

Coexistence among South African carnivores: spatial and temporal partitioning and their ecological correlates

by

Kyle Smith

u12049523

Supervisor: Prof. M. J. Somers

Co-supervisors: Prof. J. A. Venter

Prof. M. Keith

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Declaration

I, Kyle Smith, declare that this dissertation, which I hereby submit for the degree M.Sc. Wildlife Management at the University of Pretoria is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:



Date:

3 January 2023

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Supervisor: Prof. M. J. Somers

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Faculty of Natural and Agricultural Sciences,
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Summary

Carnivore species coexistence is shaped by niche partitioning that developed over evolutionary time through behavioural responses and adaptations to interspecific competition and risk. Minimising lethal and sub-lethal deleterious pressures from dominant species will aid the subordinate individual's fitness and survival.

This study aimed to test hypotheses concerning interspecific avoidance behaviour within carnivore communities and identify the potential for spatial and temporal partitioning as interspecific coexistence strategies used by South African Carnivora. Multi-seasonal data from large-scaled camera trapping networks in four South African protected areas were analysed. They are the Associated Private Nature Reserves (APNR) which encompasses Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and the Tswalu Kalahari Reserve (TKR).

Spatial avoidance behaviour was analysed using occupancy modelling, selectivity of vegetation types, and quantitative spatial overlap using Pianka's index. Only 21% of the species-pairs across all combinations and protected areas showed signs of spatial avoidance behaviour. In some cases among this minority, spatial partitioning could not be attributed to active avoidance behaviour with certainty due to a lack of biological reasoning supported by empirical evidence of competition and risk (e.g., genet-associated species-pairs) and differences in vegetation type preferences (e.g., TKR's Cape foxes *Vulpes chama* in relation to brown hyaenas *Hyaena brunnea*). No species-pairs in KPNR or MGR demonstrated clear evidence of spatial avoidance behaviour. Avoidance behaviour was observed among medium-sized and smaller carnivore species such as bat-eared foxes and aardwolves (*Proteles cristata*), but not among large predators (e.g., lions *Panthera leo*, leopards *Panthera pardus*, and spotted hyaenas *Crocuta crocuta*). Furthermore, TKR's bat-eared foxes appear to avoid areas used by brown hyaenas.

Temporal avoidance behaviour was analysed by comparing the kernel density estimates of each species' diel activity patterns and core activity periods (50% isopleths). Furthermore, interspecific spatiotemporal behaviour was examined using time-to-event analyses. Most species-pairs (63%) across all combinations and protected areas showed no clear indications of using temporal avoidance behaviour as a coexistence strategy with the potentially risk-associated, dominant species. However, temporal partitioning was clearly observed in African wild dog (*Lycaon pictus*) and caracal (*Caracal caracal*) associated species-pairs due to their distinct temporal niche classifications (crepuscular and cathemeral, respectively). The potential for temporal avoidance behaviour was also evident between bat-eared foxes and aardwolves, particularly during the dry season. The remaining species-pairs that displayed potential temporal avoidance behaviour were primarily nocturnal and showed finer-scaled asynchronization of core activity periods (e.g., subordinate carnivore species appeared to avoid lions' core activity periods, and black-backed jackals also avoided spotted hyaenas).

This study shows that spatial and temporal avoidance behaviour among South African carnivores should be considered rare, at least on the scale conducted in this study. In addition, it is shown that these carnivore species coexist in fenced, space-restricted protected areas without requiring drastic behavioural adaptations to intraguild competition and risk. This study recommends that dietary aspects, seasonality at high latitudinal regions, and finer-scaled avoidance of, for example, core activity periods should be included and receive more focus in future analyses of interspecific avoidance behaviour among carnivores.

Key words: activity patterns, behaviour, camera traps, Carnivora, interspecific avoidance, overlap, spatial

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Ethical considerations

This work was conducted with ethical approval from the Nelson Mandela University Animal Ethics Committee (A. 19- SCI-NRM-001).

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CHAPTER 1

General introduction

An important component of efficient wildlife management efforts and conservation strategies is a better understanding of the interspecific relationships within carnivore communities and the key drivers that allow carnivore species to coexist (Karanth et al. 2017). Co-existence among carnivores developed over evolutionary timescales through behavioural responses and adaptations to potential risk of direct and indirect competition (Creel and Creel 1996, Neale and Sacks 2001, Palmer et al. 2022). Minimising the risk of detrimental encounters with more dominant species will ultimately maintain fitness and ensure the survival of the subordinate individual (Linnell and Strand 2000). Two main strategies available to subordinate carnivores to avoid encounters with dominant predators are spatial and temporal avoidance behaviour (Carothers and Jaksic 1984, Linnell and Strand 2000). This means that subordinate species may be active at times of the day or occupy areas that will minimise the potential for encounters with dominant carnivores. However, avoiding certain periods of the day or areas may result in the species being excluded from favourable resources, which can have deleterious consequences at a population-level (Creel and Christianson 2008, Ritchie and Johnson 2009). Therefore, a trade-off exists between maintaining fitness and the risk associated with sympatric predators in carnivore communities.

1.1 Carnivore community structure and associated interspecific competition

Carnivores (species of the order Carnivora) are essential members of naturally functioning ecosystems. A carnivore community presents various direct interspecific interactions such as resource exploitation and intraguild killing, and indirect biotic interactions and abiotic effects with outcomes such as behaviourally induced reduction in population growth rates (Linnell and Strand 2000) and changes in habitat structure via seed and plant dispersal through ingestion (Kamler et al. 2020a) and secondary dispersion (i.e., diplotendozoochory; Hämäläinen et al. 2017), and stable soil and water dynamics (Beschta and Ripple 2019). Species extirpations and other major disturbances, such as keystone population declines within a carnivore community's structure, force pronounced stress on ecosystem functioning (Elmhagen et al. 2010, Estes et al. 2011, Ripple et al. 2014). This may destabilise vital ecosystem processes (e.g., top-down regulation of herbivores) and will ultimately require intense management by land owners (e.g., population control of prey species) to maintain healthy and functioning biological communities that provide the necessary ecosystem services (Elmhagen et al. 2010, Estes et al. 2011).

A natural carnivore community generally consists of single or multiple large apex predators, midranking mesocarnivores and subordinate, small carnivore species (Rosenzweig 1966, Prugh and Sivy 2020). Traditional carnivore ecology and hypotheses describe mainly negative interference and exploitative interactions between large predators and subordinate carnivores (Linnell and Strand 2000). The interplay between large, dominant carnivores and mesopredators is usually dictated by suppressive interactions like intraguild predation and exploitation of resources (Prugh and Sivy 2020). However, positive and neutral interactions in intraguild dominance hierarchies are equally integral in maintaining carnivore assemblages (Prugh and Sivy 2020). Most notable are the facilitative events provided by large predators in the provisioning of large herbivore carrion and thus scavenging opportunities for mesocarnivore species (Pereira et al. 2013, Yarnell et al. 2013). The strength of facilitative and

suppressive interactions is also likely dictated by the resource productivity of the ecosystem (Elmhagen and Rushton 2007, Elmhagen et al. 2010, Hoeks et al. 2020). A trade-off revolves around the availability of regular sources of nutrition when during periods of low ecosystem productivity, subordinate mesocarnivores will more readily risk intraguild killing to have scavenging access to carrion provided by large, dominant predators. In turn, during periods where resources are readily available for mesocarnivores, scavenging may not be as high a priority, and therefore the need to risk close spatial overlap with potential predators is alleviated. In addition, intense suppression of mesocarnivores by large apex predators should, according to the carnivore trophic cascade hypothesis, alleviate risk and competition experienced by smaller, more subordinate carnivores (Elmhagen et al. 2010, Gordon et al. 2015). Thus, a dominance hierarchy among carnivore species plays an integral part in maintaining ecosystem stability.

Interspecific dominance hierarchies among terrestrial carnivores generally follow a gradient according to body size (Rosenzweig 1966, Palomares and Caro 1999). This means that the species with the larger body size are, in most cases, the dominant species. However, exceptions to this rule-of-thumb exist and are mainly influenced by group size, age and sex ratio (Trinkel and Kastberger 2005). Lions (*Panthera leo*) are larger in body size compared to spotted hyaenas (*Crocuta crocuta*); however, the dominance relationship between the two top predators is dictated by a number of factors. Spotted hyaena clans with more members are more likely to be dominant over lions, especially at recent predation events (Kissui and Packer 2004, Trinkel and Kastberger 2005, Périquet et al. 2015, Lehmann et al. 2017). A higher density of mature male lions occupying an area result in more dominance being displayed by lions over spotted hyaenas (Trinkel and Kastberger 2005, Lehmann et al. 2017). Black-backed jackals (*Lupulella mesomelas*) have been shown to aggressively displace and therefore be dominant over the larger side-striped jackal (*Lupulella adusta*) (Loveridge and MacDonald 2003).

Behavioural differences among individuals of a species in terms of risk avoidance and vigilance also exist and have a direct influence on the intensity of interspecific competition (Watts et al. 2010). In addition, prey availability also influences dominance hierarchies within carnivore communities. Périquet et al. (2015) showed that as prey availability increases, spotted hyaena clan size also increases. This results in higher clan densities, ultimately followed by dominance over lions within the specific area.

Major perturbations in a carnivore community, such as the local extinction of apex predators, may result in top-down, trophic cascades that drastically impact ecosystem dynamics and biodiversity (Linnell and Strand 2000, Elmhagen et al. 2010, Estes et al. 2011). Loss of large apex predators from a community relieves the competitive pressure on mesocarnivores which may allow for rapid increases in their population density, expansion of their range and changes in their behaviour (Prugh et al. 2009, Ritchie and Johnson 2009). This ecological phenomenon, termed mesopredator release, results in significant biodiversity and economic losses worldwide (Prugh et al. 2009, Brashares et al. 2010). Mesopredator release can negatively impact predator and prey species from lower trophic levels (Brashares et al. 2010, Tambling et al. 2018).

However, recent studies argue against the mesopredator release hypothesis and claim that the loss of large apex predators does not necessarily result in mesopredator release (Comley et al. 2020b, Gigliotti et al. 2020, Castle et al. 2021). This is because mesopredator release depends on the level of productivity within an ecosystem, the number of dominant predator species present, and the strength of interactions among trophic levels, namely apex predators, mesocarnivores and the available prey species (Brashares et al. 2010). In theory (Holt and Polis 1997, Brashares et al. 2010), ecosystems with high productivity levels, meaning greater food availability, should experience top-down control where large apex predators would dominate and suppress mesocarnivores (empirically shown in Elmhagen and Rushton 2007, Prugh et al. 2009, Feit et al. 2019). In addition, high productivity areas should be more susceptible to

mesopredator release upon loss of apex predators due to greater prey availability (Prugh et al. 2009, Feit et al. 2019). However, this depends on the species diversity within the carnivore community (Prugh et al. 2009). In less productive ecosystems, theory predicts that mesocarnivores should more likely be bottom-up controlled by the limited availability of prey rather than interference competition by apex predators (Holt and Polis 1997, Prugh et al. 2009). This is because large apex predators would be more susceptible to extinction in low productivity systems (Prugh et al. 2009). The natural coexistence of carnivores is thus, according to theory, more likely at intermediate productivity levels (Holt and Polis 1997, Brashares et al. 2010). In addition, ecosystems are also, according to theory, more resilient to disturbances in its carnivore community at levels of intermediate productivity (Brashares et al. 2010). Furthermore, severe instances of mesopredator release are less likely to occur in ecosystems of high species diversity (i.e., many apex predators, mesopredators, and prey species; Prugh et al. 2009, Brashares et al. 2010). For example, the void left by the loss or removal of one apex predator species from a system will be filled by another apex predator, rather than a mesopredator species (Prugh et al. 2009, Brashares et al. 2010).

Interspecific competition is the main factor that shapes relationships within a carnivore community and includes aggressive, interference interactions such as kleptoparasitism (stealing captured prey) and intraguild killing, and exploitative competition that involves carnivores competing for similar, limited prey species (Creel and Creel 1996, Caro and Stoner 2003). An African example of intense interspecific competition is the relationships between lions and other large carnivore species. Lions, being apex predators, are responsible for a large proportion of kleptoparasitic events and intraguild killing of leopards (*Panthera pardus*; Balme et al. 2017a, 2017b), hyaenas (Trinkel and Kastberger 2005, Sogbohossou et al. 2018) and cheetahs (*Acinonyx jubatus*; Broekhuis et al. 2013). Competitive interactions such as intraguild killing have been observed among carnivores of all body sizes. For example, mesocarnivores

like black-backed jackals have been shown to kill smaller carnivore species like bat-eared foxes (*Otocyon megalotis*), Cape foxes (*Vulpes chama*) and black-footed cats (*Felis nigripes*) in territorial defence (Kamler et al. 2012, Kamler et al. 2015).

Intense competition between carnivore species does not guarantee behavioural changes in subordinate species at a population-level, even if substantial dietary overlap occurs (Darnell et al. 2014, Balme et al. 2017b). This means that even though direct interference events such as intraguild killing or kleptoparasitism may occur, the population-level behaviour of the subordinate species is sometimes more likely dictated by resource acquisition or mating potential (Broekhuis et al. 2013).

Certain carnivore species may benefit and be attracted to the presence of larger, more dominant carnivore species. This is the case with mesocarnivores that rely heavily on scavenging opportunities (Pereira et al. 2013, Yarnell et al. 2013, Allen et al. 2015, Prugh and Sivy 2020). An example includes black-backed jackal diets changing significantly with the inclusion of carrion from larger prey species (e.g., eland *Taurotragus oryx*, mountain zebra *Equus zebra*, and kudu *Tragelaphus strepsiceros*) due to the reintroduction of lions to the Karoo National Park, South Africa (Fourie et al. 2015, Codron et al. 2018). Therefore, the black-backed jackals would benefit from occupying similar areas to the lions, but will risk predation.

Carnivore communities within South Africa's major protected areas are largely intact assemblages that are ecologically diverse (Vanak et al. 2013, Searle et al. 2021). Many protected areas within Southern Africa and especially South Africa, are fenced reserves and national parks. This means that carnivore communities within these protected areas are subject to increased possible competitive interactions as space is restricted for most species (Bissett and Bernard 2011, Packer et al. 2013). Intensively managed, fenced reserves also generally maintain carnivore populations, such as lion populations, closer to carrying capacity than is

observed for unfenced reserves (Packer et al. 2013). Even though lions have been extirpated from approximately 90% of their historical range (Bauer et al. 2016), they occur in most of the larger protected areas within Southern and East Africa. Lions, and to a lesser extent spotted hyaenas, fill the role of the top predator and, therefore, the most dominant among carnivores in most areas they exist in. Other large predators such as leopards, cheetahs, brown hyaenas (*Hyaena brunnea*) and African wild dogs (*Lycaon pictus*) are considered subordinate to lions and spotted hyaenas (Cozzi et al. 2012, Swanson et al. 2014, Dröge et al. 2017, Marneweck et al. 2019). The aforementioned species are followed by other medium-sized, midranking carnivore species such as black-backed jackals, side-striped jackals, and caracals (*Caracal caracal*) within the typical dominance hierarchy (Ramnanan et al. 2016, Kamler et al. 2020b). Smaller carnivore species such as bat-eared foxes, Cape foxes and African wildcats (*Felis silvestris lybica*) are again subordinate to the medium-sized carnivore species mentioned (Kamler et al. 2013, Bagniewska and Kamler 2014). Interspecific dominance can also be observed among small carnivore species where, for example, African wildcats can be considered dominant over smaller carnivores such as mongoose species (de Satgé et al. 2017). Carnivora species in Africa, and specifically Southern and East Africa, range from the largest species, the African lion, with an average body mass of approximately 180 kg (Smuts et al. 1980), to the smallest species, namely dwarf mongooses (*Helogale parvula*) with an average body mass less than 400 g (Creel et al. 1992).

1.2 Behavioural adaptations that allow coexistence among sympatric carnivore species

Subordinate carnivore species are behaviourally adapted to respond to intensified competition exerted by dominant carnivores (Durant 1998). Studying behavioural adaptations associated with risk of competition is important in identifying the realised ecological niche that each carnivore species occupy (see Neale and Sacks 2001, Schuette et al. 2013, Kamler et al. 2015;

Hardin 1960, Schoener 1974). These behavioural adaptations generally follow components or combinations of spatial segregation, alterations in activity periods, and aspects of diet or resource partitioning (Lima and Dill 1990, Ritchie and Johnson 2009, Palmer et al. 2022). This allows the subordinate species to minimise competition and avoid the risk of aggressive encounters. However, a trade-off generally exists where preferred habitat or diel period is exchanged for conditions of lower probability of risk and, therefore, vital resource availability may not be favourable (Mukherjee et al. 2008, Ritchie and Johnson 2009). This may even lead to severe negative demographic effects (see Creel and Christianson 2008).

Avoidance behaviour may be most prominent among carnivore species that occupy similar ecological niches with high dietary overlap, seeing that a dominance hierarchy is present among the species (Hardin 1960, Schoener 1974, Creel and Creel 1996, Ramesh et al. 2012, Dröge et al. 2017). Interspecific relationships among carnivores and the associated behavioural adaptations of risk avoidance are dictated by a number of different factors, such as the local habitat characteristics, preferred prey availability, and the density and diversity of carnivore species (Palomares and Caro 1999, Elmhagen and Rushton 2007, Swanson et al. 2014, Balme et al. 2017b, Karanth et al. 2017, Vilella et al. 2020). Behavioural adaptations associated with risk avoidance are also influenced by physiological, morphological and behavioural evolutionary adaptations (Donadio and Buskirk 2006, Dibner et al. 2010). These adaptations include body size, sociality, hunting strategies and sexual cycles (O'Donoghue et al. 1998, Ramesh et al. 2012). In addition, abiotic environmental factors such as temperature (Cozzi et al. 2012, Rabaiotti and Woodroffe 2019), precipitation (Bryce et al. 2022), the amount of daylight (Heurich et al. 2014), and even moonlight intensity (Broekhuis et al. 2014) also influences when carnivore species are active and what areas they prefer to occupy (Patterson et al. 1999, Hayward and Slotow 2009).

Risk avoidance behaviour by subordinate carnivores can range from complete temporal, spatial or spatiotemporal avoidance to avoidance within short timescales (Broekhuis et al. 2013, Creel 2018). This means that the subordinate carnivore will avoid predation risk or competition proactively or reactively (Berger and Gese 2007, Broekhuis et al. 2013, Creel 2018). Proactive or predictive avoidance is based on past experiences and knowledge of the dominant species' dynamics, for example, avoiding areas and habitat types favoured by the species associated with risk (Broekhuis et al. 2013, Creel 2018). Reactive avoidance involves instantaneous decision making to avoid species of risk when they are in the vicinity (Broekhuis et al. 2013, Creel 2018). An example of reactive avoidance is where cheetahs would consider occupying habitats first based on prey availability, followed by the fine-tuning of habitat use based on risk associated with dominant predators such as hyaenas and lions (Broekhuis et al. 2013, Swanson et al. 2014, 2016). Therefore, cheetahs coexist with lions but would avoid them at short spatial scales by maintaining a considerable distance between them and the nearest lions (Broekhuis et al. 2013). López-Bao et al. (2016) suggest that risk avoidance among large predators, specifically Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*), is a response of fine-scaled reactive, rather than predictive, avoidance. Searle et al. (2021) also found that leopards reactively avoid lions. This allowed leopards to remain in areas of favourable prey densities but still minimise risk encounters with lions. Carnivore species that rely heavily on scavenging opportunities as a major resource also show indications of reactive avoidance towards dominant competitors (Allen et al. 2015, Prugh and Sivy 2020). For example, black-backed jackals would benefit from occupying similar areas to larger predators such as lions and spotted hyaenas, possibly providing carrion from large ungulates to scavenge (Hunter et al. 2006, Fourie et al. 2015).

1.3 Camera trapping and how it is useful in carnivore research

A method of studying various aspects of carnivore ecology that has seen growing popularity in the last few decades is the use of camera traps (Swanson et al. 2015). These are remotely triggered cameras placed strategically or in uniform grids of a predetermined size that use infrared or motion sensors to photo-capture animals (Swanson et al. 2015, Caravaggi et al. 2017).

Camera traps allow researchers to study species non-invasively over a long, continuous period (Swanson et al. 2015, Caravaggi et al. 2017). In addition, it enables the possibility of studying elusive species that are rarely observed, thus producing novel research and insights that were otherwise impossible to obtain (Carbone et al. 2001, Caravaggi et al. 2017). Camera trap studies for mammal research are usually large-scaled, span entire landscapes and incorporate many camera stations, thus producing large amounts of data (Caravaggi et al. 2017, Karanth et al. 2017). Therefore, camera trap surveys are appropriate methods of gathering data on the activity periods and spatial uses of carnivores, especially since carnivores are generally elusive, often nocturnal and occur at low densities with large spatial requirements (Burton et al. 2015, Karanth et al. 2017). Camera trap surveys are also ideal for studying carnivore communities as information from multiple species can be gathered on a single dataset (Monterroso et al. 2014b, Swanson et al. 2015).

1.4 Research aims, hypotheses, and predictions

This thesis aims to examine the potential for interspecific avoidance behaviour within South African carnivore communities over two niche axes, i.e., spatial and temporal dimensions, by using standardised methodologies and data collection procedures in four protected areas. Examining multiple carnivore communities from environmentally diverse regions will allow

for a better understanding of the many different species' behaviours. This thesis aims to answer the following questions: 1) Do subordinate carnivore species use space within South African protected areas that will minimise the potential for encounters with more dominant species? 2) If these subordinate carnivore species use similar areas than dominant species, do they then rely on temporal avoidance behaviour to avoid the more dominant species?

Relative body size is an important factor driving antagonistic interactions between carnivores, with aggression and intraguild killings reportedly more common among carnivore species with intermediate differences in relative body size (Donadio and Buskirk 2006, Curveira-Santos et al. 2022). Large differences in body size rarely result in attacks by the larger species (Donadio and Buskirk 2006). Therefore, small carnivores (e.g., genets and African wildcats) may not need to avoid large predators such as lions and hyaenas on a large scale but will more likely rely on reactive avoidance (Herbst 2009). It is hypothesised that indications of avoidance behaviour will generally follow the same trends in this study. It is predicted that avoidance behaviour will be more pronounced between species with intermediate than large differences in body size. However, due to their opportunistic predatory behaviour, hypercarnivorous felids such as lions, leopards, and caracals are responsible for most intraguild killings (Donadio and Buskirk 2006, Curveira-Santos et al. 2022). It is thus further hypothesised that subordinate carnivore species will more likely avoid these hypercarnivorous felids than the other species, which could potentially be a risk for their survival. Leopards have been observed killing carnivore species as small as genets (Curveira-Santos et al. 2022). From this, it is predicted that subordinate carnivore species of all body sizes will show signs of avoiding leopards. Interspecific antagonism and killing are not limited to large carnivores, but are also observed among mesopredators. For example, black-backed jackals have been shown to kill smaller carnivore species such as bat-eared foxes, Cape foxes, and black-footed cats in territorial

defence (Kamler et al. 2012, Kamler et al. 2015). Avoidance behaviour is, therefore, predicted to also manifest among the smaller carnivore species.

Due to South Africa's higher latitudes, pronounced seasonal variation in environmental characteristics are experienced (Daan and Aschoff 1975). These differences range from unimodal rainfall seasons that result in clear seasonal differences in vegetation quality (i.e., wet and dry seasons), to marked differences in temperature ranges between seasons (i.e., hot and cold seasons), and changes in the availability of resources that could affect the behaviour of carnivores. For example, diet overlap between bat-eared foxes and aardwolves is likely to occur only during the colder months of the year, when aardwolves shift a considerable portion of their diet to *Hodotermes* termites due to less availability of the preferred *Trinervitermes* termites (Williams et al. 1997, Kamler et al. 2013). As a result, the two species may experience potential for competition during the winter. Furthermore, Périquet et al. (2021) showed that there is a greater possibility of facilitation between lions and spotted hyaenas during the wet seasons when encounters between the two species are mainly centred around carcasses. However, interference competition dominates interactions between the two species during the dry seasons when carcasses are more readily available, and thus the need for scavenging lion kills is reduced. The authors also showed that interactions between lions and spotted hyaenas occurred primarily at or near waterholes during the dry seasons, where spotted hyaenas appeared to be dominant. This could be due to increased prey availability near waterholes during the dry season when prey species congregate around waterholes, and there is an increased likelihood of spotted hyaenas actively hunting prey during the dry season (Périquet et al. 2021). In addition, Kamler et al. (2017) showed that bat-eared foxes have significantly larger group sizes during the dry seasons in Benfontein Game Reserve in the Northern Cape, South Africa. This was proposed as a possible response of bat-eared foxes to increased temporal overlap with black-backed jackals in the reserve during the dry season (Kamler et al.

2017). Ultimately, it is hypothesised in this study that indications of interspecific avoidance behaviours among carnivores will vary with the different climatic seasons and to different degrees depending on the temporal scale considered.

