Land use influence on biodiversity and activity patterns of predators and prey in the semi-arid drylands of South Africa

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ABSTRACT

The unprecedented rise in anthropogenic activity worldwide has left wildlife with no other choice but to find means to coexist with humans across a range of different land uses. While some animals have developed strategies to adapt to the gradual and long-term modifications to the environment as a result of anthropogenic disruptions, rapid and pervasive changes often result in drastic reduction in species abundance causing local extirpation and posing a threat to ecosystem sustainability. Some behaviourally plastic species may be able to cope in real time to changes brought about by anthropogenic disruptions in their habitat, but they may have to compete with humans directly for space and food prompting negative interactions between people and wildlife which in turn lead to conflicts between conservation bodies on how best to mitigate these interactions. Understanding these interactions and how they influence ecosystem level functions, community interactions and the long-term persistence of wildlife is essential to achieving biodiversity goals. Most studies on wildlife in South Africa have focussed on protected areas but given that most animals still persist outside protected areas, it is imperative to expand research to include human modified landscapes too. The goal of my study was to 1) explore how wildlife adjust their activity with land use and, 2) determine whether heavily persecuted species adjust their activity more in human modified landscapes compared to protected areas and 3) how prey species adjust their activity with and without apex predators and 4) whether lunar illumination influences the activity of heavily persecuted species on farmland and predator-prey interactions in protected areas. I used camera trap surveys conducted on farmland between September 2012 and March 2013, in Anysberg Nature Reserve between the end of September 2013 and May 2014 and in Sanbona Wildlife Reserve between the end of August and November 2015 to provide insights into the relationships between land use, biodiversity, and predator-prey dynamics in the semi-arid drylands of South Africa. My study showed that semi-arid drylands of South Africa are important refugia for wildlife which is evident in the high species richness found in my study. I found that the temporal overlap for the same species living in Anysberg Nature Reserve and the nearby small livestock commercial farmland of Koup were not dissimilar. However, heavily persecuted (e.g., black backed jackal) and harvested species (e.g., steenbok) exhibited greater nocturnality on farmland presumably to avoid the diurnal peaks in farm worker activity. The presence and absence of apex predators had minimal influence on the activity of both smaller predators and a large size range of potential prey. That said both plains zebra and kudu showed increased nocturnal behaviour in the absence of lion which typically hunt at night. The response of wildlife to moon phase in different land uses was mixed with no clear patterns in the proportion of activity at night with different moon phases in either Anysberg or the farmland. This dissertation highlights the complex interplay between human activities and wildlife populations and provides important baseline information on the relationships between land use, biodiversity, and predator-prey dynamics that can be used to explore future shifts in both land use and climate in the drylands of the Karoo.

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1.0 GENERAL INTRODUCTION

1.1 Wildlife in the Anthropocene

Environmental change as a result of anthropogenic activity is occurring at unprecedented rates and is a major threat to wildlife worldwide (Pimm & Raven, 2000). With the predicted addition of 1.4 billion people in the next twenty years, most wildlife has no other choice but to share space with humans across a range of land uses (Carter et al., 2012; Venter et al., 2016). Given increasing levels of spatial overlap between people and wildlife it is imperative to know how varying land uses affect the distribution, abundance and behaviour of local fauna in a bid to adequately conserve biodiversity in productive human managed landscapes (Ceballos & Ehrlich, 2002; Hilty et al., 2006; Kauffman et al., 2007; Stein et al., 2008; Trolle, 2003).

While organisms may adapt to gradual and long-term human alterations of the environment, rapid and pervasive change often results in a drastic reduction in species abundance which in turn may lead to local extinctions (McDonnell & Hahs, 2015; Sih et al., 2011) and poses a threat to ecosystem sustainability (Seno & Shaw, 2002). Some behaviourally flexible species may be able to adapt in real time to changes (Fehlmann et al., 2021) but this may require competing directly with humans for resources (e.g., space and food) driving negative interactions between people and wildlife and leading to conflicts between stakeholders on how best to mitigate these interactions (Morehouse and Boyce, 2017; Redpath et al., 2013).

Although negative human-wildlife interactions are inevitable, the severity of interaction and its consequences differ significantly across a range of contexts (Angelici, 2016; Rissman et al., 2007). Wild animals typically avoid human-dominated habitats (Harihar & Pandav, 2012; Paudel & Kindlmann, 2012) because they have an innate fear of humans (Frid & Dill, 2001). However, the lack of natural resources including natural habitat and prey may force wildlife to consume crops (Gillingham & Lee, 2003; Linkie et al., 2007; Sapkota et al., 2014; Thapa, 2010) and livestock (Dar et al., 2009; Karanth et al., 2013) to survive. The sharing of space and competition for scarce resources (Carter et al., 2012) can lead to the injury and death of both wildlife (Oli et al., 1994; Paudel, 2012) and humans. Thus, foraging in human transformed landscapes is typically a balancing act for animals with the threat of persecution by humans being weighed up against the high quality foraging resources available (Brown et al., 1999; Chiyo et al., 2011).

Anthropogenic impacts invariably result in the decimation of fauna in heavily transformed habitats (Hilty et al., 2006; Kauffman et al., 2007; Rouget et al., 2003) or fundamental shifts in the range and abundance of species due to the extirpation of apex predators and/or access to human derived food resources (Prugh et al., 2009; Ripple & Beschta, 2004). Animals may also partition themselves temporally from human activity so as to minimise threats (Kronfeld-

Schor & Dayan, 2003). The partitioning of animals in time is an important characteristic of ecosystem functioning which in turn helps to shape the spatiotemporal patterns of predation and competition (Carothers & Jaksić, 1984; Kronfeld-Schor & Dayan, 2003; Lesmeister et al., 2015).

1.2 Human influences on animal activity patterns

Numerous wild animals respond significantly to human leisure activities and hunting by altering their daytime activity cycles to be more active at night (Brivio et al., 2017; Enggist-Düblin & Ingold, 2003; Oberosler et al., 2017; Raveh et al., 2012). For instance, carnivores avoid humans in time, suspending their activity when in contact with humans (Carter et al., 2015; Ciuti et al., 2012; Clinchy et al., 2016). Furthermore, animals have adapted to the changing climatic conditions by reducing their levels of activity during warmer parts of the day to prevent thermal stressors (Brivio et al., 2017; Rabaiotti & Woodroffe, 2019; Terrien et al., 2011) and hence dissipate more energy by becoming more active at night (Grignolio et al., 2018). Since anthropogenic disruptions are at their highest during the day, mammals globally are showing an increasing drift towards nocturnality (Gaynor et al., 2018).

At an evolutionary scale human disturbance affects ecological processes which in turn have altered the distribution of species in time (Wong & Candolin, 2015). At a more proximate level humans, as apex super-predators (Clinchy et al., 2016; Darimont et al., 2015), disturb the habitat animals live in and create new landscapes of fear (Frid & Dill, 2001). The majority of animals respond to anthropogenic disruptions by changing their choice of habitat, becoming more elusive, increasing alertness levels at the expense of feeding time, and becoming less active in preferred habitats (Frid & Dill, 2001). Together these changes can have negative impacts on animal physiology and well-being and can also trigger ecosystem imbalance (Preisser et al., 2005). This is evident in studies documenting abrupt changes in animal's movement (Tucker et al., 2018), feeding routine (Smith et al., 2015), and choice of habitat as a result of human activities (Cristescu et al., 2013; Eldegard et al., 2012).

Anthropogenic impacts have had a disproportionate impact on large carnivores and their extirpation from substantial parts of their historical distribution has contributed to the creation of 'fearless landscapes' in which smaller carnivores and prey species thrive (Bonnot et al., 2016; Creel et al., 2002). The disruption of complex predator/prey dynamics (Hintz & Relyea, 2017) has shifted how predators and prey use natural habitat (Djagoun et al., 2014; Wang et al., 2015) in addition to temporal patterns of activity in some species (Pagon et al., 2013; Wang et al., 2015). In many cases human impacts on animal activity patterns extend beyond the immediate activity. For example traffic caused by vehicles and also pedestrians have measurable impacts on animal activity at distances over 0.5 kilometres away (Andersen &

Aars, 2007; Andersen et al., 1996). Wide road networks, pathways, and other topographical features relating to human movement disrupt how animals make use of their habitats, and bring about shifts in the structure of the local faunal community in ways that increase lethal effects (Benítez-López et al., 2010; Griffiths & van Schaik, 1993).

In cases where wildlife have got no other choice but to share resources and live in close proximity to humans, they often tend to avoid people in time (Leighton et al., 2022; Oriol-Cotterill et al., 2015; Rasmussen & Macdonald, 2012). There is also a global trend that mammal species adjust their daily activity periods from being crepuscular to becoming more nocturnal to avoid peaks in human activity (Gaynor et al., 2018). Even in the case of animals that adapt easily to changing environmental conditions, such adaptations occur at fine spatial scales (Carter et al., 2012), in which animals avoid habitat with extensive human activity during the day and migrate into human occupied areas at night (Barnes et al., 2007; Graham et al., 2009; Gunn et al., 2014; Valeix et al., 2009).

1.3 Other factors influencing patterns of activities in animals

The need for animals to adapt physiologically and behaviourally to variation in environmental factors on a daily, seasonal and regional scale necessitated the evolution of activity patterns (Bennie et al., 2014; Kronfeld-Schor & Dayan, 2003; Roll et al., 2006). Patterns of activity in animals are mostly influenced by seasonal variation which influences both light/dark cycles and climatic conditions (Halle & Stenseth, 2000). At a local scale activity patterns are also affected by food availability (Larivière et al., 1994; Pereira, 2010), foraging efficacy (Lode, 1995; Prugh & Golden, 2014), predator/prey interactions (Fenn & Macdonald, 1995; Middleton et al., 2013), presence and activity of mates (Halle & Stenseth, 2000), and competition (Monterroso et al., 2014; Rychlik, 2005). Many of these factors act in concert, thus predators are obliged to improve their hunting efficacy by hunting at periods when prey are most available and vulnerable, while still avoiding competition with other predators (Ross et al., 2013). Disruptions in patterns of activity in animals have the propensity to alter the physiology (Creel et al., 2002; Millspaugh et al., 2001) and interspecific interactions (Barrueto et al., 2014; Hebblewhite et al., 2005), and also promote conservation conflicts (Redpath et al., 2015). Arguably the single most pervasive disruption to animal activity patterns is human activity (Barrueto et al., 2014; Vistnes & Nellemann, 2007).

1.4 How predator-prey interactions may influence activity

Predator-prey associations pose contrasting challenges for the species involved with predators exerting considerable energy to locate, catch and handle prey species (Lima, 2002), while the latter must evolve strategies to elude or ward off predators (Kronfeld-Schor & Dayan,

2003; Wirsing et al., 2010). Prey species may avoid predators in both space and time (Kronfeld-Schor & Dayan, 2003; De Vos et al., 2015) while predators and prey can minimise competition for resources by similarly avoiding conspecifics in space and time. The dynamics of these interactions are thus largely dependent on the adaptive skills or level of displacement of the prey species in the predator-prey or competitor interactions (Carothers & Jaksić, 1984; Fedriani et al., 2000; Kronfeld-Schor & Dayan, 2003; Neale & Sacks, 2011; Schoener, 1974). Thus for example African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) may avoid habitats with abundant preferred prey simply because more dominant predators such as lion (*Panthera leo)* and spotted hyena (*Crocuta Crocuta*) frequently make use of those habitats (Durant, 1998; Pretorius et al., 2021; Schuette, 2012).

Predicting how animals adjust behaviourally to the complex dynamics of predator-prey interactions is confounded by the diverse phenotypic traits of both interactants. Interactions are thus dependent on a host of factors ranging from availability of other sympatric predators and prey species (Wirsing et al., 2010), associated cost of niche migration (Creel & Christianson, 2008; Lima, 1998), prey escape instincts (Wirsing et al., 2010), evolutionary histories (Wiens & Graham, 2005), energy requirements (Bennie et al., 2014) and the omnipresent influence of humans as super predators.

1.5 Lunar illumination influences on animal activity patterns

Numerous studies have shown that the lunar cycle influences the physiological processes of a variety of living creatures including predator-prey interactions (Grant et al., 2013; Prugh & Golden, 2014). The lunar cycle is a major factor driving activity changes in animals as most nocturnal animals have the tendency to tailor their activity relative to moonlight variations (Bhatt et al., 2021) and depending on the degree of such adjustment in activity patterns, they could be classified as lunarphobic (Bhatt et al., 2021) or lunarphilic (Gursky, 2003). For instance, animals like small rodents (Clarke, 1983; Kotler et al., 1991), armadillos (Pratas-Santiago et al., 2017), and bats (Morrison, 1978), have been observed to reduce their activity on moonlit nights and increase it during less luminous nights or darker times of the night (Daly et al., 1992; Kotler et al., 2004). Variations in lighting conditions caused by the moon's fluctuating brightness throughout the lunar cycle typically cause prey to be less active and more cautious, and to forage in safer habitats around the full moon (Brown & Kotler, 2004; Griffin et al., 2005; Vásquez, 1994). Prey species reduce predator hunting effectiveness by being more active in darker nights of the lunar phase such as the new moon (Daly et al., 1992; Mori et al., 2014; Penteriani et al., 2013). On bright nights, prey adopt more cautious foraging techniques (Kotler et al., 2010) or become less active (Berger-Tal et al., 2010; Clarke, 1983; Sábato et al., 2006). These activity patterns make them less susceptible to predators as

predators are often more active during brighter phases of the moon (Pratas-Santiago et al., 2017; Kotler et al., 1991).

However, some species, like the white-footed mouse *Peromyscus leucopus* (Zollner & Lima, 1999); the cheetah *Acinonyx jubatus* (Broekhuis et al., 2014); the striped hog-nosed skunk *Conepatus semistriatus* (Dias, 2017); the rock cavy *Kerodon rupestris*, and certain primates (Fernández-Duque et al., 2010; Gursky, 2003) are more active on nights with strong moonlight. This heightened activity during moonlit nights could be linked to better awareness of potential predators and more successful foraging (Fernández-Duque et al., 2010; Gursky, 2003; Wilson & Watts, 2006). Despite being accustomed to hunting in the dark, most nocturnal predators enhance their hunting success on luminous nights in full moon (Bhatt et al., 2021; Cozzi et al., 2012; Harmsen et al., 2011; Sábato et al., 2006).

1.6 Camera traps for estimating wildlife activity patterns

Monitoring wildlife presence, abundance and activity patterns comes with a number of challenges ranging from having to overcome the barrier of the human observer in cases where it alters the focal species behaviour (Stewart et al., 1997), to adequate data collection and statistical analyses needed to provide robust estimates of these variables (Cagnacci et al., 2010). In a bid to overcome these barriers, wildlife biologists have employed various sampling techniques like collaring, radio-tracking and live trapping with differing success rates (Caravaggi et al., 2018). Radio-tracking is constrained with sampling on a periodic basis (Lovari et al., 1994) requiring extensive surveying effort (Palomares and Delibes, 1991; Reid et al., 2010) leading to small sample sizes (Caravaggi et al., 2018) that capture a small subset of the population (Sadlier et al., 2004). It is also prone to signal errors (Cagnacci et al., 2010), and has the propensity to modify the behaviour of tagged animals (Wilson et al., 2011). Additionally, inferences drawn from data generated from VHF or GPS collars might yield deceptive results and it is largely dependent on the regularity in which positional coordinates were acquired which reduces the total time the animal(s) can be sampled (Merrill & David, 2003). Live trapping has also been a technique used in studying patterns of activity in animals with each capture interpreted as an indication of animal activity (Caravaggi et al., 2018). Nevertheless, it is time consuming, has negative consequences for animal welfare (Torre et al., 2010), and the likelihood of capture is dependent on the target species, individuals and their levels of habituation and the types of traps used (Lešo and Kropil, 2010).

Camera traps have emerged as an important sampling technique in population, behavioural, and ecological studies over the last two decades (O'Brien, 2011). Remotely enabled cameras using light beams or infrared sensors (Swann et al., 2004) are gaining prominence in ecology and conservation studies (Kucera and Barrett, 2011) due to their non-invasive nature,

technological advancements and cost reductions (Tobler et al., 2008). They clearly have some advantages as a population sampling technique because they obviate the need for human observers and produce data that can readily be analysed using constantly evolving software approaches (Lashley et al., 2018; O'Brien, 2011; Zwerts et al., 2021). Additionally, they incorporate spatiotemporal replication, and a time track of captured photos, making them efficient tools for studies relating to spatial and temporal patterns of species activity (Trolliet et al., 2014).

While different taxonomic groups need various sampling techniques as no sampling device can detect all species with equal efficiency (Gompper et al., 2006), camera-trap surveys help to negate the potential pitfalls inherent in other sampling techniques as they can continuously sample multiple species with minimal disturbance (O'Connell et al., 2011). As the cost of camera-trap studies decreases and software for processing images becomes readily available, it has become increasingly popular for constant monitoring in observational and experimental studies (Burton et al., 2015; Steenweg et al., 2017). Since camera traps take photographs of all organisms that pass by, including humans, at all hours of the day, they provide a rich data set that often extends beyond the initial scope of study (Caravaggi et al., 2017) and can explore how animals adjust their activity in accordance with other animals and humans.

Camera traps have been hugely effective in evaluating temporal patterns of activity in cryptic species (Azlan & Sharma, 2006; Dillon and Kelly, 2007), temporal partitioning in carnivore guilds (Bischof et al., 2014; Fedriani et al., 2000; Wacher and Attum, 2005), herbivore guilds (Rivero et al., 2005), and predator-prey interactions (Weckel et al., 2006). Camera trap studies have also enabled researchers to carry out long-term studies with little disturbance of the focal species (Caravaggi et al., 2018) allowing researchers to investigate wildlife activity patterns across a range of land uses and contexts (Allen et al., 2018; Carbajal-Borges et al., 2014; Di Cerbo and Biancardi, 2013).

1.7 Research problem statement

Human activities have had dire consequences for global biodiversity with an estimated rate of loss of 818 species from AD 1500 to the present (Chaudhary and Mooers, 2018) and the current Anthropocene being characterised by the sixth great extinction (Dirzo et al., 2014). Many of the surviving species are adapting to living in human modified landscapes where they experience a multitude of non-lethal impacts. Understanding these impacts and how they influence ecosystem level functions, community interactions and the long-term persistence of wildlife is essential to achieving biodiversity goals. Most research on wildlife has focussed on protected areas (PAs) but given most animals still live outside of PAs it is imperative to expand

research to include human modified landscapes too. In a bid to fill knowledge gaps this dissertation seeks to explore how different land uses in the semi-arid drylands of South Africa influence biodiversity and the activity patterns of both predators and prey.

1.8 Wildlife and land use patterns in South Africa

The provinces with the most commercial agricultural practices in the country are the Western Cape, KwaZulu-Natal, and the Free State in which crop cultivation, mixed farming, cattle ranching, sheep farming, dairy farming, game ranching, aquaculture, beekeeping, and winemaking are the main agricultural activities (AGRI-SETA, 2010). Land use for domestic livestock farming and game ranching constitutes approximately 68.6% (839 281km^2) of the total land area in South Africa (Thorn et al., 2012). Sheep farming is practiced nationwide but is more prevalent in the arid regions of most provinces (Department of Agriculture Forestry and Fisheries, 2012). Most of the land in the semi-arid Karoo landscape which encompasses nearly 33% of South Africa's land mass (400 000 km^2) is dominated by sheep farming. Due to the regions low carrying capacity, 99% of the land is farmed extensively, with only one small-stock unit per 3-6 ha on average (Hoffman et al., 1999).

Since the 1980s, South Africa has witnessed a dramatic change in land use from livestock farming to game farming (Mann et al., 2015). Even though game farming is regarded as an environmentally friendly alternative to livestock farming in that it provides more habitat for indigenous animals (Lindsey et al., 2009), stocking beyond the carrying capacity and the widespread introduction of exotic species may have detrimental impacts on native biodiversity (Castley et al., 2001; Mann et al., 2015). Such impacts include vegetation changes, behavioural shifts in endemic species as a result of exposure to exotic species, inter breeding, and the introduction of harmful genetic strains (Castley et al., 2001; Goss and Cumming, 2013). In addition, game farms are usually fenced in a bid to restrict animal movement leading to habitat fragmentation (Hayward and Kerley, 2009) and the eradication of predators within fenced areas.

The transformation and degradation of land as a result of agriculture (Hof et al., 2012), deforestation (Sahlén et al., 2016) and pollution have all been shown to influence the structure, functioning, and integrity of ecosystems (Balmford et al., 2001; Brooks et al., 2002; Kerby and Wehrmann, 2012). Despite this a substantial proportion of biodiversity is currently living within human-modified landscapes but with severe changes to habitat functionality and cascading effects on species interactions (Lazenby and Dickman, 2013; Crooks and Soulé, 1999; Lewis et al., 2015). Habitat conversion has been shown to reduce natural resource availability and cause species to concentrate in remaining patches of natural habitat, increasing the likelihood of encountering competing species either directly or indirectly (Lewis et al., 2015). Thus

throughout much of Africa, livestock are reared alongside wild ungulates (Charles et al., 2017) and while a low abundance of domestic ungulates may allow wild ungulates to persist (Charles et al., 2017) excessive bushmeat harvesting often further suppresses their numbers in shared landscapes (Rogan et al. 2015).

1.9 Study objectives

The main objective of this study is to assess how different wildlife species adjust their activity patterns in response to a gradient of human land use ranging from a private protected area to a public reserve and private farmland. I use existing data from three independent camera trap surveys that employed the same survey design to: 1) explore how wildlife adjust their activity with land use and, 2) determine whether heavily persecuted species adjust their activity more on human modified landscapes (i.e., farmland) compared to protected areas and 3) how prey species adjust their activity with and without apex predators and 4) whether lunar illumination influences the activity of heavily persecuted species on farmland and predator-prey interactions in protected areas. These data will allow me to test three main hypotheses; firstly, whether fear of humans due to hunting and persecution will drive increased nocturnality among select prey (hunted) and predator (persecuted) species on farmland. Secondly whether prey species and smaller members of the predator guild will adjust their activity patterns to avoid temporal overlap with apex predators in protected areas. Thirdly, whether prey species will reduce their activity during moonlit nights (full moon) to avoid predators while predators will increase their activity during moonlit nights (full moon) in search of prey.

