaging in vigilance or resting behaviour depending on temperature and/or time of day, vegetation cover, and predator densities. Furthermore, it is possible that vigilance behaviour could, to some extent, be considered rest, specifically quiet wakefulness, as less energy is spent than on foraging, grooming, and mating. To investigate this, I would add an actigraph accelerometer to the collar to measure heart rate and activity levels (Rothney et al., 2008). Measuring heart rate could allow us to differentiate more accurately between inactive and active behaviours in the field. Adding actigraph accelerometers to the collars could even allow us to differentiate between REM and light sleep under varying environmental factors (temperature, vegetation cover) as has been done in dogs (Ortmeyer et al., 2018; Yam et al., 2011), horses, sheep, goats, cattle (Giannetto et al., 2017), and humans (Jean-Louis et al., 2001).

Human Presence and Hunting Risk

Human activities are continuously expanding around the globe (Venter et al., 2016; Watson et al., 2016) due to population growth, agricultural and urban development, and technology allowing us to access formerly isolated areas (Pertierra et al., 2017; Ramirez-Llodra et al., 2011). Growing participation in outdoor recreational activities further expands our impact on natural habitats (Gonson et al., 2016; Watson et al., 2016). Furthermore, pollution (including noise and light; Halfwerk & Slabbekoorn, 2015; Longcore & Rich, 2014; Zala & Penn, 2004), habitat modification (Fischer & Lindenmayer, 2007), invasive species (Murphy & Romanuk, 2014), and climate change (Evans & Moustakas, 2017) impacts habitats long

after humans have left a habitat. These human-mediated changes in environments are so swift that evolutionary processes might not be able to keep up (Chevin & Lande, 2010; Sinervo et al., 2010). The growing body of research on the effects of humans on animal behaviour helps us in understanding our human footprint. We now understand that humans have top-down effects on animal behaviour by changing animals' perception of risk (Miller & Schmitz, 2019; Suraci et al., 2019).

The effect of human disturbance on animal behaviour could be greater than that of natural predators, as humans affect all trophic levels and kill prey at much higher rates than other predators (Darimont et al., 2015, 2023; Hill et al., 2019), leading to humans being labelled the new apex predator or the "super predator" (Darimont et al., 2023; Dorresteijn et al., 2015; Suraci et al., 2019). For example, humans on foot lead to increased vigilance and decreased foraging in elk, more so than wolves and grizzly bears (Ciuti et al., 2012). Furthermore, hunted ungulate populations show significantly greater flight initiation responses to humans than non-hunted populations (Stankowich, 2008). When broadcasting playbacks of humans, lions, and hunting sounds, a wide variety of mammalian species (from lion to kudu and warthog) were twice as likely to run and ran 40% faster from waterholes in reaction to human sounds compared to lion (Zanette et al., 2023). Human disturbance also leads to an increase in animal nocturnality (Gaynor et al., 2018).

Alternatively, humans could create a safe space for prey by interfering in predator-prey interactions, reducing predators, and altering predators' landscape of fear (Miller & Schmitz, 2019; Shukla et al., 2021). When human voices were played in natural environments, large carnivores (mountain lions) avoided the area, while medium-sized carnivores (bobcats, striped skunks) reduced foraging and became elusive, and small mammals (deer mouse) increased foraging and habitat use (Suraci et al., 2019). Another study suggested that predators were less abundant in areas with high human activity, but that prey species were more abundant in these areas than areas with low human activity (Muhly et al., 2011).

Studies on the impact of human activity and accompanying risk on resting behaviour are limited. One study on American elk found a decrease in both feeding and resting time when subjected to mountain biking and hiking (Naylor et al., 2009). Elk also change their rest timing to avoid humans, specifically during hunting seasons (Visscher et al., 2017). Furthermore, wolves select resting sites offering more cover after encountering humans (Wam et al., 2012). Wild boar revisited resting spots close to or within villages more than

those far away from villages when there was no risk of being hunted, due to the benefits of resource acquisition (Fradin & Chamaillé-Jammes, 2023). Yet, when being hunted, wild boars revisited previous resting spots less frequently (Fradin & Chamaillé-Jammes, 2023). An extensive review paper on the effects of noise on wildlife found no papers on the effect on resting behaviour, but multiple on the effects on vocalization, movement, vigilance, mating, and foraging behaviour (Shannon et al., 2016). As such, studying the impact of human activities and hunting risk on resting behaviour should be a priority.

To test the impact of human activities and hunting risk on resting behaviour, I would advise using GPS collars with accelerometers on a variety of predator and prey species, as to test the impact of human activity and hunting risk on all trophic levels. Furthermore, I would collar these animals on neighbouring farms with varying hunting pressures and a tar road crossing through or alongside them. With this study design, one can test the effect of cars and noise on both predator and prey distribution and activity. Furthermore, this study design tests the effect of human activity and hunting pressure on prey distribution and activity. Alternatively, one could deploy camera traps, in a similar design as mentioned above, although this study design and data analysis could be more time consuming.

General Advice for Future Studies

It seems that there is a bias in the literature towards laboratory studies on resting behaviour (Acerbi et al., 2008; Rattenborg et al., 2017; Voirin et al., 2014) where the ecological drivers of rest are neglected (Shukla et al., 2021). For future studies, I would advise not only studying animals in a laboratory or zoo environment, but rather studying animals under natural circumstances, as our ultimate aim is to conserve animals under natural conditions.

Chapter 3 highlights the differences in diurnal and nocturnal wildebeest resting probabilities and behaviour. Chapter 3 also suggests that diurnal behaviour is not always an indication of nocturnal activities, and that the drivers of resting behaviour can differ between day and night. Furthermore, due to both logistical and financial limitations, previous research shows a bias towards diurnal behavioural studies. As such, I would suggest focusing on resting behaviour throughout the diel cycle.

Observational studying of animal behaviour may result in observer bias and thus may not truly reflect the patterns observed (Rattenborg et al., 2017; Wilmers et al., 2015). Thus, it can become problematic when studying cryptic and elusive animals and can be quite time consuming. Yet, GPS collars and accelerometery (Brown et al., 2013) offer ways to

overcome these challenges. Accelerometers can be fit to all species (Wilmers et al., 2015) and are small and affordable. Furthermore, resting is easy to identify from an accelerometric record (Brivio et al., 2021) and analysing the data from accelerometers is relatively simple. As such, I would suggest utilizing these new technologies in any future study of resting behaviour.

CHAPTER 5   REFERENCES

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