The vegetation structure of an area also influences the risk avoidance behaviour of mammals (Lima and Dill 1990). Thicker vegetation may provide better concealment and protective cover for species that attempt to avoid detection by larger, more dominant species (Lima and Dill 1990, Potash et al. 2019). However, thicker vegetation also provides better cover for ambush predators, such as lions, which may increase fear in subordinate carnivores (Davies et al. 2016). However, it may also impair the detection of prey and cooperative hunting behaviour of the lions (Loarie et al. 2013). Thicker vegetation may also obstruct the sightlines of carnivores. Less dense open vegetation provides subordinate carnivores with a better view of their surroundings, and, as a result, they can more easily detect and respond earlier to the threat posed by dominant carnivores (Camp et al. 2013). In contrast, predators can more easily detect subordinate carnivores in less dense open vegetation from whence antagonistic interactions may arise. If regular detection of risk-associated species is impaired by thicker vegetation, then subordinate carnivores may rather rely on temporal avoidance behaviour. It is, therefore, predicted that temporal interspecific avoidance behaviour among carnivores will be more evident than spatial avoidance behaviour in protected areas with denser vegetation. Furthermore, since detection is easier in open environments through improved sightlines, it is predicted that spatial interspecific avoidance behaviour among carnivores will be more evident in more open environments with less dense vegetation.

Most of Southern Africa's carnivore species are nocturnal (i.e., most active between dusk and dawn; Satterfield 2014, de Satgé et al. 2017, Comley et al. 2020b, Greco et al. 2021, Webster et al. 2021, Vissia and van Langevelde 2022). Therefore, it is predicted that interspecific temporal avoidance behaviour among the carnivores in this study will more likely manifest as

finer-scaled asynchronization of their core activity periods than complete avoidance throughout the 24-hour diel period (Vissia and van Langevelde 2022).

1.5 Short methodological review of recent studies that examined avoidance behaviour among African carnivores

Recently, an increasing number of studies from a vast array of ecosystems worldwide have investigated interspecific temporal and spatial use of sympatric carnivores in relation to available resources, competition and predation avoidance. However, these studies differ greatly in data collection methods, analysis techniques, and the associated parameters used to determine the degree of interspecific spatial and temporal overlap. In addition, studies vary in the number of potentially important factors assessed that may dictate or alter the degree of temporal and spatial overlap among carnivore species, such as predator-prey relationships, seasonal and climatic differences, and habitat characteristics.

For this study, the data collection and analytical methods used in 54 published articles that examined the temporal and/or spatial overlap among African carnivore species were reviewed (Table 1.1). These articles were sourced by using relevant combinations of key words such as “avoidance”, “behaviour”, “overlap”, “spatial”, “temporal”, “activity”, “South Africa”, “Africa”, “carnivores”, and “interspecific” in the Google Scholar search engine and the University of Pretoria’s online library. To maintain relevancy and include current methods of analysing carnivore coexistence, only studies published within the 21st century were examined. These studies were all conducted in Africa and used either activity patterns, spatial use or both temporal and spatial behaviour to describe interspecific relationships and coexistence among terrestrial, mammalian carnivores. Most (32 out of 54) of these studies used camera trap surveys as the data collection method (Table 1.1). The other studies made use of VHF radio or

GPS collars (19 out of 54) to track the movement of individuals, with only Balme et al. (2017b), Cristescu et al. (2013), and Strampelli et al. (2022) using alternative methods of data collection that entailed field observations by employed guides within the protected area, direct observations by the researchers, and data collected from animal tracks, respectively.

Table 1.1. All relevant published studies that were reviewed in this thesis. These studies entail the comparison of temporal and spatial use of carnivore species in Africa.

Method of data collection		
Camera trap surveys	GPS or radio-collars	Other
Allen et al. 2018	Broekhuis et al. 2013	Balme et al. 2017b
Balme et al. 2019	Comley et al. 2020a	Cristescu et al. 2013
Bashant et al. 2020	Cozzi et al. 2012	Strampelli et al. 2022
Comley et al. 2020b	Darnell et al. 2014	
Cronk and Pillay 2020	Davies et al. 2021	
Cusack et al. 2017	Dröge et al. 2017	
Davis et al. 2021	Goodheart et al. 2022	
de Satgé et al. 2017	Hayward and Hayward 2006	
Easter et al. 2020	Hayward and Slotow 2009	
Edwards et al. 2015	Kamler et al. 2012	
Evers et al. 2022	Kamler et al. 2015	
Greco et al. 2021	Kamler et al. 2020b	
Havmøller et al. 2020	Loveridge and MacDonald 2003	
Kheswa et al. 2018	Maputla et al. 2015	
Miller et al. 2018	Périquet et al. 2021	
Mills et al. 2019	Rafiq et al. 2020b	
Mugerwa et al. 2017	Saleni et al. 2007	
Muller et al. 2022	Swanson et al. 2014	
Mwampeta et al. 2020	Vanak et al. 2013	

Paúl et al. 2020
Ramesh et al. 2017
Rich et al. 2017
Schuette et al. 2013
Searle et al. 2021
Sogbohossou et al. 2018
Swanson et al. 2016
Tambling et al. 2015
Van der Hoek et al. 2022
Verschueren et al. 2021
Vissia and Van Langevelde 2022
Vissia et al. 2021
Webster et al. 2021

Apart from Sogbohossou et al. (2018) and Paúl et al. (2020), which were conducted in West Africa, and Van der Hoek et al. (2022) from central Africa, all the studies reviewed stem from Southern and East Africa. The reviewed studies, therefore, encompass various environments and ecosystems and covers a considerable latitudinal and longitudinal range. This includes, for example, arid and semi-arid areas such as the Namib desert and Nama Karoo, where the average annual rainfall can be as low as 80 mm (Edwards et al. 2015), the Succulent Karoo of Namaqualand (de Satgé et al. 2017), the tropical forests of Uganda (Mills et al. 2019), urban environments (Cronk and Pillay 2020), and the thicket biome present in Addo Elephant National Park (Hayward and Hayward 2006, Tambling et al. 2015). However, most of the studies were conducted in savanna and woodland ecosystems.

Most of the studies (33 out of the 54) only compared spatial and/or temporal use of sympatric large carnivores such as lions, spotted hyaenas, brown hyaenas cheetahs, leopards and African

wild dogs. Out of the 32 studies that utilised camera trapping surveys (Table 1.2), 18 included small to medium sized carnivores such as black-backed jackals, African wildcats, slender mongooses (*Herpestes sanguineus*), bat-eared foxes, and African civets (*Civettictis civetta*). There were only 10 studies out of the 54 reviewed that solely compared temporal and/or spatial use of small to medium sized carnivores and thus did not include any large carnivores (Loveridge and MacDonald 2003, Kamler et al. 2012, Kamler et al. 2015, de Satgé et al. 2017, Mills et al. 2019, Cronk and Pillay 2020, Easter et al. 2020, Mwampeta et al. 2020, Paúl et al. 2020, Webster et al. 2021).

The studies that used camera trapping surveys vary greatly in the methods used to analyse the spatial and temporal overlap of carnivore species and the number of influential variables assessed (Table 1.2). Temporal activity was compared using kernel density functions and coefficient of overlap (Δ), simple relative percentages at time intervals using a number of different statistical tests (Saleni et al. 2007, Dröge et al. 2017, Mugerwa et al. 2017), linear mixed-effect models of mean activity periods (Rafiq et al. 2020b), examining detection probability at a temporal scale (Schuette et al. 2013), circular statistical testing of discrete transformed time data (Cristescu et al. 2013) and a number of other statistical methods. However, the majority of studies that utilised camera trapping surveys applied nonparametric kernel density estimation, followed by comparing daily activity periods using the coefficient of overlap (Δ) developed by Ridout and Linkie (2009). This involves converting the time-of-activity, recorded on each photo-capture, to circular radians followed by calculating kernel density estimates and finally determining the coefficient of overlap (Δ) between a specific species pair. The coefficient of overlap ranges from 0 to 1, where 0 means that the activity periods of the species-pair show no overlap, and 1 indicates total overlap of activity periods (Ridout and Linkie 2009).

Table 1.2. Published articles reviewed for this thesis that used camera trap surveys to examine interspecific avoidance behaviour of African carnivores related to spatial and temporal use.

Article	Region	Variables included			Analyses (S or T) ^a	Only large carnivores?
		Prey	Season	Habitat		
Allen et al. 2018	Serengeti NP ^b		✓	✓	S+T	No
Balme et al. 2019	Sabi Sand GR ^c	✓		✓	S+T	Yes
Bashant et al. 2020	Waterberg, SA ^d	✓		✓	S	Yes
Comley et al. 2020b	Limpopo, SA ^d	✓	✓	✓	S+T	No
Cronk and Pillay 2020	Johannesburg, SA ^d		✓	✓	S+T	No
Cusack et al. 2017	Tanzania	✓	✓		S+T	Yes
Davis et al. 2021	Malawi	✓		✓	S+T	Yes
de Satgé et al. 2017	Namaqualand				S+T	No
Easter et al. 2020	Mozambique		✓	✓	S+T	No

Edwards et al. 2015	Namibia			✓	S+T	No
Evers et al. 2022	Madikwe GR ^c , SA ^d			✓	S+T	Yes
Greco et al. 2021	Limpopo, SA ^d		✓		T	No
Havmøller et al. 2020	Tanzania	✓			T	Yes
Kheswa et al. 2018	iSimangaliso WP ^e			✓	S	No
Miller et al. 2018	KZN ^f , Limpopo	✓		✓	S+T	Yes
Mills et al. 2019	Uganda		✓	✓	S+T	No
Mugerwa et al. 2017	Zimbabwe	✓			T	Yes
Müller et al. 2022	Western Cape, SA ^d	✓	✓	✓	S+T	No
Mwampeta et al. 2020	Serengeti NP ^b		✓	✓	S+T	No
Paúl et al. 2020	Senegal				S+T	No
Ramesh et al. 2017	Maputaland			✓	S+T	No
Rich et al. 2017	N Botswana	✓	✓	✓	S	No

Schuette et al. 2013	Kenya			✓	S+T	No
Searle et al. 2021	Tanzania			✓	S+T	Yes
Sogbohossou et al. 2018	Benin				S+T	Yes
Swanson et al. 2016	Serengeti NP ^b	✓		✓	S+T	Yes
Tambling et al. 2015	Addo Elephant NP ^b	✓	✓		T	Yes
Van der Hoek et al. 2022	DRC ^g	✓			T	No
Verschueren et al. 2021	Namibia		✓		S+T	Yes
Vissia and Van Langevelde 2022	Botswana		✓	✓	S+T	No
Vissia et al. 2021	Botswana	✓		✓	S+T	Yes
Webster et al. 2021	Highveld, SA ^d			✓	T	No

^aS = Spatial analysis, T = Temporal analysis, S+T = Both spatial and temporal analyses performed; ^bNP = National Park; ^cGR = Game Reserve;

^dSA = South Africa; ^eWP = Wetland Park; ^fKZN = KwaZulu-Natal; ^gDRC = Democratic Republic of the Congo.

Analyses and statistical methods used to describe spatial overlap between species-pairs also differed among the reviewed studies. Methods ranged from Pianka's overlap index (Sogbohossou et al. 2018, Cronk and Pillay 2020, Vissia and Van Langevelde 2022) to comparing relative abundances at each site using Spearman's rank correlation (Edwards et al. 2015), and examining relative intensity of use for each site by comparing distributions using utilisation distribution overlap indices (Dröge et al. 2017, Kamler et al. 2020b). Furthermore, hurdle models have also been used to compare spatial avoidance (Swanson et al. 2016). However, a large majority of the reviewed studies used occupancy modelling and detection probabilities to compare overlap in spatial use.

Spatiotemporal analysis involves both spatial and temporal activity of co-occurring carnivore species. This entails the comparison of the temporal period between detections of a carnivore species (reference species) and the closest subsequent or previous detection of the competing species (proximal species) at sites where spatial coexistence is confirmed (Cusack et al. 2017, Karanth et al. 2017). Results from these time-to-event analyses reveal fine-scaled temporal behaviour of competing species. Of the 54 studies examined, only eight incorporated spatiotemporal overlap of competing species using some form of time-to-event analysis (Cusack et al. 2017, Swanson et al. 2016, Balme et al. 2019, Mills et al. 2019, Paúl et al. 2020, Davis et al. 2021, Searle et al. 2021, Verscheuren et al. 2021). There is, however, variation in the methodology surrounding spatiotemporal analysis. The methodology of most studies that utilise a time-to-event analysis to determine fine-scaled spatiotemporal overlap of carnivore species stems from either Karanth et al. (2017) or Cusack et al. (2017). Karanth et al. (2017) used multi-response permutation procedures where observed time differences between reference and proximal detections are compared with bootstrapped, randomly generated time differences. Cusack et al. (2017) compared observed detection probabilities within time intervals of temporal differences between reference and proximal detections with expected,

randomly generated detection probabilities. Variation between studies that use the aforementioned methods exists among the limits of time intervals between detections. Where Cusack et al. (2017) classed proximal detections into 24-hour periods, five days before and after the reference detection, Searle et al. (2021) examined proximal detections before or after 12 hours from reference detections, classed into 1-hour intervals. Verscheuren et al. (2021) used linear mixed models of time intervals between detections to discern spatiotemporal overlap. Swanson et al. (2016) also compared the expected versus the random number of detections between reference and proximal photo-captures binned within 12-hour intervals.

1.6 Study areas

Five protected areas within South Africa were included in the study (Figure 1.1, Table 1.3): Associated Private Nature Reserves (APNR), Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR). These protected areas span a considerable latitudinal and longitudinal range, allowing for variation in climatic conditions, environmental characteristics, and ecological diversity.

All the protected areas are in summer rainfall regions. Average monthly temperatures (Figure 1.2) and rainfall (Figure 1.3) were determined between one year before the cameras were deployed until one year after the last photo-capture occurred within each protected area from nearby automatic weather stations (South African Weather Service 2016-2020). These stations were Hoedspruit Air Force Base (Coordinates: -24.3526, 31.0493) for APNR and KPNR, Madikwe Game Reserve Station (Coordinates: -24.6884, 26.1964) within MGR, Cradock-Mun (Coordinates: -32.1675, 25.6253) for MZNP, and Van Zylsrus (Coordinates: -26.8774, 22.0499) for TKR. Subsequent months that obtained as close to 95% of the annual rainfall as possible were classified as the wet season, and the remaining months as the dry season. Because

of the high seasonality of rainfall in South Africa, this resulted in seasonal classifications that are in congruence with previous literature.

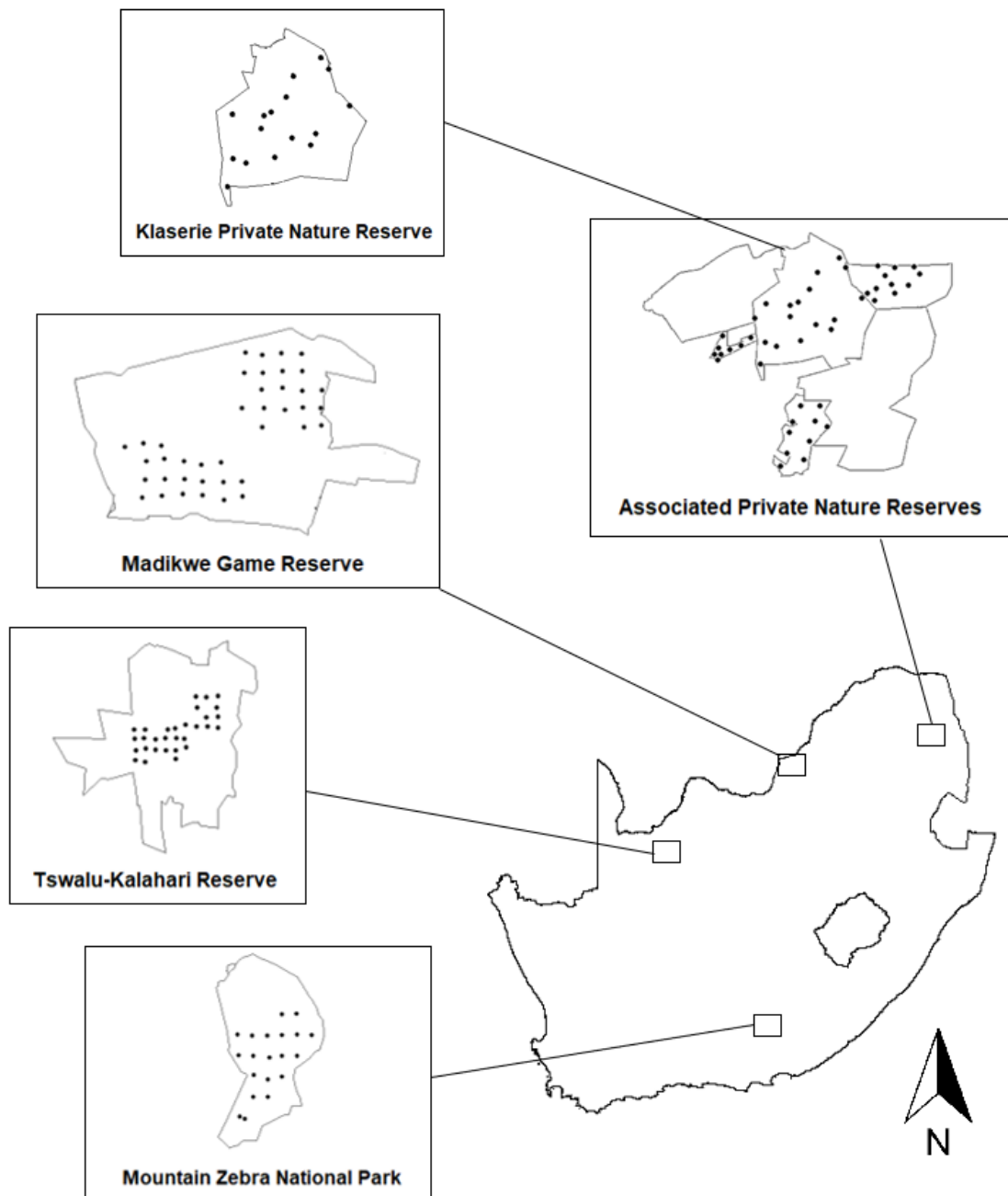


Figure 1.1. Camera trapping networks in the five protected areas included in the study. The size of each protected area is not according to relative scale. Outlines represent the borders of each protected area.

Table 1.3. Characteristics of the Snapshot Safari camera trap networks in four South African protected areas: Associated Private Nature Reserves (APNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR).

	APNR ^a	MGR	MZNP	TKR
Size	2055 km ²	750 km ²	214 km ²	1100 km ²
Fencing	Fenced border, but open to Kruger National Park along eastern border	Fenced border	Fenced border	Fenced border, separated into two fenced camps ^b
Biome	Semi-arid savanna	Semi-arid savanna	Albany thicket, Nama-Karoo, and grassland	Arid Kalahari savanna
Rainfall seasons	Summer	Summer	Summer	Summer
Wet seasons	Oct – Apr	Oct – Apr	Oct – May	Oct – Apr
Dry seasons	May – Sep	May – Sep	Jun – Sep	May – Sep
Annual rainfall	Approx. 500 mm	Approx. 500 mm	Approx. 400 mm	Approx. 360 mm
Hottest months	Dec, Jan	Nov, Dec, Jan	Jan, Feb	Dec, Jan, Feb
Coldest months	Jun, Jul	Jun, Jul	Jun, Jul, Aug	Jun, Jul

^aKlaserie Private Nature Reserve is encompassed within APNR.

^bKorannaberg, the main section of TKR, and Lekgaba, which supports TKR's lion population.

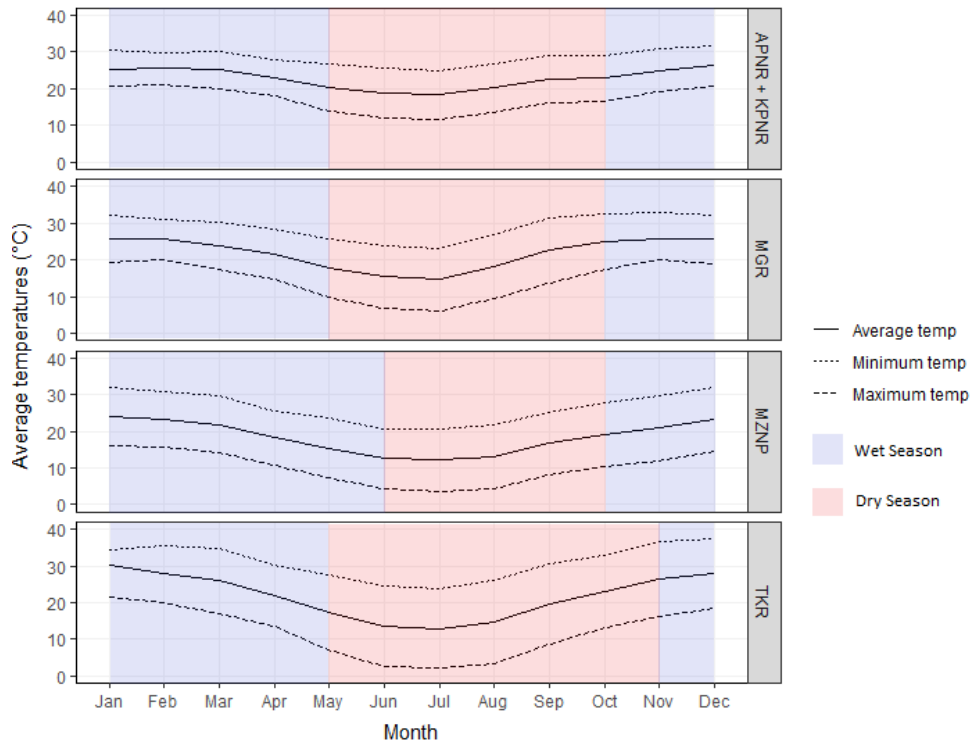


Figure 1.2. Average monthly temperatures for the four protected areas from one year before data collection commenced to one year after data collection was completed.

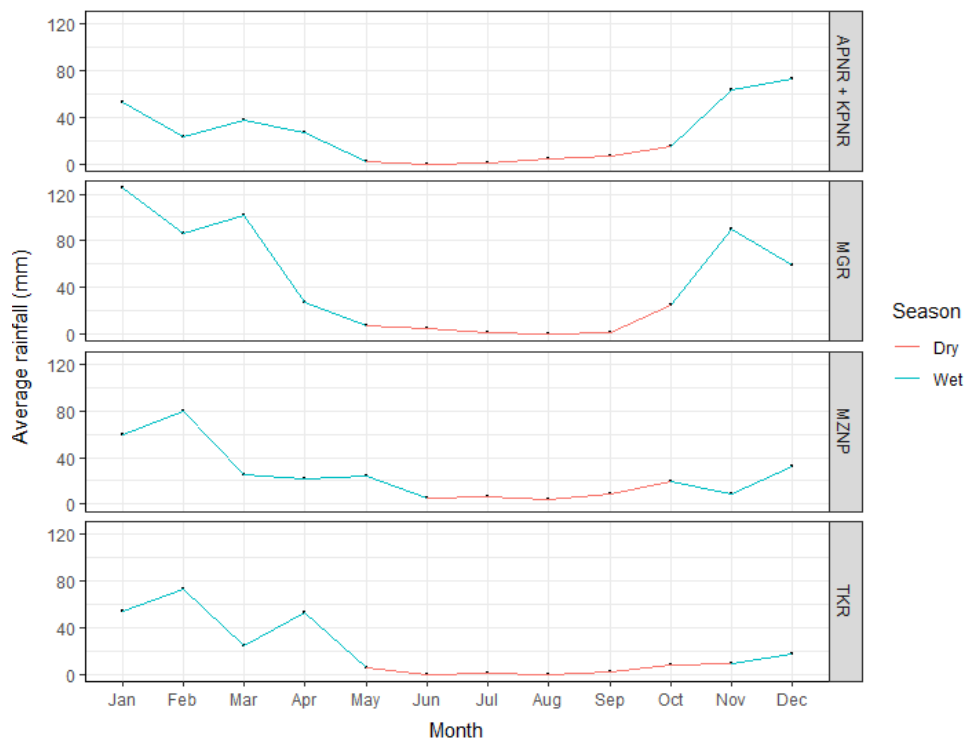


Figure 1.3. Average monthly rainfall for the four protected areas from one year before data collection commenced to one year after data collection was completed.

APNR and MAD are characterised by more dense vegetation compared to MZNP and TKR (Figure 1.4).