2.0 METHODS AND MATERIALS

2.1 Study sites

Data used in this study were collected firstly by Drouilly (2019) who surveyed the 22 neighbouring small-livestock farms in the Koup region, in addition to the Anysberg Nature Reserve, a public protected area approximately 48 km from the border of the Koup farms (Figure 1). Additionally, I used data collected by Woodgate (2021) who surveyed Sanbona Wildlife Reserve, a private protected area adjacent to the southern border of Anysberg Nature Reserve. All the three study areas (Anysberg Nature Reserve, Koup farms and Sanbona Wildlife Reserve) are located within less than 60km of one another, thus while they do not control for geographical variation between sites there are no other regions within the Karoo that have three similar sized areas of land that differ in land use and are all in proximity. Additionally, all three surveys used the same survey design (see below, Camera trapping)

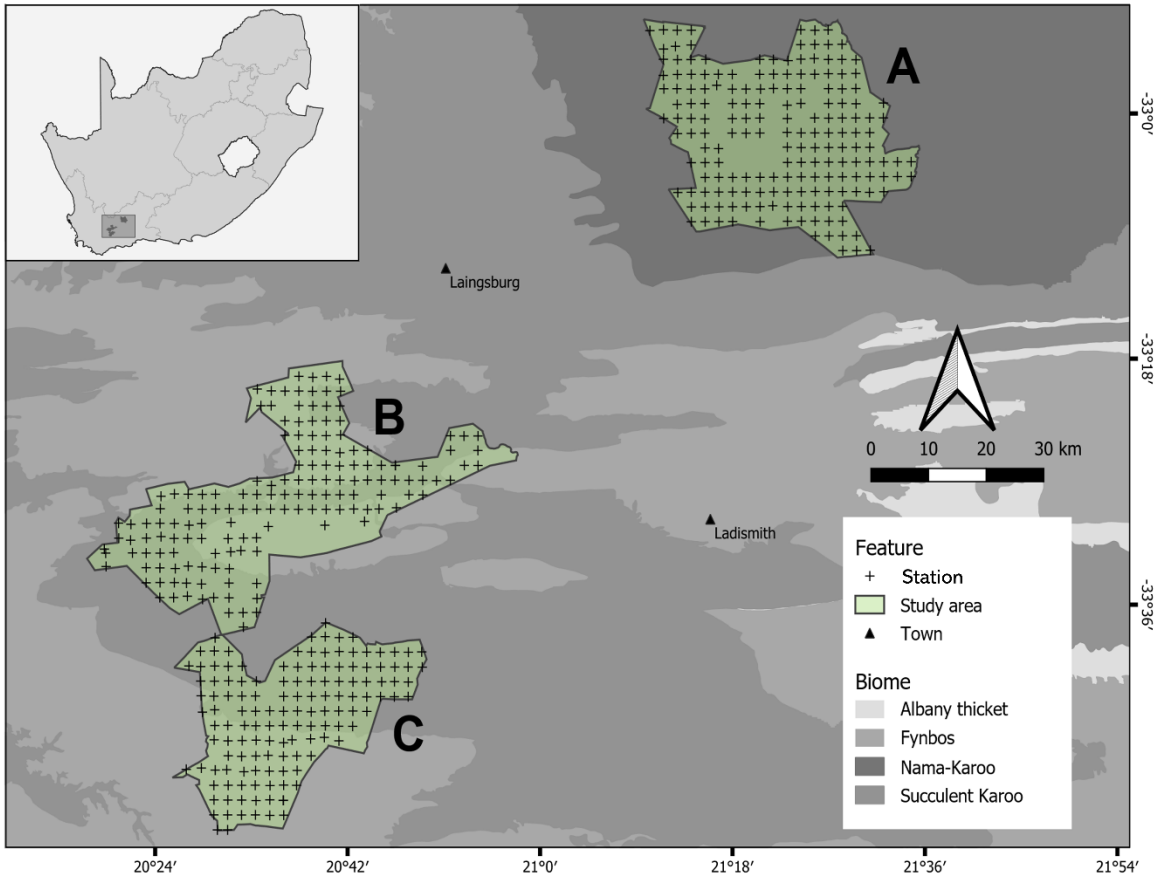


Figure 1: Location of the three study sites [A (Koup farms), B (Anysberg Nature Reserve), and C (Sanbona Wildlife Reserve); green polygons] in South Africa and their associated camera stations (denoted by the crosses). Map of South Africa showing the location of the three study sites (Insert).

2.1.1 Koup farms

The farmland in this study was comprised of 22 adjoining farms that collectively are part of the Koup district in the Central Karoo region and covers an area of roughly 80,000 ha. Domestic sheep are the most prevalent livestock on the farms with the two major breeds being Dorper and Merino, while Boer and Angora goats accounted for less than 4% of the livestock on the farms (Drouilly et al., 2018). Each farm in the Karoo is partitioned into fenced camps made of three simple wires to prevent livestock crossing between them and enable rotational grazing. Each fenced camp has its own artificial water source powered by a windmill which has replaced the orthodox “shepherding-plus-kraaling” arrangements (Archer, 2000; Drouilly, 2019).

Each farm's perimeter is enclosed with a mix of old and new ‘predator-proof’ fences made of 1.4m high wire mesh with boulders placed at the base to deter animal digging (Drouilly, 2019). In 2010 the perimeters of all the 22 farms were re-fenced with new jackal-proof fencing and re-packed with anti-digging stones that commenced under the auspices of “Koup jackal-proof Fence Project” which was supported by the farmers in conjunction with LandCare (community based) and the government (Nattrass et al., 2015). By mid-2014, a total of 238 kilometers of renovated and new fencing had been completed, accounting for 86.5% of the total circumference of the Koup farms (Nattrass et al., 2015). The fence is aimed at restricting predator movement into the Koup, thereby reducing negative interactions with livestock and minimizing farmer retaliation through indiscriminate lethal management methods. Despite these concerted efforts to limit predator movement into the farms, burrowing species frequently breached the fence, providing other wildlife with temporary passageways between farms (Drouilly et al., 2017; Kamler, Klare, et al., 2012).

In the Karoo most farmers employ lethal measures to reduce jackal and caracal numbers (Nattrass et al., 2017) including poisoning, trapping with steel jawed gin-traps and night hunting (Drouilly et al. 2020). A combination of non-lethal and lethal methods to reduce predation of livestock on farms is common both globally (Creel & Rotella, 2010; Treves & Karanth, 2003) and nationally (McManus et al., 2015) but how these methods are executed varies substantially between properties and their efficacy remains controversial (Nattrass & Conradie, 2018; Kerley et al. 2018). In addition most farmers actively hunt antelope species on their farm either for both recreational and consumptive purposes (Carruthers, 2008) in an effort to reduce competition for grazing with domestic livestock (du Plessis et al. 2018).

2.1.2 Weather and climate

The Central Karoo is widely regarded as a semi-arid region with frequent droughts and rainfall that is both unpredictable and seasonal, peaking in the hot summer months of December and March. Annual precipitation in the Koup is usually from isolated summer thundershowers, with infrequent cut-off low pressure systems generating stronger and sustained rainfall events that are frequently associated with significant floods (Desmet & Cowling, 1999). The climate in the Karoo is extreme, with significant seasonal and daily temperature variations. Average monthly temperature in the summer (October- April) frequently exceeds 32^{o}C, whilst in the winter (May-September), average monthly temperatures are regularly below 5^{o}C and frost is widespread (Drouilly et al., 2017).

2.1.3 Vegetation

The farmland is located in South Africa's second-largest biome, the Nama Karoo, which is characterized by low shrubs and grasses, with shrub cover increasing with increasing aridity. Overgrazing by livestock frequently degrades the grass component (Palmer & Hoffman, 1997; Todd, 2006). The area is dominated by shrub species such as *Drosanthemum spp*., *Eriocephalus spp*., *Galenia spp*, *Pentzia spp*., *Pteronia spp*., and *Ruschia spp*., while grass species such as *Aristida spp*., *Digitaria spp*., *Enneapogon spp*., and *Stipagrostis spp*. are also prevalent. *Vachellia karroo*, *Diospyros lycioides*, *Grewia robusta*, *Rhus lancea*, and *Tamarix usneoides* were usually confined to watercourses (Palmer and Hoffman, 1997; Todd, 2006).

2.1.4 Topography and geology

Farmlands are covered by shallow, poorly developed lime-rich soils that are primarily underlain by Dwyka Formation sediments, which are in turn covered by the Ecca and Beaufort groups (Desmet & Cowling, 1999). The terrain is flat partitioned with dry riverbeds and undulating hills, and is surrounded by mountains with maximum elevation of 1,200 m (Drouilly et al., 2018). The northern section is made up of hills that are flat at the top and are covered by dolerite sills which are more resistant to weathering than the sandstones and shale in the surrounding (Desmet and Cowling, 1999). The Dwyka River flows through the Koup, joining the Gamka River as a tributary at the Gamka Dam. Gullies with nonperennial rivers and streams are found throughout farmlands and flow momentarily following heavy rainfall.

2.2 Anysberg Nature Reserve

Anysberg Nature Reserve was established out of land formerly used for small livestock farming in 1987 and it lies between 33^{0} 31'S and 020^{0} 37'E. It is managed by CapeNature, Western Cape's public entity charged with biodiversity conservation. It covers an area of

82,300ha making it one of the largest protected areas in the Western Cape Province (Drouilly et al., 2018). The reserve is located in the Little Karoo approximately halfway between Touws River, which is 47 kilometers to the west, and Ladismith, 48 kilometers to the east (Rust, 2000) (Figure 1).

The Reserve falls within the Succulent Karoo and Fynbos biomes- a global significant winter-rainfall arid hotspot that occupies 112,000km^2 on the outskirt of the South Africa's Cape Floristic Region which is home to outstanding diversity and rarity of plant species (Cowling et al., 1999; Drouilly et al., 2018). Additionally, it comprises 4849 species of vascular plants out of which 40% are endemic to the country and is also home to the world's richest succulent flora (Drouilly, 2019).

2.2.1 Climate

Anysberg Nature Reserve has a bi-modal rainfall pattern that alternates between summer and winter rainfall seasons (Rust, 2000; Brand et al., 2018). However, rainfall varies according to the terrain, with the northern and southern mountain ranges receiving a greater amount of rainfall annually (500 mm) than the lowlands (200 mm), while the centrally located mountain region, Matjiesgoedberg, receives roughly 400 mm of rainfall per annum (Rust, 2000). Snowfalls may be experienced in July, August, and on rare occasions, September. There is presence of fog on high elevation summit all year round (Brand et al., 2018). Temperature varies from -5°C in winter to 38°C in the summer, with frost occurring between March and October. The maximum day lengths in January and December is roughly 15hours, while the minimum day lengths in June and July is around 9hours (Brand et al., 2018).

2.2.2 Vegetation

Anysberg Nature Reserve is situated in the succulent Karoo biome, particularly in the biome's less arid region (Rust, 2000). The reserve is characterised by four major habitat types namely the Succulent Karoo, Renosterveld, Montane fynbos, and Riverine/ floodplain vegetation (Vlok et al., 2005). The Succulent Karoo comprises of xeric adapted dwarf scrub of the Aizoaceae, Amaranthaceae and Asteraceae families on valleys and low hills (Desmet and Cowling, 1999; Vlok et al., 2005). The Renosterveld is characterised by low shrub layers from 1-2 metres tall composed mainly of Ericoids in hilly areas exposed to fire and could also have a significant grass component (*Ehrharta* spp., *Pentameris* spp., *Pentaschistis* spp. and *Themeda triandra*) (Vlok et al., 2005).

The Montane fynbos at higher altitude comprises of Proteaceae, Ericaceae and Restionaceae occurring on shallow, acidic, nutrient-poor sandy soils (Burger, 1993; Vlok et al., 2005). The Riverine and floodplain vegetation that line the mostly dry riverbeds is dominated by *Vachellia*

karroo, Rhus lancea and reeds Phragmitis australis) and create a network of trees that stretch throughout the reserve's plains (Vlok et al., 2005). Anysberg Nature Reserve's plant diversity is enhanced by its varied topography and substrates (Brand et al., 2018). Microhabitats are also formed by pockets of soil that support diverse plant communities. Although it is an arid habitat, it supports Cape hares, small steenbok, duiker, leopard, jackal, and caracal, as well as a diverse herpetofauna (Burger, 1993).

2.2.3 Topography and geology

Anysberg Nature Reserve is typified by rough, undulating, semi-arid terrain owing to its position in the centre of South Africa's Cape Fold Belt (Brand et al., 2018). The reserve is divided by three mountain ranges- the Anysberg in the south, Matjiesgoedberg in the centre, and the western extension of Suurkloof se Berg in the north, all of which are partitioned by two east-west valleys (Burger, 1993). Elevation in the reserve ranges from 1621 meters above sea level along the summit of the Anysberg Mountain to little less than 500 meters above sea level along the Buffels River on the reserve's eastern boundary (Brand et al., 2018). The reserve is traversed by numerous rivers, the most notable of which are the Touws, Anys, Prins and Buffels Rivers (Brand et al., 2018).

The reserve's geology is comprised of the Table Mountain Group, the Bokkeveld Group, and the Witteberg Group. Quartzitic sandstone, sandstone, siltstone, shale, tillite, and diamictite are among the geological constituents of these groupings. Shallow Mispah and Glenrosa soils, as well as Clovelly soils with a depth lesser than 30 cm, are the prominent soils in the reserve (Burger, 1993).

2.3 Sanbona Wildlife Reserve

Sanbona Wildlife Reserve was founded in 2002 following the integration of 19 agricultural farms that were previously used for lucerne and wheat cultivation, domestic livestock production (sheep and goats), game farming, recreation farming and tourism (Gordon et al., 2016). The farms were merged by removing their internal fences, crops like lucerne and wheat were cleared, exotic vegetation was removed and a boundary fence was established (Gordon et al., 2016). Sanbona is the largest privately owned game reserve in the Western Cape, covering an area of approximately 54,000 hectares (Gordon et al., 2016). The reserve (33°43'24'' south and 20°36'55'' east) is situated in the Little Karoo, a semi-arid region approximately 27 kilometers northwest of the town of Barrydale and 49 kilometers northeast of Montagu (Gordon et al., 2016). The reserve is demarcated into management units viz Sanbona south and Sanbona north with Sanbona south comprising the largest part of the reserve and forms the hotspot of tourism activities. Lions and cheetahs were introduced into

the northern section (Vorster, 2017) which serves as a basis for me to explore predator prey associations with and without apex predators.

2.3.1 Vegetation

The reserve is home to two of the world's thirty-four vegetation biodiversity hotspots- the Fynbos Biome and the Succulent Karoo Biome (Mucina and Rutherford, 2006), and is abundant in plant diversity, with approximately 600 species identified within the Renosterveld, Central Mountain Fynbos, Succulent Karoo, Thickets, Riverine and floodplain vegetation types (Vlok et al., 2005). Variation in vegetation is mostly determined by rainfall, topography and soil properties of which the most prominent are Western Little Karoo, Little Karoo Quartz Vygieveld, Montagu Shale Renosterveld, Matjiesfontein Quartzite Fynbos, Montagu Shale Fynbos, Northern Langeberg Sandstone Fynbos and South Langeberg Sandstone Fynbos (Hoffman et al., 2009; Mucina and Rutherford, 2006).

2.3.2 Topography and Geology

Sanbona Wildlife Reserve is made up of Devonian sedimentary sandstone, mudstone, and siltstone (Norman and Whitfield, 2006). The terrain is quite varied, undulating in some places and flat in other parts. Rolling hills are predominant in the South-eastern section of the reserve, while the South-western region is characterised by open plains. The reserve's central and western sections are typified by deep river valleys and steep mountains (Norman and Whitfield, 2006). Elevation in the reserve ranges from 430 meters above sea level in the Brak River to 1344 meters above sea level in the Warmwaterberg mountain range (Swanepoel, 2019). The Warmwaterberg range comprises the oldest geological formations and serves as a natural boundary between the reserve's northern and southern sections. The mountain is dominated by sandstones and quartzite and falls within the Rietvlei Formation and Skurweberg Formation (Vorster, 2017), which forms part of the Table Mountain Group. The mountain range is characterised by steep to very steep slopes and consists predominantly of exposed rock with little soil. The dominant soil formations for the reserve are the Mispah and Glenrosa formations, with some Oakleaf, Hutton and Swartland (Vorster, 2017).

2.3.3 Climate

Sanbona Wildlife Reserve is located in South Africa's transition zone between summer and winter rainfall regions (Gordon et al., 2016). Although the reserve can receive rainfall throughout the year, it occasionally experiences drought conditions but prolonged droughts are uncommon (Desmet and Cowling, 1999; Swanepoel, 2019; Vorster, 2017).

Due to the reserve's size and topographical heterogeneity, rainfall varies significantly. Rainfall variation across the reserve is also strongly influenced by the centrally positioned, east-west orientated, Warmwaterberg mountain which effectively divides the reserve into a northern section (Sanbona North) and a southern section (Sanbona South). As a result of the rainfall shadow cast by the Warmwaterberg mountain, Sanbona South receives more rainfall than Sanbona North (Gordon et al., 2016; Mucina and Rutherford, 2006).

Annual temperature in the reserve ranges from -2 to 41.8°C, with the summer months (December, January, and February) being extremely hot, with a mean maximum ambient temperature of 35°C. The winter months (June, July, and August) are extremely cold, with an average daily temperature of 4.9°C and temperatures often dipping below the freezing point in the early hours of the day. Frost also covers the ground in the winter months early in the morning (Gordon et al., 2016; Swanepoel, 2019; Vorster, 2017).

2.4 Camera Trapping

All three study sites were surveyed using the same systematic sampling technique with a randomized starting point (Kinnaird and O'Brien, 2012; Meek et al., 2014) and cameras placed in a grid arrangement with a 2km inter-camera distance (Fig. 1). This design allows for habitat characteristics such as riverbeds, trails and cliffs to be sampled in proportion to their occurrence on the landscape (Cusack et al., 2015; Rowcliffe et al., 2013) and is suitable for multi-species surveys (Cusack et al., 2015; Harmsen et al., 2010; Larrucea et al., 2007; Mann, et al., 2015). The sampling unit centroids of the survey grids were located with the aid of ArcView 3.2 (ESRI, Redlands, CA, USA) and cameras were positioned within 50 m (with the exception of certain cases in which cameras were placed up to 200 m due to topographical barriers) of the centroid mostly on animal trails or where there were other signs of animal activity (Drouilly et al. 2019) so as to be able to increase the maximum likelihood of obtaining photographs of a wide variety of species (Colyn et al., 2018; O'Brien et al., 2010). Due to the preference of light emitting diodes as opposed to white flashes which are known to influence species' detectability in ecological surveys (Caravaggi et al., 2020), all three study sites were surveyed using digital Bushnell Trophy CAM HD (Bushnell Outdoor Products, Overland Park, Kansas, USA) with Passive Infra-Red (PIR) motion sensors. The cameras were programmed to take three pictures each time they were triggered, with a 1-minute delay between triggers to minimise the number of photos of species living in groups (e.g., chacma baboons, springboks, and small livestock).

Camera traps were deployed at a total of 176 locations on farmland between the end of September 2012 and March 2013, and at 156 locations in Anysberg Nature Reserve between the end of September 2013 and May 2014 (Drouilly,2019). In Sanbona Wildlife Reserve,

camera traps were deployed at 132 locations between the end of August and November 2015 Woodgate (2022) (see Figure 1).

2.5 Data processing and analysis

The resultant photograph database was cleaned by deleting pictures of non-focal species (birds, insects and bats) and images where it was difficult to identify the species. Furthermore, the database was also cleaned of instances where the camera captured blank images and recorded incorrect date or time. A 24 hour duration commencing at 00:00 and ending at 23:59 denotes an independent trap night (Meek et al., 2014). To investigate the potential shifts in wildlife activity patterns between different land uses (farmland versus protected area) and management approaches (commercial small livestock farming versus conservation) without the confounding effects of seasonality, I had to restrict my analyses to Anysberg Nature Reserve and Koup farms which were sampled at a similar time of year. Similarly, to understand the impacts of lunar illumination on the activity patterns of species that are hunted on farms, without the confounding effects of seasonality, I restricted my comparison to Anysberg and Koup. Lastly, to explore the impacts of trophic interactions on activity patterns I only compared wildlife on Sanbona which has a diverse predator guild including large apex predators. Furthermore, the broad division of Sanbona into a northern section with lion and southern section without allowed for a comparison of both prey species and mesopredators with and without this apex predator.

I only included species in analyses for which I had sufficient photographic captures (n>10) at each site (Gerber et al., 2012; Ota et al., 2019). I used the overlap package (Ridout & Linkie, 2009) to compare the activity patterns of target species within and between the study sites. The time data from each photographic capture was converted to radians and used to construct non-parametric kernel density distributions of each species' diel activity data (Linkie & Ridout, 2011; Noor et al., 2017; Ridout & Linkie, 2009). To account for minor seasonal differences in sunrise and sunset between the Koup and Anysberg study sites, I standardised observations by transforming the clock-recorded time of each detection to a relative sun time corresponding to the actual sunrise and sunset (Nouvellet et al., 2012) instead of using the raw observation time. For each pairwise comparison (between species and across sites), I calculated the coefficient of overlap (Δ). Δ is defined as the proportion under the curve created by 2 minimum density functions at each time point (i.e., Δ is the proportion of overlap between the 2 species' diel activity curves; Ridout and Linkie, 2009). Δ is presented as a spectrum of proportional values, with 1 indicating complete overlap and 0 indicating no overlap. For instance, $\Delta = 0$ could occur if one species was entirely diurnal and the other entirely nocturnal. I used a cut-off value of $\Delta \geq 0.70$ to signify high overlap in diel activity, and $\Delta < 0.35$ to signify low overlap,

following Lynam (2013). Furthermore, following Schmid and Schmidt (2006), the coefficient of overlap was quantified using the Δ_1 overlap estimator for species with small (< 50 independent events) sample sizes while Δ_4 estimator was used to quantify the coefficient of overlap for species with large (> 50 independent events) sample sizes (Ridout and Linkie, 2009). Schmid and Schmidt (2006) introduced five broad nonparametric estimators (designated as Δ1 through Δ5) for measuring the coefficient of overlapping. In circular distributions, the first two estimators (Δ1 and Δ2) are the same, while the third (Δ3) is not workable (Ridout & Linkie, 2009). Δ5 is not stable, as minor changes in the data can cause abrupt shifts in the estimate, potentially resulting in estimates exceeding one and thus rendering it ineffective (Schmid & Schmidt, 2006). The selected approach for overlap computation involved utilizing Δ1 and Δ4 estimators, contingent upon the sample size. For each of the comparisons the coefficient of overlap was bootstrapped 1000 times to generate 95 % confidence limits (Linkie and Rideout, 2011).

To assess the potential effects of lunar illumination on the activity patterns of species with at least 10 independent photo-capture events in both study areas and which are known to be actively persecuted by commercial farmers because of their perceived or actual competition with, or predation of, livestock, I filtered the dataset to nocturnal activity by selecting only those records occurring between sunset and sunrise and removing photographs captured an hour before and after sunrise and sunset (i.e., crepuscular activity) (Linkie and Ridout, 2011). I characterised lunar activity using the 'lunar.phase' function from the package lunar in R to obtain the moon phase for each observation based on its date. The records from each moon phase were selected to assess the effect of moonlight on the activity patterns of selected species during the lunar cycle. I classified the moon phase of records, according to the percentage of visible moon surface into four categories: 0%–25% [New Moon (New)], >25%–75% [first quarter—Waxing Moon (Waxing); last quarter—Waning Moon (Waning)], and 75%–100% [Full Moon (Full)] using the lunar package in R-software version 4.1.2 (R Development Core Team, 2021).

3.0 RESULTS

A total of 8930 independent detections of 43 species were recorded across the 26 331 camera trap days in all three study sites (Table 1). The total number of independent trap nights was lowest for Sanbona Wildlife Reserve (n=5951) and highest for the Koup farms (n=10 842) with effort in Anysberg Nature Reserve similar to the farmland (n=9538). Weather events (e.g., extreme rainfall and wind) and disturbance (by humans and animals) resulted in 62 cameras across all three sites (13.36%) experiencing significant data loss. A further 334 (3.74%) detections were missing time stamps and were subsequently omitted from the analyses.

Table 1. Summary of camera trap surveys in the three study sites. Data include the total extent of each study area, the period over which the survey was conducted, the total number of stations at which camera traps were deployed, the proportion of those stations where the camera trap failed, the number of trap days or effort for each site, total number of independent captures (≥ 30 min between successive images of the same species) and the total number of wildlife species detected at each site.

Study area	Size of study area (km^2)	Sampling period	Active camera stations	Camera trap failure (%)	Effort	Total independent captures	Total detected species
Koup farms	754	2012-2013	156	10.2	10842	3480	27
Anysberg	802	2013–2014	176	16.1	9538	2966	30
Sanbona	540	2015	132	10.3	5951	2484	36
Total	**2096**		**464**		**26331**	**8930**	

Data from 464 camera trap locations yielded a total of 43 species of wild animals. Sanbona Wildlife Reserve had the highest number of species detected (n=36), with Koup farms the lowest (27) and Anysberg an intermediate number (30). Common duikers (*Sylvicapra grimmia)* were detected the most across all three study sites, while Cape grysbok (*Raphicerus melanotis)* had the lowest number of detections across the study sites. On Koup farms, common duikers were detected the most, while suricate had the fewest detections. In Anysberg Nature Reserve, chacma baboon (*Papio ursinus*) accounted for the highest number of detections, while striped polecat (*Ictonyx striatus*) and water mongoose (*Atilax paludinosus*) were detected the least. In Sanbona Wildlife Reserve, hares (*Lepus spp*) were detected the most, while mountain zebra (*Equus zebra*) had the lowest detection rate.

Table 2. Total number of independent detections for each wildlife species across the three study sites.

Species	Koup farms	Anysberg Nature Reserve	Sanbona Nature Reserve	Total
Aardvark	41	26	19	86
Aardwolf	96	20	2	118

African elephant	0	0	12	12
African lion	0	0	33	33
African wildcat	9	96	32	137
Bat eared fox	213	7	7	227
Black backed jackal	103	230	131	464
Black wildebeest	0	0	9	9
Blesbok	26	0	0	26
Brown hyena	0	13	47	60
Bushpig	0	4	0	4
Cape fox	16	0	0	16
Cape grey mongoose	37	45	14	96
Cape grysbok	0	0	2	2
Cape porcupine	64	103	47	214
Caracal	23	8	21	52
Chacma baboon	82	493	112	687
Cheetah	0	0	5	5
Common duiker	897	280	158	1335
Eland	0	61	227	288
Fallow deer	18	0	0	18
Gemsbok	20	416	177	613
Giraffe	0	0	28	28
Greater kudu	131	67	94	292
Grey rhebok	64	72	22	158
Hare	523	133	232	888
Honey badger	0	17	3	20
Klipspringer	50	188	67	305
Leopard	0	23	6	29
Mountain zebra	0	19	1	20
Plains zebra	0	0	97	97
Red hartebeest	0	115	10	125
Rock hyrax	14	37	5	56
Small spotted genet	38	17	30	85
Smiths red rock rabbit	30	95	41	166
Springbok	82	86	23	191
Steenbok	682	103	84	869
Striped polecat	35	1	0	36
Suricate	3	0	0	3
Vervet monkey	8	16	0	24
Water mongoose	0	1	2	3
White rhino	0	0	12	12
Yellow mongoose	15	0	3	18
Total number of detections	3320	2792	1815	

3.1 Comparing the activity of select species in Koup farms and Anysberg Nature Reserve

I selected species for which I had at least 10 independent photo-capture events in both study areas, and which are known to be actively persecuted by commercial farmers because of their perceived or actual competition with, or predation of, livestock (Table 2 and 3). This resulted in a total of 3712 independent detections of the 10 species with common duiker comprising

32% (n = 1177) of the detections, steenbok (*Raphicerus campestris*) 21% (n = 785), gemsbok (*Oryx gazella*) 12% (n = 436), black backed jackal (*Canis mesomelas*) 9% (n = 333), klipspringer (*Oreotragus oreotragus*) 6% (n = 238) greater kudu (*Tragelaphus strepsiceros*) 5% (n =198), springbok (*Antidorcas marsupialis*) 5% (n = 168), grey rhebok (*Pelea capreolus*) 4% (n = 136), aardwolf (*Proteles cristata*) 3% (n = 116) and aardvark (*Orycteropus afer*) 2% (n = 67) (Table 2 and 3).

Of the 10 selected wildlife species across both study sites, common duiker had the most detections (n = 1177) and were also detected at the most stations (n = 164; 22%) while springbok was the least detected (168) and were also detected at the fewest stations (35; 5%) (Table 2 and 3).

Table 3: The total number of independent detections for each species of interest (grouped by guild) in Anysberg Nature Reserve and Koup farms and the total number of stations in each site that each species was detected.

Species	**Guild**	**Number of detections in each study site**			**No. of camera stations species was detected**		
		Anysberg	Koup	Total	Anysberg	Koup	Total
Aardvark	Prey	26	41	67	21	22	53
Aardwolf	Mesopredator	20	96	116	15	47	62
Black backed jackal	Mesopredator	230	103	333	49	31	80
Common duiker	Prey	280	897	1177	63	101	164
Gemsbok	Prey	416	20	436	67	3	70
Greater kudu	Prey	67	131	198	18	25	43
Grey rhebok	Prey	72	64	136	19	19	38
Klipspringer	Prey	188	50	238	48	14	62
Springbok	Prey	86	82	168	22	13	35
Steenbok	Prey	103	682	785	37	112	149
Total		1557	2155				756

Temporal overlap was generally high (Mean = 0.83; 99% of all species had $\Delta_4 > 0.70$ in the sites; Table 4). None of the Δ_4 estimates were below 0.35 which is the cut off for 'low temporal overlap' and ranged from 0.60 [CI =0.43-0.77] for gemsbok (*Oryz gazella*), to 0.95 [CI =0.90-0.98] for common duiker.

Table 4: Coefficients of overlaps (Δ_4), associated 95% confidence intervals of temporal activity patterns for species of interest in both Anysberg Nature Reserve (ANYS) and Koup farms (FARM). Bold values indicate overlap in activity pattern considered to be strong ($\Delta_4 \geq 0.70$).

Species	ANYS and FARM
Aardvark	**0.93 (0.79-1.02)**
Aardwolf	**0.92 (0.77-1.03)**
Black backed jackal	**0.80 (0.71-0.88)**
Common duiker	**0.95 (0.90-0.98)**
Gemsbok	0.60 (0.43-0.77)
Greater kudu	**0.80 (0.70-0.89)**
Grey rhebok	**0.78 (0.66-0.89)**
Klipspringer	**0.80 (0.70-0.90)**
Springbok	**0.85 (0.74-0.94)**
Steenbok	**0.87 (0.80-0.94)**
Mean overlap	**0.83**

3.2 A comparison of activity patterns of select wildlife in a protected area (Anysberg) versus commercial small livestock farmland (Koup) with active hunting

Aardvark exhibited predominantly nocturnal activity in both Anysberg and Koup with activity peaks around 22:00-23:00. Aardwolf activity was similar to aardvark in both study sites but with a peak in activity around 0:00. Black backed jackal activity was predominantly nocturnal in farmland with a peak in activity around 0:00. In Anysberg the species was less nocturnal than on farmland with a small early evening peak in activity around (18:00-19:00). The activity of common duiker was similar at both study sites with an early morning peak between 04:00 and 06:00 and an evening peak between 18:00-20:00.

Gemsbok showed a clear nocturnal peak (22:00-23:00) in activity on farmland but were active at moderate levels throughout both the day and at night in Anysberg. Greater kudu activity in Koup followed a bimodal pattern, with an early morning peak around 04:00-06:00 and an evening peak around 16:00-17:00. In Anysberg, greater kudu showed a similar early morning peak (04:00-06:00), but with a distinct nocturnal peak at 00:00. Grey rhebok were mostly diurnal on farmland with a morning peak between 08:00-10:00, whereas the species exhibited a bimodal activity pattern in Anysberg with an early morning peak around 04:00-05:00 and an afternoon peak around 14:00- 17:00.

Klipspringer exhibited a bimodal peak in activity in Koup with a morning peak in activity between 08:00-10:00 and an early evening peak in activity between 16:00-17:00. In Anysberg Nature Reserve, they were still diurnal but with a morning peak at 06:00-07:00 and a second early evening peak in activity around 16:00-17:00 and then a gradual drop-off in activity. Springbok on farmland showed a unimodal activity pattern being active exclusively during the

day with a peak in activity between 10:00-11:00. In Anysberg they were still diurnal but with an early morning peak between 08:00 and 09:00 and second early evening peak around 16:00- 17:00. Steenbok activity in Koup followed a bimodal pattern, with an early morning peak around 04:00-05:00 and a smaller early evening peak from 16:00-17:00. In Anysberg, they showed a similar early morning peak but from (06:00-07:00) and a smaller late evening peak from 16:00-17:00 and a nocturnal peak around 22:00-23:00. All results are shown in figure 2.

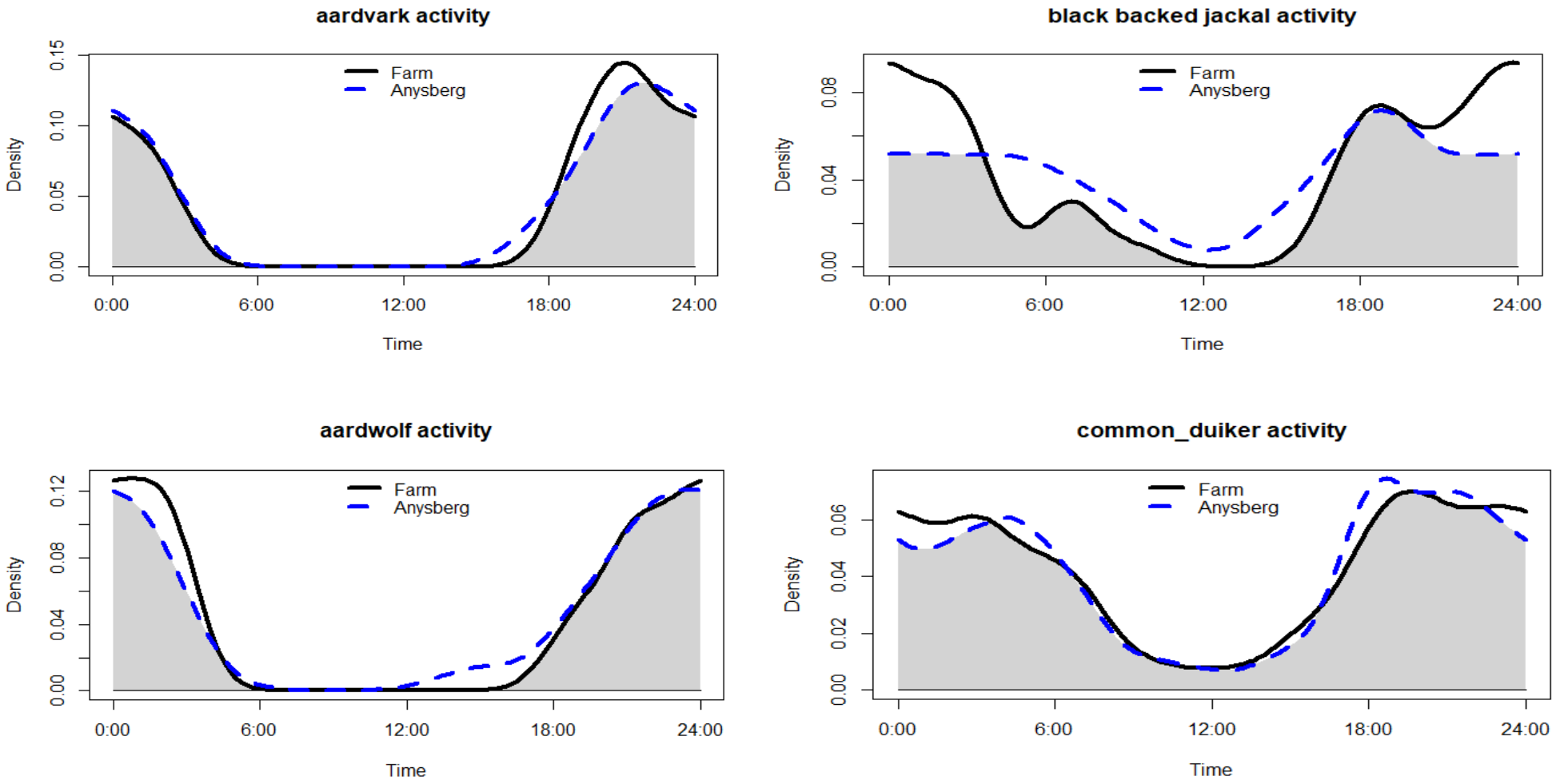


Figure 2: Activity patterns of species that are routinely hunted on Koup farms.

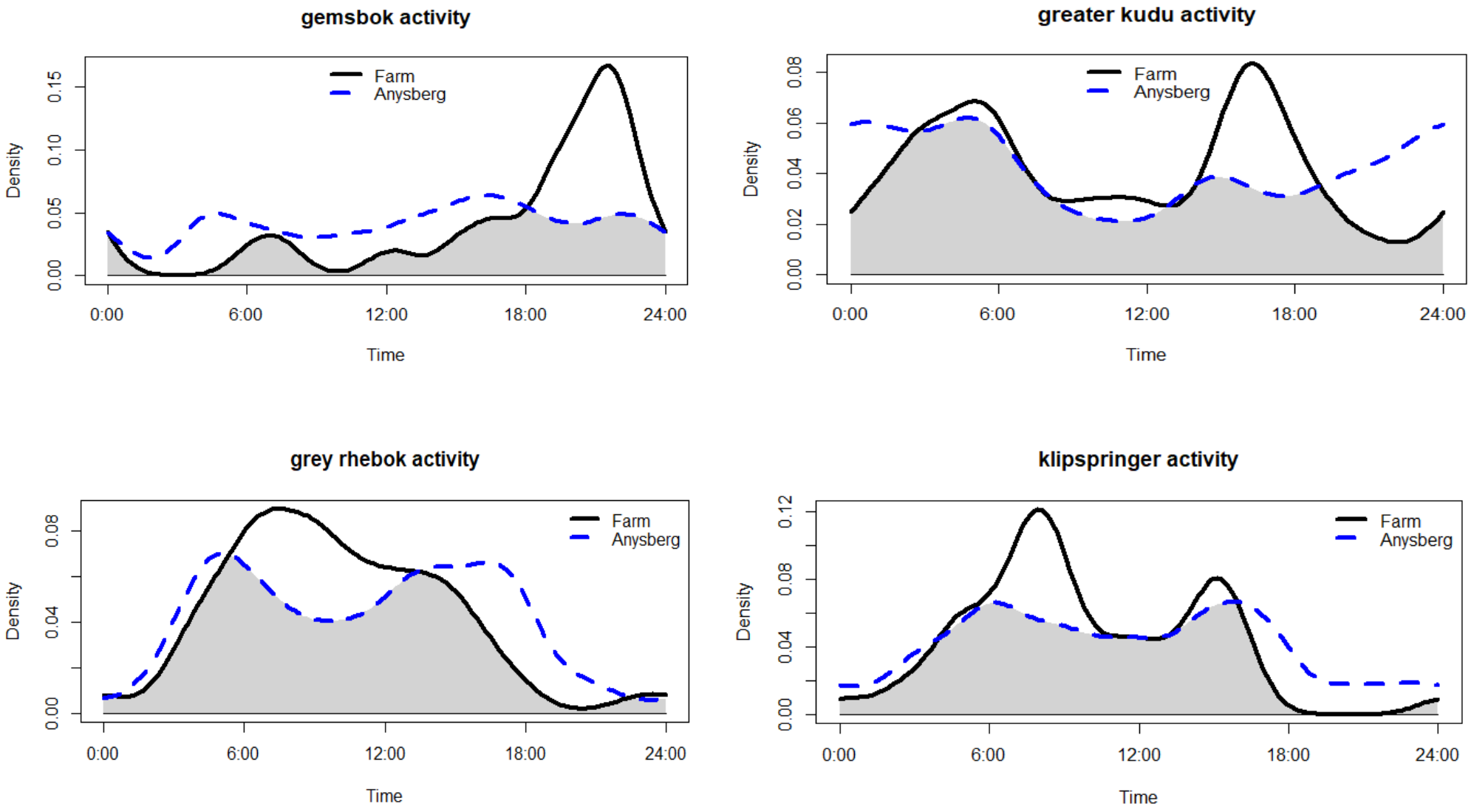
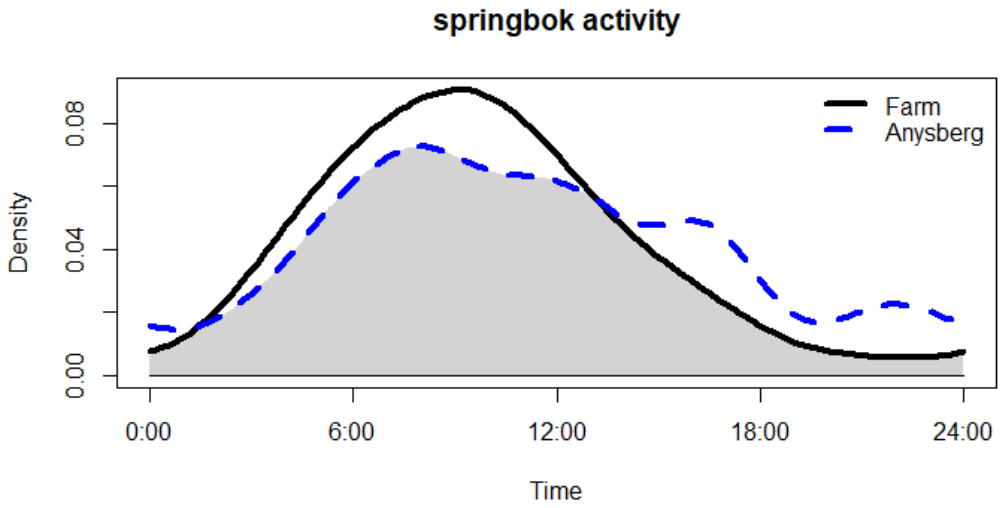


Figure 2 Continued.



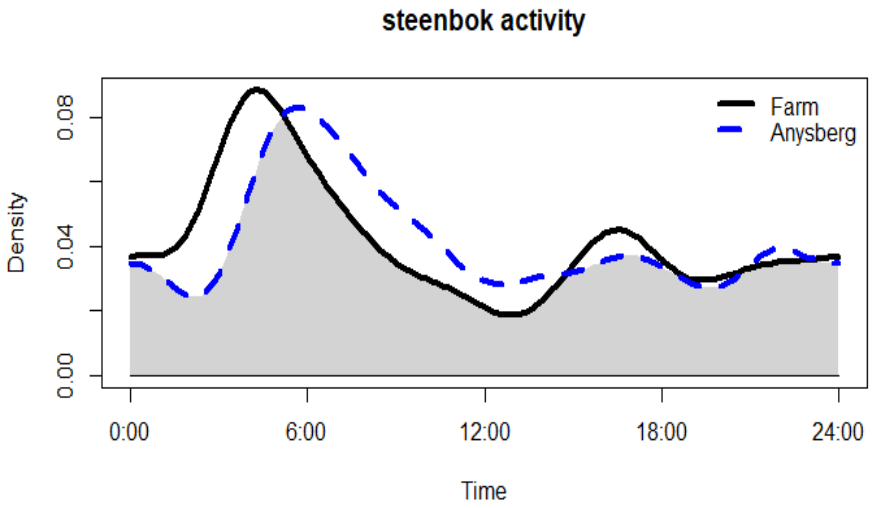


Figure 2 continued.