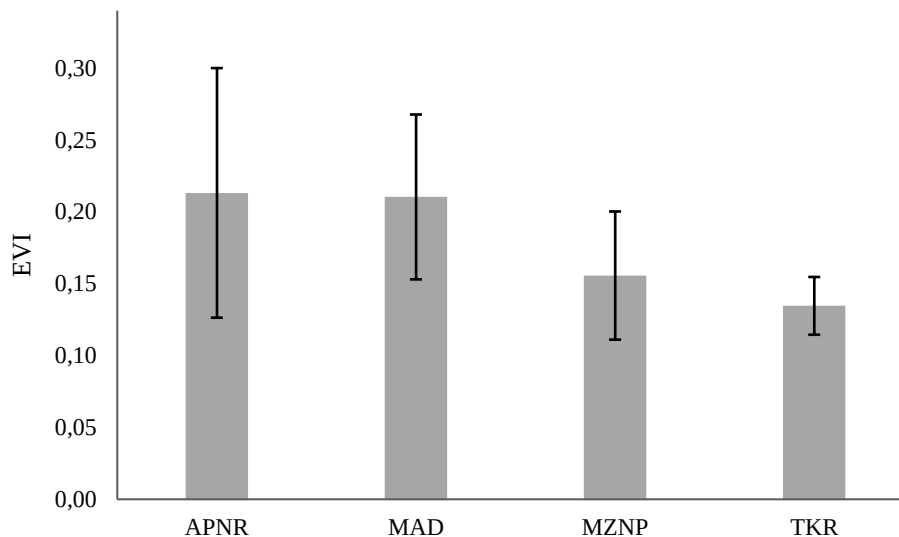


Figure 1.4. Average Enhanced Vegetation Index (EVI) and its standard deviation during the survey period within the four protected areas included in the study.

1.6.1 Klaserie Private Nature Reserve and the Associated Private Nature Reserves

The Associated Private Nature Reserves (APNR) is a conglomerate of private nature reserves in the Limpopo and Mpumalanga provinces that share an unfenced border on the western side of Kruger National Park and forms part of the Greater Kruger system. Fences have also been removed within the APNR, creating a large open ecological system that allows wildlife to freely move between the protected areas.

Seasonality within APNR is characterised by unimodal wet and dry seasons where temperatures are high during wet seasons and low during dry seasons. Wet and warm seasons typically range from October to March, and dry and colder seasons from April to September. Wet season temperatures within APNR range from an average minimum of around 21 °C to an

average maximum of approximately 33 °C. During the dry seasons, average temperatures generally range from a minimum of 11 °C to a maximum of 28 °C (Ryan et al. 2006, Turner 2007). APNR is situated within the savanna biome of the Lowveld bioregion with vegetation classifications mainly consisting of woodland and shrubveld of the Granite Lowveld, Phalaborwa-Timbavati Mopaneveld, and Lowveld Rugged Mopaneveld (Rutherford et al. 2006, South African National Biodiversity Institute 2006-2018). APNR is largely flat, with no major change in elevation within the protected area.

Klaserie Private Nature Reserve (KPNR) is a ~600 km² unfenced private nature reserve that forms part of the Associated Private Nature Reserves in the Greater Kruger system. The reserve also consists of Granite Lowveld vegetation dominated by *Combretum* spp., *Terminalia sericea*, *Sclerocarya birrea*, *Senegalia* spp., and *Vachelia* spp., with Mopane bushveld of the Phalaborwa-Timbavati Mopaneveld and Lowveld Rugged Mopaneveld dominated by *Colophospermum mopane* to the north and northeast of the reserve (Figure 1.5; Rutherford et al. 2006). KPNR range in elevation from 278 meters above sea level (m.a.s.l.) to 514 m.a.s.l.

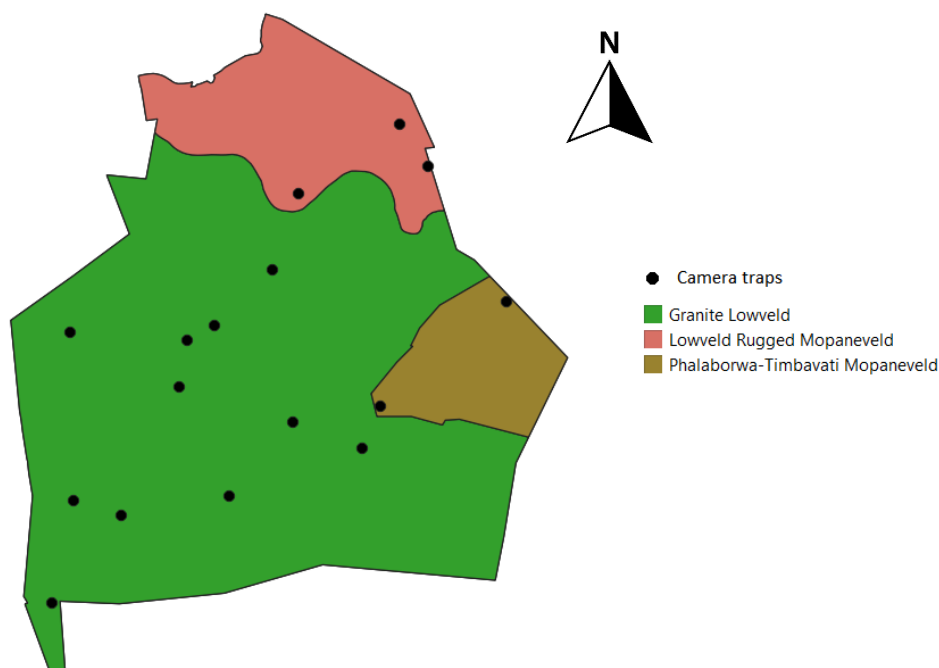


Figure 1.5. The vegetation types of Klaserie Private Nature Reserve (Rutherford et al. 2006).

1.6.2 Madikwe Game Reserve

Madikwe Game Reserve (MGR) is a ~750 km² provincial protected area situated in the semi-arid savanna of the North West province.

Seasonality within MGR is characterised by distinct wet and dry seasons that typically span from October to March and April to September, respectively (Louw et al. 2019). Temperatures during wet seasons can reach highs above 35 °C, while dry seasons experience distinctly lower averages where daily minimum temperatures can reach as low as just above 0 °C.

Being situated within the Central Bushveld bioregion, the vegetation within MGR is mainly made up of the Dwaalboom Thornveld in the lower elevations of the northern and southern sections of the reserve, Madikwe Dolomite Bushveld in the central region associated with higher elevations, and a small portion of Dwarsberg-Swartruggens Mountain Bushveld to the far south of the reserve (Figure 1.6; Rutherford et al. 2006, South African National Biodiversity Institute 2006-2018). Dwaalboom Thornveld consists of mainly microphyllous *Senegalia* and *Vachelia* spp. with only a few broad-leaved trees of mainly *Combretum* species. Madikwe Dolomite Bushveld consists of mixed bushveld mainly dominated by *Combretum apiculatum*. Grasses dominate the herbaceous layer within the reserve.

Lower elevations are found within the reserve's northern and far southern sections, with the Dwarsberg Mountain Range spanning east and west through the reserve (Figure 1.7). Elevations range between 919 m.a.s.l. to 1252 m.a.s.l.

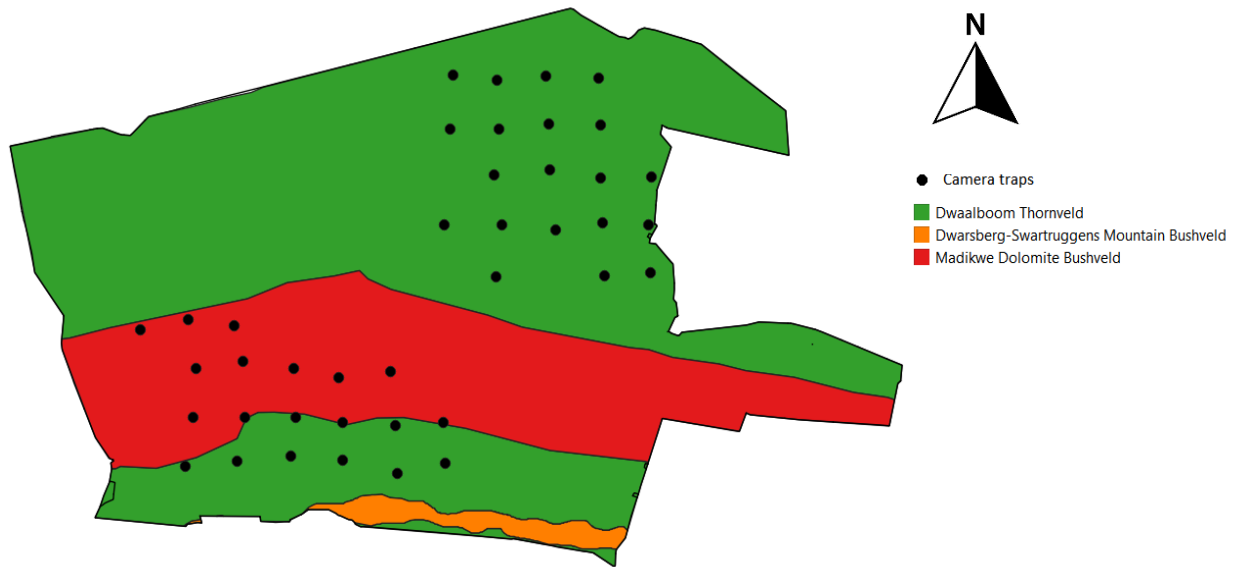


Figure 1.6. The vegetation types of Madikwe Game Reserve (Rutherford et al. 2006).

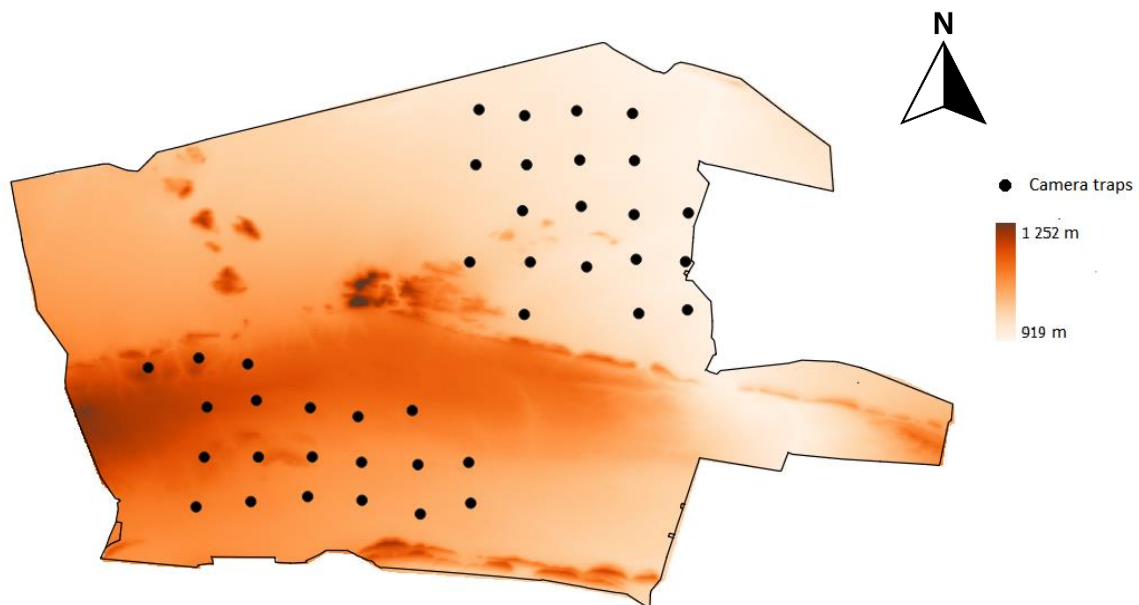


Figure 1.7. The elevational range within Madikwe Game Reserve.

1.6.3 Mountain Zebra National Park

The Mountain Zebra National Park (MZNP) is a state-owned national park of just over 214 km² situated within the Eastern Cape province.

Generally, most rainfall is recorded from December to March, with the lowest rainfall period being between May and August (Bezuidenhout and Brown 2021). Summer temperatures average from a minimum of approximately 6 °C to a maximum between 23 °C and 30 °C. During the winter months, temperatures range from an average minimum of 4 °C to a maximum of between 17 °C to 24 °C, approximately (Brown and Bezuidenhout 2000, Bezuidenhout and Brown 2021).

Three biomes can be found within MZNP: Albany Thicket, Nama-Karoo, and Grassland. MZNP's vegetation types are described as Karoo Escarpment Grassland, mainly in the southern region of the park; Escarpment Arid Thicket, which occurs in a narrow region through the park; and Eastern Upper Karoo, which is mainly found within the northern section (Figure 1.8; Rutherford et al. 2006, South African National Biodiversity Institute 2006-2018). Therefore, MZNP mainly consists of open shrubland and grassland, with a minority of semi-open to closed thicket vegetation.

MZNP has a wide range of elevations, with steep to moderately steep mountain ranges dominating the park's southern half and lower lying areas characterizing the park's northern section (Figure 1.9). Elevations within the park range between 991 m.a.s.l. to 1960 m.a.s.l.

Most of the natural mammalian fauna has been reintroduced within the park since its proclamation in 1937 (Parker 2021). Naturally occurring large predators, i.e., cheetahs, brown hyaenas, and lions, were only reintroduced in 2008, 2007, and 2013 respectively (Parker 2021). There are, however, no reliable records of leopards within MZNP.

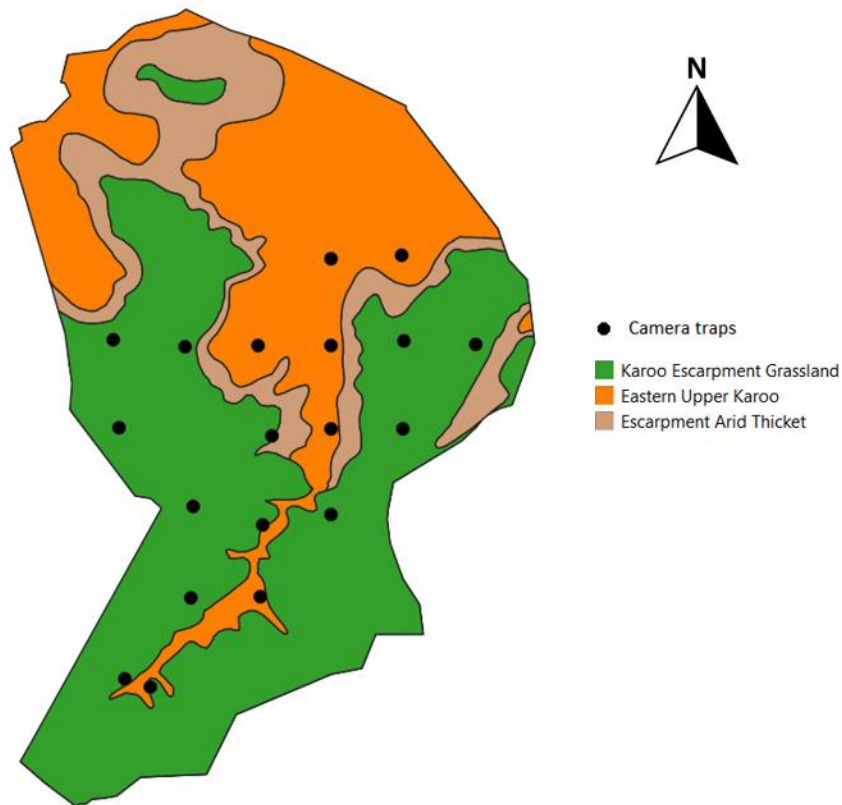


Figure 1.8. The vegetation types of Mountain Zebra National Park (Rutherford et al. 2006).

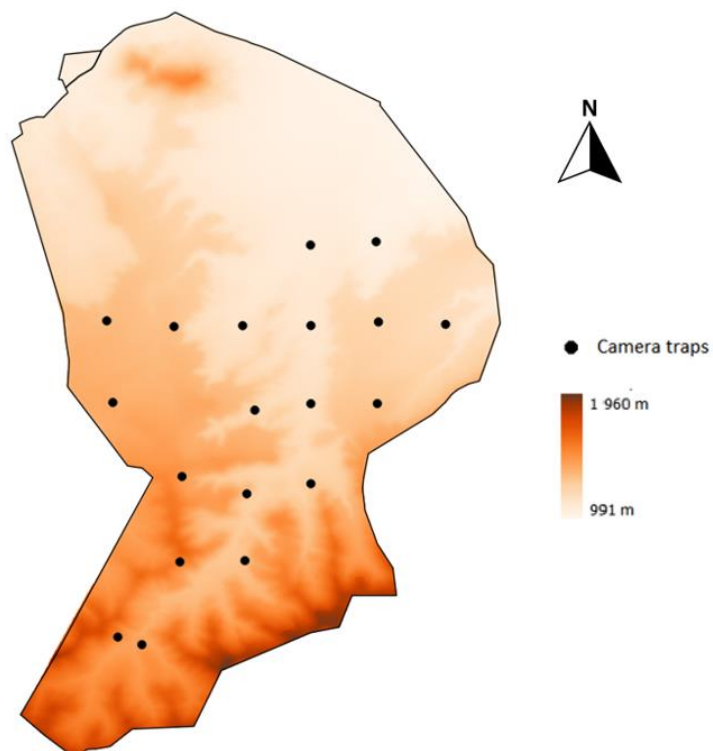


Figure 1.9. The elevational range within Mountain Zebra National Park.

1.6.4 Tswalu Kalahari Reserve

Tswalu Kalahari Reserve (TKR) is a ~1100 km² privately owned fenced game reserve situated in the arid Kalahari savanna region of the Northern Cape province. The reserve is separated into 2 main fenced camps: Korannaberg, the larger section where no lions are present, and Lekgaba, which supports the lion population in TKR and is located in the north-eastern section.

TKR is situated within the summer rainfall region of South Africa, with an average annual rainfall of approximately 360 mm and a standard deviation of 170 mm (Tokura et al. 2018). Therefore, rainfall during the summer months can vary considerably between seasons. The wet season in TKR typically runs from October to April, and the dry season from May to September (Dippenaar-Schoeman et al. 2018). Temperatures also vary considerably among seasons, with an annual average temperature of around 17 °C. However, temperatures can vary from a minimum of below 0 °C during the coldest period of the year to a maximum of over 40 °C during the warmest (Lowney et al. 2020). Similarly, temperatures can vary significantly between midnight and midday within TKR (Lowney et al. 2020).

The vegetation in TKR is categorised into five separate types, namely Gordonia Duneveld, Gordonia Plains Shrubland, Kathu bushveld, Koranna-Langeberg Mountain Bushveld, and Olifantshoek Plains Thornveld (Figure 1.10; Rutherford et al. 2006, South African National Biodiversity Institute 2006-2018). TKR, therefore, consists of open shrubland and grass ridges among parallel dunes within the centre of the Korannaberg section, and a mixture of duneless shrub and grassland with few trees, typical open arid bushveld, and rugged slopes of open grassland and shrub cover along the Korannaberg mountains in the eastern part of the reserve. The reserve ranges in elevation from 1023 m.a.s.l. to 1544 m.a.s.l. (Figure 1.11).

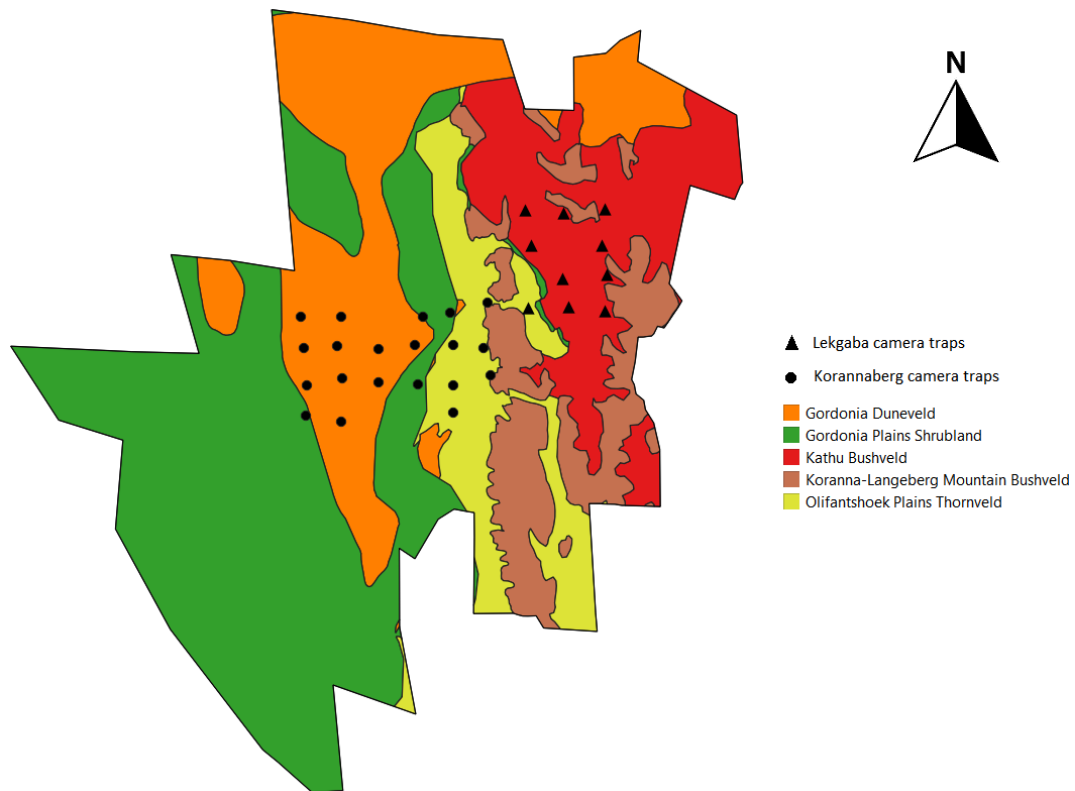


Figure 1.10. The vegetation types of Tswalu Kalahari Reserve (Rutherford et al. 2006).

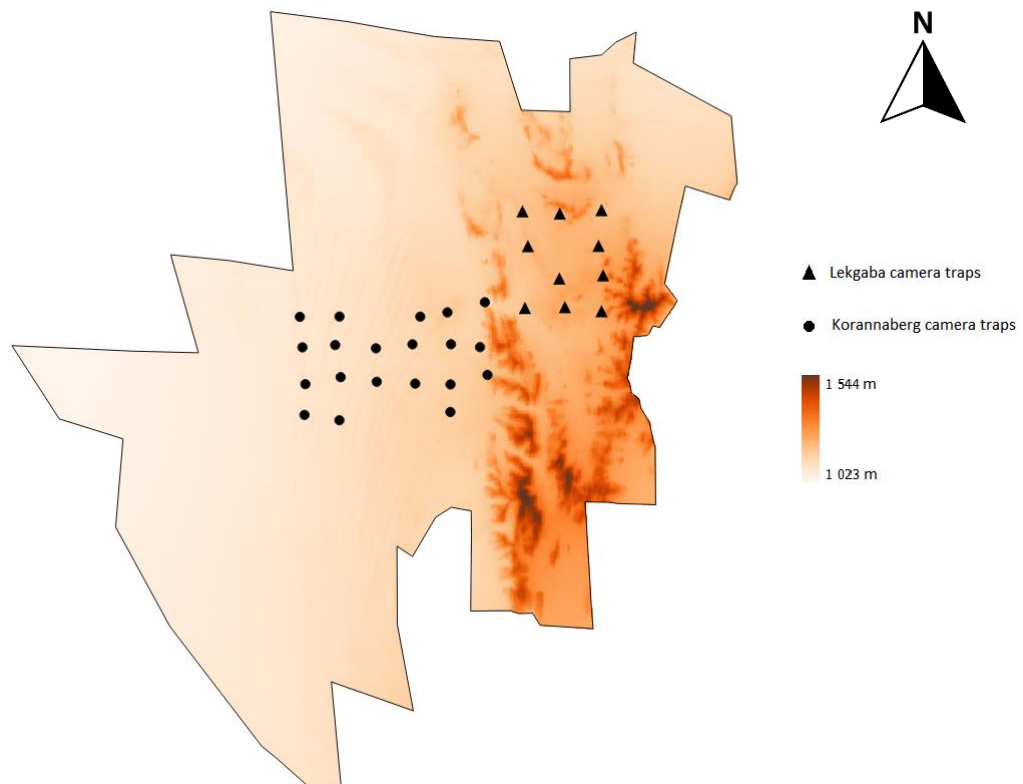


Figure 1.11. The elevational range within Tswalu Kalahari Reserve.

Within TKR, lions, leopards, and brown hyaenas can be found within the Lekgaba section, whereas brown hyaenas, cheetahs, leopards, and African wild dogs are present within the Korannaberg section.

1.7 Data collection and pre-analysis processing

Camera trap data from the five protected areas were sourced from the Snapshot Safari project (Pardo et al. 2021, Figure 1.1). Snapshot Safari comprises a large number of clustered camera trapping networks across southern and eastern Africa with the purpose of long-term monitoring and studying of the regions' mammal communities with the help of citizen science participation and the development of innovative machine learning techniques (Pardo et al. 2021). Snapshot Safari provides a large amount of data that allows for the non-invasive research of common and more cryptic mammal species. Apart from APNR and KPNR, the protected areas followed a standardised camera trapping system where cameras were placed facing game paths at the centre of a grid network of 5 km² per camera placement (Pardo et al. 2021). Camera trapping deployments ran for multiple seasons and years (Table 1.4).

Camera trap photos collected from Snapshot Safari's camera networks are processed through the Zooniverse citizen science platform (www.zooniverse.org) where the public can participate in identifying species from the photos, thereby processing the camera trap photos into a raw data form. I examined each carnivore record in the raw data by accessing links to the camera trap photos to correct misidentifications and time-stamp errors.

Unless specifically mentioned, carnivores (species of the order Carnivora) with more than 20 independent detections within a specific protected area were included in the analyses. Independent detections are defined as subsequent photo-captures of a species that are unlikely to include the same individual triggering the specific camera trap on multiple occasions.

Table 1.4. Deployment data of the Snapshot Safari camera trap networks in five South African protected areas: Associated Private Nature Reserves (APNR), Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR).

Site	Number of cameras	Camera brands	Camera flash types	Camera deployment	Camera days ^a
APNR	49	Cuddeback	Strobe - White	Jun 2017 – Oct 2019 ^b	33 000
KPNR	16	Cuddeback	Strobe - White	Jun 2017 – Oct 2019	12 350
MGR	40	Cuddeback	IR - Black	Aug 2017 – Oct 2019	15 900
MZNP	19	Cuddeback/ Scoutguard	IR - Black IR - White Strobe - White	Aug 2017 – Oct 2019	7 900
TKR	30 ^c	Cuddeback	Strobe - White	Nov 2018 – Nov 2019	9 800

^aThe number of cumulative days (24-hour cycles) that all cameras were active

^bDifferent deployment dates within each private nature reserve that is encompassed by the APNR's.

^c20 cameras in Korannaberg and 10 in Lekgaba.

Photo-captures were rendered independent by limiting the intermission length between subsequent photo-captures of the same species at a specific camera station to a minimum of 60 minutes, reducing the possibility of pseudoreplication. This time interval was validated by comparing the proportion of photo-captures removed within incremental increases in the intermission length for each included carnivore species in the respective protected areas. The intermission lengths used were 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 20, 25, 30, 40, 50, 60, 120, 240, 360, 480, 600, 720, and 1440 minutes. The average rate of slope decline for all the species in each separate protected area was then examined with the same incremental increases in the intermission length. The average rate of slope decline was considered small enough from a 30-minute intermission length and longer, whereafter, the average rate of slope decline neared zero (Figure 1.12). Therefore, an independence interval of 60-minutes was used to accommodate all species within the protected areas.

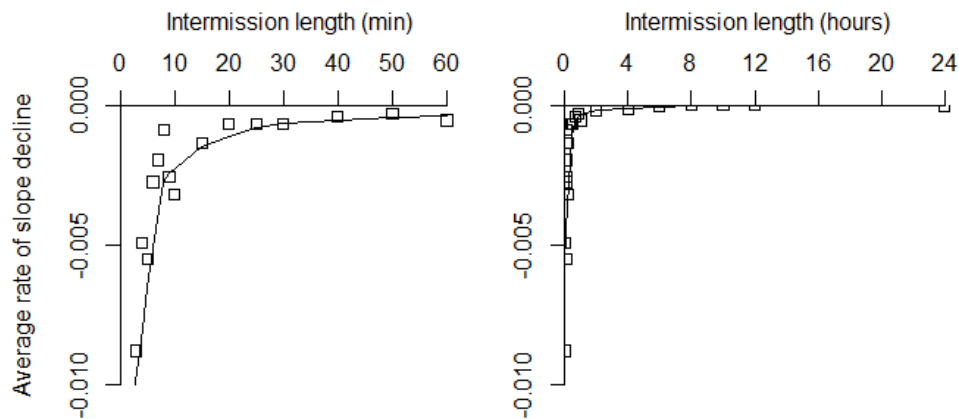


Figure 1.12. The average rate of slope decline of the proportion of photo-captures removed within incremental increases in the intermission length for carnivore species with more than 50 camera trap detections. This was performed to determine the ideal independent interval length that will reduce pseudoreplication, while minimising the number of detections removed.

CHAPTER 2

Spatial partitioning and the potential for large-scaled avoidance among South African Carnivora

2.1 Abstract

Competition between carnivores (species of the order Carnivora) is fundamental in shaping the dynamics of healthy, naturally functioning ecosystems. Behavioural adaptations in response to competitive pressure and risk facilitate coexistence within carnivore communities, which include segregation along a variety of possible axes in order to avoid threats to survival or fitness (e.g., spatial, temporal, and dietary partitioning).

Multi-seasonal camera-trapping data from four South African protected areas were used in this study to investigate the potential for interspecific avoidance behaviour among carnivores via spatial partitioning. These areas are Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNK), and Tswalu Kalahari Reserve (TKR). Analyses were performed using occupancy modelling, vegetation type preferences using Jacobs Index, and quantitative spatial overlap analysis using Pianka's index.

Only 21% of the species-pairs analysed across all combinations, and protected areas showed signs of spatial avoidance behaviour. In some cases among this minority, spatial partitioning could not be attributed to active avoidance behaviour with certainty due to a lack of biological reasoning supported by empirical evidence of competition and risk (e.g., genet-associated species-pairs), differences in vegetation type preferences (e.g., TKR's Cape foxes *Vulpes chama* in relation to brown hyaenas *Hyaena brunnea*), and wide confidence intervals (e.g.,

MZNP's bat-eared foxes *Otocyon megalotis* in relation to black-backed jackals *Lupulella mesomelas*). Indications of avoidance behaviour were observed among the medium-sized and smaller carnivore species such as bat-eared foxes and aardwolves (*Proteles cristata*), whereas avoidance was lacking among large predators (e.g., lions *Panthera leo*, leopards *Panthera pardus*, and spotted hyaenas *Crocuta crocuta*). Furthermore, TKR's bat-eared foxes appear to avoid areas used by brown hyaenas. None of the species-pairs in KPNR and MGR showed clear evidence of spatial avoidance behaviour.

The data show that spatial avoidance behaviour among African carnivores, at least on the scale conducted in this study, should be considered a rarity. Factors such as resource acquisition, intraspecific territoriality, and fine-scaled reactive avoidance are presumed to outweigh the need for large-scaled spatial partitioning to avoid the risk of rare encounters with larger, more dominant species.

Key words: behavioural ecology, carnivores, dominance, interspecific avoidance, occupancy, predation risk, spatial overlap

2.2 Introduction

Carnivores (species of the order Carnivora) are at the top of most trophic niche structures (Elmhagen et al. 2010, Estes et al. 2011, Hoeks et al. 2020). They are, therefore, vital to the health and natural functioning of ecosystems through top-down regulation in the form of lethal and sub-lethal effects on species at lower levels of the trophic structure; including other carnivores (see Kamler et al. 2013). Competition between carnivore species can exist in a variety of forms (Linnell and Strand 2000, Caro and Stoner 2003, Prugh and Sivy 2020), from interference competition which involves direct antagonistic interactions such as

kleptoparasitism, predation or territorial killings, to exploitative competition where dominant species outcompete subordinates for shared, limited prey (e.g., see Tallian et al. 2022). Subordinate carnivores' behavioural responses to competitive pressure facilitate coexistence within carnivore communities (Lima and Dill 1990, Karanth et al. 2017). This entails niche segregation along a variety of possible axes (e.g., spatial, temporal, and dietary niches). One method of partitioning is to occupy or frequent areas that are not inhabited or are used less frequently by dominant carnivore species that may pose a threat to survival or fitness upon encounter, i.e., spatial avoidance (Linnell and Strand 2000, Darnell et al. 2014, Davies et al. 2021). These landscapes of fear (see review by Gaynor et al. 2019 and its references) exist as a potential trade-off in which preferred habitat is exchanged for low-risk probability, and as a result, areas of poor resource availability may be inhabited (Mukherjee et al. 2008, Ritchie and Johnson 2009). This may lead to population suppression and severe negative demographic consequences for the subordinate or prey species (Creel and Christianson 2008, Miller et al. 2018).

An important component of efficient wildlife management efforts and conservation strategies is a better understanding of interspecific relationships within carnivore communities and the key drivers that allow carnivore species to coexist (Glen and Dickman 2005, Karanth et al. 2017). Therefore, multi-seasonal data from large-scaled camera trapping networks in four South African protected areas were analysed in this study with the aim of identifying the potential for spatial partitioning as a method used by terrestrial carnivores to facilitate interspecific coexistence. In addition, spatial-use information regarding habitat preferences is also investigated. Whole carnivore communities were considered in the analyses as this chapter of the study is mainly focussed on exploratory research.

Comparisons of potential avoidance behaviour among carnivore species from different previous studies are, in some cases, difficult due to varying methodologies. Therefore, this

study strives to ease comparisons between regions with varying environmental characteristics by using standardised data collection and analysis methods. In addition, this study strives to provide information regarding spatial avoidance behaviour of understudied carnivore species, owing to the indiscriminate data collection of camera traps.

2.3 Methods

Four protected areas across South Africa were analysed in this chapter: Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR). KPNR, instead of the entire APNR, was analysed in this chapter due to the latter's camera traps being deployed at considerably different periods within each reserve. Therefore, only camera data from KPNR were analysed in order to improve uniformity.

Unless specifically mentioned, carnivores (species of the order Carnivora) with more than 20 independent detections within a specific protected area were included in the analyses.

2.3.1 Occupancy analysis

Single-species, single-season occupancy model analyses were performed using the *unmarked* package (Fiske and Chandler 2011) in R (R Core Team 2021). Occupancy models determine the probability of occupancy (Ψ) and detection (ρ) given that imperfect detection is accounted for with variables at each site and during each survey occasion (MacKenzie et al. 2018). Due to the cryptic nature of many carnivore species and the resultant scarcity of detection data, multi-season occupancy models were not performed.

Firstly, detection histories of each carnivore species with more than 30 photo-captures at the specific protected area were created using the *camtrapR* package (Niedballa et al. 2016) in R. This involves creating a matrix of camera trap stations versus occasion events in each protected area where a “1” indicates that the species was detected and a “0” indicates that the species was not detected during the specific occasion at the specific camera trap station. Various occasion lengths were tested during the occupancy analysis process by examining model fit using the MacKenzie and Bailey Goodness-of-Fit test (MacKenzie and Bailey 2004). An occasion length of 60 days was selected based on the ability to include most carnivore species in the analysis while still providing biologically relevant information. It is acknowledged that this occasion length is unconventionally long relative to previous studies; however, due to the scarcity of detection data for many carnivore species, this length was deemed adequate. Extended occasion lengths have also been used in previous studies that looked at interspecific spatial use, which proved adequate (see Lombardi et al. 2020).

Various biotic and abiotic variables were collected as potential site covariates in the occupancy models using camera trap data and satellite imagery, respectively. Abiotic environmental variables were determined using QGIS (QGIS Development Team 2021) and consisted of mean zonal values derived from 100 m radiuses around each camera trap site. These variables included Enhanced Vegetation Index (EVI) and topographic roughness. Two-band EVI at a 30 m resolution, an indicator of vegetation density or productivity (“greenness”), was derived from Landsat 8 collection 2 level-2 products collected from the U.S. Geological Survey’s EarthExplorer (<https://earthexplorer.usgs.gov/>). EVI values range from 0 (bare ground) to 1 (dense vegetation). Topographic roughness, an indicator of elevational variation over an area, was derived from digital elevation models sourced from NASA’s Shuttle Radar Topography Mission (SRTM) at 30 m resolution (see Farr et al. 2007). The elevation of each camera trap site was also obtained from SRTM products. A sampling effort variable was also included and

comprised the number of active camera trap days at each camera trap site. Biotic variables consisted of encounter rates of specific species or combinations of species. Encounter rates were calculated using $ER = \left(\frac{E}{TD}\right) \times 100$, where E is the number of encounters of the species at the specific camera trap site, and TD is the total number of camera trap days that the specific camera trap site was active. Detailed descriptions of biotic covariates related to combined encounter rates of different species can be found in Table 2.1. Potential covariates were tested for dependence (i.e., covariates that will have similar effects) using Spearman's rank correlations in R. This was performed to prevent multicollinearity of covariates. Potential covariates that correlated by more than 80% were deemed highly correlated. As a result, only the covariate deemed most relevant to the species' spatial use was included in the analysis (Long et al. 2011).

Next, null occupancy models were examined where occupancy and detection probabilities were kept constant to determine these probabilities at a pre-covariate inclusion state. Occupancy probability (Ψ) is the proportion of all the sites that are occupied by the specific species as determined by photo-captures of the species at the specific sites, and by accounting for imperfect detection (i.e., the species is present but not photo-captured at the specific site) through inclusion of detection probabilities (ρ) at each site (MacKenzie and Nichols 2004). High null model occupancy probabilities prevented the inclusion of occupancy covariates in the final models. This is because the species occupies nearly all the camera trap sites surveyed, and therefore all the covariates will have equal effect on the occupancy probability. Lastly, final occupancy models were discerned by including a maximum number of biologically relevant covariates that produced a good model fit. Model fit was calculated using the MacKenzie-Bailey goodness-of-fit tests (MacKenzie and Bailey 2004) at 1000 simulations in the *AICcmodavg* package (Mazerolle 2020) in R. Next, 95% confidence intervals (CI's) of the beta values of each included covariate were calculated. These CI's were then used to discern

the effect direction and strength of each covariate on the occupancy and detection probabilities for each carnivore species included in the analysis. Covariate effects were deemed to be strong if the CI did not range over zero, moderate if the CI ranged over zero but with the effect still skewed towards a certain direction, and a covariate with no effect was identified by having a CI that ranged roughly equally over zero in both the negative and positive directions (Comley et al. 2020b).

Occupancy probabilities obtained in this study were viewed as spatial use rather than true occupancy (MacKenzie et al. 2004). This stems from the relaxation of a basic assumption of occupancy models: sites are closed to changes in occupancy during each occasion or survey. Detection probabilities are adopted as indications of continuous use of a specific occupied site, where more detections during separate occasions at occupied sites result in higher detection probabilities. Therefore, detection probability was viewed as a proxy for preference behaviour.

Table 2.1. Detailed descriptions of biotic covariates of combined species encounter rates included in the single-season, single species occupancy models.

Protected area	Covariate (species model)	Description	References
KPNR	Lion prey	Combined encounter rate of larger ungulate species that are considered as preferred prey species: blue wildebeest, buffalo, giraffe, and zebra.	Maruping-Mzileni et al. (2017), Owen-Smith and Mills (2008), Hayward and Kerley (2005)
	Hyaena prey	Combined encounter rate of species over a wide range of body sizes: Blue wildebeest, buffalo, common duiker, impala, kudu, steenbok, warthog, waterbuck, and zebra.	Hayward (2006), Owen-Smith and Mills (2008), Henschel and Skinner (1990)
	Leopard prey	Combined encounter rate of species that are considered as preferred prey for leopards:	Owen-Smith and Mills (2008), Hayward et al. (2006)

		bushbuck, common duiker, impala, steenbok, and warthog.	
	Hyaena competition	Combined encounter rate of competition species, i.e., leopards and African wild dogs, that have a considerable overlap in diet with spotted hyaenas.	Owen-Smith and Mills (2008), Hayward and Kerley (2008)
	Large predators (leopard)	Combined encounter rate of carnivore species from the large predator guild that are larger than leopards: lions and spotted hyaenas.	
MGR	Lion prey	Combined encounter rate of ungulate species that are considered as preferred prey species: blue wildebeest, buffalo, giraffe, impala, kudu, and zebra.	Owen-Smith and Mills (2008), Hayward and Kerley (2005)
	Leopard prey	Combined encounter rate of species that are considered as preferred prey for leopards: bushbuck, impala, klipspringer, kudu, steenbok, and warthog.	Owen-Smith and Mills (2008), Hayward et al. (2006)
	Hyaena competition	Combined encounter rate of competition species, i.e., leopards and African wild dogs, that have a considerable overlap in diet with spotted hyaenas.	Owen-Smith and Mills (2008), Hayward and Kerley (2008)
	Brown hyaena comp	Combined encounter rate of leopards and black- backed jackals that are considered as competition species, in potential scavenging opportunities and competition at kill sites.	Creel et al. (2001), Yarnell et al. (2013), Van der Merwe et al. (2009)
	Large predators (brown hyaena)	Combined encounter rates of carnivores that are larger than brown hyaenas and not included in other covariates: lions and spotted hyaenas.	
	Large predators (black-backed jackal)	Combined encounter rates of carnivores that are larger than black-backed jackals: African wild dogs, brown hyaenas, leopards, lions, and spotted hyaenas.	
MZNP	Lion prey	Combined encounter rate of larger ungulate species that are considered as preferred prey species: Buffalo, eland, and red hartebeest	Owen-Smith and Mills (2008), Hayward and Kerley (2005)

	Large predators (bat-eared fox and aardwolf)	Combined encounter rates of species from the large carnivore guild in MZNP: Cheetahs, brown hyaenas, and lions.	
TKR	Scavenging opportunity	Combined encounter rates of species from the large predator guild that could present regular scavenging or kleptoparasitic opportunities in the form of provisioned prey carcasses: Cheetahs, leopards, and lions.	Yarnell et al. (2013), Van de Ven et al. (2013), Owens and Owens (1978)
	Large predators (bat-eared foxes and African wildcats)	Combined encounter rates of species from the large carnivore guild in TKR: African wild dogs, cheetahs, brown hyaenas, leopards and lions.	
	Mesopredators	Combined encounter rates of the two main mesopredators in the reserve, caracals and black-backed jackals.	

2.3.2 Vegetation type preferences

The location of each camera trap site within each protected area was categorised into vegetation types, as identified by Rutherford et al. (2006). This was performed in QGIS using shapefile data from the South African National Biodiversity Institute's (SANBI) National Vegetation Map (South African Biodiversity Institute 2006-2018). Carnivore species that recorded 20 or more photo-captures were included. The species' encounter rates at each camera trap site were then used to calculate Jacob's Index values for vegetation type preference using the *ivlev* function in the *selectapref* package (Richardson 2020) in R. Jacob's Index values range between -1 (complete avoidance) and 1 (complete preference). To allow comparison, species detections from camera trap sites located in the two Mopaneveld vegetation types found within KPNR, Lowveld Rugged Mopaneveld and Phalaborwa-Timbavati Mopaneveld, were combined due to low separate representation among camera trap sites.

2.3.3 Spatial overlap

To quantitatively estimate spatial co-occurrence between carnivore species, Pianka's index of spatial overlap (Pianka 1973, 1974) was calculated using the species encounter rates at each camera trap site using the *spaa* package (Zhang 2016) in R. In addition, 90% bootstrapped confidence intervals were calculated at 5000 iterations using the *niche.overlap.boot* function of the *spaa* package. Species that recorded 20 or more photo-captures at the specific protected area were analysed. Pianka's index range between 0 (no spatial overlap) to 1 (complete spatial overlap). Encounter rates over the entire study period were analysed, as well as during the wet and dry seasons separately within each protected area. Furthermore, to investigate the effect of lion presence on the spatial overlap of other carnivore species, Pianka's index was calculated separately for carnivores within TKR's Korannaberg section, where lions are absent, and the Lekgaba section, where lions are present.

2.4 Results

Across all four protected areas, 12 species of the order Carnivora obtained more than 20 independent photo-captures (Table 2.2). These species range in size from the largest, lions (*Panthera leo*), to the smallest genets (*Genetta* spp.).

Table 2.2. The number of independent camera trap photo-captures (> 60 min apart) for South African carnivore species (species of the order Carnivora) within the Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR).

Site	Common name	Scientific name	Total	Wet season	Dry season
KPNR	Spotted hyaena	<i>Crocuta crocuta</i>	491	207	284

	Lion	<i>Panthera leo</i>	40	15	25
	Leopard	<i>Panthera pardus</i>	44	19	25
	African civet	<i>Civettictis civetta</i>	34	10	24
	African wild dog	<i>Lycaon pictus</i>	15	7	8
	Honey badger	<i>Mellivora capensis</i>	14	10	4
	Genet	<i>Genetta</i> spp.	13	3	10
	Side-striped jackal	<i>Lupulella adustus</i>	9	5	4
	Black-backed jackal	<i>Lupulella mesomelas</i>	5	0	5
	Caracal	<i>Caracal caracal</i>	4	2	2
	White-tailed mongoose	<i>Ichneumia albicauda</i>	2	0	2
	Banded mongoose	<i>Mungos mungo</i>	1	0	1
	Dwarf mongoose	<i>Helogale parvula</i>	1	1	0
	African wildcat	<i>Felis silvestris lybica</i>	1	0	1
	Meller's mongoose	<i>Rhynchogale melleri</i>	1	0	1
MGR	Brown hyaena	<i>Hyaena brunnea</i>	216	86	130
	Spotted hyaena	<i>Crocuta crocuta</i>	173	78	95
	Black-backed jackal	<i>Lupulella mesomelas</i>	70	24	46
	Leopard	<i>Panthera pardus</i>	44	17	27
	Lion	<i>Panthera leo</i>	36	12	24
	African wildcat	<i>Felis silvestris lybica</i>	25	7	18
	Banded mongoose	<i>Mungos mungo</i>	13	11	2
	Genet	<i>Genetta</i> spp.	10	4	6
	Slender mongoose	<i>Galerella sanguinea</i>	10	2	8
	Caracal	<i>Caracal caracal</i>	8	4	4
	African civet	<i>Civettictis civetta</i>	8	3	5
	Honey badger	<i>Mellivora capensis</i>	7	4	3
	African wild dog	<i>Lycaon pictus</i>	6	4	2
	Aardwolf	<i>Proteles cristata</i>	4	2	2
	Cheetah	<i>Acinonyx jubatus</i>	4	2	2
	Serval	<i>Leptailurus serval</i>	4	1	3
	White-tailed mongoose	<i>Ichneumia albicauda</i>	2	2	0
MZNP	Black-backed jackal	<i>Lupulella mesomelas</i>	816	456	368
	Aardwolf	<i>Proteles cristata</i>	175	119	59

	Brown hyaena	<i>Hyaena brunnea</i>	108	76	32
	Bat-eared fox	<i>Otocyon megalotis</i>	57	23	34
	Lion	<i>Panthera leo</i>	49	19	30
	Small-spotted genet	<i>Genetta genetta</i>	25	20	5
	Caracal	<i>Caracal caracal</i>	23	14	9
	Cheetah	<i>Acinonyx jubatus</i>	6	4	2
	Cape grey mongoose	<i>Herpestes pulverulentus</i>	6	4	2
	Meerkat	<i>Suricata suricatta</i>	5	5	0
	Striped polecat	<i>Ictonyx striatus</i>	4	4	0
	Yellow mongoose	<i>Cynictis penicillata</i>	3	1	2
	Water mongoose	<i>Atilax paludinosus</i>	2	2	0
	Black-footed cat	<i>Felis nigripes</i>	1	0	1
	African striped weasel	<i>Poecilogale albinucha</i>	1	0	1
TKR	Bat-eared fox	<i>Otocyon megalotis</i>	260	149	111
	Black-backed jackal	<i>Lupulella mesomelas</i>	234	134	100
	Brown hyaena	<i>Hyaena brunnea</i>	85	45	40
	Cape fox	<i>Vulpes chama</i>	44	20	24
	African wildcat	<i>Felis silvestris lybica</i>	36	19	17
	Aardwolf	<i>Proteles cristata</i>	21	12	9
	Cheetah	<i>Acinonyx jubatus</i>	16	9	7
	Meerkat	<i>Suricata suricatta</i>	13	9	4
	African wild dog	<i>Lycaon pictus</i>	12	5	7
	Caracal	<i>Caracal caracal</i>	12	9	3
	Lion	<i>Panthera leo</i>	9	5	4
	Leopard	<i>Panthera pardus</i>	6	5	1
	Yellow mongoose	<i>Cynictis penicillata</i>	4	3	1
	Genet	<i>Genetta spp.</i>	3	2	1
	Striped polecat	<i>Ictonyx striatus</i>	3	1	2

2.4.1 Occupancy analysis

2.4.1.1 Klaserie Private Nature Reserve

All carnivore species analysed in KPNR had high null model occupancy probabilities and low detection probabilities (Table 2.3). This prevented any occupancy covariates from being included in the analyses. Regarding abiotic covariates, lions and leopards (*Panthera pardus*) showed moderate positive responses to EVI values, while spotted hyaenas (*Crocuta crocuta*) and African civets (*Civettictis civetta*) displayed moderate negative relationships to EVI values. Biotic factors were more prominent in the models. Lions and spotted hyaenas displayed moderate negative effects in response to the encounter rates of preferred prey species, while leopards had a strong positive relationship with the combined encounter rate of their preferred prey species. Encounter rates of lions had a moderate negative effect on the detection probability of spotted hyaenas, while it had a moderately positive effect on the detection probability of African civets. Combined encounter rates of large predators (i.e., lions and spotted hyaenas) had a moderately positive effect on the spatial detection probability of leopards in KPNR. Carnivore species that were considered to be competition to spotted hyaenas or could provide them with kleptoparasitic opportunities (i.e., African wild dogs and leopards) had a strong positive relationship with the detection probabilities of spotted hyaenas in KPNR. All KPNR's analysed carnivore species obtained adequate fit of the final model according to the MacKenzie-Bailey goodness-of-fit test.