3.3 Effect of lunar illumination on activity patterns

Aardvark activity peaked during the waxing moon phase in Anysberg Nature Reserve (36%), with a decline in activity in the new moon phase. In Koup farms, the species was mostly active in the new moon phase (34%) with a dip in activity during the waning moon phase. Aardwolf showed high affinity for lunar illumination in Koup with most activity occurring in the full moon phase (32%) and activity dropping during the less bright phases of the lunar illumination of new (24%), waning (24%) and waxing (23%) moon phases. In Anysberg, the species activity peaked at waning moon phase (32%), and with a similar level of activity in the new and waxing moon phases (26%) and a decline in activity during the full moon phase (16%).

There was a uniform marked peak in activity for jackals during the full (39%) and waning (39%) moon phases with a dip in activity recorded during the waxing moon phase (10%) in Koup. Their activity also peaked in the full moon phase in Anysberg (30%), with a fairly uniform level of activity across the waxing (24%) and waning (26%) moon phases with the lowest activity occurring during the new moon phase (20%). Common duiker exhibited similar levels of activity across the four lunar phases in both Anysberg and Koup.

Gemsbok showed a clear affinity for moon illumination in Koup with 36% of activity occurring during the full moon. Activity declined thereafter with 29% of activity occurring at new moon, 21% at waning moon and 14% at waxing moon. Gemsbok had similar activity patterns in Anysberg with a peak in activity at full moon (28%) and their activity also decreases across the less illuminated lunar phase with 25% activity at waxing moon and a uniform activity pattern during the new and waning moon phases. Grey rhebok activity peaked during the waxing moon phase (43%), with the lowest activity occurring during the new moon phase (5%) in Anysberg. In Koup the activity peaked at full and waxing moon phases (33%), with a dip in activity (13%) during the new moon phase.

Springbok activity was at its peak during the waning moon phase in Koup (39%) which was followed by a uniform activity pattern in the full and new moon phases (22%), with the least activity occurring during the waxing phase in Koup. The species exhibited a uniform peak in activity in the full and waxing moon phases (29%) in Anysberg, which was followed by a 25% activity in the new moon phase and the lowest level of activity occurring in the waning moon phase (17%). Steenbok showed high affinity for moon light in Anysberg with its highest activity occurring in the full moon phase (32%) and a gradual decline in activity occurring in the less bright phases of the waning (26%), new (24%) and waxing (18%) lunar phases. In Koup farms, the species activity peak uniformly in the full and waxing moon phases (28%), with a gradual drop off in activity in the waning (26%) and new (24%) moon phases. All results are shown in figure 3.

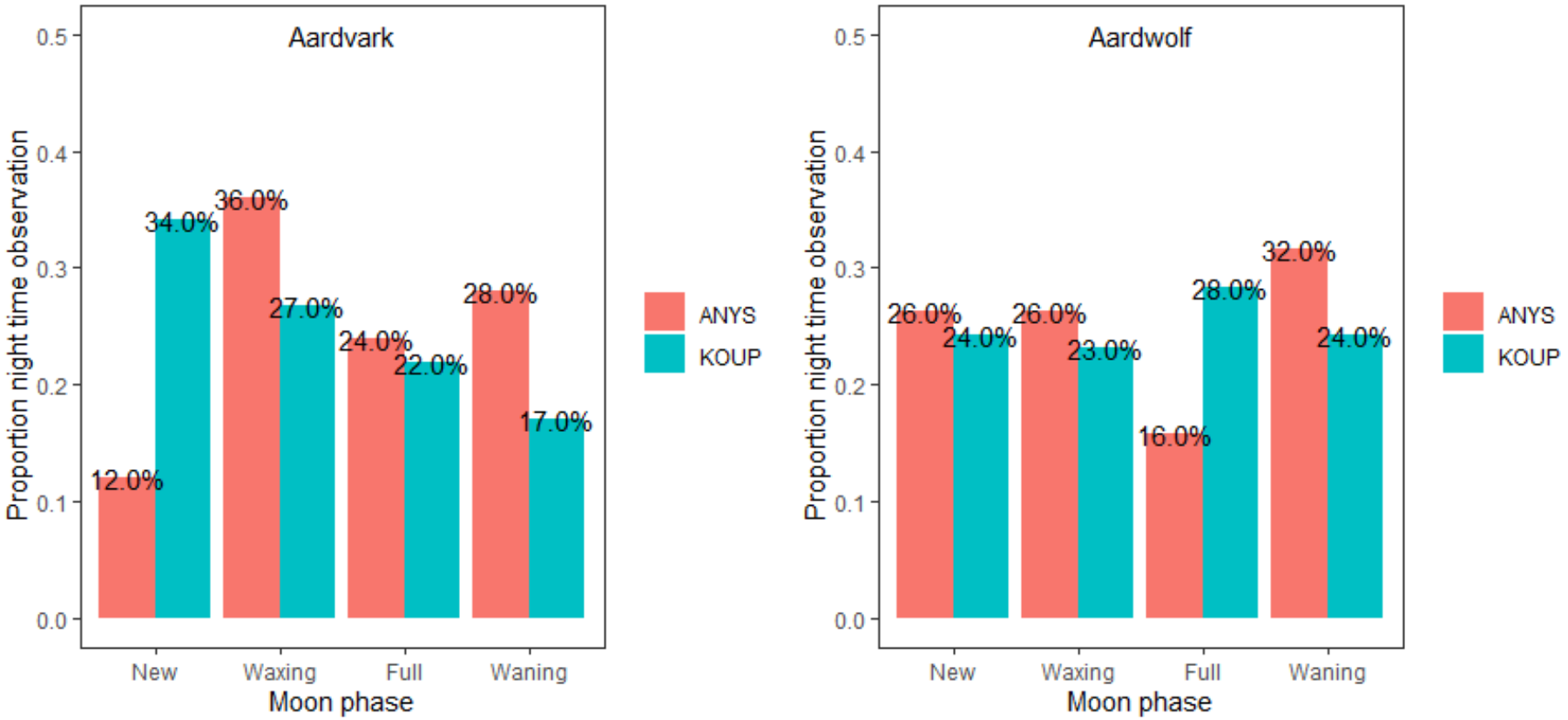


Figure 3: The proportion of night-time activity with moon phase for select species in both Anysberg Nature Reserve and the Koup farms

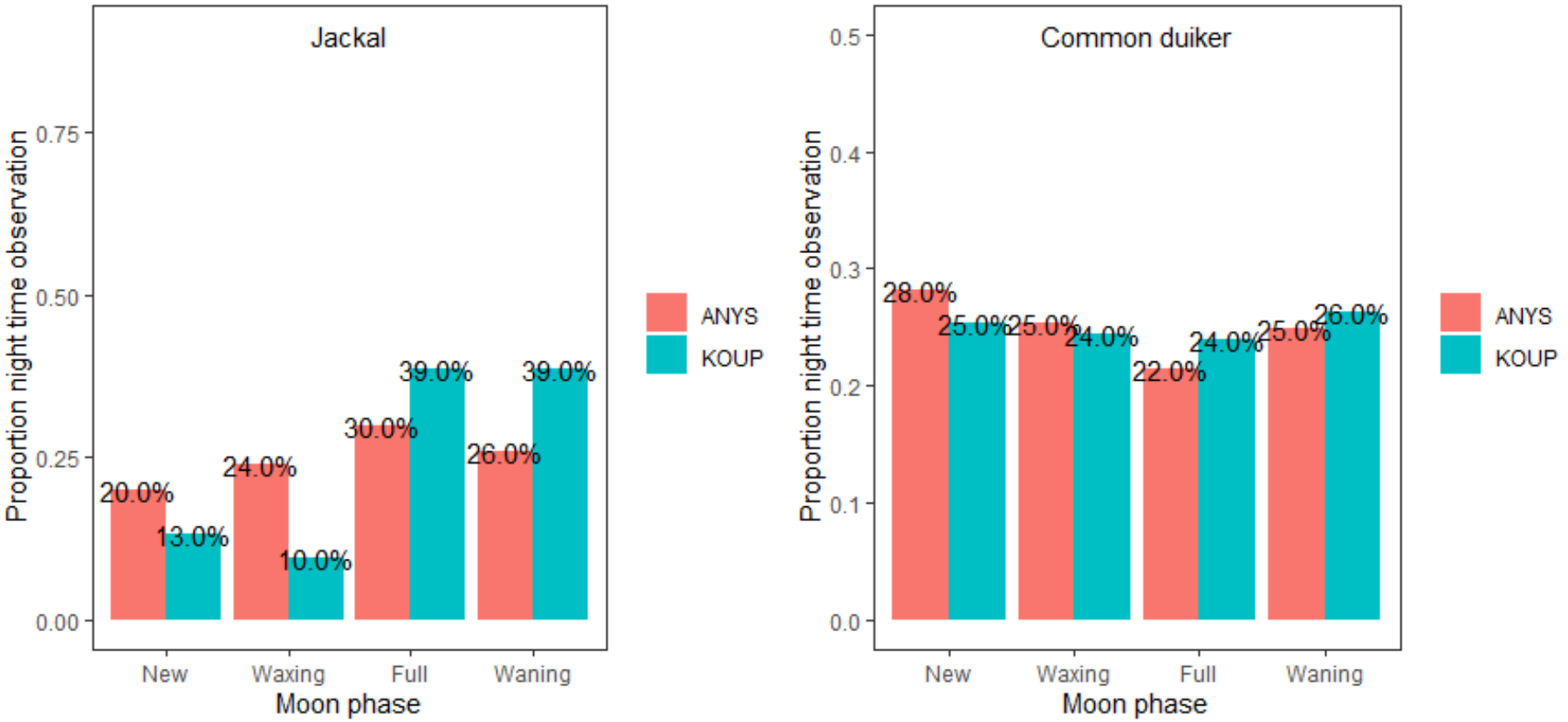
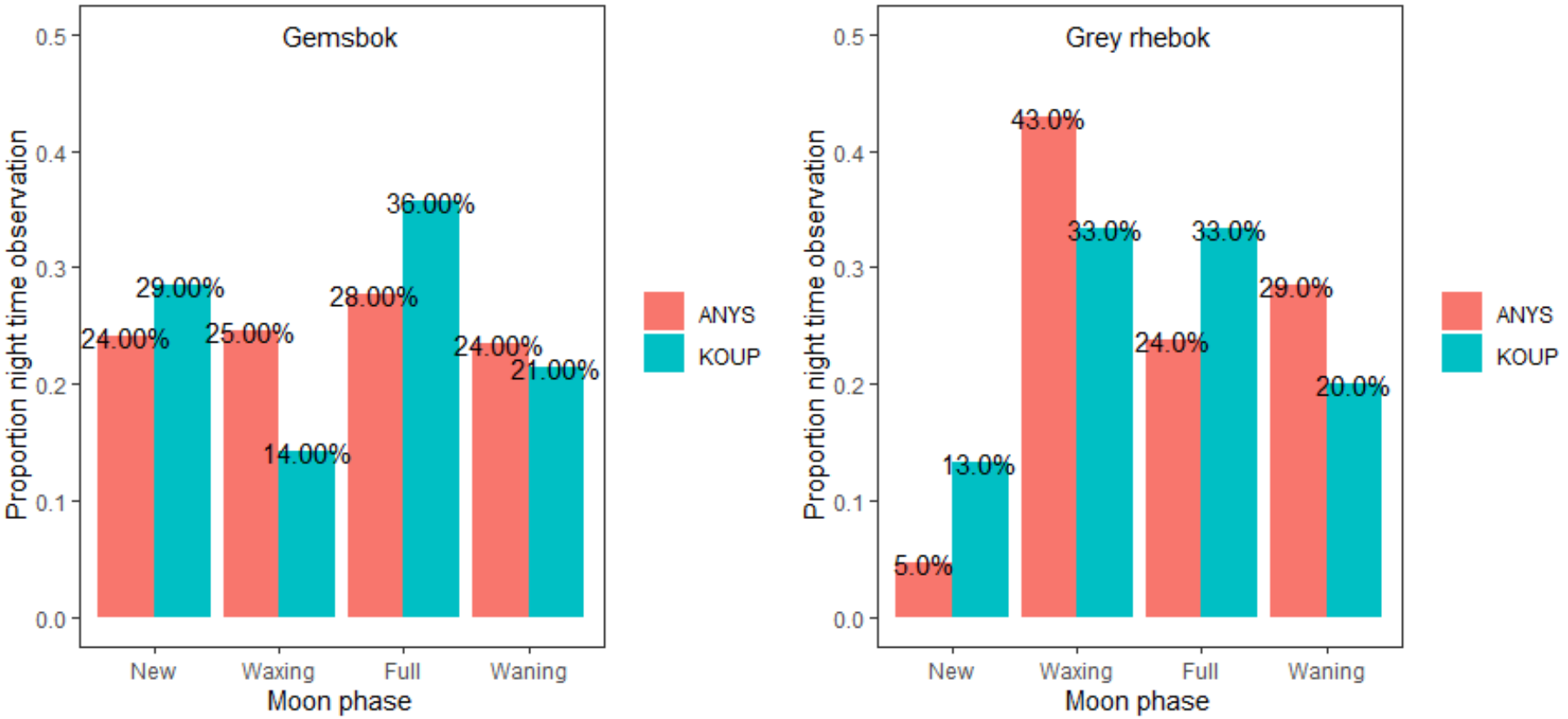


Figure 3 continued



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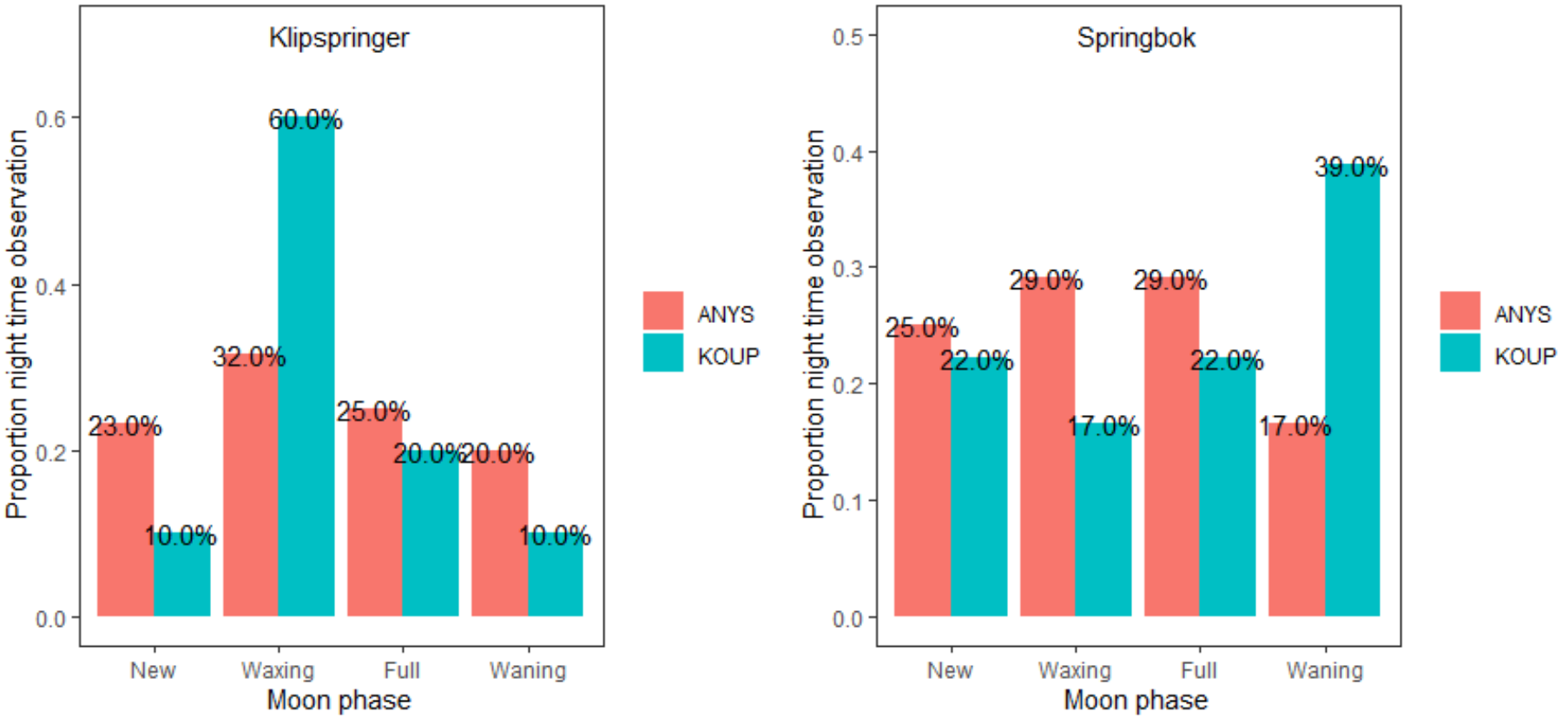

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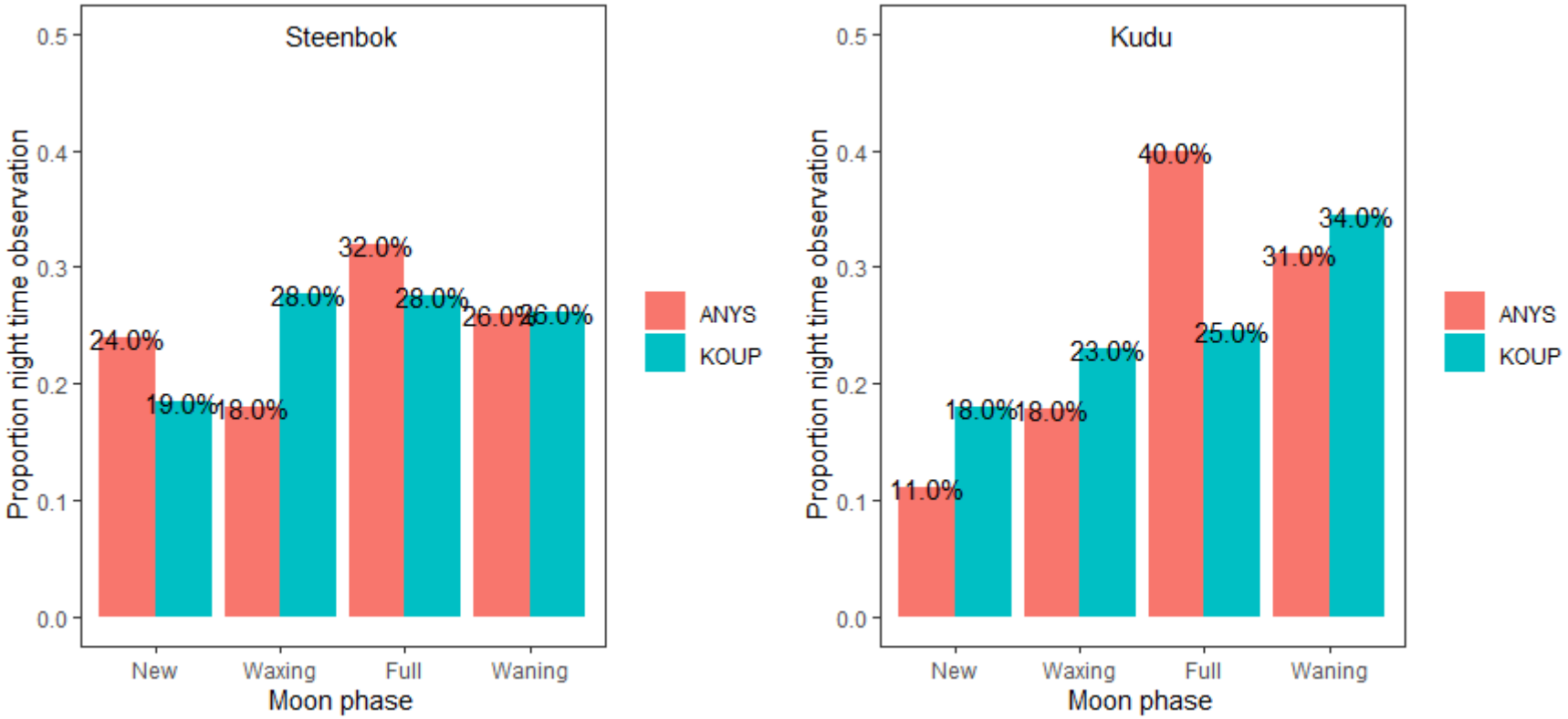


Figure 3 continued

3.4 Proportion of nocturnal activity of the species of interest in Anysberg Nature Reserve and Koup farms

Black-backed jackal, gemsbok, and steenbok were more active at night on farmland than in Anysberg Nature Reserve, whereas greater kudu, grey rhebok, klipspringer, and springbok exhibited greater nocturnality in Anysberg compared to Koup farms. There was no distinct difference in the nocturnality activity pattern of common duiker in both Koup and Anysberg. Additionally, aardvarks and aardwolf activity were mostly nocturnal in both Koup and Anysberg (Fig 4).