2.4.1.2 Madikwe Game Reserve

Lions, spotted hyaenas, and brown hyaenas (*Hyaena brunnea*) had high null model occupancy probabilities and therefore did not have any occupancy covariates included in the final model (Table 2.3). All analysed carnivore species, except for brown hyaenas, had a negative detection

response to elevational variation. In addition, EVI had little to no effect on the detection probabilities of MGR's carnivores, apart from a moderate negative response by leopards. Concerning biotic covariates, lions had a strong positive detection relationship, whereas leopards had a moderate negative relationship with the encounter rates of their respective preferred prey species. Black-backed jackals (*Lupulella mesomelas*) and both hyaena species analysed in MGR had positive spatial relationships with other large carnivores and competing species. In contrast, leopards had a negative occupancy relationship with lions and a moderate positive spatial relationship with spotted hyaenas in MGR. Final occupancy models for lions and black-backed jackals showed evidence of noticeable underdispersion according to the MacKenzie-Bailey goodness-of-fit tests. These were included in the final results as information could still be extracted from the models. All other species obtained good model fits.

2.4.1.3 Mountain Zebra National Park

MZNP's brown hyaenas did not provide any evidence of good model fit ($P < 0.05$) for all biologically relevant covariates and were therefore excluded from the occupancy analysis. Apart from aardwolves (*Proteles cristata*) that showed slight underdispersion, all species-pairs obtained good model fits according to the MacKenzie-Bailey goodness-of-fit tests. Nonetheless, brown hyaenas and black-backed jackals had high null model occupancy probabilities, whereas bat-eared foxes (*Otocyon megalotis*) had the lowest (Table 2.3). Apart from lions, all carnivore species analysed in MZNP had negative detection responses to EVI values. Black-backed jackals and bat-eared foxes had a strong negative response of detection to topographic roughness values, whereas topographic roughness negatively affected lion occupancy to a moderate degree. Regarding biotic factors, lions had a moderate positive relationship with the combined encounter rate of their preferred prey species, both in detection and occupancy. Black-backed jackals showed a moderate negative detection relationship with

lion encounter rates while having a positive relationship with brown hyaenas. Regarding MZNP's smaller carnivores, i.e., bat-eared foxes and aardwolves, combined encounter rates of large predators in the park (i.e., lions, cheetahs *Acinonyx jubatus*, and brown hyaenas) had moderate positive effects on both detection and occupancy probabilities. In contrast, bat-eared foxes displayed a moderate negative occupancy response to black-backed jackal encounter rates.

2.4.1.4 Tswalu Kalahari Reserve

African wildcats (*Felis silvestris lybica*) and Cape foxes (*Vulpes chama*) had the lowest occupancy probabilities, both for naïve occupancy and null model outputs in TKR (Table 2.3). Regarding abiotic covariates, black-backed jackals were detected more consistently at TKR's lower elevations located on the western side of the reserve. The two larger carnivore species analysed in TKR, brown hyaenas and black-backed jackals, both displayed a negative response of detection probability to EVI values, while the smaller carnivores, i.e., African wildcats, bat-eared foxes, and Cape foxes, had a positive response. This was especially noticeable for bat-eared foxes, owing to their strong positive detection relationship with EVI values. However, black-backed jackals occupied more sites with higher EVI values. Black-backed jackals displayed a strong negative response to topographic roughness. In terms of potential scavenging opportunities provided by larger carnivores, both species in TKR that are known to scavenge carcasses, brown hyaenas and black-backed jackals, had positive spatial relationships with the combined encounter rates of the aforementioned large carnivores. In addition, black-backed jackals' occupancy and detection probabilities were negatively and positively affected to a moderate extent, respectively, by brown hyaena encounter rates in the reserve. Combined encounter rates of large predators positively affected bat-eared foxes' occupancy; in contrast, it had a strong negative effect on their detection probability. In addition, TKR's bat-eared foxes displayed a positive spatial relationship with black-backed jackals.

Cape foxes had a strong positive response of detection probability to the combined encounter rates of TKR's main mesopredators, black-backed jackals and caracals (*Caracal caracal*). African wildcats displayed a moderate positive relationship with the site encounter rates of black-backed jackals and caracals, combined. In contrast, African wildcats had a moderate negative relationship to the combined encounter rates of all large predators in the reserve. All species obtained a good final model fit according to MacKenzie-Bailey goodness-of-fit tests.

Table 2.3. Single-species, single-season occupancy model result outputs (Ψ = occupancy probability, ρ = detection probability) for carnivore species (species of the order Carnivora) from four South African protected areas: Klaserie Private Nature Reserve (KPNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR). The covariate ‘Large predators’ entails combined encounter rates of more dominant species, based on body size, from the large predator guild (i.e., lions, spotted hyaenas, leopards, cheetahs, brown hyaenas, and African wild dogs) that were not included in other covariates. Detailed descriptions of covariates can be found in Table 2.1. The Naïve Occupancy refers to the proportion of sites where the species was detected at least once without accounting for imperfect detection. The Null Model represents the model with occupancy and detection probability kept constant and without any covariates included.

Species		Naïve Occupancy	Null Model (SE)		$\Psi()$	Occupancy Model		
			$\Psi(.)$	P(.)		95% CI	$\rho()$	95% CI
KPNR	Lion	0.813	0.884	0.158	.		Effort	-0.286 – 0.713
			(0.113)	(0.030)			EVI	-0.120 – 0.714
							Lion prey	-0.591 – 0.293
	Spotted hyaena	1.000	1.000	0.691	.		Effort	0.117 – 0.776
			(0.002)	(0.031)			EVI	-0.611 – 0.052
							Hyaena prey	-0.403 – 0.286
							Hyaena competition	0.055 – 0.806
							Lions	-0.666 – 0.076
	Leopard	0.938	1.000	0.148	.		Effort	-0.655 – 0.236
			(0.003)	(0.023)			EVI	-0.100 – 0.650
							Leopard prey	0.123 – 1.017
							Large predators	-0.234 – 0.539
	African civet	0.688	0.770	0.142	.		Effort	-1.677 – -0.468
			(0.139)	(0.031)			EVI	-0.920 – 0.296

MGR	Lion	0.525	0.905 (0.219)	0.101 (0.030)	.		Leopards	0.016 – 1.207
							Spotted hyaenas	-0.256 – 0.707
							Lions	-0.224 – 0.737
							Effort	-0.513 – 0.500
							Elevation	-0.707 – 0.201
							Lion prey	0.110 – 0.722
	Spotted hyaena	0.775	0.803 (0.069)	0.373 (0.031)	.		Effort	-0.026 – 0.701
							Elevation	-0.569 – 0.089
							Hyaena competition	0.012 – 0.539
							Lions	0.109 – 0.639
	Leopard	0.525	0.673 (0.118)	0.171 (0.034)		Lions Spotted hyaenas	Elevation	-0.720 – 0.252
							EVI	-1.110 – 0.147
							Leopard prey	-1.654 – 0.022
							Effort	-0.050 – 0.571
MZNP	Brown hyaena	0.900	0.915 (0.049)	0.396 (0.030)	.		Elevation	-0.223 – 0.481
							EVI	-0.253 – 0.385
							Brown hyaena comp	0.332 – 1.057
							Large predators	-0.217 – 0.459
							Effort	-0.738 – 0.301
							Elevation	-1.735 – -0.142
	Black-backed jackal	0.500	0.559 (0.092)	0.240 (0.038)		EVI Large predators	EVI	-0.532 – 0.525
							Large predators	-0.063 – 0.609
							Effort	-0.866 – 0.211
							EVI	-0.031 – 0.747
	Brown hyaena	0.579	0.601 (0.117)	0.300 (0.047)		Roughness Lion prey	Lion prey	-0.262 – 0.715
							Effort	-0.420 – 0.488
							EVI	-0.698 – 0.077
							Roughness	-1.356 – -0.472

							Lions	-0.675 – 0.085
							Brown hyaenas	-0.115 – 1.012
TKR	Bat-eared fox	0.421	0.472 (0.129)	0.221 (0.050)	Large predators	-5.332 – 10.780	Effort	-0.033 – 1.822
					Black-backed jackals	-5.261 – 2.854	Roughness	-3.511 – -0.120
							EVI	-1.098 – 0.224
	Aardwolf	0.632	0.648 (0.113)	0.377 (0.045)	Large predators	-1.788 – 7.038	Effort	-0.288 – 0.882
							EVI	-1.300 – -0.340
							Large predators	-0.074 – 0.806
	Brown hyaena	0.733	0.835 (0.102)	0.302 (0.047)	.		Effort	-0.456 – 0.521
							Roughness	-0.418 – 0.449
							EVI	-0.705 – 0.157
							Scavenging opportunity	0.058 – 0.834
	Black-backed jackal	0.733	0.736 (0.081)	0.615 (0.044)	EVI	-0.646 – 1.348	Effort	-0.925 – 0.132
					Scavenging opportunity	-0.917 – 1.407	Elevation	-1.069 – 0.040
					Brown hyaenas	-1.313 – 0.847	Roughness	-1.462 – -0.455
							EVI	-0.844 – 0.067
							Scavenging opportunity	0.077 – 1.598
							Brown hyaenas	-0.410 – 2.006
	Bat-eared fox	0.500	0.505 (0.092)	0.546 (0.055)	Large predators	-3.154 – 19.494	Effort	-0.460 – 0.560
					Black-backed jackals	-1.053 – 5.545	EVI	0.074 – 1.168
							Large predators	-1.000 – -0.008
							Black-backed jackals	0.358 – 1.563
Cape fox	0.367	0.383 (0.093)	0.419 (0.067)	Bat-eared foxes	-1.050 – 6.067	Effort	-0.864 – 1.027	
						EVI	-0.163 – 1.348	
						Mesopredators	0.581 – 3.219	
African wildcat	0.367	0.369 (0.097)	0.362 (0.067)	Mesopredators	-1.010 – 3.833	Effort	-0.930 – 0.583	
						EVI	-0.370 – 1.329	
						Mesopredators	-0.674 – 3.494	
						Large predators	-1.527 – 1.108	

2.4.2 Vegetation type preferences

2.4.2.1 Klaserie Private Nature Reserve

Apart from spotted hyaenas, all carnivore species analysed in KPNR were detected more often in the Granite Lowveld vegetation than the Mopaneveld, owing to their higher positive Jacob's Index value (Figure 2.1). Although distinction or preference was less prominent due to low Jacob's Index values, spotted hyaenas showed a slight preference for the Mopaneveld vegetation.

2.4.2.2 Madikwe Game Reserve

Apart from brown hyaenas, all carnivore species analysed in MGR had positive Jacob's Index values for the Dwaalboom Thornveld vegetation in the reserve (Figure 2.1). Brown hyaenas did not display any clear preferences for a specific vegetation type.

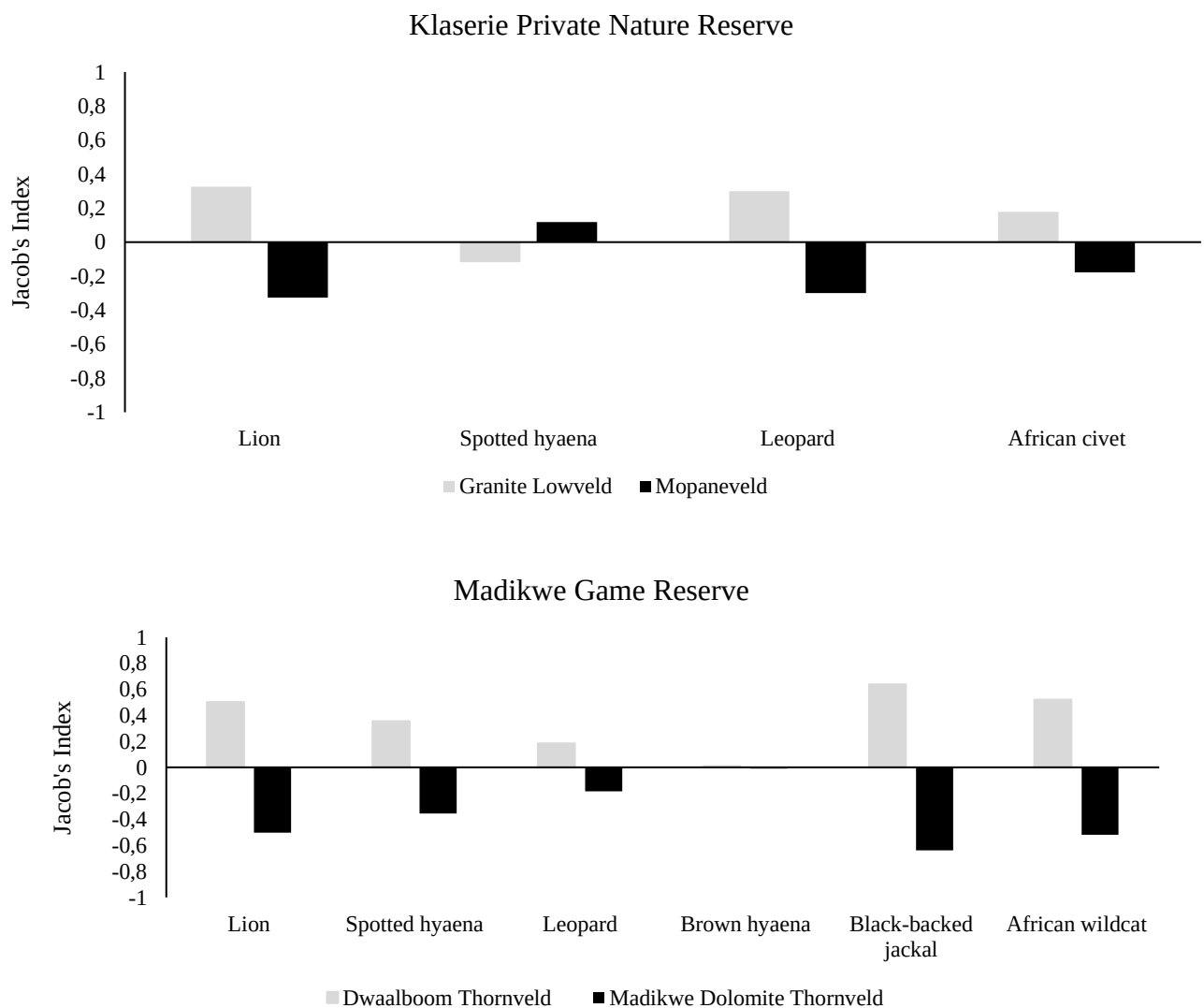
2.4.2.3 Mountain Zebra National Park

Black-backed jackals showed no clear preference for a vegetation type as they were detected equally often in both the Eastern Upper Karoo and the Karoo Escarpment Grasslands (Figure 2.1). In contrast to the other remaining carnivore species analysed in MZNP, aardwolves displayed a positive Jacob's Index relationship to the Karoo Escarpment Grassland areas.

2.4.2.4 Tswalu Kalahari Reserve

The two larger carnivore species analysed in the reserve, brown hyaenas and black-backed jackals, obtained similar Jacob's Index values over TKR's four vegetation types, with negative values most noticeably displayed for the Olifantshoek Plains Thornveld (Figure 2.1). In

contrast, bat-eared foxes and Cape foxes showed positive Jacob's Index values for the Olifantshoek Plains Thornveld vegetation, whereas aardwolves had negative index values. Aardwolves and Cape foxes had high positive Jacob's Index values for the Gordonia Duneveld region. Regarding the Kathu Bushveld vegetation, both fox species had highly negative Jacob's index values, whereas African wildcats had contrasting positive values for the Kathu Bushveld. African wildcats were never detected within the Gordonia Plains Shrubland vegetation.



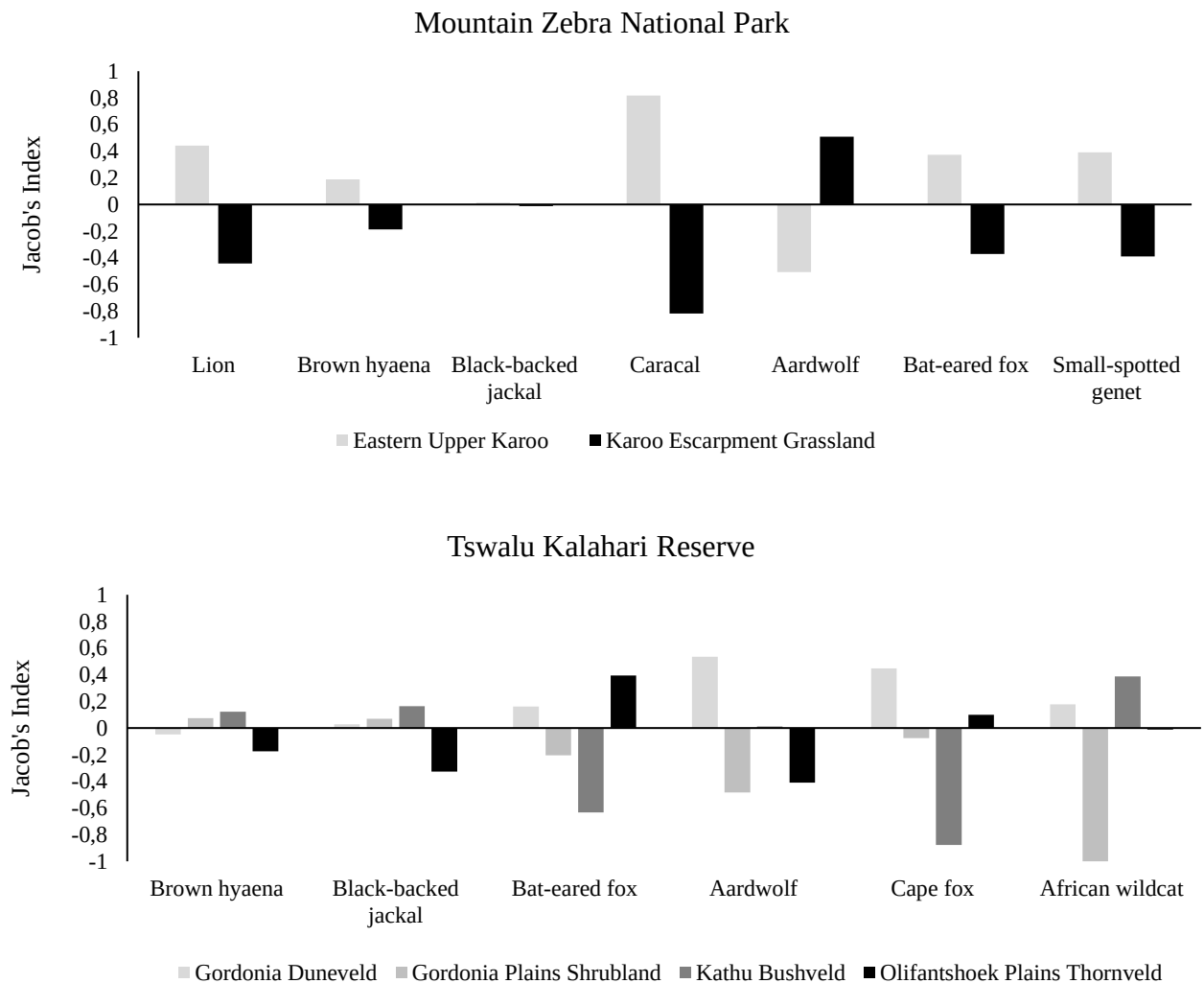


Figure 2.1. Habitat preferences of carnivores (species of order Carnivora) in four South African protected areas based on Jacob's index. Positive values indicate preference, whereas negative values indicate avoidance.

2.4.3 Spatial overlap

2.4.3.1 Klaserie Private Nature Reserve

All carnivore species-pairs in KPNR obtained relatively high spatial overlap values (Pianka's index > 0.500 , Figure 2.2). However, a spatial association was most apparent between spotted hyaenas and leopards in KPNR, owing to the narrow 95% confidence interval.

Only spotted hyaenas obtained more than 20 detections during both the wet and dry seasons; therefore, seasonal comparisons of spatial overlap between carnivore species in KPNR were not considered for analysis.

2.4.3.2 Madikwe Game Reserve

All the carnivore species-pairs in MGR had some degree of spatial association (Figure 2.2). The majority of these species-pairs (10 out of 15) had relatively high spatial overlap (Pianka's index > 0.500). The lowest spatial overlap values were associated with species-pairs that included African wildcats. While obtaining narrow confidence intervals, the highest spatial overlap was between lions and spotted hyaenas, spotted hyaenas and brown hyaenas, and spotted hyaenas and black-backed jackals.

Considering the variation in spatial overlap between wet and dry seasons in MGR (Figure 2.3), black-backed jackals had considerably more spatial overlap with both spotted hyaenas (Pianka's index = 0.674, 95% CI: 0.542 – 0.835) and brown hyaenas (Pianka's index = 0.717, 95% CI: 0.542 – 0.836) in the dry season than during the wet season (with spotted hyaenas: Pianka's index = 0.447, 95% CI: 0.190 – 0.686; with brown hyaenas: Pianka's index = 0.439, 95% CI: 0.221 – 0.720).

2.4.3.3 Mountain Zebra National Park

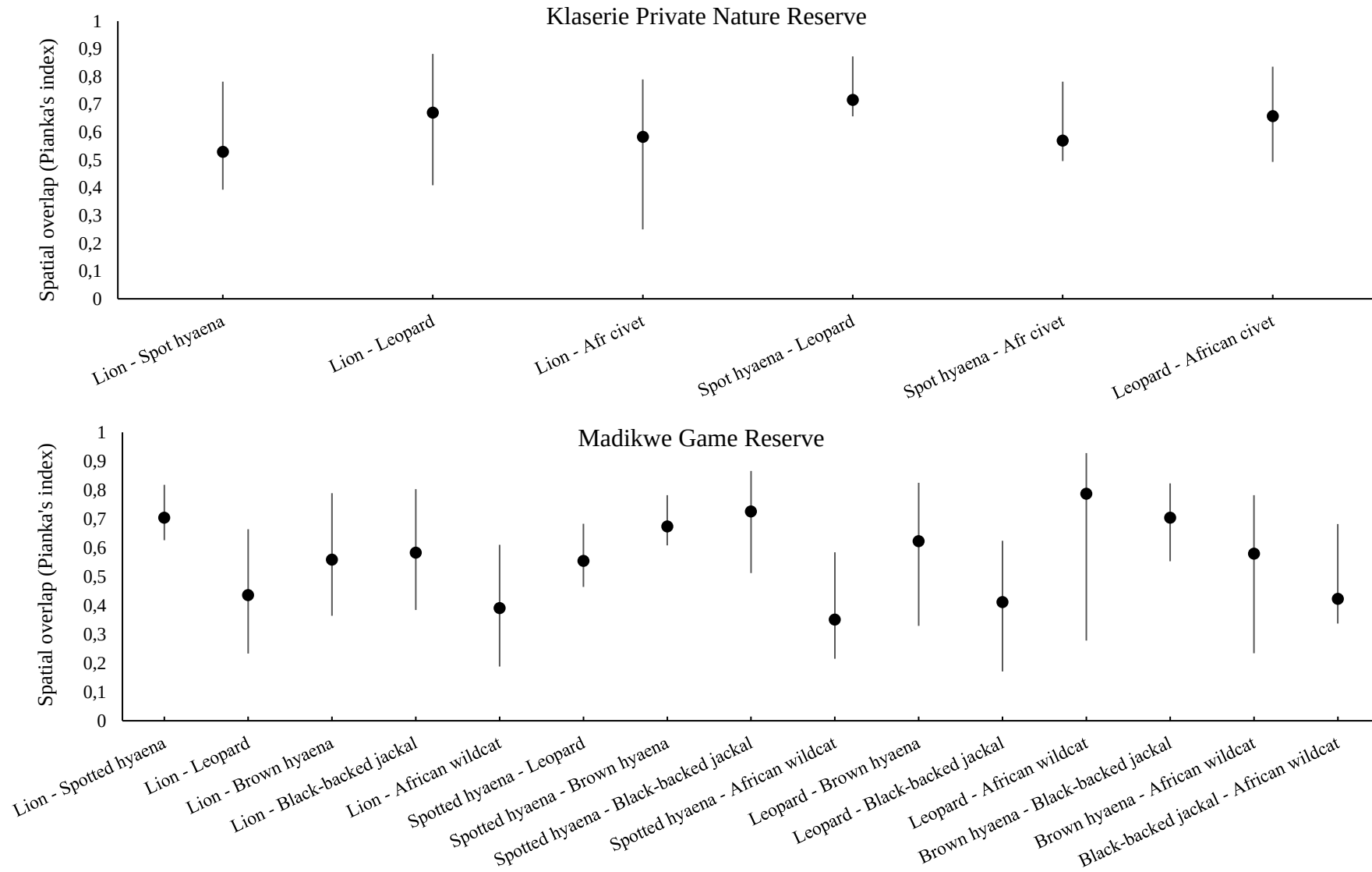
Most carnivore species-pairs analysed in MZNP (15 out of 21) had relatively low spatial overlap in terms of Pianka's index (Figure 2.2). The highest spatial overlap, with noticeably less variation, was between brown hyaenas, black-backed jackals, and aardwolves. The lowest spatial overlap was with genet-associated species-pairs.