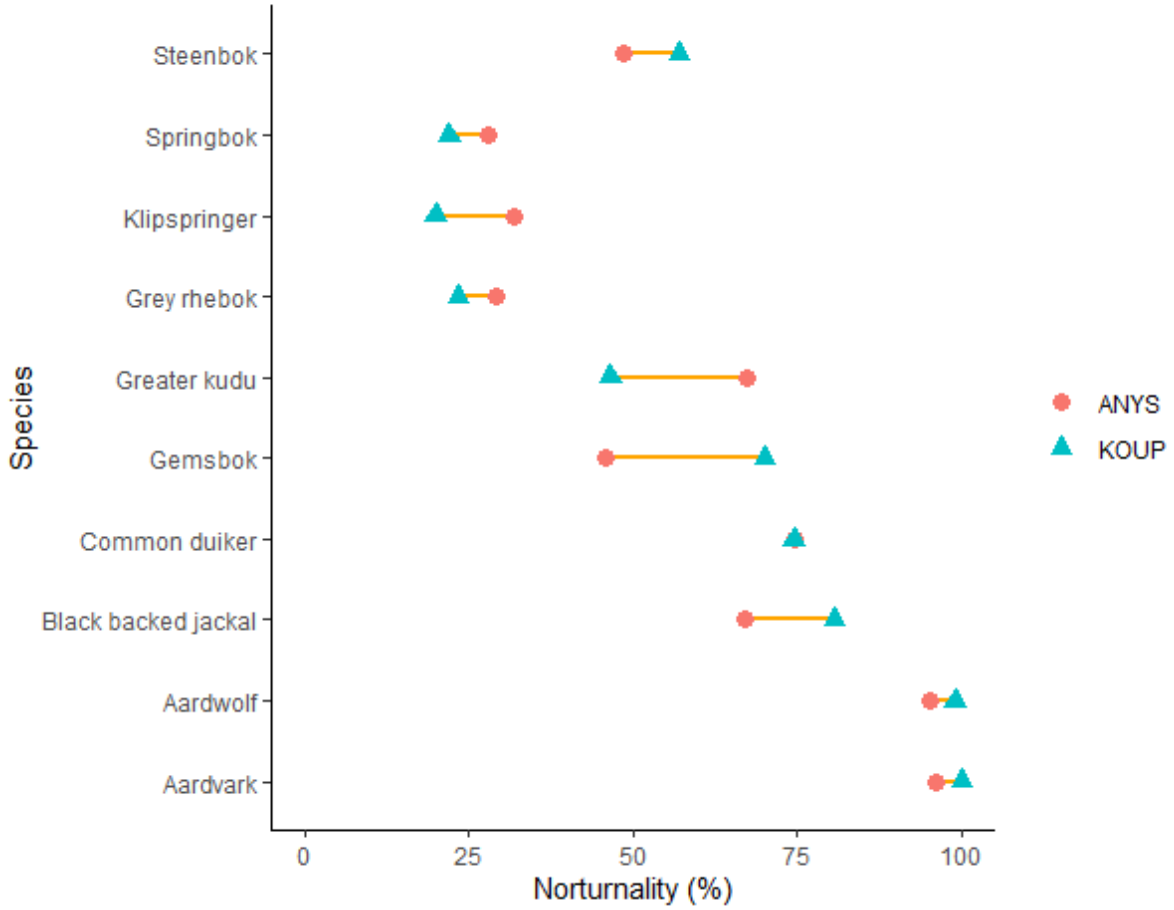


Figure 4: A comparison of the percentage nocturnality of select wildlife species in Anysberg Nature Reserve and Koup farms.

3.5 Species detected in the northern section Sanbona Wildlife Reserve

A total of 964 independent detections of 35 species were recorded in the northern section of Sanbona Wildlife Reserve. Hares (*Lepus victoriae*) were detected the most (n=156), while cape grey mongoose (*Herpestes pulverulentus*), cape mountain zebra and marsh mongoose (*Atilax paludinosus*) had the lowest detections (n=1). African lion (*Panthera leo*) (n=33) was the only apex predator detected in the northern part of the reserve (Table 5).

Table 5. Total number of independent detections for each wildlife species in Sanbona Wildlife Reserve northern section

Species	Number of Detections
Aardwolf	2
African elephant	11
African lion	33
African wildcat	16

Bat eared fox	4
Black backed jackal	74
Brown hyena	33
Cape grey mongoose	1
Cape mountain zebra	1
Caracal	17
Chacma baboon	47
Cheetah	5
Common duiker	78
Eland	97
Gemsbok	96
Giraffe	27
Greater kudu	41
Hare	156
Hippopotamus	4
Honey badger	3
Klipspringer	17
Large spotted genet	2
Large grey mongoose	2
Leopard	4
Marsh mongoose	1
Plains zebra	42
Porcupine	22
Red hartebeest	3
Rock hyrax	5
Small spotted genet	13
Smith's red rock rabbit	29
Springbok	18
Steenbok	46
White rhino	12
Yellow mongoose	2
Total	964

3.6 Species of interest in the northern section Sanbona Wildlife Reserve

I selected predator and prey species for which I had at least 10 independent photo-capture events which resulted in a total of 15 species of 789 independent detections. Hare comprised the majority of the detections (20%; n = 156), while small spotted genet (*Genetta genetta*) had the fewest detections (2%; n =13). Of the selected species, eland was detected at the most stations (15%; 35), while small spotted genet and Smith's red rock rabbit (*Pronolagus rupestris*) were detected at the fewest stations (3%; 7) (Table 6).

Table 6. Species of interest, their guild, the number of independent detections and the number of camera stations they were detected at in the northern section of Sanbona Wildlife Reserve.

Species	Guild	Number of Detections	Number of camera stations detected
African lion	Apex predator	33	10

Black backed jackal	Mesopredator	74	28
Caracal	Mesopredator	17	8
Common duiker	Prey	78	17
Eland	Prey	97	35
Gemsbok	Prey	96	27
Giraffe	Prey	27	11
Greater kudu	Prey	41	16
Hare	Prey	156	16
Plains zebra	Prey	42	19
Porcupine	Prey	22	13
Small spotted genet	Prey	13	7
Smith's red rock rabbit	Prey	29	7
Springbok	Prey	18	8
Steenbok	Prey	46	15
Total		789	237

3.7 Overlap in activity between lion and both smaller predators and potential prey species in the northern section of Sanbona Wildlife Reserve

Lion had high levels of activity overlap with 11 of the 12 species (Mean = 0.80; S.D.= 0.07) with the highest overlap between lion and Smith's red rock rabbit and porcupine (*Hystrix africaeaustralis*) (Δ_1 = 0.88 [CI =0.70-0.97]) and (Δ_1 = 0.88 [CI =0.71-1.01]) respectively. The lowest overlap was between lion and caracal (Δ_1 = 0.62 [CI =0.42-0.81]) (Table 7; Fig 5).

Table 7. Coefficients of overlap and 95% confidence intervals between lion and both smaller predators and potential prey species in Sanbona Wildlife Reserve northern section. Overlap is considered high when $\Delta_1 \geq 070$.

Species	Coefficient of overlap
Lion-black backed jackal	**0.80 (0.66-0.92)**
Lion-caracal	0.62 (0.42-0.81)
Lion-common duiker	**0.78 (0.64-0.90)**
Lion-eland	**0.79 (0.65-0.91)**
Lion-gemsbok	**0.87 (0.74-0.97)**
Lion-giraffe	**0.79 (0.63-0.93)**
Lion-hare	**0.85 (0.73-0.95)**
Lion-kudu	**0.84 (0.69-0.96)**
Lion-porcupine	**0.88 (0.71-1.01)**
Lion-Smith's red rock rabbit	**0.88 (0.70-0.97)**
Lion-steenbok	**0.76 (0.61-0.90)**
Lion-springbok	**0.71 (0.51-0.89)**
Mean overlap	**0.80**

3.8 Overlap in activity between mesopredators and antelope species in the northern section of Sanbona Wildlife Reserve

Black backed jackal had high levels of overlap (Mean = 0.70; S.D.= 0.05) with five antelope species ($\Delta_1 \geq 0.70$) including common duiker, hare, klipspringer, and Smith's red rock rabbit and gemsbok. The highest overlap in activity was between black-backed jackal and common duiker ($\Delta_1 = 0.75$ [CI =0.63-0.85]) and the lowest was between black-backed jackal and springbok ($\Delta_1 = 0.60$ [CI =0.39-0.79]) (Table 8; Fig 6).

Table 8. Coefficients of overlaps and 95% confidence intervals between black backed jackal and antelope species in the northern section of Sanbona Wildlife Reserve. Overlap is considered high when $\Delta_1 \geq 070$ and represented in bold.

Species	Coefficient of overlap
Black backed jackal-common duiker	**0.75 (0.63-0.85)**
Black backed jackal-gemsbok	**0.72 (0.61-0.83)**
Black backed jackal-hare	**0.71 (0.61-0.81)**
Black backed jackal-klipspringer	**0.70 (0.53-0.86)**
Black backed jackal-kudu	0.69 (0.54-0.82)
Black backed jackal-smith's red rock rabbit	**0.74 (0.59-0.87)**
Black backed jackal-steenbok	0.65 (0.51-0.78)
Black backed jackal-springbok	0.60 (0.39-0.79)
Mean overlap	**0.70**

The only instance of high temporal overlap between caracal (*Caracal caracal*) and an antelope species was with springbok ($\Delta_1 = 0.71$ [CI =0.51-0.88]), while the lowest overlap was with steenbok ($\Delta_1 = 0.59$ [CI =0.41-0.77]) (Table 9; Fig 7).

Table 9. Coefficients of overlap and 95% confidence intervals between caracal and antelope species in the northern section of Sanbona Wildlife Reserve. Overlap is considered high when $\Delta_1 \geq 070$ and represented in bold.

Species	Coefficient of overlap
Caracal-common duiker	0.65 (0.46-0.82)
Caracal-gemsbok	0.64 (0.46-0.81)
Caracal-hare	0.66 (0.48-0.81)
Caracal-klipspringer	0.62 (0.40-0.81)
Caracal-kudu	0.62 (0.43-0.79)
Caracal-smith's red rock rabbit	0.62 (0.41-0.81)
Caracal-springbok	**0.71 (0.51-0.88)**
Caracal-steenbok	0.59 (0.41-0.77)

Mean overlap	0.64

3.9 Influence of lion presence and absence on the activity pattern of prey species in the northern and southern section of Sanbona Wildlife Reserve

The activity pattern of the prey species in the presence and absence of lion in both the northern and southern section of Sanbona Wildlife Reserve were not dissimilar with the highest temporal overlap found in hare $\Delta_4 = 0.85$ [CI =0.75-0.93]), while the lowest overlap was with plains zebra ($\Delta_1 = 0.56$ [CI =0.41-0.71]) (Table 10; Fig 8).

Table 10. Coefficients of overlap and 95% confidence intervals between prey species in the northern and southern sections of Sanbona Wildlife Reserve in the presence and absence of lion. Overlap is considered high when $\Delta_1 \geq 070$ and represented in bold.

Species (Sanbona North/South)	Coefficient of overlap
Common duiker	**0.73 (0.61-0.84)**
Eland	**0.82 (0.73-0.91)**
Gemsbok	**0.80 (0.69-0.89)**
Hare	**0.85 (0.75-0.93)**
Kudu	**0.74 (0.61-0.86)**
Smith's red rock rabbit	0.61 (0.38-0.81)
Steenbok	**0.79 (0.65-0.91)**
Plains zebra	0.56 (0.41-0.71)
Mean overlap	**0.74**

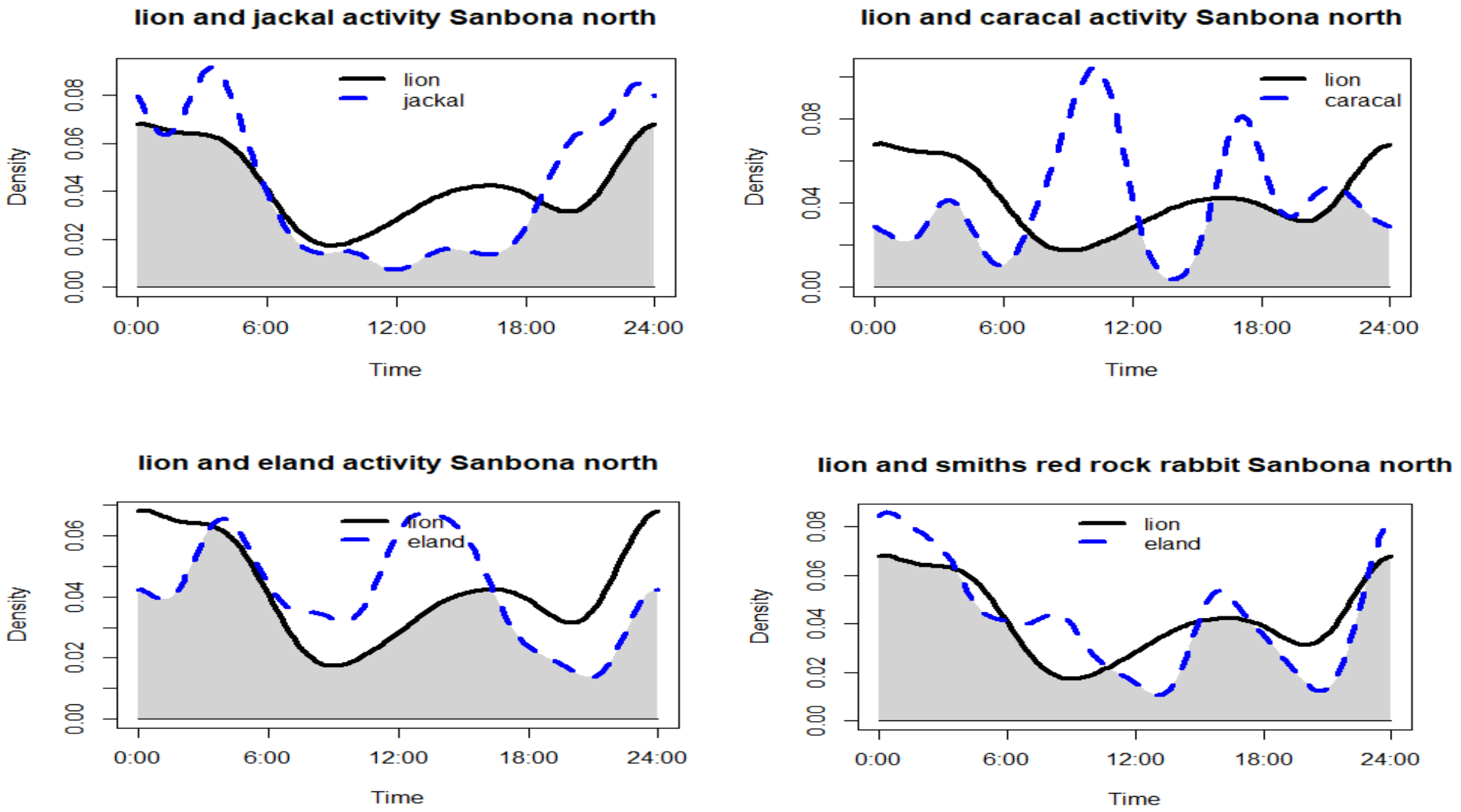
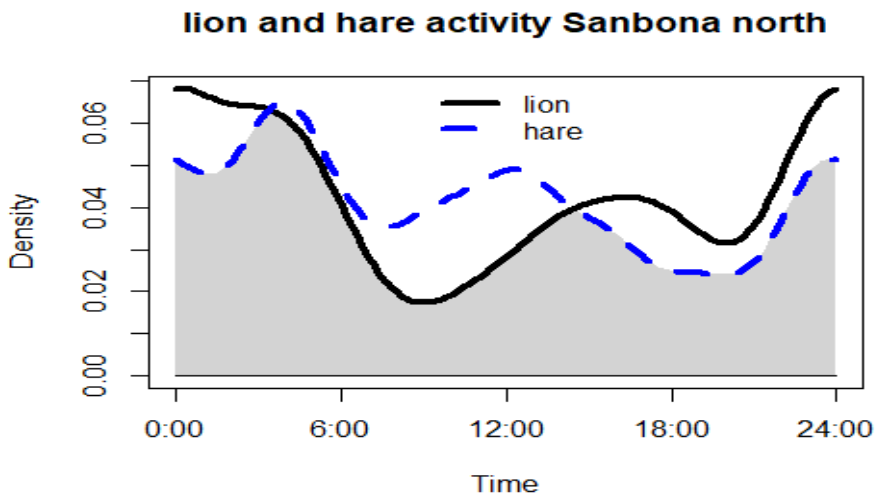
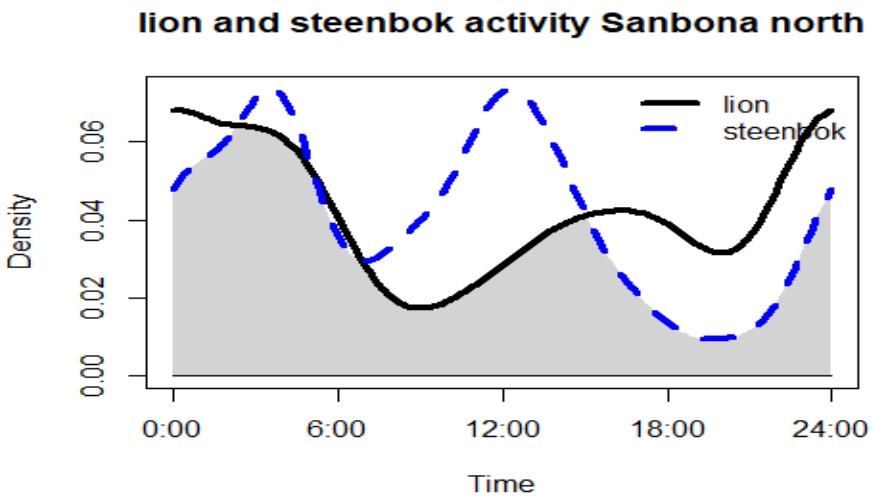
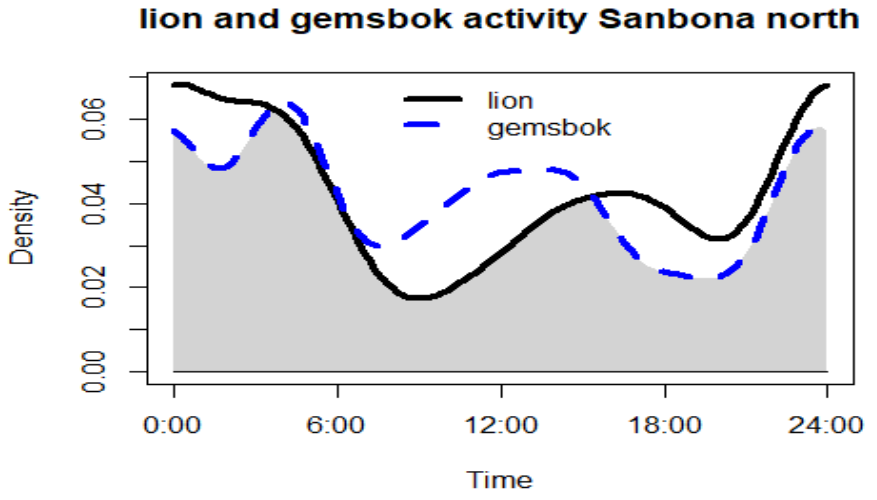
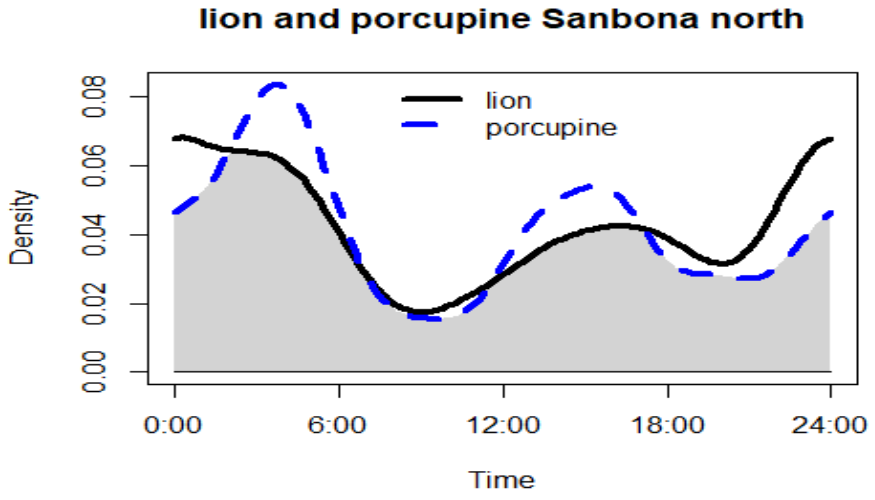


Figure 5: Lion and both smaller predators and potential prey species activity in Sanbona Wildlife Reserve northern section.









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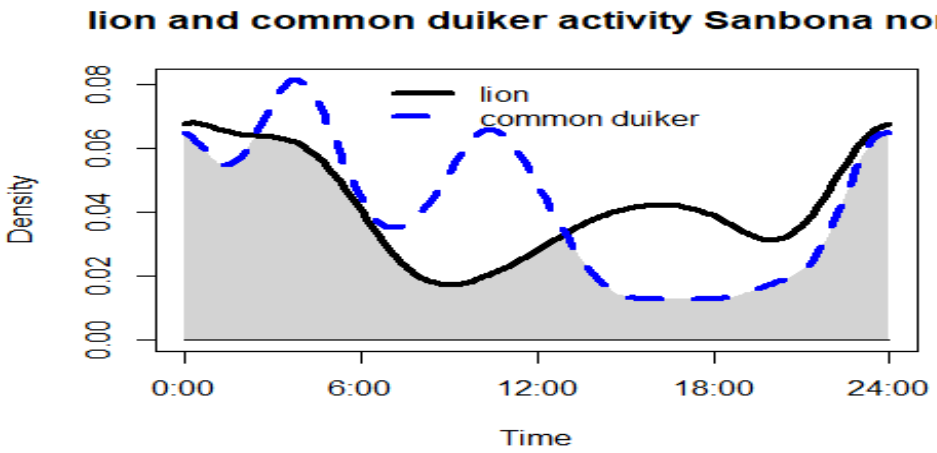

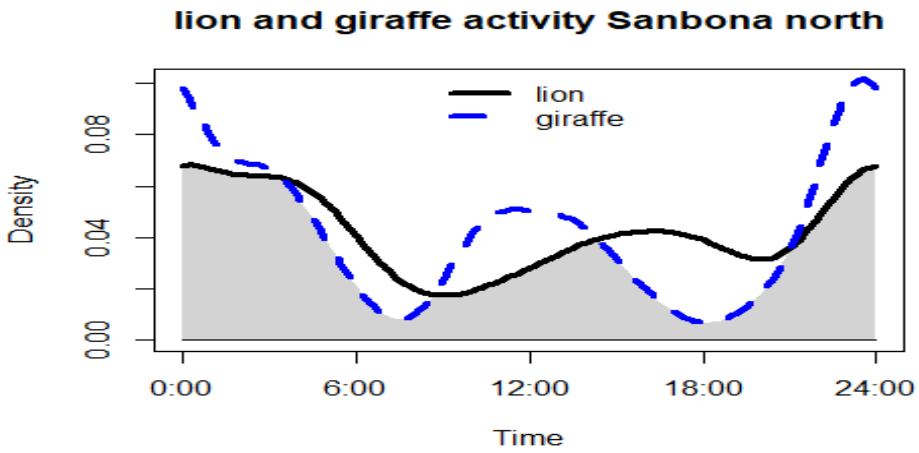

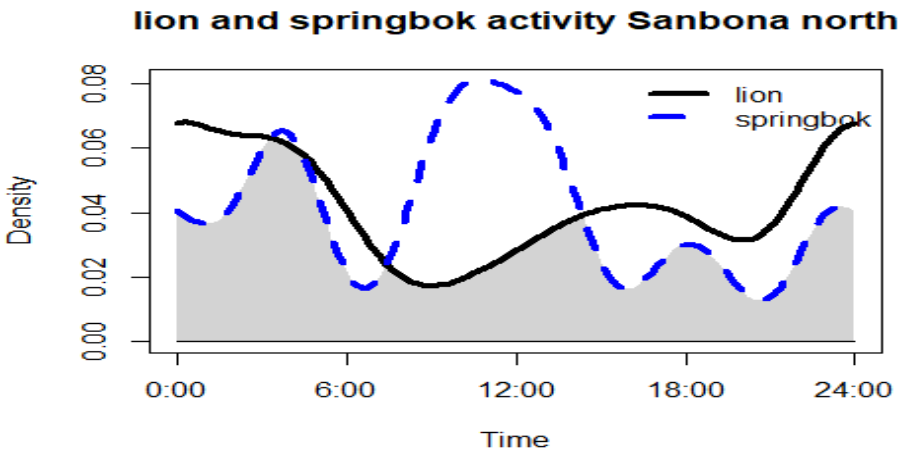

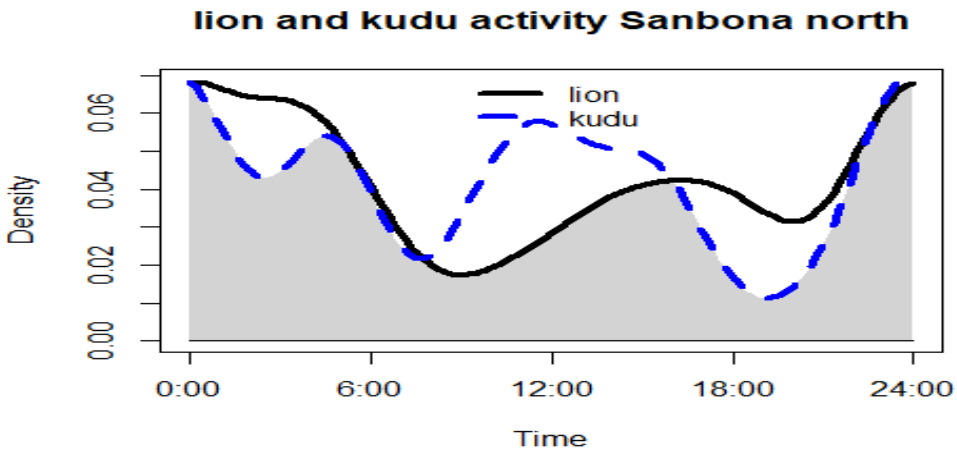

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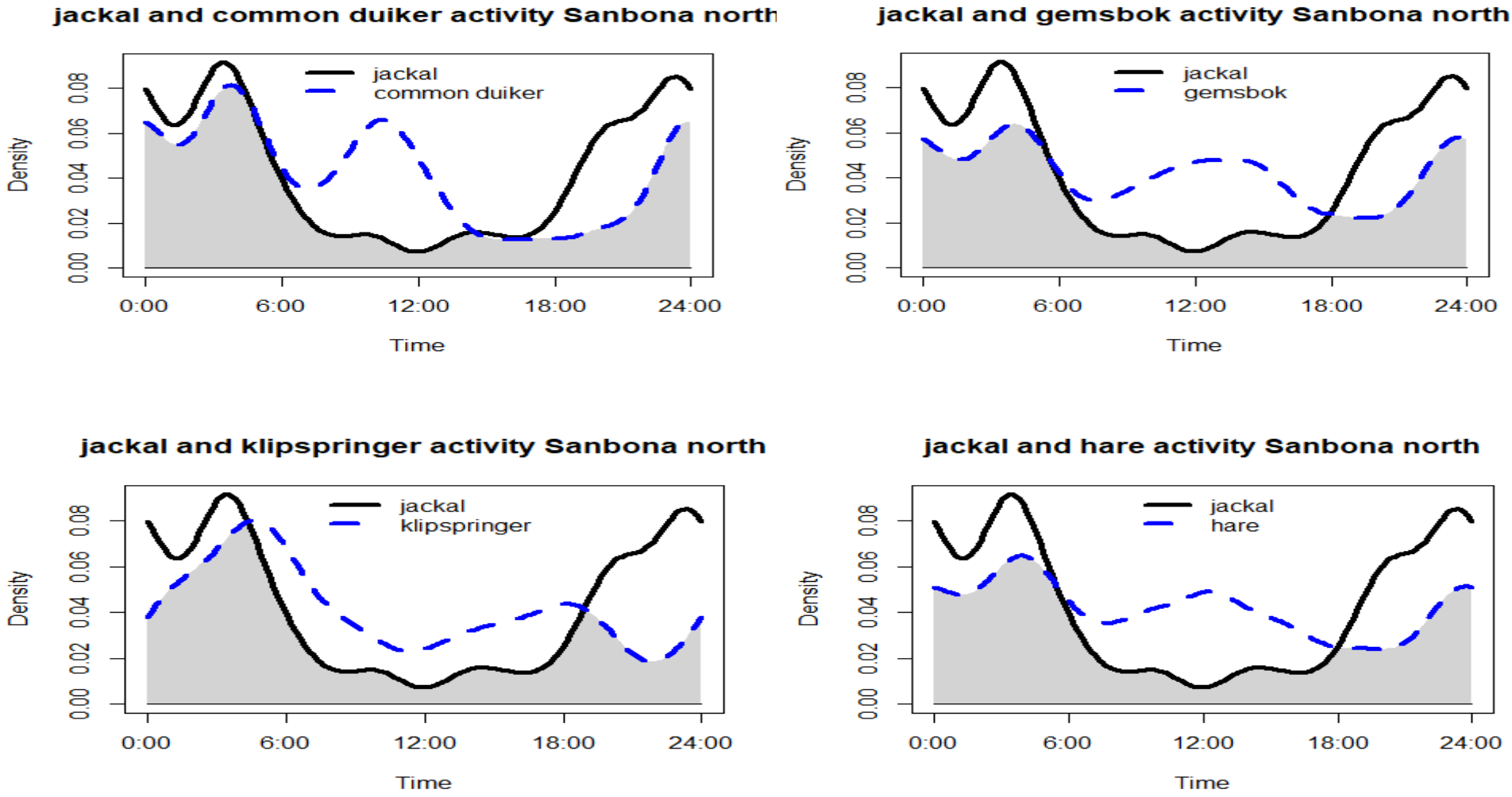
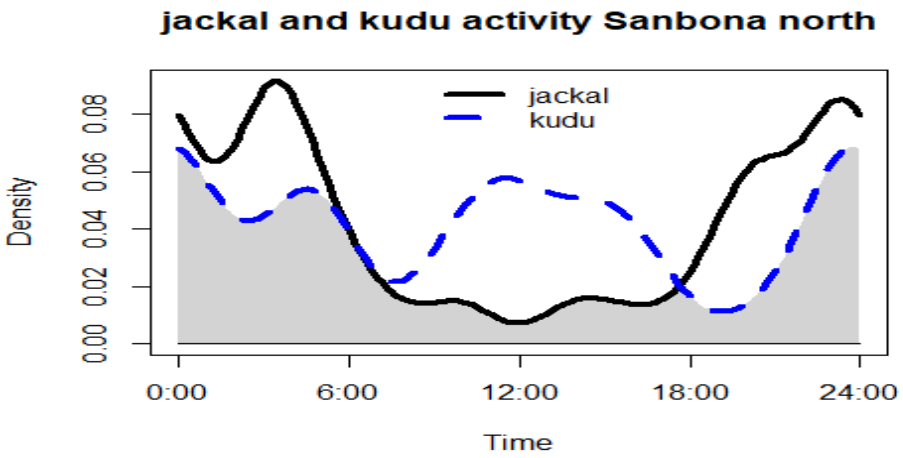
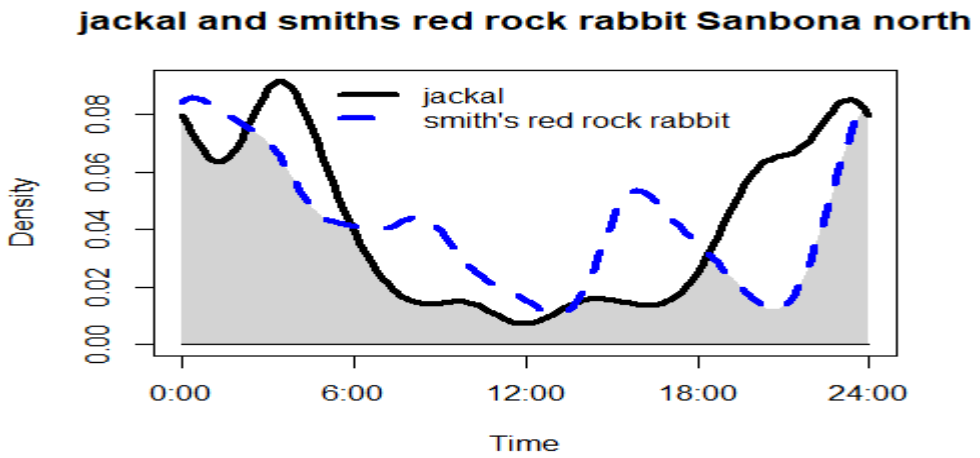
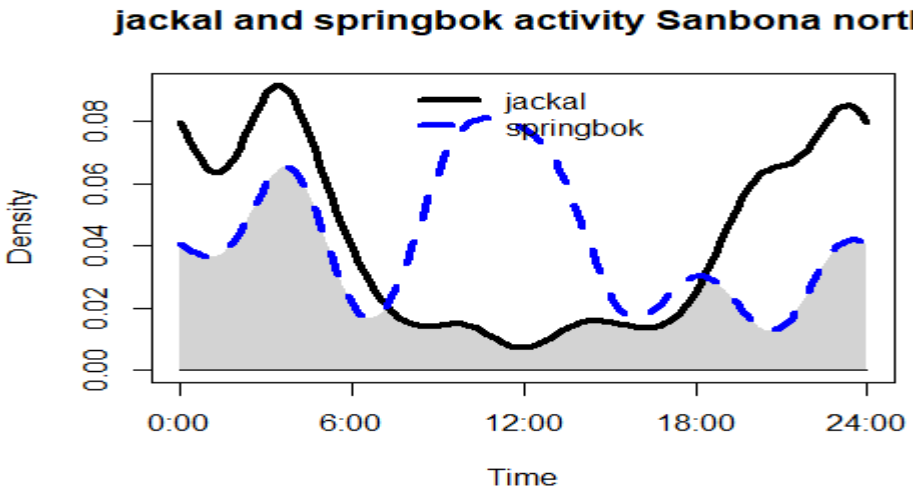
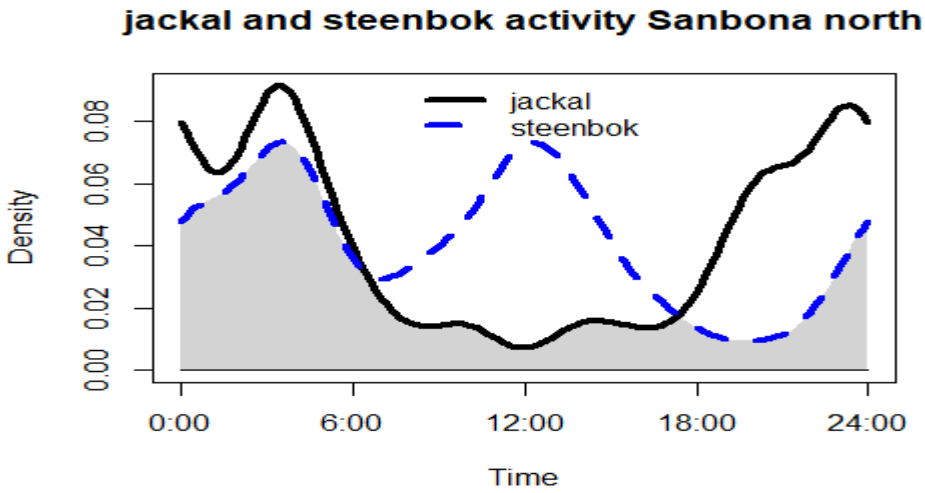


Figure 6: Black backed jackal and its potential prey species activity in Sanbona Wildlife Reserve northern section.









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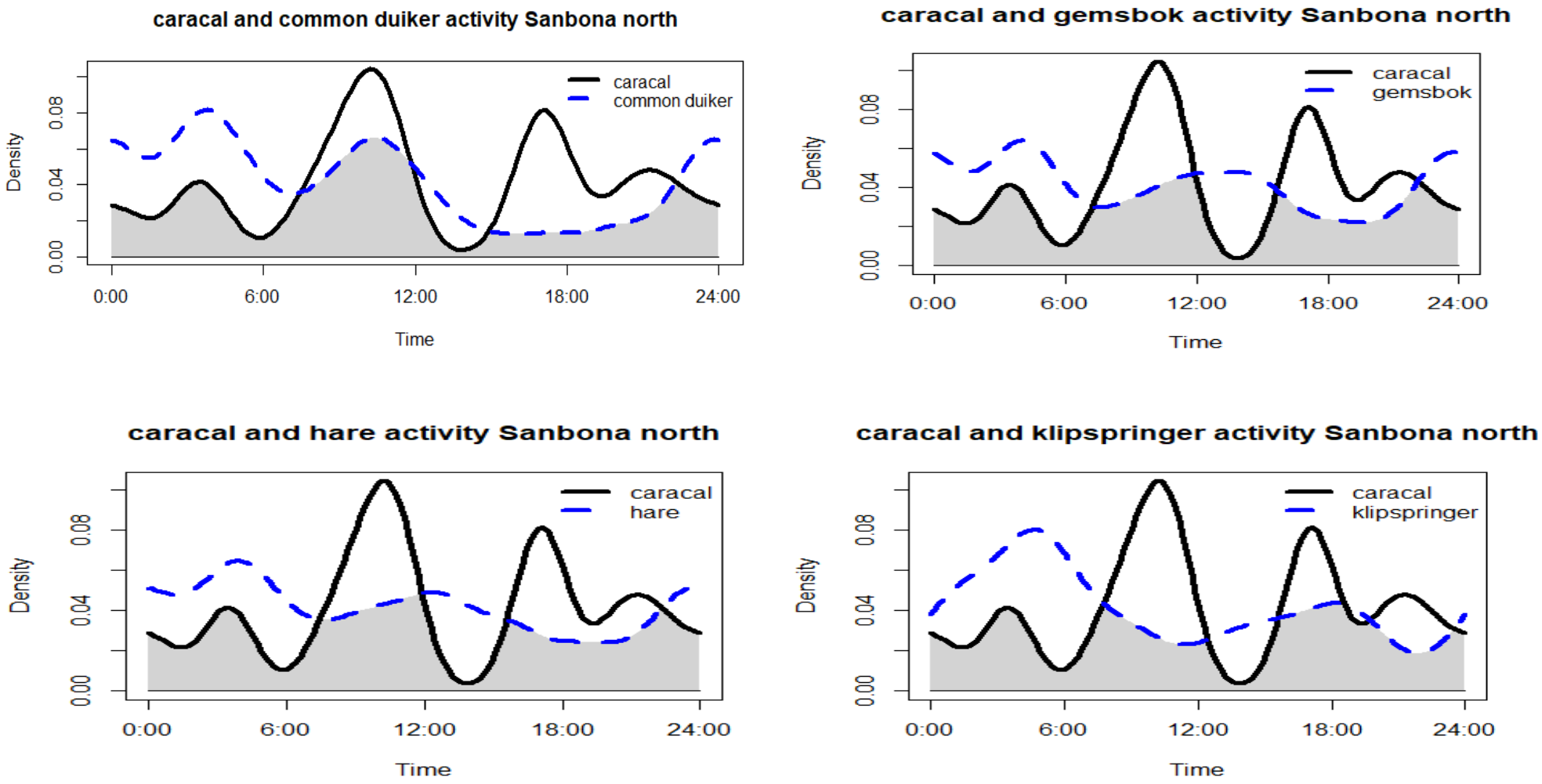
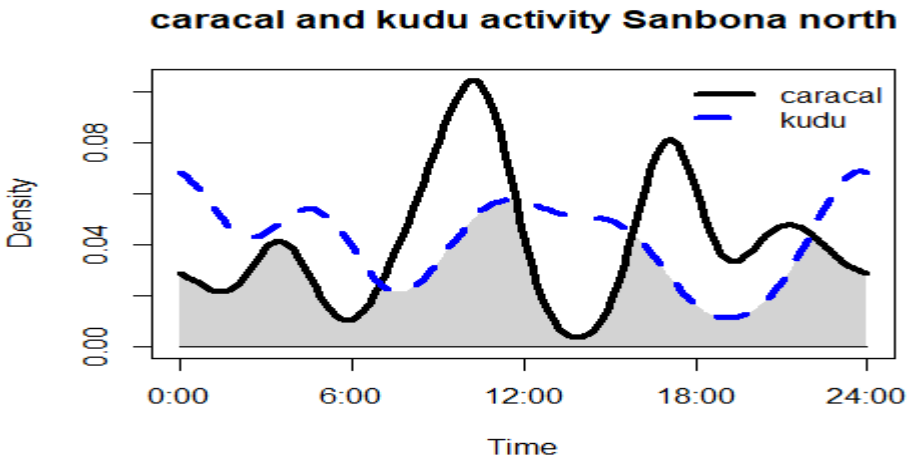
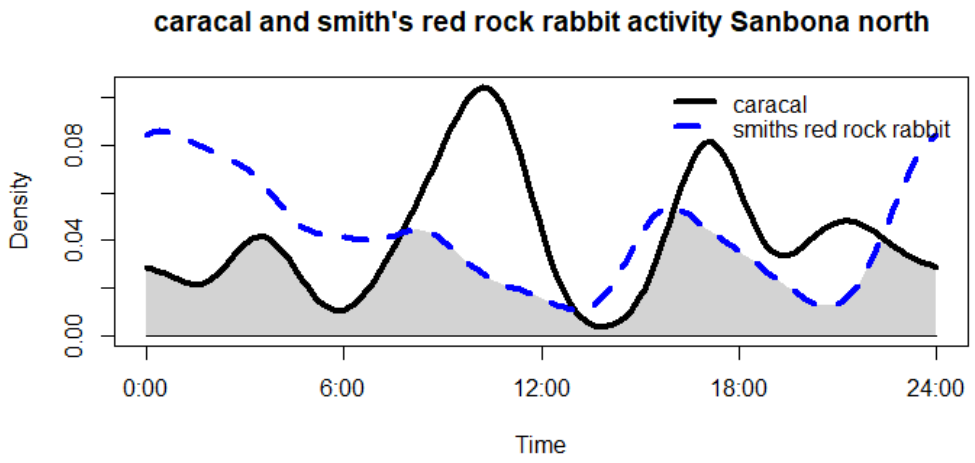
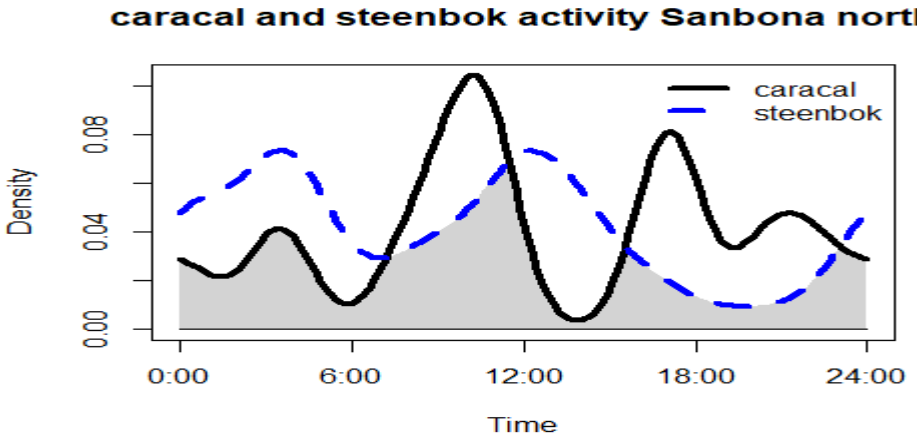
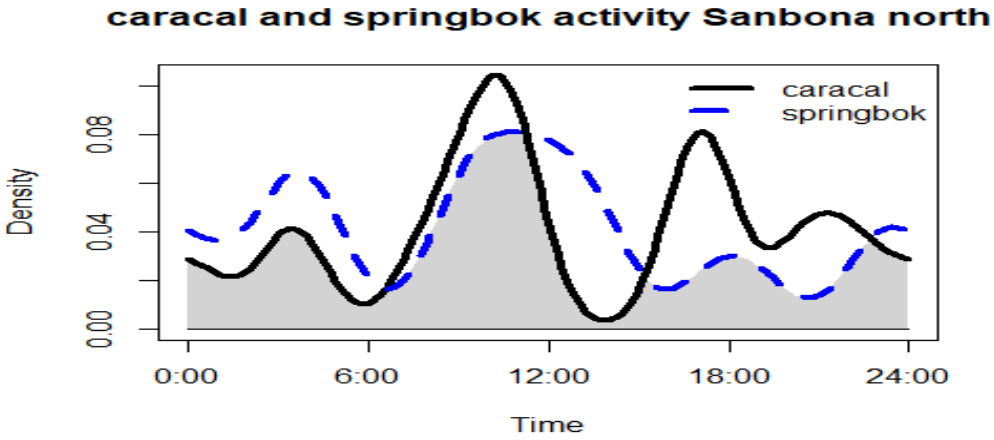


Figure 7: Caracal and its potential prey species activity in Sanbona Wildlife Reserve northern section.