All species-pairs that obtained sufficient detections during both MZNP's wet and dry seasons separately showed less spatial overlap during the dry compared to the wet season (Figure 2.3).

2.4.3.4 Tswalu Kalahari Reserve

The lowest spatial overlap in TKR among carnivore species-pairs was observed between brown hyaenas and both fox species, and bat-eared foxes and aardwolves. In contrast, the highest was between black-backed jackals and African wildcats (Figure 2.2). Black-backed jackals had relatively high spatial overlap with all other carnivore species analysed in TKR. There was no apparent seasonal variation in the spatial overlap between carnivore species in TKR (Figure 2.3).

Regarding the two separate sections of the reserve (Figure 2.4), Korannaberg (no lions present) and Lekgaba (lions present), spatial overlap was noticeably less between brown hyaenas and black-backed jackals in Korannaberg (Pianka's index = 0.376, 95% CI: 0.238 – 0.615) compared to the Lekgaba section (Pianka's index = 0.878, 95% CI: 0.359 – 0.974). Similarly, less spatial overlap was observed between brown hyaenas and bat-eared foxes in the Korannaberg section (Pianka's index = 0.194, 95% CI: 0.120 – 0.436) than the Lekgaba section (Pianka's index = 0.572, 95% CI: 0.050 – 0.983). It should, however, be noted that the confidence intervals of spatial overlap were very wide during comparisons between Korannaberg and Lekgaba.



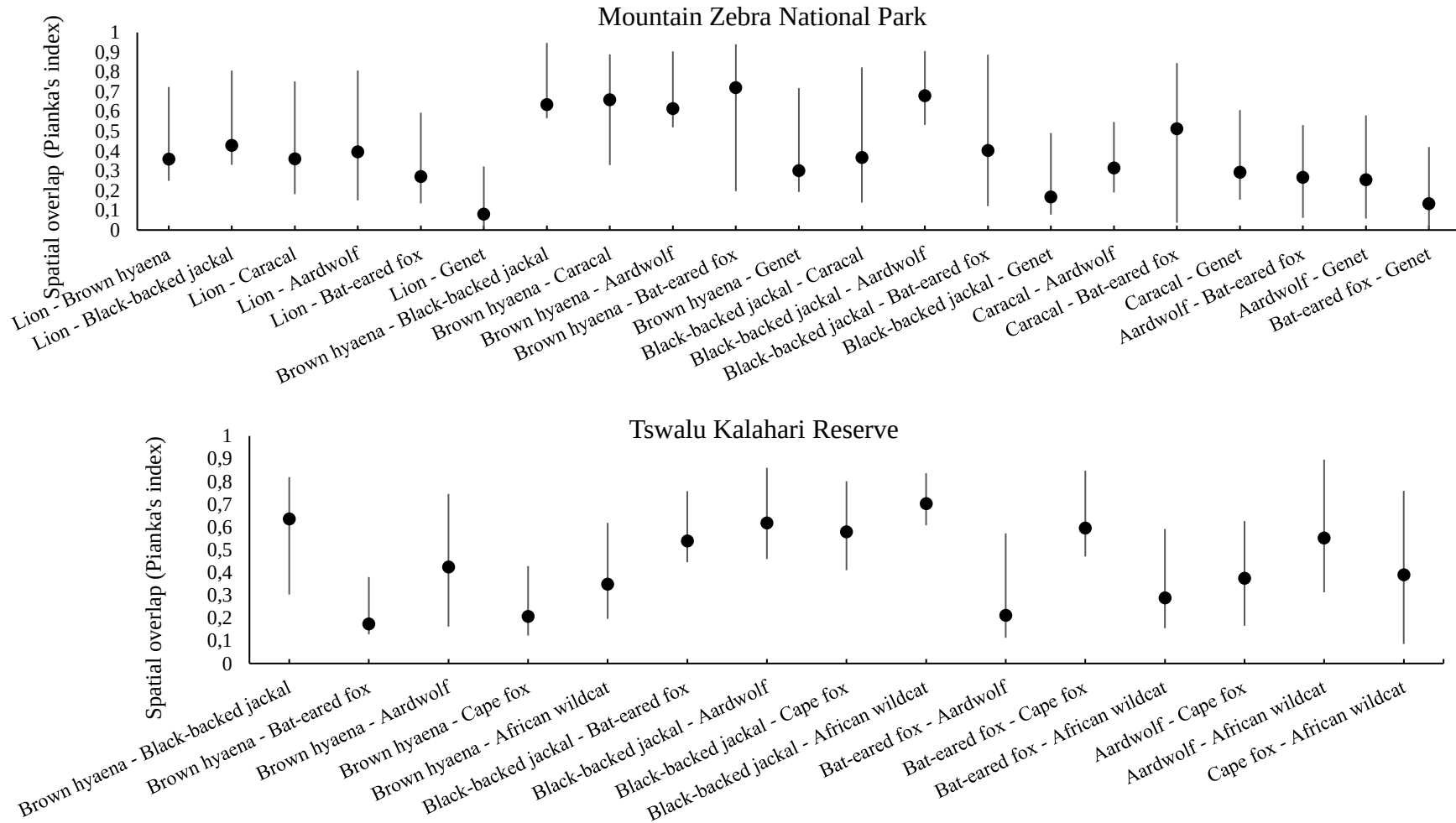
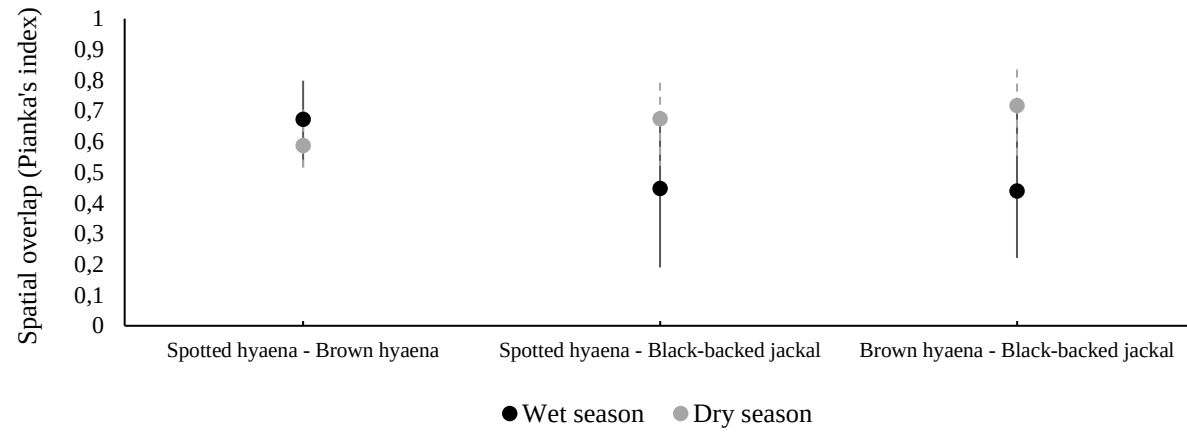


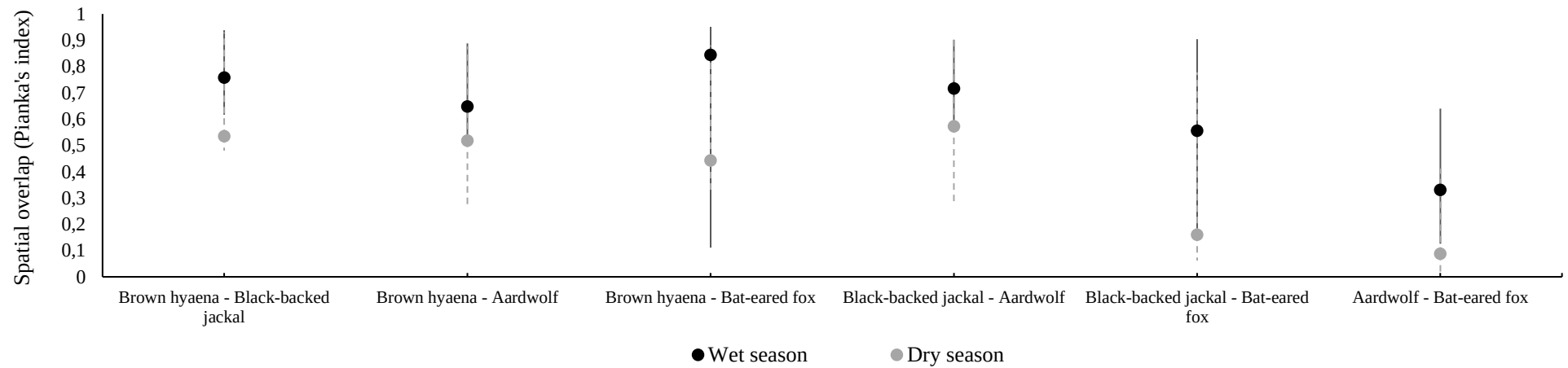
Figure 2.2. Spatial overlap, according to Pianka's index, of carnivores (species of the order Carnivora) from four South African protected areas.

The vertical lines indicate 95% confidence intervals.

Madikwe Game Reserve



Mountain Zebra National Park



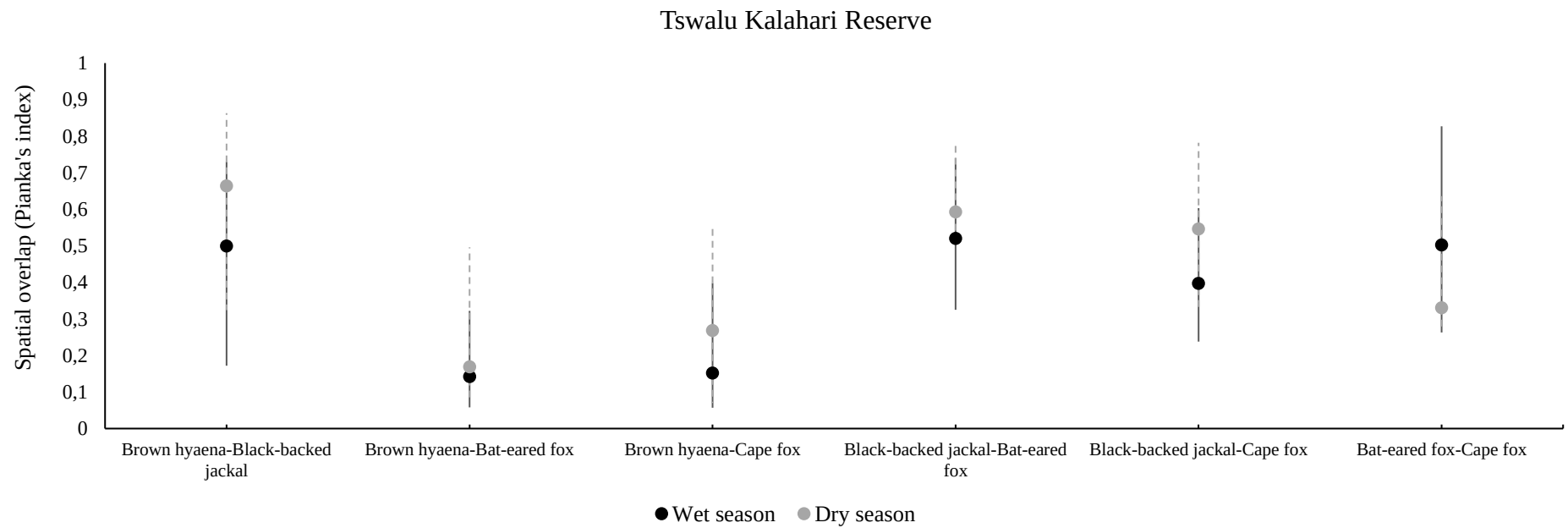


Figure 2.3. Seasonal spatial overlap, according to Pianka's index of spatial overlap, of carnivore species (species of the order Carnivora) in three South African protected areas.

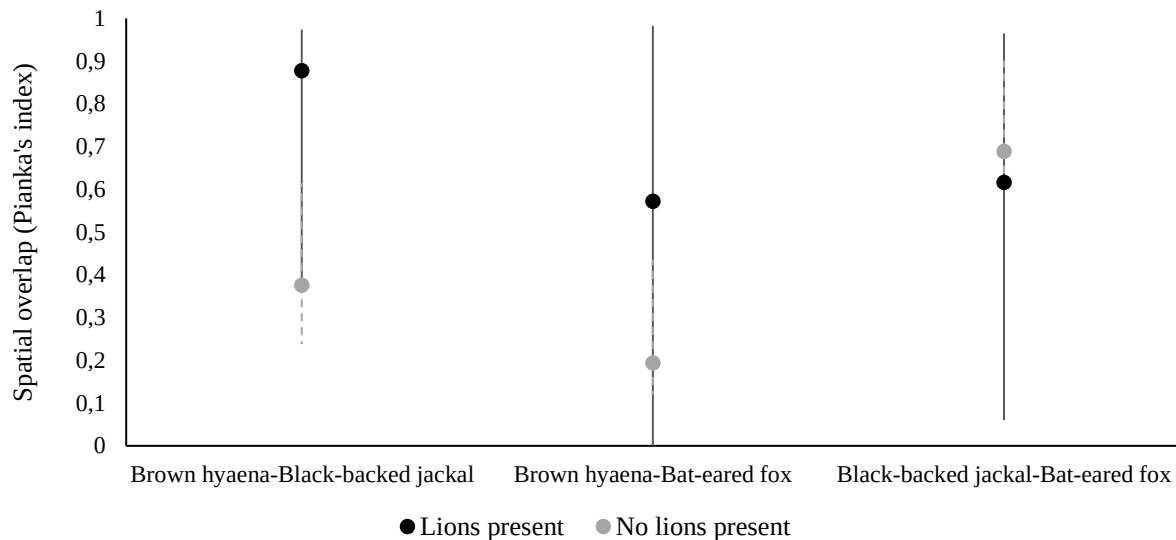


Figure 2.4. Spatial overlap, according to Pianka's index, of carnivore species (species of the order Carnivora) from the Lekgaba and Korannaberg fenced sections of the Tswalu Kalahari Reserve, South Africa, where lions are present and absent, respectively.

2.5 Discussion

This study used camera-trapping data to investigate the potential for interspecific spatial avoidance behaviour among South African Carnivora species. Only 21% of the species comparisons across all the protected areas and considering all species combinations revealed possible spatial avoidance behaviour. In addition, the apparent spatial partitioning between some of these species cannot be confidently attributed to avoidance behaviour based on biologically relevant reasoning (e.g., documented cases of interspecific aggression and killings, and subordinate species forming part of dominant carnivore diets). MZNP's small-spotted genets (*Genetta genetta*), for example, appear to avoid larger carnivore species through spatial segregation. It is important to consider the actual biological likelihood of avoidance behaviour by the subordinate genets. This requires empirical evidence of the potential risk of antagonistic interactions between species (see Curveira-Santos et al. 2022). This is especially relevant

regarding the potential avoidance behaviour exhibited by MZNP's small-spotted genets in response to other small and medium-sized carnivores such as bat-eared foxes and aardwolves. Competition and the threat of interspecific killings or aggression between these species, as well as genets and apex predators such as lions, are deemed negligible, and thus avoidance should not be required (Donadio and Buskirk 2006, Prugh and Sivy 2020). Small-spotted genets are more likely to avoid the movements and habitats of caracals due to the intermediate body size differences and caracals' highly adapted ability to kill vertebrate prey (Donadio and Buskirk 2006).

Furthermore, certain species-pairs where potential avoidance behaviour was shown, such as between brown hyaenas and Cape foxes in TKR, displayed distinct habitat preferences; thus, spatial partitioning is more likely the result of opposing preferences for certain vegetation types than active avoidance behaviour. None of the species-pairs in KPNR and MGR showed clear evidence of spatial avoidance behaviour, at least not on the spatial scale considered in this study. It is speculated that this could be due to the thicker vegetation in the two protected areas, which provides refuge and better concealment for subordinate species while still allowing them to use areas frequented by larger risky species (Broekhuis et al. 2013, Oriol-Cotterill et al. 2015, Rostro-García et al. 2015).

Black-backed jackals and caracals in MZNP displayed a noticeable degree of spatial partitioning, particularly in terms of vegetation type preferences, where caracals were more selective compared to black-backed jackals, which showed no preference for a specific vegetation type. Interspecific killings, particularly of juveniles, and a considerable amount of diet overlap occur between caracals and black-backed jackals (Kok and Nel 2004, Melville et al. 2004, Do Linh San et al. 2009, Curveira-Santos et al. 2022). However, because detection rates for MZNP's caracals were low and occupancy modelling was not performed, inferences about spatial avoidance may be insufficient to draw confident conclusions. Spatial associations

and the potential for aggressive interactions between these two main mesopredator species remain poorly understood and understudied. MZNP's bat-eared foxes may also avoid black-backed jackals on a large spatial scale. This was noticeably more evident during the park's dry seasons when spatial overlap was low. However, it is important to note the high variation in spatial overlap between the two species, as indicated by wide confidence intervals. This could imply that bat-eared foxes' spatial use is less dependent on that of black-backed jackals, and thus active spatial avoidance is less likely. This is supported by TKR's bat-eared foxes, which showed no indications of spatially avoiding black-backed jackals. Even though black-backed jackals are known to kill bat-eared foxes, previous research has shown that they coexist through means other than spatial avoidance (e.g., diet partitioning and increased group sizes), but may seek refuge in areas away from jackal core home ranges for denning activities (Kamler et al. 2012, 2013, 2017). Thus, the high variation in spatial overlap between the two species in MZNP may have resulted from spatial segregation of different activities. Compared to caracals, MZNP's aardwolves showed relatively low spatial overlap and distinct differences in vegetation type preferences. This could imply that aardwolves in MZNP avoid areas frequented by caracals. As previously stated, detection rates of MZNP's caracals were low, making population inferences about interspecific spatial avoidance less robust. In addition, documented cases of aggressive interactions between the two species are lacking in the literature (Curveira-Santos et al. 2022). Therefore, the potential for avoidance behaviour is based on theoretical assumptions confounded by a lack of empirical evidence. More research is needed to determine whether this is true active avoidance behaviour. Aardwolves and bat-eared foxes, two arthropophagous carnivores, appear to use spatial partitioning as a method of interspecific avoidance in MZNP and TKR. This was especially noticeable during MZNP's dry seasons when there is some dietary overlap in the form of *Hodotermes* termite species (Williams et al. 1997, Kamler et al. 2013). They also vary in their preference for different vegetation types.

Aardwolves are more likely to inhabit grassland and duneveld habitat in MZNP and TKR, respectively, as their main prey (i.e., termites of the *Trinervitermes* and *Hodotermes* genera; Cooper and Skinner 1979) prefer to inhabit the softer soils of grasslands (Kruuk and Sands 1972, Schuette et al. 2013). On the other hand, bat-eared foxes prefer to use the shrub-dominated Eastern Upper Karoo vegetation and thornveld habitat in MZNP and TKR, respectively (Périquet and le Roux 2017). Therefore, potential avoidance behaviour between bat-eared foxes and aardwolves is most likely motivated by access to localised termite colonies. Furthermore, TKR's bat-eared foxes spatially avoid species from the large predator guild. Large predators such as lions, leopards, cheetahs, brown hyaenas, and black-backed jackals kill bat-eared foxes (Mills 1984, Kamler et al. 2013, Curveira-Santos et al. 2022), and therefore avoidance behaviour displayed by bat-eared foxes would result in increased survival. In particular, bat-eared foxes have clear opposite vegetation type preferences and little spatial overlap with brown hyaenas in TKR. This is exacerbated by the fact that there is little spatial overlap during both the wet and dry seasons. Furthermore, they showed little overlap with brown hyaenas in TKR's Korannaberg section. Bat-eared foxes, particularly younger foxes, are vulnerable to predation by brown hyaenas (Mills 1978, Mills and Mills 1978), even though adult bat-eared foxes can chase away brown hyaenas through aggression, particularly at fox dens (Pauw 2000). However, bat-eared foxes in MZNP do not appear to avoid brown hyaenas via spatial partitioning. Brown hyaena densities, group sizes of bat-eared foxes, and denning locations may all play a role in the varied indications of spatial avoidance behaviour in the two protected areas; however, these variables were not determined or included in this study, necessitating additional research to identify possible reasoning. Similarly, TKR's Cape foxes appear to avoid brown hyaenas via spatial partitioning. Cape foxes and brown hyaenas prefer opposite habitat types in TKR, with Cape foxes favouring *Gordonia* Duneveld vegetation and avoiding Kathu Bushveld. Aside from possible scavenging behaviour (Owens and Owens

1978), documented cases of antagonistic encounters between Cape foxes and brown hyaenas are lacking in the literature (Curveira-Santos et al. 2022). Therefore, it may not be that Cape foxes actively avoid brown hyaenas on a large spatial scale but that they rather prefer to use different vegetation types.

Among the remaining species-pairs analysed, subordinate species displayed no clear indications of avoidance behaviour via spatial partitioning at the scales presented in this study. It can be inferred that species of the large predator guild from this study (lions, spotted hyaenas, leopards, and brown hyaenas) do not use spatial partitioning on a large scale to avoid encountering risk-associated species. More specifically, MGR's spotted hyaenas and lions appear to be drawn to similar habitats occupied by preferred prey species. In KPNR, however, spotted hyaenas' generalist proclivity to also use Mopaneveld vegetation, whereas lions strongly prefer Granite Lowveld vegetation, likely resulted in lower overlap values than in MGR. Previous research has shown that spotted hyaenas and lions follow a relationship of both benefit and risk, and therefore, complete avoidance would be less likely (Périquet et al. 2015). Both species can coexist in prey-rich environments; however, finer-scaled avoidance of interspecific core home ranges and reliance on reactive avoidance may persist (Broekhuis et al. 2013, Périquet et al. 2015, Swanson et al. 2016, Dröge et al. 2017). Leopards in KPNR and MGR do not avoid areas used by lions and spotted hyaenas. This is consistent with previous research (Vanak et al. 2013, Balme et al. 2017b, Miller et al. 2018, Rafiq et al. 2020a). Spotted hyaenas may even be attracted to leopard habitat as scavenging or kleptoparasitic opportunities are presented (Balme et al. 2019, Searle et al. 2021). Furthermore, potential spatial partitioning between leopards and lions in MGR is outweighed by exceptionally high variation in spatial overlap (i.e., wide confidence intervals), which may indicate independent spatial use. Nonetheless, on the scale presented in this study, avoidance behaviour can be ruled out. Spatial use of leopards may be dictated by the spatial use of their preferred prey species, such as

warthogs and medium-sized antelope (Hayward et al. 2006, Balme et al. 2019). Because of their strict scavenging behaviour, brown hyaenas should be drawn to areas frequented by other large carnivores (Yarnell et al. 2013, Bashant et al. 2020). This study found that brown hyaenas do not avoid other large carnivores on a broad spatial scale, correlating with previous research that revealed similar behaviour (Owens and Owens 1978, Vissia et al. 2021, Gush et al. 2022). However, finer-scaled spatial avoidance or reactive avoidance are likely to manifest in brown hyaena behaviour, as observations made by Owens and Owens (1978). It should, however, be noted that they showed a high degree of variation in spatial overlap with lions and leopards. Because their reliance on scavenging carcasses rules out the independence of relative spatial use, this high variation may be attributed to brown hyaenas' spatial partitioning of different activities. For example, denning sites and daytime resting may be in areas away from regular lion and leopard use, while interspecific spatial overlap occurs when brown hyaenas forage for scavenging opportunities on forays outside of core areas. This hypothesis could be supported by brown hyaenas' preference for vegetation types avoided by leopards and, particularly, lions. However, denning locations in response to the spatial use of other large carnivores are lacking in the literature, and thus, the above hypothesis will need to be confirmed by future research. Black-backed jackals, another species known to regularly scavenge off carcasses provided by large carnivores (Yarnell et al. 2013, Fourie et al. 2015), also showed high variation in spatial overlap with MGR and MZNP's top predators, lions and spotted hyaenas. This could again indicate that spatial overlap is greater during foraging periods and less during periods of rest or that intraspecific competition leads to territorial partitioning and, eventually, high variation in spatial overlap with other carnivore species due to differentiation of core and home ranges (Kamler et al. 2019, 2020b). Nonetheless, spatial partitioning is not a population-wide strategy used by black-backed jackals to coexist with large predators such as lions, spotted hyaenas, and brown hyaenas, at least not on the spatial scale examined in this study. Furthermore, due

to their high spatial overlap with brown hyaenas and spotted hyaenas during MGR's dry seasons, black-backed jackals may rely more on scavenging opportunities during the dry seasons, particularly in MGR with its high densities of large predators. This means that the risk of coexistence may be reduced due to increased availability and easier detection of carcasses to scavenge during the dry seasons (Ferguson et al. 1983, Pereira et al. 2013, Moleón et al. 2015, Temu et al. 2016). It may also represent extra-territorial movements associated with reproductive cycles or the search for vacant territories by displaced or dispersing individuals (Kamler et al. 2019). This is supported by Kaunda (2001), who reported larger black-backed jackal home ranges during the drier winter months. However, the reasoning behind the seasonality in spatial overlap observed among jackals and hyaenas in MGR would require more in-depth research. Furthermore, it appears that black-backed jackal ranges overlap more with lions and hyaenas in areas with higher densities of these species, as observed in MGR (Honiball et al. 2021), whereas in MZNP there is less evidence of spatial attraction but still a lack of avoidance behaviour (Kaunda and Skinner 2003). Black-backed jackals used very similar areas to brown hyaenas in TKR's Lekgaba section, where lions will provide regular sources of carrion to scavenge, whereas, in the Korannaberg section where lions are absent, overlap between black-backed jackals and brown hyaenas is much less. Furthermore, large predator diversity is higher in the Korannaberg section, which may reduce competition between the two scavenger species (Yarnell et al. 2013) by providing more spatially varied scavenging opportunities as opposed to more predictable and localised lion-kill carcasses available to scavenge in the Lekgaba section. Future studies of black-backed jackal diets and densities in the reserve's two sections will reveal their reliance on scavenging in areas with varying large predator assemblages and densities that may direct reasoning to the varied spatial overlap observed in this study. African civets in KPNR use similar areas and habitats to sympatric large carnivores and, as a result, do not use large-scaled spatial partitioning to coexist with large carnivores.

However, reactive spatial avoidance may persist (Mills et al. 2019). MZNP's bat-eared foxes also use similar vegetation and occupy similar areas to lions, but showed relatively low spatial overlap. This could imply that bat-eared foxes in MZNP use finer-scaled spatial partitioning to avoid core lion ranges; however, more research is required to confirm this. Bat-eared foxes also showed no clear indications of avoiding areas frequented by black-backed jackals; however, finer-scaled avoidance of core jackal ranges may have been used by the foxes but was missed in this study due to an inappropriate scale of analyses. Despite preferring different habitat types, aardwolves do not avoid MZNP's lions or MZNP's and TKR's brown hyaenas spatially. Furthermore, aardwolves do not avoid areas frequented by black-backed jackals in both MZNP and TKR. It can thus be deduced that aardwolves' spatial use preferences are more likely dictated by access to termite colonies, open areas devoid of dense vegetation, and potential avoidance of areas frequented by bat-eared foxes due to potential dietary overlap during the dry seasons rather than avoidance of larger species that may pose a threat to their survival. This is supported by the lack of documented cases of aggressive encounters between aardwolves and lions, as well as brown hyaenas (Curveira-Santos et al. 2022).

Regarding the smaller carnivores, Cape foxes frequently use areas favoured by the main mesopredator species in TKR, namely caracals and particularly black-backed jackals. Concerning the latter in particular, even though they largely preferred to use different habitat types, they showed a moderate degree of spatial overlap. This points to the general absence of large-scaled spatial avoidance behaviour by Cape foxes in response to black-backed jackal movement patterns but does not rule out the use of finer-scaled avoidance of core jackal ranges. This contrasts with previous studies that revealed lethal and sub-lethal effects of black-backed jackals on Cape fox populations, ultimately leading to population suppression and avoidance of jackal-used space (Kamler et al. 2012, 2013). Cape foxes and bat-eared foxes appear to be drawn to similar environments. Coexistence between the two fox species may be explained by

a possible lack of overlap in dietary preferences (Bothma et al. 1984, Kamler et al. 2012), as well as possible mutual avoidance of core ranges of species such as black-backed jackals, as observed by Kamler et al. (2012). Cape foxes and aardwolves both prefer to use Gordonia Duneveld habitat and appear to use space independently of each other due to the high variation in spatial overlap observed in this study, a lack of documented cases of interspecific aggression (Bothma et al. 1984, Curveira-Santos et al. 2022), and no dietary overlap (Bothma et al. 1984). As evidence for competition is lacking, avoidance is likely negligible between the two species. Despite having similar habitat preferences, African wildcats had relatively moderate to low spatial overlap with larger carnivores in MGR. This could imply finer-scaled spatial partitioning. However, the high variation in spatial overlap may suggest that African wildcats use space independently of larger carnivores in MGR. Given the findings and methods employed, the latter is regarded as more likely in this study. Comley et al. (2020b) showed that African wildcats are detected less in areas occupied by lions and spotted hyaenas but not by leopards. This study partially supports the findings of Comley et al. (2020b), as MGR's African wildcats had less overlap with lions and spotted hyaenas compared to a relatively high overlap with leopards. Documented cases of African wildcat killings by larger predators are dominated by hyper-carnivorous felids that are well adapted to hunting vertebrate prey (Curveira-Santos et al. 2022); therefore, more research is needed to explain their greater overlap with leopards than spotted hyaenas, for example. In addition, African wildcats showed no indication of spatial avoidance behaviour with regards to the movement of main mesopredator species, namely black-backed jackals and caracals. A degree of diet overlap is likely among the three species, which would benefit African wildcats from overlapping spatially with caracals and jackals (Kok and Nel 2004). Due to their solitary, cryptic nature and generally low densities, African wildcats appear to use areas independently of most larger carnivore species and may rather rely

on reactive, finer-scaled avoidance behaviour than large-scaled spatial partitioning (Herbst 2009, Edwards et al. 2015).

In conclusion, at least on the scale conducted in this study, spatial avoidance behaviour among carnivores in South African protected areas should be considered a rarity. This supports the findings of Swanson et al. (2016), who found no evidence of long-term spatial displacement of subordinate carnivores in the Serengeti National Park due to the presence of more dominant species. Carnivore species are typically found in low densities, are mostly solitary or move in a cohesive social group, and exhibit cryptic and secretive behaviour. Low encounter rates raise the question of the potential for encounters between carnivore species and whether spatial avoidance is considered a requirement for coexistence (Romero-Muñoz et al. 2010). Spatial avoidance behaviour will most likely exclude a subordinate carnivore species from its preferred habitat and resources. The need for adequate resource intake to increase fitness likely outweighs the need to avoid the risk associated with rare encounters with larger, more dominant species. As stated by Broekhuis et al. (2013), spatial use and habitat selection could be a hierarchical process in which resource acquisition takes precedence over predator avoidance. However, this can only be confirmed through empirical evidence of encounter rates and levels of antagonism between species over a dominance hierarchy, such as that presented by Curveira-Santos et al. (2022). However, this study cannot rule out finer-scaled spatial avoidance in the form of reactive responses to the presence of a dominant carnivore (Broekhuis et al. 2013, Vanak et al. 2013). Intraspecific avoidance on a spatial scale, especially regarding large carnivores such as lions and spotted hyaenas (Dheer 2016, Comley et al. 2020a), is likely to have a greater influence on a species' spatial use than interspecific avoidance. This is particularly relevant at larger spatial scales that represent distinct territorial ranges.

CHAPTER 3

Temporal partitioning and the potential for avoidance behaviour among South African carnivore species

3.1 Abstract

Carnivora occupy many ecological niches fundamental to ecosystem functioning. As a result, carnivores compete on a variety of levels to establish dominance and ensure survival while maintaining fitness. Subordinate carnivores must therefore adapt their behaviour to coexist with more dominant species. One such strategy is the partitioning of temporal activity patterns.

This chapter investigated temporal partitioning as an interspecific avoidance strategy among carnivores. The diel activity patterns and core activity periods of carnivore species were compared using multi-seasonal camera trapping data from four protected areas across South Africa: Associated Private Nature Reserves, Madikwe Game Reserve, Mountain Zebra National Park, and Tswalu Kalahari Reserve. Furthermore, interspecific spatiotemporal behaviour among carnivores was examined using time-to-event analyses.

Most species-pairs (63%) across all combinations and sites in this study showed no clear evidence of using temporal partitioning as a strategy to coexist with potentially risk-associated carnivores. However, potential avoidance behaviour revolved around species-pairs associated with African wild dogs (*Lycaon pictus*) and caracals (*Caracal caracal*), owing to their unique temporal niche classifications. The remaining species-pairs that displayed potential avoidance behaviour were predominantly nocturnal and relied on finer-scaled temporal partitioning of core activity periods.

Overall, this study shows the importance of seasonality and temporal scale regarding interspecific avoidance behaviour, while highlighting the need for fine-scaled behavioural analyses. Temporal avoidance among South African carnivores is more likely to manifest as adaptations to core activity periods. Furthermore, potential underlying factors that will increase the reliability and relevance of future studies that examine temporal avoidance behaviour among carnivores are also addressed. In conclusion, this study suggests that the daily activity patterns of most African carnivores are more likely influenced by bottom-up forces such as potential hunting success, than top-down forces in the form of suppression by more dominant species.

Key words: activity patterns, behavioural ecology, Carnivora, coexistence, dominance, temporal overlap

3.2 Introduction

Temporal avoidance behaviour is a form of resource partitioning whereby animal species, constrained by morphological characteristics and adaptations, are active at different periods of the 24-hour day to reduce the risk posed by species that occupy higher levels of the dominance hierarchy (Schoener 1974, see review by Kronfeld-Schor and Dayan 2003, Hayward and Slotow 2009, Bennie et al. 2014). Temporal partitioning is thus a behavioural adaptation that species could employ to coexist with other species that are deemed a threat to their survival or fitness (Carothers and Jaksic 1984). Avoidance behaviour constitutes many dimensional considerations related to niche theory, ranging from spatial, temporal, and diet partitioning, to reliance on reactive or predictive decision making in response to various forms of interspecific competition (Carothers and Jaksic 1984, Linnell and Strand 2000, Hayward and Kerley 2008, Broekhuis et al. 2013).

Spatial partitioning may force subordinate species to occupy areas with unfavourable resource availability (Ritchie and Johnson 2009). In response, these species may resist exclusion from favourable habitat by being active at different times of the day which will reduce the likelihood of encounters with the dominant species (Swanson et al. 2014).

Carnivores (i.e., species of the Carnivora order) occupy many ecological niches fundamental to ecosystem functioning (Ripple et al. 2014, Hoeks et al. 2020). Carnivores have a major role in maintaining trophic stability within ecosystems through top-down regulation (Elmhagen et al. 2010, Estes et al. 2011). Therefore, by providing information about the dynamics of interspecific interactions and competition among carnivores, we can better understand community functioning and the drivers of community structure (Ritchie and Johnson 2009, Karanth et al. 2017). This will aid in improving management decision-making and conservation strategies.

Carnivores are subject to a wide range of interspecific competition, from indirect exploitation of limited resources to interference competition that involves direct interactions of an aggressive nature, such as kleptoparasitism, predation, and territorial killings (Carothers and Jaksic 1984, Creel and Creel 1996, Palomares and Caro 1999, Linnell and Strand 2000, Caro and Stoner 2003). Outcomes of interspecific competition among carnivores are usually dictated by body size, predatory behaviour, morphological adaptations, age structure, social organisation, as well as species diversity and richness within the region (Cooper 1991, Trinkel and Kastberger 2005, Donadio and Buskirk 2006, Cozzi et al. 2012, Lehmann et al. 2017). Even though interspecific avoidance behaviour is adaptive and manifested over evolutionary timescales, subordinate carnivores must often adjust their behaviour to ensure coexistence with more dominant carnivores due to population-wide changes of, for instance, demographics and sex ratios (Lima and Dill 1990, Linnell and Strand 2000, Kronfeld-Schor and Dayan 2003, Trinkel and Kastberger 2005, Lehmann et al. 2017).

Carnivore communities within South Africa's major protected areas are considered largely intact assemblages that are ecologically diverse and species rich (Dalerum et al. 2009, Dalerum 2013). These protected areas are mostly fenced nature reserves or national parks. This means that the carnivore communities within the protected areas may be subjected to intensified competitive interactions as most species have restricted space (Bissett and Bernard 2011, Packer et al. 2013). Intensively managed, fenced reserves also generally maintain carnivore populations, such as lions (*Panthera leo*), closer to carrying capacity than is observed for unfenced reserves (Packer et al. 2013). Competition for ecological niches is, therefore, likely amplified. Furthermore, with the increased popularity of fencing as a management tool in Africa (Pekor et al. 2019), along with Africa's apparent increasing human population growth, communities' proximity to protected areas, and the continent's natural landscapes becoming more fragmented (Pekor et al. 2019), the need for fencing as a conservation tool might offset the preservation of Africa's remaining natural, unfenced protected areas in the future (Pekor et al. 2019). As a result of all those mentioned above, major fenced protected areas in South Africa are ideal study sites to examine interspecific relationships and possible associated patterns of temporal avoidance behaviour among carnivore species.

In this study, data derived from Snapshot Safari's extensive camera-trapping surveys (Pardo et al. 2021) conducted within four South African protected areas were utilised to assess the use of temporal partitioning as a method of interspecific avoidance behaviour among carnivores. Given sufficient detections, the overlap in diel activity patterns of sympatric carnivore species was examined within the entire data collection period, during both wet and dry seasons, and the hottest and coldest months of the year in each specific region. Finally, temporal spacing behaviour was examined to identify spatiotemporal avoidance or aggregation between carnivore species using time-to-event analyses. Temporal avoidance behaviour would be unnecessary if a subordinate carnivore species spatially avoids a dominant carnivore. However,

given the rarity of spatial avoidance behaviour observed in chapter 2 and the potential ancillary information that can be provided, all species-pairs were considered in this chapter.

3.3 Methods

Camera trap data from four protected areas within South Africa were analysed in this chapter: Associated Private Nature Reserves (APNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZNP), and Tswalu Kalahari Reserve (TKR).

Apart from wet and dry seasons, average monthly temperatures (South African Weather Service 2016-2020) across all years were used to identify the two or three, depending on the number of species-detections within each month, hottest (e.g., December and January) and coldest (e.g., June and July) subsequent months of the year. As all four protected areas are in South Africa's summer rainfall region, the hottest months are encompassed within the wet seasons, and the coldest months of the year are within the dry seasons. Interspecific comparisons of activity patterns during the hottest and coldest months of the year were included to investigate seasonal differences at more extreme levels of climatic variation.

Sunrise and sunset times for each temporal-scale categorisation were calculated by averaging the collective monthly sunrise and sunset times, respectively. Times of sunrise and sunset at each protected area were sourced from the NOAA (National Oceanic and Atmospheric Administration) Global Monitoring Laboratory's NOAA Solar Calculator (<https://www.gml.noaa.gov/grad/solcalc/>).

The temporal classifications in each protected area were defined as follows: dawn as the period between an hour before and an hour after the average time of sunrise during each categorisation (i.e., entire study period, wet and dry season, and hottest and coldest months of the year); dusk as the period between an hour before and an hour after the average time of sunset during each

categorisation; the diurnal period between dawn and dusk; and conversely the nocturnal period between dusk and dawn.

The analyses included species of the Carnivora order that had at least 20 independent detections within a specific protected area but did not exhibit any clear spatial avoidance behaviour in chapter 2. Previous studies have included species with as low as 10 independent detections (Nakabayashi et al. 2021, Gerber et al. 2012), but reliability in daily activity patterns increases with an increasing number of detections (Niedballa et al. 2019). Therefore, 20 independent detections were considered as this allowed the inclusion of several elusive species into the analyses.

3.3.1 Interspecific activity overlap

Daily activity patterns derived from kernel density estimates were compared between species-pairs within each protected area. This was done by calculating the coefficient of overlap ($\hat{\Delta}$) and the associated 95% smoothed bootstrapped confidence intervals with 10000 resamples using the *overlap* package (Ridout and Linkie 2009, Meredith and Ridout 2021) in R (R Core Team 2021). The coefficient of overlap is a proportional value representing the possible similarity in diel activity patterns of species-pairs and ranges from 0 to 1, indicating dissimilar and identical activity patterns, respectively. According to Meredith and Ridout (2021), when one or both species in a pair obtain less than 50 photo-captures, the overlap estimator $\hat{\Delta}_1$ was calculated, and when both species obtained more than 50 photo-captures, $\hat{\Delta}_4$ was calculated.

Given that most of the carnivore species included in this study are predominantly active between dusk and dawn (i.e., primarily nocturnal; Figure S3.1), overlap in core activity periods (50% core isopleths) was calculated between species using the highest species-specific bandwidth estimation within each species-pair. Appropriate bandwidth values for each species

were calculated in RStudio using the *circular* package (Agostinelli and Lund 2022) with a maximum moment, $k_{max} = 3$. Core activity periods were calculated using the *modal.region.circular* function in the *circular* package (Agostinelli and Lund 2022) and the overlap in core activity periods between species were determined using the *totalvariation.circular* function, also in the *circular* package (Agostinelli and Lund 2022).

The two separated sections of TKR, Lekgaba (lions present) and Korannaberg (lions absent), presents a unique opportunity where the behaviour of a mammal species can be compared within the same region, but where lions are present and absent. Therefore, to test the effect of lion presence on the daily activity patterns of carnivore species in TKR, similar steps as described above were followed to compare each carnivore species' diel activity pattern separately between the Lekgaba (lions present) and Korannaberg (lions absent) sections of TKR.

Given enough detections, the daily activity patterns of each species-pair were also compared using the aforementioned methods during the wet seasons, dry seasons, hottest months of the year, and coldest months of the year in each protected area.

3.3.2 Spatiotemporal behaviour between species

A time-to-event analysis, derived from Karanth et al. (2017) and Cusack et al. (2017), was performed to determine spatiotemporal avoidance or aggregation between carnivore species. This entailed extracting the time period from each photo-capture of a specific species (reference species) to the nearest single photo-capture, before or after, of the comparing species (proximate species) at shared camera trapping stations. The species with the fewest total photo-captures among each species-pair was designated as the reference species. A maximum of seven days before and after each reference detection was used to include proximate detections,

as this allowed for enough comparisons among species while still likely maintaining biological relevance. To increase reliability, only species-pairs with more than 20 total comparisons across all camera stations within seven days before and after the reference detections were included in the analysis. The observed median of all time intervals between reference and proximate detections within the 7-day relevance period was calculated.

A randomisation process was then applied to each photo-capture of the proximate species. This entailed randomly selecting a camera station, date, and time from the original dataset for the specific proximate species, thereby preserving biological relevance in activity period preferences. This was repeated 1000 times to generate 1000 randomised datasets against which the reference species detections were compared in the time-to-event analysis. The median of the minimum time between proximate and reference detections for each 1000 randomised datasets was then calculated and plotted as a density distribution of medians. Similar to standard permutation tests, a proportional value (p-value) was then calculated as $p = n/N$, where n is the number of randomised medians greater than the observed median and N is the total number of randomised medians for the specific species-pair. A two-tailed significance level ($\alpha = 0.05$) was considered, where a $p > 0.975$ indicated a significant possibility of spatiotemporal aggregation and $p < 0.025$ indicated a significant possibility of avoidance behaviour.

3.4 Results

Across all four protected areas, 14 species of the order Carnivora obtained more than 20 independent photo-captures in total (Table 3.1). These species range in size from the largest, lions, to the smallest, genets (*Genetta* spp.).

Table 3.1. The number of independent camera trap photo-captures (> 60 min apart) for South African Carnivora species within the Associated Private Nature Reserves (APNR), Madikwe Game Reserve (MGR), Mountain Zebra National Park (MZN), and Tswalu Kalahari Reserve (TKR).

Site	Common name	Scientific name	Total	Wet season	Dry season	Hot months	Cold months
APNR	Spotted hyaena	<i>Crocuta crocuta</i>	1712	853	859	275	399
	Lion	<i>Panthera leo</i>	190	97	93	20	31
	Leopard	<i>Panthera pardus</i>	165	82	83	20	37
	African civet	<i>Civettictis civetta</i>	72	20	52	10	27
	African wild dog	<i>Lycaon pictus</i>	46	17	29	4	15
	Honey badger	<i>Mellivora capensis</i>	24	15	9	5	4
	Genet	<i>Genetta spp.</i>	19	7	12	3	6
	White-tailed mongoose	<i>Ichneumia albicauda</i>	16	10	6	3	2
	Black-backed jackal	<i>Lupulella mesomelas</i>	15	3	12	1	8
	Side-striped jackal	<i>Lupulella adustus</i>	13	8	5	5	3
	Caracal	<i>Caracal caracal</i>	7	3	5	0	1
	African wildcat	<i>Felis silvestris lybica</i>	3	0	3	0	2
	Dwarf mongoose	<i>Helogale parvula</i>	2	2	0	1	0
	Banded mongoose	<i>Mungos mungo</i>	1	0	1	0	0
	Cheetah	<i>Acinonyx jubatus</i>	1	0	1	0	1
	Meller's mongoose	<i>Rhynchogale melleri</i>	1	0	1	0	0
MGR	Brown hyaena	<i>Hyaena brunnea</i>	216	86	130	28	70
	Spotted hyaena	<i>Crocuta crocuta</i>	173	78	95	18	51

	Black-backed jackal	<i>Lupulella mesomelas</i>	70	24	46	3	27
	Leopard	<i>Panthera pardus</i>	44	17	27	8	11
	Lion	<i>Panthera leo</i>	36	12	24	3	14
	African wildcat	<i>Felis silvestris lybica</i>	25	7	18	3	15
	Banded mongoose	<i>Mungos mungo</i>	13	11	2	4	1
	Genet	<i>Genetta spp.</i>	10	4	6	1	3
	Slender mongoose	<i>Galerella sanguinea</i>	10	2	8	1	8
	Caracal	<i>Caracal caracal</i>	8	4	4	1	4
	African civet	<i>Civettictis civetta</i>	8	3	5	1	1
	Honey badger	<i>Mellivora capensis</i>	7	4	3	1	2
	African wild dog	<i>Lycaon pictus</i>	6	4	2	0	2
	Aardwolf	<i>Proteles cristata</i>	4	2	2	0	0
	Cheetah	<i>Acinonyx jubatus</i>	4	2	2	1	1
	Serval	<i>Leptailurus serval</i>	4	1	3	1	2
	White-tailed mongoose	<i>Ichneumia albicauda</i>	2	2	0	0	0
MZNP	Black-backed jackal	<i>Lupulella mesomelas</i>	816	456	368	140	230
	Aardwolf	<i>Proteles cristata</i>	175	119	59	42	32
	Brown hyaena	<i>Hyaena brunnea</i>	108	76	32	24	20
	Bat-eared fox	<i>Otocyon megalotis</i>	57	23	34	2	7
	Lion	<i>Panthera leo</i>	49	19	30	5	10
	Small-spotted genet	<i>Genetta genetta</i>	25	20	5	3	1
	Caracal	<i>Caracal caracal</i>	23	14	9	2	5
	Cheetah	<i>Acinonyx jubatus</i>	6	4	2	1	0

	Cape grey mongoose	<i>Herpestes pulverulentus</i>	6	4	2	2	0
	Meerkat	<i>Suricata suricatta</i>	5	5	0	1	1
	Striped polecat	<i>Ictonyx striatus</i>	4	4	0	0	0
	Yellow mongoose	<i>Cynictis penicillata</i>	3	1	2	0	0
	Water mongoose	<i>Atilax paludinosus</i>	2	2	0	0	0
	Black-footed cat	<i>Felis nigripes</i>	1	0	1	0	1
	African striped weasel	<i>Poecilogale albinucha</i>	1	0	1	0	1
TKR	Bat-eared fox	<i>Otocyon megalotis</i>	260	149	111	23	44
	Black-backed jackal	<i>Lupulella mesomelas</i>	234	134	100	53	42
	Brown hyaena	<i>Hyaena brunnea</i>	85	45	40	23	12
	Cape fox	<i>Vulpes chama</i>	44	20	24	8	6
	African wildcat	<i>Felis silvestris lybica</i>	36	19	17	4	6
	Aardwolf	<i>Proteles cristata</i>	21	12	9	5	6
	Cheetah	<i>Acinonyx jubatus</i>	16	9	7	2	2
	Meerkat	<i>Suricata suricatta</i>	13	9	4	6	2
	African wild dog	<i>Lycaon pictus</i>	12	5	7	4	2
	Caracal	<i>Caracal caracal</i>	12	9	3	5	2
	Lion	<i>Panthera leo</i>	9	5	4	0	3
	Leopard	<i>Panthera pardus</i>	6	5	1	2	0
	Yellow mongoose	<i>Cynictis penicillata</i>	4	3	1	0	0
	Genet	<i>Genetta spp.</i>	3	2	1	1	0
	Striped polecat	<i>Ictonyx striatus</i>	3	1	2	1	0

3.4.1 Interspecific activity overlap

3.4.1.1 Associated Private Nature Reserves

The majority of species-pairs in APNR obtained moderate to high coefficients of overlap ($\hat{\Delta} > 0.700$) when the diel activity periods over the entire study period were considered (Table 3.2, Figure 3.1). In contrast, African wild dogs (*Lycaon pictus*) exhibited relatively low overlap in activity patterns with all other species ($\hat{\Delta} < 0.600$), which was especially evident when the 50% core isopleths were compared ($\hat{\Delta} < 0.100$) (Table 3.2). However, African wild dogs and honey badgers (*Mellivora capensis*) had a core activity overlap of 0.400. Lions and spotted hyaenas (*Crocuta crocuta*), and lions and leopards (*Panthera pardus*) had high overlap in overall core activity periods ($\hat{\Delta} > 0.850$) while all other species-pairs displayed moderate to low overlap in their core activity periods ($\hat{\Delta} < 0.570$). The highest overlap in activity patterns ($\hat{\Delta} = 0.949$, 95% CI: 0.886-0.999) and core activity periods ($\hat{\Delta} = 0.943$) were observed between lions and leopards. Although honey badgers and African civets (*Civettictis civetta*) had moderate overlap ($\hat{\Delta} = 0.691$, 95% CI: 0.521-0.847) in their activity patterns, they displayed very low overlap in their overall core activity periods ($\hat{\Delta} = 0.019$).