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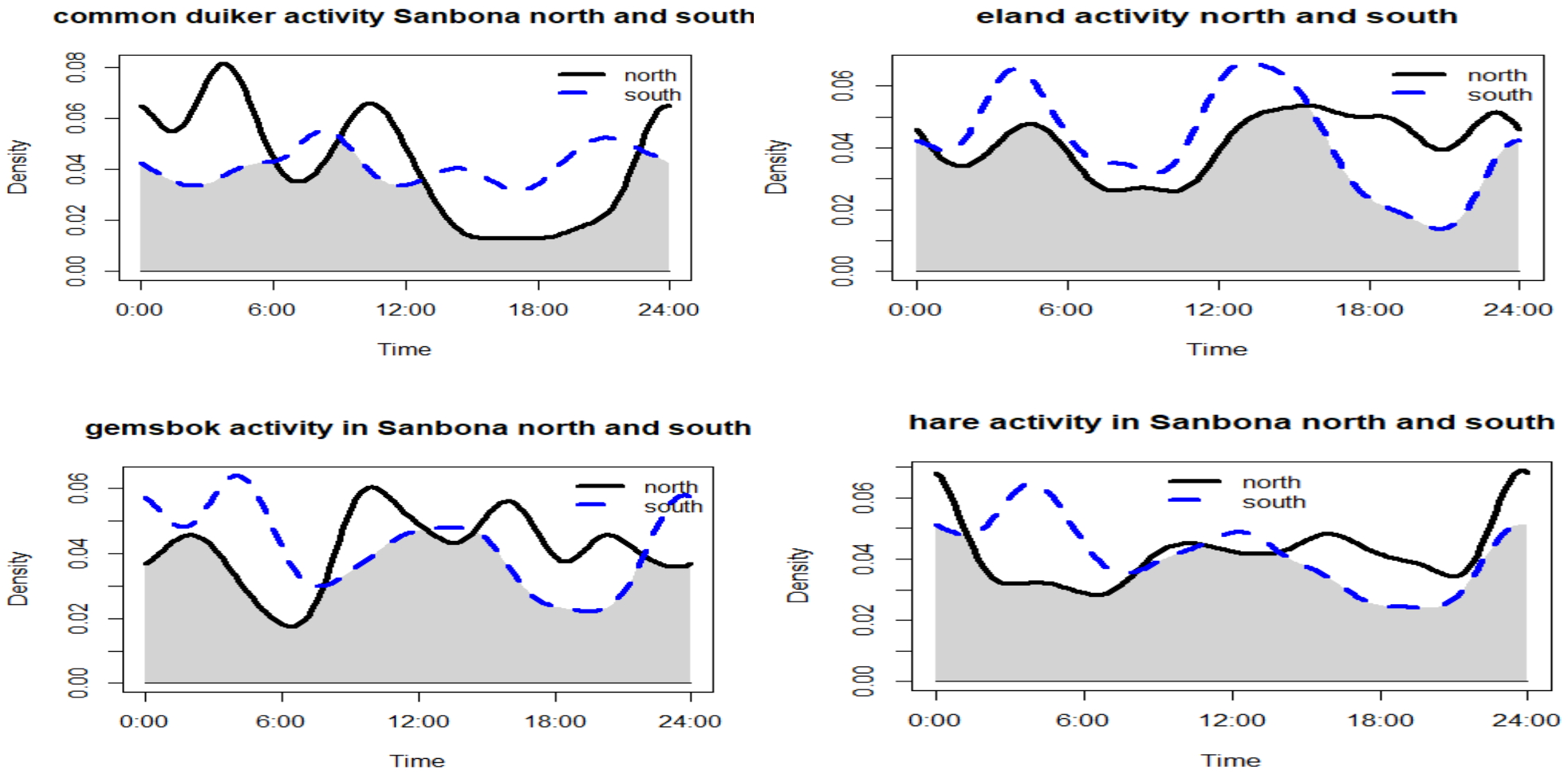
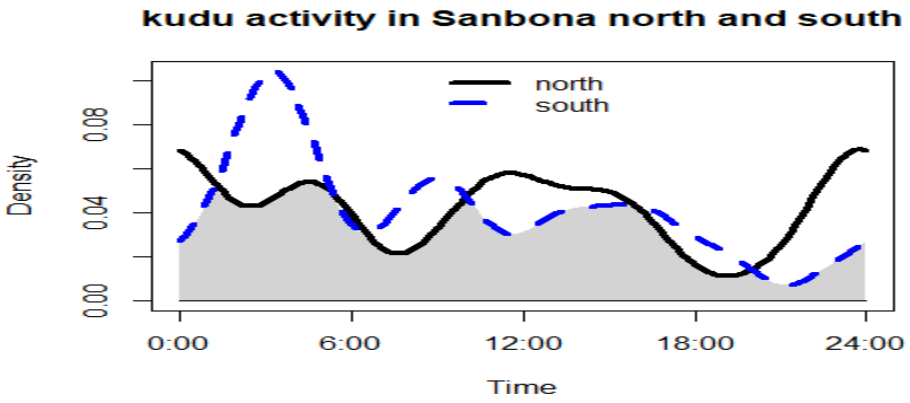
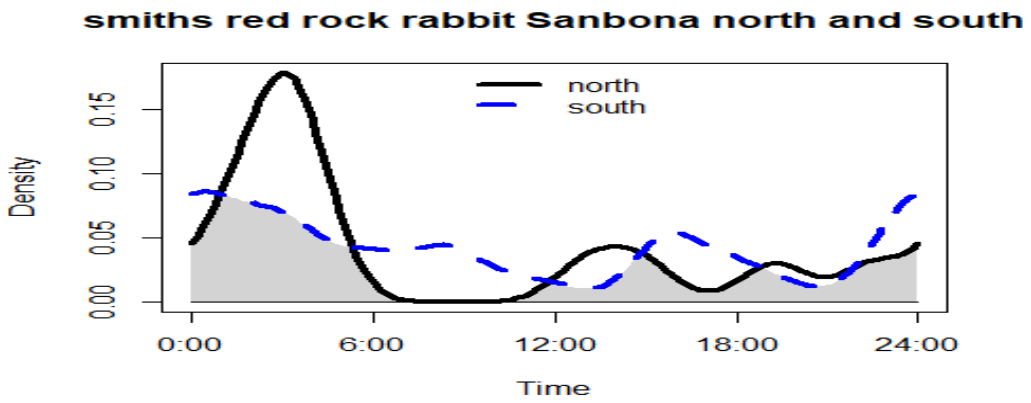
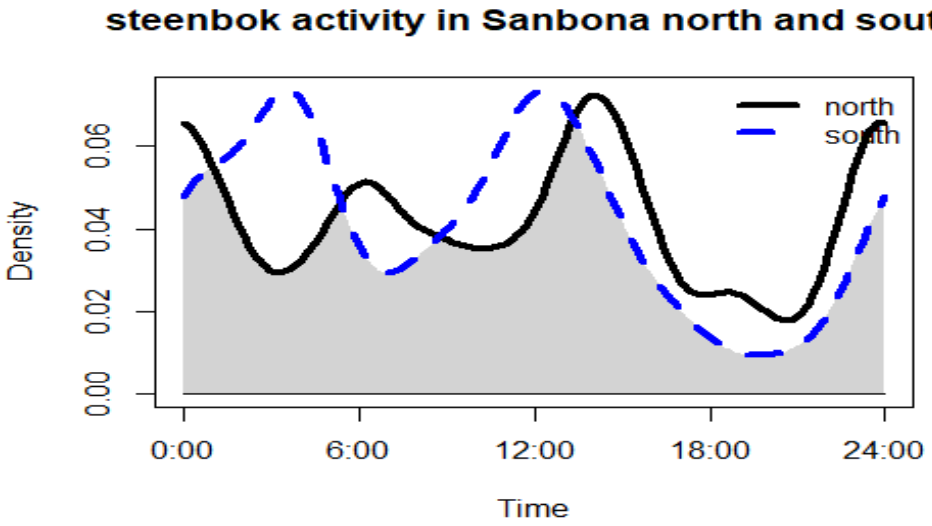


Figure 8: Activity pattern of prey species in the presence and absence of apex predator in the presence and absence of apex predator in the northern and southern section of Sanbona Wildlife Reserve.







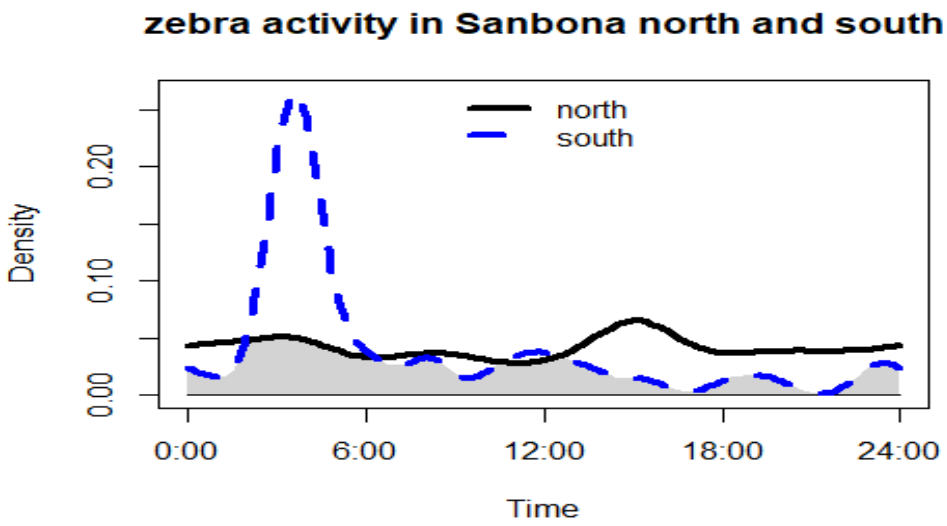


Figure 8 Continued.

3.9 Species detected in the southern section Sanbona Wildlife Reserve

A total of 858 independent detections of 32 species were recorded with eland detected the most (n=130), while African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), large spotted genet (*Genetta tigrina*), marsh mongoose and yellow mongoose (*Cynictis penicillata*) had the lowest detections (n=1). Black-backed jackal (n=57) was the most frequently detected mesopredator (Table 11).

Table 11. Total number of independent detections for each wildlife species in Sanbona Wildlife Reserve southern section.

Species	Number of Detections
Aardvark	19
African elephant	1
African wild cat	16
Bat eared fox	3
Black backed jackal	57
Black wildebeest	9
Brown hyena	14
Cape grey mongoose	6
Cape grysbok	2
Caracal	4
Chacma baboon	65
Common duiker	80
Eland	130
Gemsbok	81
Giraffe	1
Greater kudu	53
Grey rhebok	22
Hare	76
Hippopotamus	3
Klipspringer	50
Large spotted genet	1
Large grey mongoose	5
Leopard	2
Marsh mongoose	1
Plains zebra	55
Porcupine	25
Red hartebeest	7
Small spotted genet	14
Smith's red rock rabbit	12
Springbok	5
Steenbok	38
Yellow mongoose	1
Total	**858**

3.10 Species of interest in the southern section Sanbona Wildlife Reserve

I selected predator and prey species for which I had at least 10 independent photo-capture events which resulted in a total of 12 species with a total of 679 independent detections. Eland (*Taurotragus oryx*) had the most detections (19.2%, n = 130), while Smith's red rock rabbit had the fewest detections (1.8%, n =12). Of the selected species, eland was detected at the most stations (34; 17%), while Smith's red rock rabbit was detected at the fewest stations (7; 3.4%) (Table 12).

Table 12. Species of interest in Sanbona Wildlife Reserve southern section

Species	Guild	Number detections	No. camera stations
Black backed jackal	Mesopredator	57	23
Common duiker	Prey	80	27
Eland	Prey	130	34
Gemsbok	Prey	81	28
Greater kudu	Prey	53	14
Grey rhebok	Omnivore	22	9
Hare	Prey	76	12
Klipspringer	Prey	50	12
Plains zebra	Prey	55	13
Porcupine	Prey	25	11
Smith's red rock rabbit	Prey	12	7
Steenbok	Prey	38	16
Total		679	206

3.11 Black backed jackal and its potential prey species activity in the southern section of Sanbona Wildlife Reserve

Black backed jackal's (*Canis mesomelas*) activity had high levels of overlap (Mean = 0.68; S.D.= 0.06) with two herbivore species (viz., common duiker and hare) all of which are potential prey. The highest overlap in activity was between black backed jackal and common duiker (Δ_1 = 0.75 [CI =0.62-0.86]) and the lowest overlap was between black backed jackal and Smith's red rock rabbit (Δ_1 = 0.58 [CI =0.35-0.79]) (Table 13; Fig 9).

Table 13. Coefficients of overlaps and 95% confidence intervals between lion and its potential prey species in Sanbona Wildlife Reserve northern section. Overlap is considered high when $\Delta_1 \geq 070$.

Species	**Coefficients of overlap**
Black backed jackal-common duiker	**0.75 (0.62-0.86)**
Black backed jackal-gemsbok	0.68 (0.55-0.81)
Black backed jackal-hare	**0.74 (0.61-0.85)**
Black backed jackal-klipspringer	0.68 (0.54-0.82)
Black backed jackal-kudu	0.63 (0.51-0.76)
Black backed jackal-smith's red rock rabbit	0.58 (0.35-0.79)

Black backed jackal-steenbok	0.68 (0.53-0.82)
Mean overlap	0.68

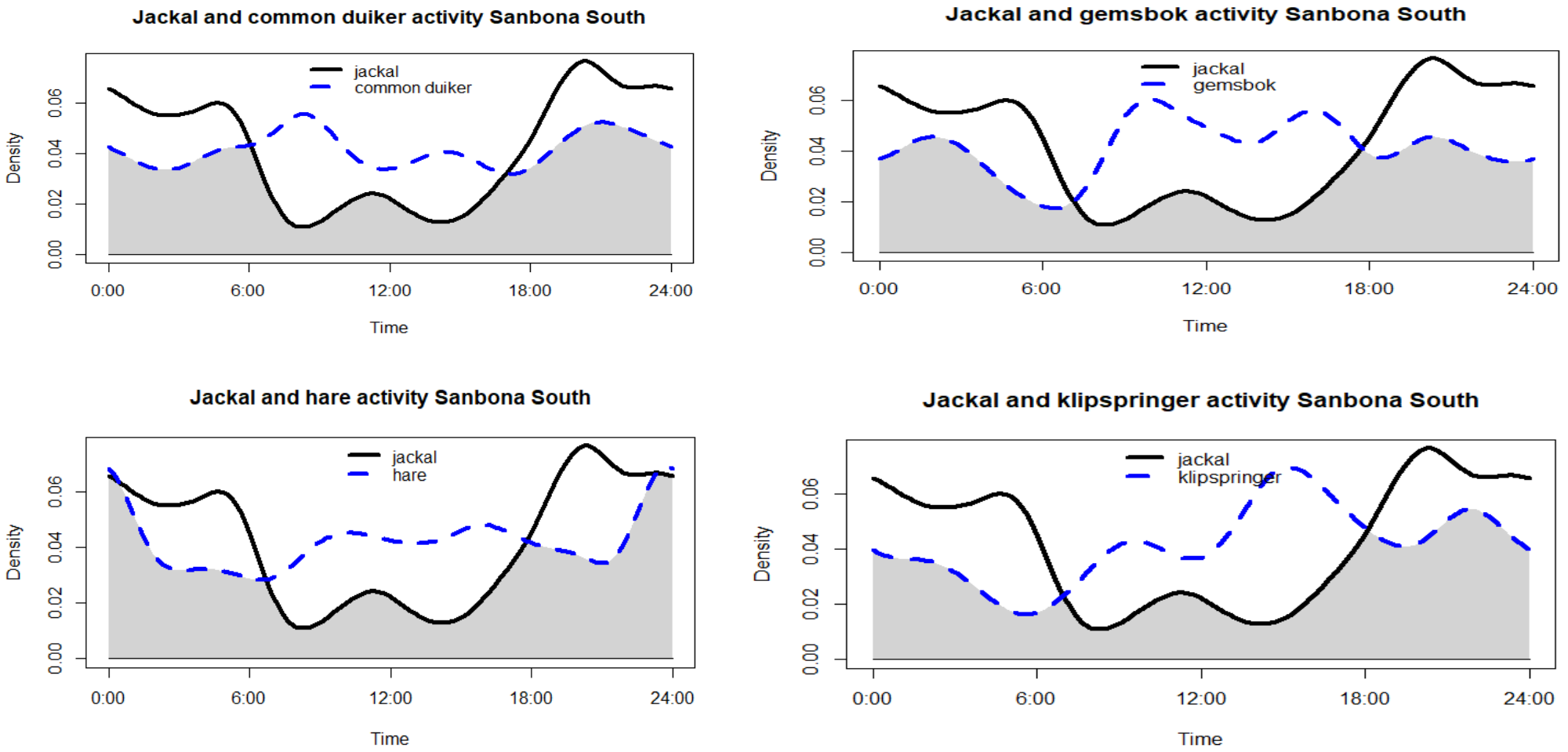
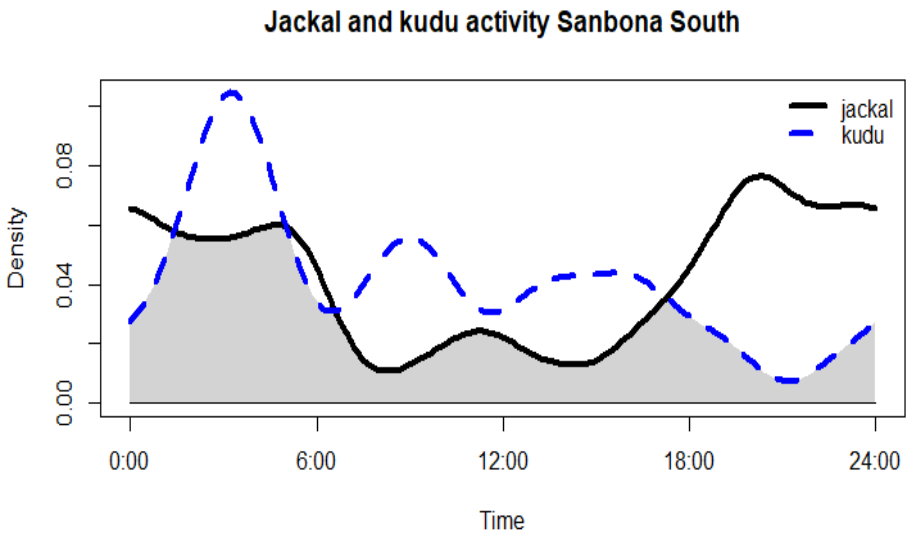
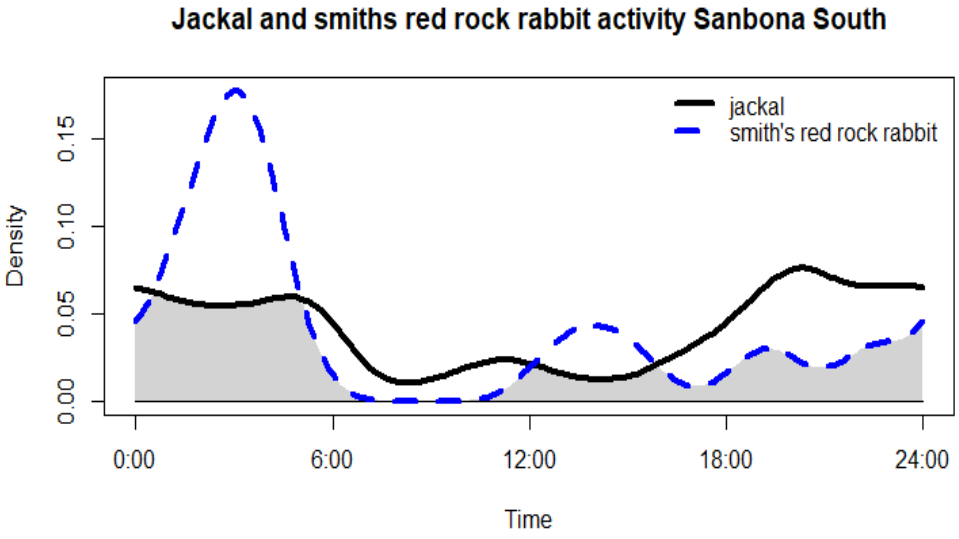


Figure 9 Black backed jackal and its potential prey species activity in Sanbona Wildlife Reserve southern section.





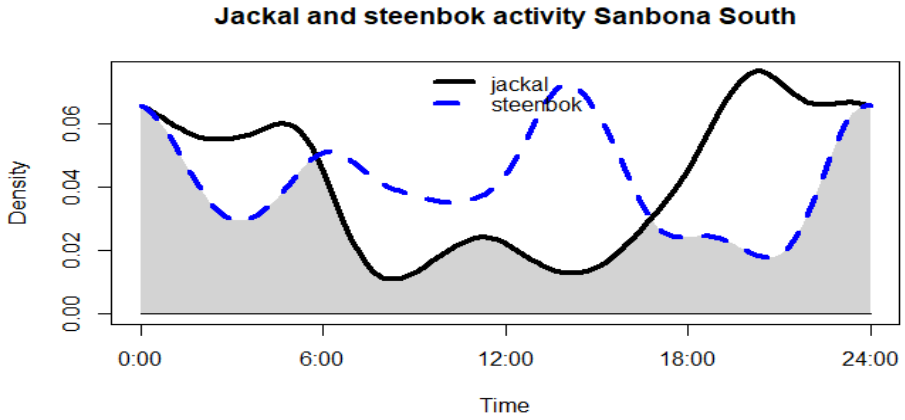


Figure 9 Continued.

4.0 Discussion

Protected areas are widely regarded as a critical intervention for biodiversity conservation across the globe (Kareiva & Marvier, 2012; Soulé, 2013). Evidence for their success in realizing this goal is primarily measured through the higher species richness found in protected areas compared to land used for urban, industrial and agricultural uses (Gray et al. 2016). The results of my study support this finding with species richness increasing from commercial farmland (27) to public (30) and then private protected areas (36). Despite this, biodiversity on small livestock farms was still high relative to both urban (Schnetler et al. 2019) and more intensive agricultural land uses (Allan et al., 2015).

Other studies in South Africa (Drouilly and O'Riain 2019; Mann et al. 2015) and elsewhere in Africa (Kiffner et al., 2015; Kinnaird & O'brien, 2012; Msuha et al., 2012; Rannestad et al., 2006) have shown the compatibility of wildlife with low intensity small livestock farming in rangelands. Two of these studies (Kiffner et al. 2015; Msuha et al. 2012) attributed their findings to the intermediate disturbance hypothesis, proposing that with low levels of disturbance in terms of frequency and intensity, wildlife diversity is higher (Connell, 1978; Huston, 1979). However, the intermediate disturbance hypothesis has since been strongly contested (Fox, 2013). It is important to note that the Karoo ecosystem has had a long history of herbivory by both medium and large native herbivores, resulting in moderate levels of disturbance (Dean, 1999). Karoo vegetation may thus be more tolerant of the effects of small livestock grazing than other ecosystems (Todd, 2006) and may thus continue to support native grazers and their predators.

Unsurprisingly large predators such as lion and leopard, which pose a threat to both livestock and human lives were absent from farmland in this study. Local extirpation of megaherbivores, large predators and large antelope species is common throughout the world and has led to trophic downgrading of ecosystems worldwide (Estes et al., 2011). In South Africa local extirpation of large mammals typifies landscapes used primarily for agricultural and urban activities (Boshoff et al., 2016). The extirpation of apex predators in agricultural landscapes has conversely led to thriving populations of mesocarnivores (Beinart, 1998; Kerley et al., 2017, Drouilly et al. 2018). Lion were also absent from the public protected area as the fencing is inadequate for containing this species. While lion do occur in the Karoo National Park they frequently escape into neighbouring farmland and cause both considerable damage to livestock and foment conflict amongst stakeholders on how best to manage them in this context (Geldenhuys, 2019; Head, 2020; Stoddard, 2020). Invariably it is only private protected areas like Sanbona that have the resources to adequately contain large carnivores

and megaherbivores through expensive fencing and maintenance plans (Hayward & Somers, 2012).

4.1 Temporal activity patterns of species in a protected area and farmland

Many species persist in human modified landscapes by adjusting their activity patterns to reduce temporal overlap with people (Carter et al., 2015; Leighton et al., 2022), domestic animals (Zapata-Ríos & Branch, 2016) and vehicles (Andersen & Aars, 2007; Andersen et al., 1996). In farmland used for low intensity livestock grazing, temporal avoidance is more common than spatial, with animals typically shifting to a more nocturnal activity pattern to avoid the peak in human activity (Shamoon et al., 2018). This pattern may be more pronounced for actively persecuted species such as coyote in the USA (McClennen et al., 2001), fox in Europe (Gálvez et al., 2021), boar in Europe (Keuling et al., 2008).

My results show high levels of temporal overlap (mean coefficient of overlap, $\Delta \geq 0.83$) for the same species living in Anysberg Nature Reserve and the nearby small livestock commercial farmland of Koup. This corroborates the findings of Winterton et al. (2020) who reported high temporal overlap in small antelope and domestic ungulates between the West Coast National Park and a farm outside of the park. Further afield in Brazil, Ferreira et al. (2022) reported only modest effects of anthropogenic pressure on the temporal activity patterns of Cerrado mammals under varying levels of protection. Ferreira et al. (2022) found that most mammals did not adjust their activity patterns in response to anthropogenic pressure in the protected areas of Cerrado or in areas where small-scale agriculture and cattle ranching is practiced. This once again underlines compatibility between wildlife and low intensity pastoralism (Blaum et al., 2007).

By contrast, several studies have reported consistent increases in the nocturnality of wildlife as a result of anthropogenic disturbance (Gaynor et al., 2018; Grignolio et al., 2018), including a shift in wildlife activity away from locations experiencing greater anthropogenic pressure. Where temporal shifts to avoid human peaks in activity are not apparent it may be because species exhibit strong spatial response to differences in levels of anthropogenic activity (Cruz et al., 2018; Di Bitetti et al., 2008, 2020; Massara et al., 2018; Norris et al., 2010; Paviolo et al., 2009) or wildlife communities already have low levels of diurnal activity and thus lack flexibility in activity patterns (e.g. aardvark which are nocturnal).

My results showed greater nocturnality on farmland than the protected area particularly among species that are heavily persecuted like the black backed jackal (Drouilly et al., 2018; Kamler et al., 2020; Minnie et al., 2016). The ability of black-backed jackals to depredate medium sized mammals using cooperative and opportunistic hunting behaviour (Humphries et al.,

2016; Krofel, 2008; Nattrass et al., 2020), coupled with their wide distribution in human-dominated landscapes means that they invariably face high levels of negative interactions with farmers (Kerley et al., 2018). It is pertinent to note that the activity patterns of black-backed jackals are not known in all parts of its range as it is poorly studied outside of protected areas (Plessis et al., 2015). However, available evidence reveals that black-backed jackal display predominantly crepuscular and nocturnal activity patterns, in both protected areas (Ferguson et al., 1988; Kaunda, 2000, 2001) and farming regions (Ferguson et al., 1988; Fink et al., 2020). The greater nocturnality of jackal on farmland in this study is thus almost certainly in response to higher farmer activity during the day coupled with high levels of farmer persecution. This finding complements previous studies which have found that black backed jackals become more nocturnal when experiencing negative human interactions (Ferguson et al., 1988; Fuller et al., 1989; Hiscocks, 1988).

Increased nocturnality of persecuted predators is a global phenomenon with wolves in both the United States (Chavez & Gese, 2006) and Europe (Ciucci et al., 1997) being more active at night in agricultural lands. Other large predators living in shared landscapes have also been observed to increase nocturnality to avoid peaks in human diurnal activity including tigers in India (Athreya et al., 2014), lion in Kenya (Suraci et al., 2019), leopard in India (Odden et al., 2014) and polar bears in Canada (Lamb et al., 2020). Medium sized predators including coyote (Gehrt et al., 2009), lynx (Haswell et al., 2020) and dingo (McNeill et al., 2016) have also been shown to increase nocturnality in response to human disturbance and persecution. In my study there were too few captures of caracal on farmland to include a comparison with the protected area but other heavily persecuted species on farmland with sufficient captures such as steenbok and gemsbok also exhibited greater nocturnality on farmland compared to the protected area. Farmers in the Karoo are renowned for hunting antelope on their properties both for consumption (Gordon et al., 2004) and to reduce competition for limited grazing with their livestock (Drouilly et al., 2019).

Ungulates have also adapted to anthropogenic disruptions by altering their behaviour in human-dominated landscapes (Ditchkoff et al., 2006; Riley et al., 2003; Tigas et al., 2002; Valeix et al., 2012). For instance, male white-tailed deer have been documented to evade detection by hunters by altering their resource choices and patterns of movement (Little et al., 2014). Similarly, western roe deer have been shown to evade hunters by utilising less perilous habitats (Padié et al., 2015). Most of these behavioural changes are theorised to emanate from the ecology of fear (Clinchy et al., 2016) as animals may see humans as “super predators” and exhibit higher antipredator instincts to humans than to natural predators (Bonnot et al., 2020; Zbyryt et al., 2018).

In antelopes, habitat usage and behaviour are responsive to many risk and resource variables (Anderson et al., 2010). In habitats with limited human presence, they often pay close attention to the habitat structure, which influences their interactions with natural predators. Generally, antelopes inhabit a "landscape of fear" (Anderson et al., 2010; Verdolin, 2006) weighing the danger of predation against the rewards of foraging and are believed to avoid foraging in regions with high-quality fodder if the risk of predation is sufficiently high. Prey species usually evaluate predation risk using indirect indices like habitat structure, as opposed to direct indicators like presence of predators (van der Merwe & Brown, 2008). Consequently, human presence directly or indirectly influences the "landscape of fear" and resource variables utilised by antelopes (Bonnot et al., 2013). This is evident in mule deer which greatly reduces the extent of habitat utilised (Kleist et al., 2021) experiencing a net loss in food intake in response to anthropogenic disruptions (Dwinnell et al., 2019). Elk have also been documented to respond to anthropogenic disruptions by varying the amount of time spent in a given location and by also modifying their habitat choices (Cleveland et al., 2012).

Despite the hunting of antelopes such as greater kudu, klipspringer, springbok and grey rhebok in the Karoo, these species did not alter their temporal activity pattern relative to their conspecifics in Anysberg. Greater kudu showed a late afternoon peak in activity on farmland, while klipspringer and grey rhebok both had an early morning peak in activity on farmland. It is possible that environmental and morphological constraints reduce the behavioural plasticity of these species resulting in their being active during daytime in the presence of humans (Gill et al., 2001).Thus animals habituating to anthropogenically disturbed landscapes often experience limited food availability which reduce their capacity to alter their activity pattern temporally (Martin et al., 2010). Moreover, some wildlife species are capable of altering specific behaviours by being active in safer microhabitats at daytime in anthropogenically disturbed landscapes (Dupke et al. 2016) or dissuade from anthropogenic features such as roads and buildings (Morrison et al. 2014, Stabach et al. 2016) in places where they have got no other choice but to coexist with humans. Certain species have also adapted to modifying their movement during the day (Oriol-Cotterill et al. 2015) and also increase alertness levels (Sönnichsen et al. 2013) so as to persist in human modified landscapes which could be the reason for antelopes' persistence in the Karoo in my study despite heavy persecution.

In Africa, duikers have been reported to shift towards nocturnality in areas of high anthropogenic disruptions (Ehlers Smith et al., 2019; Skinner & Chimimba, 2005). There have also been evidence of Cape bushbuck, blue duiker and grey duiker drifting towards nocturnality in human modified landscapes (Ehlers Smith et al., 2019) in a bid to avoid temporal overlap with humans. However, common duikers in my study did not show any

activity shift in response to anthropogenic disruptions on farmland and may rely on refugia to avoid detection.

Primates such as baboons are able to adapt to human induced alterations in their environment by being flexible in their patterns of movement, feeding, reproduction and social structure (Alberts & Altmann 2006; Swedell 2011). The ability of baboons to adopt selective and generalist foraging techniques in human modified landscapes (Alberts & Altmann 2006) makes it easier to avoid people in space. Additionally, baboons ability to reduce their home range size and daily path length during the day when exploiting high risk food sources in human dominated landscape (Altmann & Muruthi, 1988; Hoffman & O'Riain, 2012; Strum, 2010) have also enabled them to avoid humans spatially since they cannot be active at night. For species that are strictly nocturnal like springhare or aardvark, they have little option to shift between day and night and hence must tailor their activity relative to moonlight variations (Bhatt et al., 2021).

4.2 The effects of lunar illumination on the activity patterns of species in a protected area and farmland

There were no clear or consistent differences between the proportion of nocturnal activity and the moon phase for most species living on farmland and in protected areas. Aardwolf, common duiker, gemsbok, steenbok and springhare all showed limited variation in nocturnal activity with lunar phases. Lunar illumination is believed to increase predation risk as it helps predators to more easily locate their prey (Kotler et al., 1991; Nash, 2007), resulting in less activity or alterations in prey foraging techniques on well moonlit nights (Daly et al., 1992; Orrock et al., 2004; Prugh & Golden, 2014). However moonlit nights may also aid prey in detecting predators and darker nights may provide more cover and reduce detection by predators. It is thus not surprising that mammals' response to lunar illumination varies among taxa and is dependent on factors such as trophic level, sensory cues and habitat type (Prugh & Golden, 2014). My results showed a peak in black backed jackal activity during the brighter portion of the lunar phase in both the protected area and farmland. This corroborates the findings of Kerley et al. (2018) who posited that black backed jackals have the tendency to be more active during full moon which is more conducive for hunting. Generally, small mammals which are the preferred natural prey of jackal in this region (Drouilly et al. 2018) have low predation risk during new moons and high predation risk during full moons (Hughes & Ward, 1993). However, Sábato et al. (2006) recorded reduced activity in maned wolves during full moon which they attributed to reduced activity of small mammal prey species and a shift to more plant material in the diet.

My study is also in contrast to the findings of Ferguson et al. (1988) who reported reduced activity of black backed jackals during full moon in South Africa which they argued was to avoid detection by farmers hunting at night. However, most farmers in my study area hunt with spotlights from vehicles relying on light reflected from the eyes of predators to detect and then shoot them (Drouilly pers comm). Reflected light is easier to detect at low lunar illumination and thus farmers prefer to hunt using this method when there is minimal moonlight (J. O'Riain pers. comm).

Prey species are more likely to be detected by predators during high lunar illumination (Clarke, 1983) but predators are also more vulnerable to being detected by their prey. This dynamic may result in prey species shifting to habitats that provide more concealment on moonlit nights a hypothesis I could not test with my methods and results.

My finding that prey species such as gemsbok, grey rhebok, kudu, steenbok and springbok are more active on brighter nights also contradicts the predation risk hypothesis which posited that prey species limit their activity when risk of predation is high (Prugh and Golden 2014) such as during bright moonlit nights, when the likelihood of being easily sighted by predators is high. Mesocarnivores, may thus alter their patterns of activity and use other senses to detect prey during period of prey scarcity (Lkaundre & Keller, 1981). This pattern of activity has been observed in red foxes increasing activity during less luminous nights when visual cues of prey are harder to distinguish, and foxes relying more on senses of smell and touch to detect prey (Penteriani et al., 2011).

Gemsbok and steenbok were mostly active during the full moon phase in both the protected area and farmland. This activity pattern could be said to be in compensation for their reduced activity during daylight when the risk of detection by humans and predators is higher (Carnevali et al., 2016; Visscher et al., 2017). This pattern of activity has been noticed in lowland tapir and the white-tailed deer both of which become active at night to compensate for inactivity during the day as a result of increased predation risk (Brown et al 2011). Additionally, Lashley et al. (2014) ascertained that ungulates have a tendency to increase their foraging activity by lowering alertness times when night-time visibility improves as predators are easier to detect during moonlit nights than on darker nights.

4.3 Predator and prey interactions in Sanbona wildlife reserve

Due to the absence of human persecution in Sanbona Wildlife Reserve, I used the data from this site to explore predator and prey interactions. My results showed that the presence of apex predators did not change the activity of both smaller predators and potential prey. My results are consistent with other recent findings indicating that lions do not always have

substantial impact on sympatric predators (Balme et al., 2017; Chizzola et al., 2018; Mugerwa et al., 2017; Rafiq et al., 2020), even though such impacts have been documented (Chaudhary et al., 2020). In addition, several studies in southern Africa have documented the absence of competitive effects on sympatric carnivores diel activity (Balme et al., 2017; Miller et al., 2018; Mugerwa et al., 2017; Rafiq et al., 2020). Hence, my study adds to the burgeoning body of evidence downplaying the ecological importance of apex predators (Estes et al., 2011) especially those transcending far beyond consumptive impacts on prey populations which may not be as substantial as formerly envisaged (Chizzola et al., 2018; Hargreaves et al., 2020; Kohl et al., 2018; Middleton et al., 2013; Périquet et al., 2017). Rather, the impact of predators on sympatric species is largely context-dependent both for sympatric predators and prey (Haswell et al., 2016).

Mammalian carnivore species use a wide variety of adaptive mechanisms to partition resources and coexist. Such mechanisms of coexistence among carnivores includes spatio-temporal, habitat and food partitioning (Dröge et al., 2017; Kamler, Stenkewitz, et al., 2012; Vanak et al., 2013). When larger carnivores prey on smaller carnivores, some of the latter, may avoid the former in space and time for safe cohabitation (Kamler et al., 2003; Marneweck et al., 2019; Vanak et al., 2013). For instance, cape foxes have been reported to partition in space and time from black backed jackals' major activity areas when feeding (Kamler, Klare, et al., 2012). Contrastingly, even though bat-eared foxes and black-footed cats were also being killed by black backed jackals, they did not segregate in space and time from black backed jackals' major activity areas while foraging (Kamler et al., 2015; Kamler, Klare, et al., 2012). My results showed black backed jackal and caracal having a high level of overlap with their potential prey species suggesting that the prey species are only relying on their antipredator instincts to ward off threats posed by the mesocarnivores (Caro et al., 2004) rather than to avoid them in space and time. This finding corroborates the study of Charaspet et al. (2019) who found that golden jackal had high temporal overlap with all its potential prey species in Huai Kha Khaeng Wildlife Sanctuary, Thailand.

Amongst large carnivores, African wild dogs have been reported to avoid lion core activity areas due to predation (Darnell et al., 2014; Marneweck et al., 2019; Vanak et al., 2013). By contrast, even though lions predate on cheetahs and spotted hyenas (Périquet et al., 2016), they did not segregate in space and time from lions (Broekhuis et al., 2013; Dröge et al., 2017; Vanak et al., 2013). Hence, the dynamics of predator and prey coexistence and intraguild competition in carnivores and their potential prey species is dependent on the adaptive mechanisms of the interactants to facilitate cohabitation (Broekhuis et al., 2013; Dröge et al., 2017; Kamler, Klare, et al., 2012; Périquet et al., 2016; Vanak et al., 2013).

4.4 Conclusions and limitations

My study confirms the findings of Drouilly et al. (2018) and Woodgate et al. (2018) who showed that extensive small livestock farms support considerable biodiversity outside of protected areas. Living in proximity to humans who actively persecute, and harvest wildlife is however predicted to impact the behaviour of wildlife and in particular active avoidance of peaks in human activity in both space and time (Brivio et al., 2017; Oberosler et al., 2017; Raveh et al., 2012). My results reveal that select heavily persecuted species such as the black backed jackal adjust their temporal activity on farmlands to avoid the early mornings and evenings when farmers and their labour are more active. Similarly, Steenbok, a popular source of wild protein for people living on farms, peaked in activity before dawn while gemsbok that are hunted for sport and consumption showed a clear nocturnal peak relative to the protected area. A shift to higher nocturnality by these three species likely reflects the avoidance of human activity in the daytime and is consistent with research elsewhere in the world for persecuted species living in human modified landscapes (Shamoon et al., 2018; Gálvez et al., 2021). By contrast other actively hunted species such as kudu, grey rhebok and klipspringer were more active during daytime on farmland and it is possible these species rely on both concealment in dense vegetation in riparian zones and rocky habitat to avoid detection by people on farms. These adaptive behaviours, honed through evolution, allow them to persist in the face of human-induced changes to their environments, highlighting the importance of understanding and conserving natural behaviours in conservation efforts. Other species including aardvark, aardwolf and common duiker showed no effect of land use on their activity patterns. Together these results reveal clear variation in how wildlife adjust their activity patterns in response to land use. I was not however able to discern the relative contribution of levels of persecution, habitat use, predator-prey interactions and behaviour on the level of activity of wildlife in different land uses and this remains a challenge going forward.

There was no clear effect of moon phase on the percentage of time that animals were active in either Anysberg or on farmland. Jackals increased nocturnal activity during the full moon and this was more marked in the protected area compared to farmland. However other species which were more active at night on farmland (e.g., gemsbok, kudu and steenbok) did not show consistent variation with moon phase and land use suggesting a more complex interaction between predation, predator avoidance and thermal constraints that were not adequately measured in this study.

A limitation of this study was the failure to adequately quantify human activity. Camera placement was optimised to detect wildlife and was thus biased away from roads and other infrastructure frequented by people (e.g., walking trails, buildings and water points). In

retrospect it would have been sensible to record human activity by placing select camera traps in areas frequented by people to allow for an assessment of temporal overlap of human activity with select wildlife species. Fortunately, human activity patterns on farmland and in the protected area is very similar with established peaks in the early morning and evening corresponding to the cooler parts of the day in summer and when gates at overnight accommodation are opened to tourists in protected areas.

My study showed that the presence of apex predators did not have a marked influence on the activity of smaller predators and potential prey in a protected area with limited negative human interactions. Plains zebra, a preferred prey species of lion (Courbin et al., 2016; Funston, 1999), had the least similar activity patterns in the North compared to the South of Sanbona (i.e., with and without lions) with a clear peak in activity before dawn in the absence of lions. Kudu, another prey species routinely consumed by lions (Louw & Marshal, 2019), showed a similar peak in pre-dawn activity in the absence of lions. Given lions hunt primarily at night these two examples would appear to be an example of a prey species adjusting their activity in the absence of a predation risk by large predators.

Black backed jackal temporal activity overlapped considerably with most prey species including those that are too large to be actively hunted. By contrast caracal had much lower levels of temporal overlap with the same species but this may in part be linked to the very low levels of detection for this species in both protected areas. It is unlikely that ungulate prey would actively avoid the peaks in mesopredator activity given that both jackal and caracal in protected areas eat mostly small mammals (<5kg) and that jackal in Anysberg consumed more fruit than vertebrate prey (Drouilly et al. 2018).

Camera traps are an excellent method for sampling the temporal variation of multiple wildlife species simultaneously within a landscape. However, in the absence of behavioural observations or remote devices that can provide a proxy for animal behaviour (e.g., smart collars, Fehlmann et al. 2019) it is difficult to understand the context of temporal shifts and whether they are driven by deliberate avoidance of threats, the avoidance of competition in species whose niches overlap, avoidance of temperature extremes or evolutionary adaptations to a generally nocturnal or diurnal lifestyle. In this study I attempted to control for environmental variables by comparing sites that are geographically close to one another and within the same season. Despite this I was not able to control for year (farmland and Anysberg were sampled in successive years) and despite their proximity there are differences in both the habitat types and topography between the sites. Similarly, while I used the north (with lions and cheetah) and the South of Sanbona within pseudo-experimental design for exploring how the presence or absence of lion might influence the activity of mesopredators and prey

species, I was not able to control for topographical and climatic differences that are apparent between these two regions in the reserve.

4.5 Management implications

My study affirms that extensive small livestock farms are a rich source of biodiversity outside protected areas and as such conservation strategies tailored to protect key habitats and species habituating in this environment should be adopted. Additionally, the drift to nocturnality in a bid to avoid peaks in human activity in space and time witnessed in my study in select heavily persecuted species such as black backed jackal, steenbok and gemsbok suggests a significant behavioural mechanism by which human-induced disturbance is restructuring ecological communities. By understanding animals' perceptions and reactions to risks inherent in their habitat and human-induced stimuli, we could enhance our ability to devise management strategies that promote harmonious coexistence. The persistence of kudu, grey rhebok, and klipspringer not to adjust their overall activity in response to risk from farmers necessitates the importance of temporal risk avoidance especially when ecological or anthropogenic constraints limits the ability of animals to respond in space and time to risk. It is thus important to understand and conserve natural behaviours in conservation efforts in the Anthropocene.

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