Table 3.2. Comparison of temporal activity patterns between carnivore species within the Associated Private Nature Reserves, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

	Species	Lion	Spotted hyaena	Leopard	African wild dog	Honey badger
A	Spotted hyaena	0.874 (0.818-0.923)				
	Leopard	0.949 (0.886-0.999)	0.857 (0.795-0.910)			
	African wild dog	0.556 (0.435-0.681)	0.527 (0.415-0.642)	0.532 (0.409-0.657)		
	Honey badger	0.801 (0.656-0.926)	0.703 (0.561-0.838)	0.811 (0.661-0.934)	0.576 (0.408-0.742)	
	African civet	0.797 (0.714-0.875)	0.848 (0.774-0.913)	0.804 (0.714-0.886)	0.392 (0.266-0.520)	0.691 (0.521-0.847)
B	Spotted hyaena	0.869				
	Leopard	0.934	0.362			
	African wild dog	0.004	0.099	0.003		
	Honey badger	0.464	0.174	0.510	0.400	
	African civet	0.529	0.567	0.491	0.003	0.019

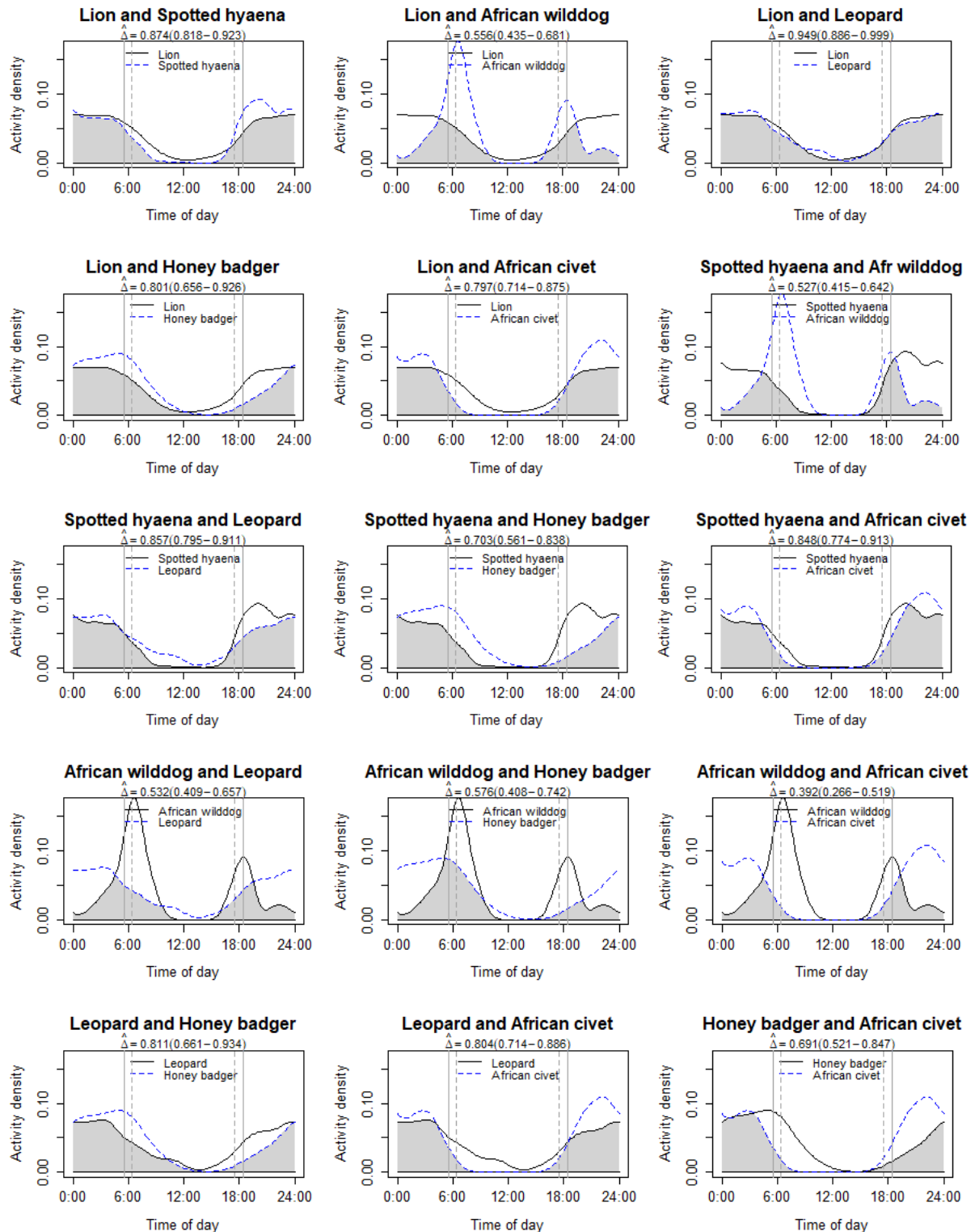


Figure 3.1. Kernel density overlap (shaded area) of carnivore species' diel activity patterns from the Associated Private Nature Reserves, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by solid vertical lines during wet seasons, and stippled vertical lines during dry seasons.

All species-pairs showed moderate to high ($\hat{\Delta} > 0.720$) overlap during wet and dry seasons (Table 3.3, Figure 3.2). Lions and spotted hyaenas had very high overlap during the wet seasons, but a clear decrease was observed during the dry seasons. In addition, lions and spotted hyaenas had moderate overlap in their core activity periods during the wet seasons but very low overlap during the dry seasons, with a marked decrease from 56.4% in the wet season to 12.6% during the dry season (Table 3.3). The same pattern was observed between lions and African civets.

Table 3.3. Comparisons of diel activity patterns between carnivores during wet and dry seasons within the Associated Private Nature Reserves, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity. B: Coefficient of overlap ($\hat{\Delta}$) in core activity periods (50% isopleths).

Season	Species	Lion	Spotted hyaena	Leopard
A	Spotted hyaena	0.900 (0.835-0.955)		
	Wet			
	Leopard	0.827 (0.711-0.925)	0.830 (0.744-0.905)	
	African civet	0.780 (0.635-0.902)	0.856 (0.719-0.954)	0.777 (0.636-0.900)
	Spotted hyaena	0.764 (0.673-0.849)		
	Dry			
	Leopard	0.850 (0.738-0.945)	0.876 (0.795-0.944)	
	African civet	0.726 (0.606-0.836)	0.822 (0.729-0.902)	0.811 (0.699-0.911)
B	Spotted hyaena	0.564		
	Wet			
	Leopard	0.425	0.406	
	African civet	0.395	0.571	0.640
	Spotted hyaena	0.126		
	Dry			
	Leopard	0.466	0.426	
	African civet	0.141	0.466	0.650

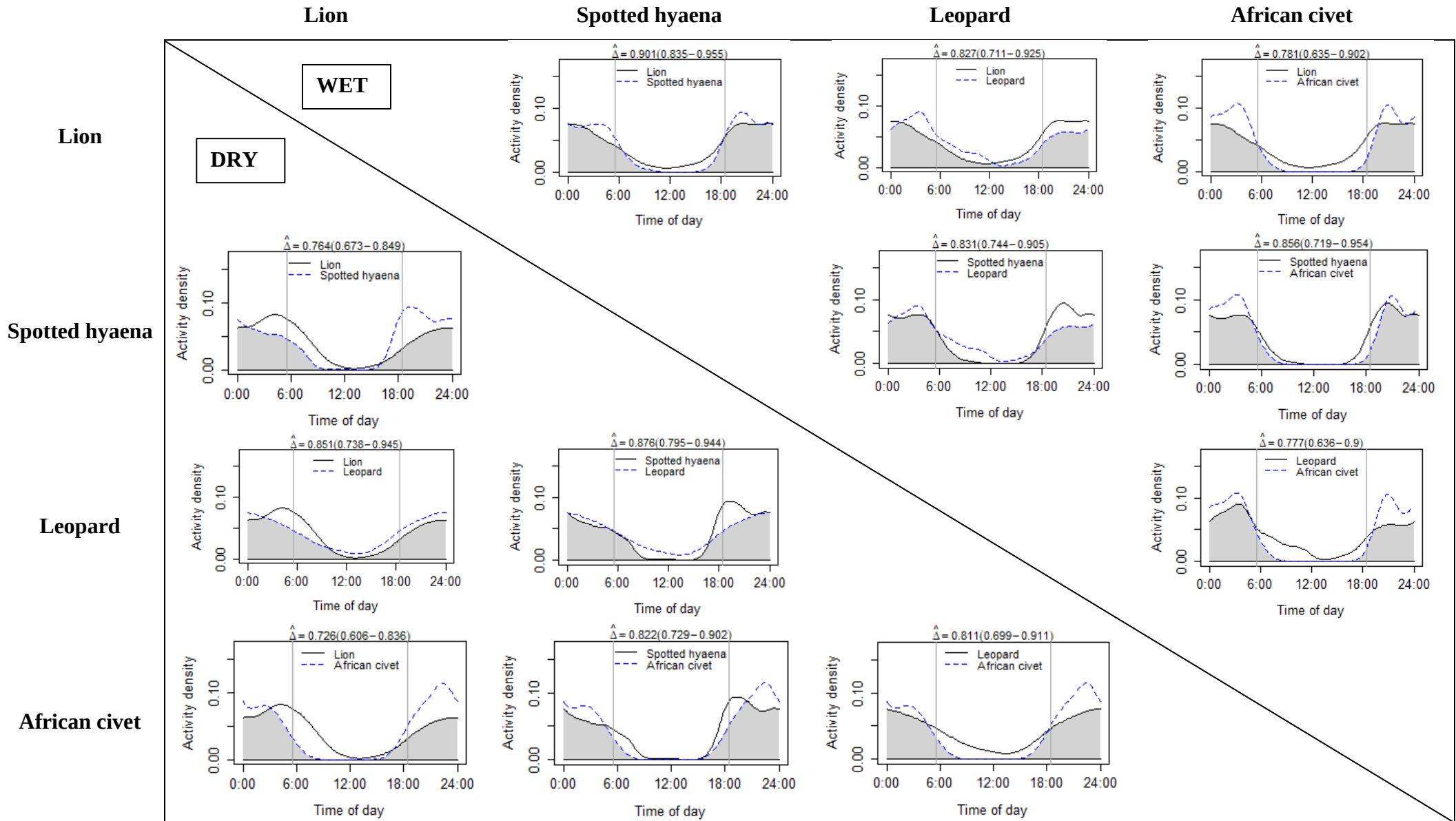


Figure 3.2. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the wet and dry seasons from the Associated Private Nature Reserves, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). The solid and vertical lines represent times of sunrise and sunset during the respective seasons.

Similar patterns in overlap were observed during APNR's hottest and coldest months of the year (Table 3.4, Figure 3.3). The least overlap in diel activity patterns during these periods was between lions and spotted hyaenas in the year's coldest months (Table 3.4). Furthermore, there was less overlap in core activity periods between the species during the hottest and coldest months of the year compared to the wet and dry seasons. In particular, lions and leopards had very low overlap in their core activity periods during both the hottest and coldest months ($\hat{\Delta} < 0.280$). Yet, a relatively high overlap in core activity periods was maintained between leopards and spotted hyaenas in the hottest and coldest months of the year ($\hat{\Delta} > 0.590$).

Table 3.4. Comparisons of diel activity patterns between carnivores during the hottest (December and January) and coldest (June and July) months of the year within the Associated Private Nature Reserves, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Species		Lion	Spotted hyaena
A	Spotted hyaena	0.834 (0.682-0.955)	
	Hottest		
	Leopard	0.753 (0.551-0.914)	0.729 (0.560-0.881)
	Spotted hyaena	0.663 (0.529-0.789)	
B	Coldest		
	Leopard	0.724 (0.559-0.876)	0.859 (0.745-0.954)
	Spotted hyaena	0.278	
	Hottest		
	Leopard	0.327	0.598
	Spotted hyaena	0.175	
	Coldest		
	Leopard	0.171	0.691

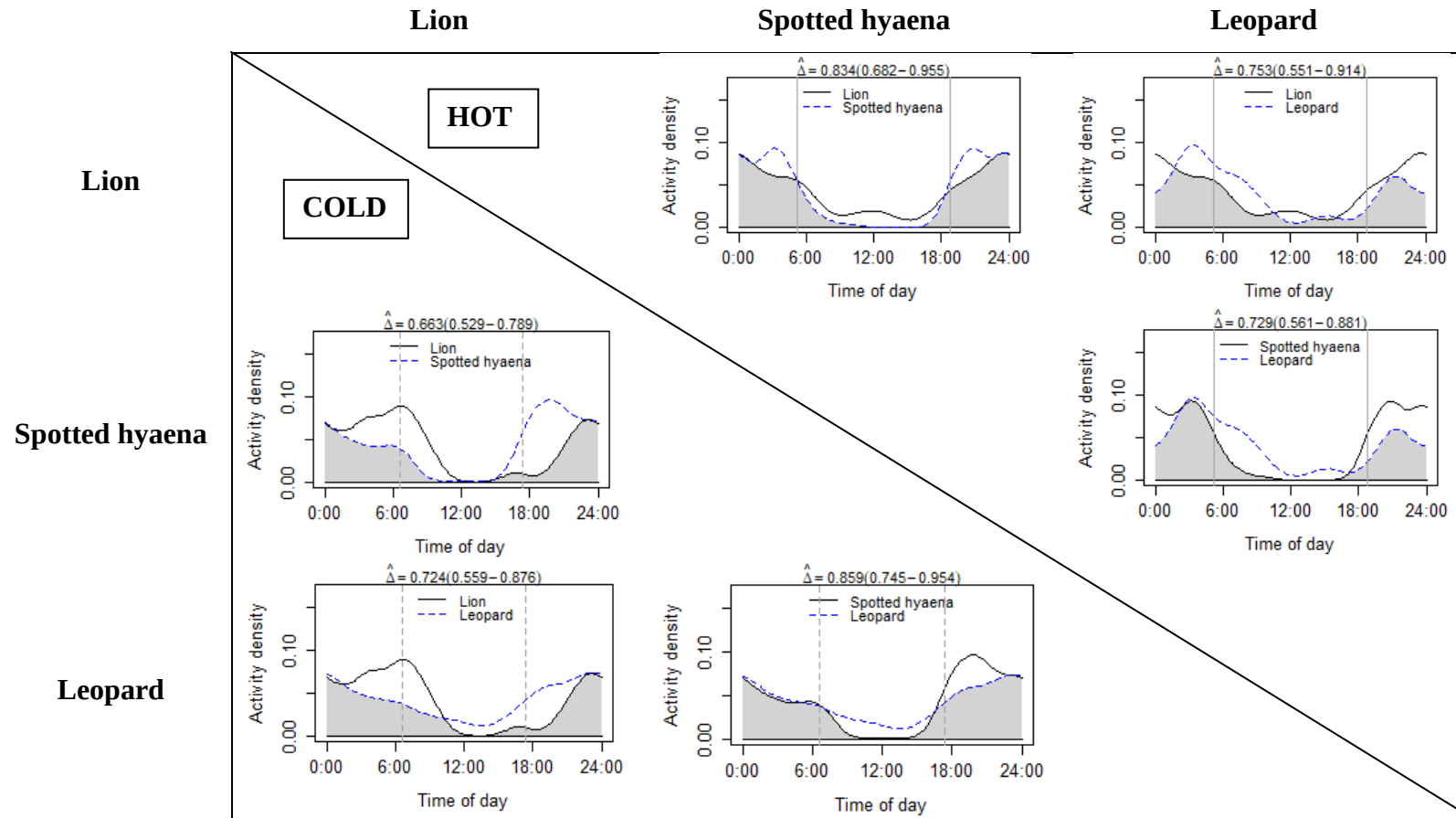


Figure 3.3. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the hottest and coldest months of the year from the Associated Private Nature Reserves, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the stippled vertical lines.

3.4.1.2 Madikwe Game Reserve

Most of MGR's species-pairs had moderate to high overlap ($\hat{A} > 0.700$) in their overall activity patterns (Table 3.5, Figure 3.4). The overall diel activity overlap in MGR was greatest between leopards and black-backed jackals (*Lupulella mesomelas*), and lowest between lions and both species of hyaenas, and African wildcats (*Felis silvestris lybica*) with leopards, brown hyaenas (*Hyaena brunnea*), and black-backed jackals. This was accentuated when core activity periods were compared, with very low overlap ($\hat{A} < 0.140$) between lions and spotted hyaenas, and lions and brown hyaenas (Table 3.5). Despite having a high overlap in overall activity patterns, spotted hyaenas and black-backed jackals had very low overlap in their core activity periods ($\hat{A} = 0.100$). The most overlap in core activity periods was found between lions and leopards, lions and African wildcats, and leopards and black-backed jackals ($\hat{A} > 0.500$).

All species comparisons undertaken in this study for wet and dry seasons displayed moderate to high overlap ($\hat{A} > 0.700$) in their activity patterns during each season (Table 3.6, Figure 3.5). However, a clear decrease in overlap in activity patterns and core activity periods was observed in the dry season between spotted hyenas and brown hyaenas (Table 3.6). Despite having high overlap in their activity patterns during both seasons, black-backed jackals and spotted hyaenas had very low overlap in their core activity periods, with even less overlap during the dry seasons. Brown hyaenas and black-backed jackals showed an increase in activity pattern overlap during the dry season, but a decrease in the overlap of core activity ranges during this period.

Only one species, brown hyaenas, recorded more than 20 photo-captures during MGR's hottest and coldest months of the year; therefore, no comparisons could be made during the months of contrasting temperature extremes in MGR.

Table 3.5. Comparison of temporal activity patterns between carnivore species within Madikwe Game Reserve, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Species		Lion	Spotted hyaena	Leopard	Brown hyaena	Black-backed jackal
A	Spotted hyaena	0.655 (0.528-0.779)				
	Leopard	0.781 (0.629-0.914)	0.712 (0.589-0.827)			
	Brown hyaena	0.656 (0.516-0.794)	0.797 (0.721-0.869)	0.776 (0.651-0.888)		
	Black-backed jackal	0.765 (0.620-0.896)	0.750 (0.635-0.852)	0.852 (0.735-0.947)	0.793 (0.687-0.890)	
	African wildcat	0.722 (0.569-0.853)	0.791 (0.628-0.927)	0.654 (0.499-0.808)	0.666 (0.520-0.810)	0.670 (0.524-0.811)
B	Spotted hyaena	0.078				
	Leopard	0.526	0.288			
	Brown hyaena	0.134	0.497	0.477		
	Black-backed jackal	0.357	0.100	0.512	0.463	
	African wildcat	0.688	0.208	0.387	0.055	0.313

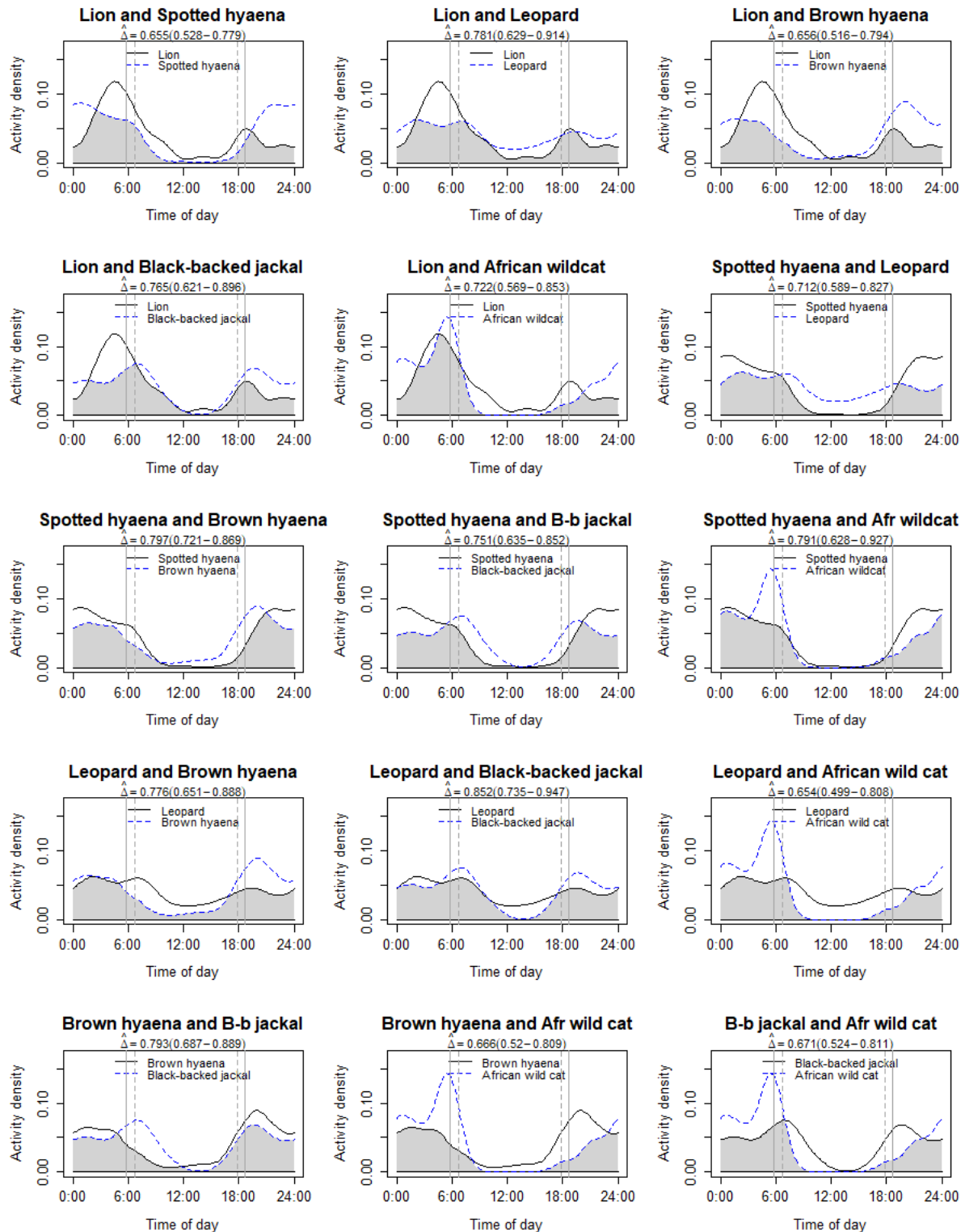


Figure 3.4. Kernel density overlap (shaded area) of diel activity patterns of carnivore species from Madikwe Game Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the solid vertical lines during wet seasons, and stippled vertical lines during dry seasons.

Table 3.6. Comparisons of diel activity patterns between carnivores during the wet and dry seasons within Madikwe Game Reserve, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Season	Species	Spotted hyaena	Brown hyaena
A	Brown hyaena	0.874 (0.769-0.956)	
	Wet		
	Black-backed jackal	0.749 (0.594-0.890)	0.744 (0.587-0.882)
	Brown hyaena	0.705 (0.606-0.800)	
Dry	Black-backed jackal	0.706 (0.576-0.829)	0.777 (0.651-0.884)
B	Brown hyaena	0.560	
	Wet		
	Black-backed jackal	0.225	0.528
	Brown hyaena	0.338	
Dry	Black-backed jackal	0.189	0.395

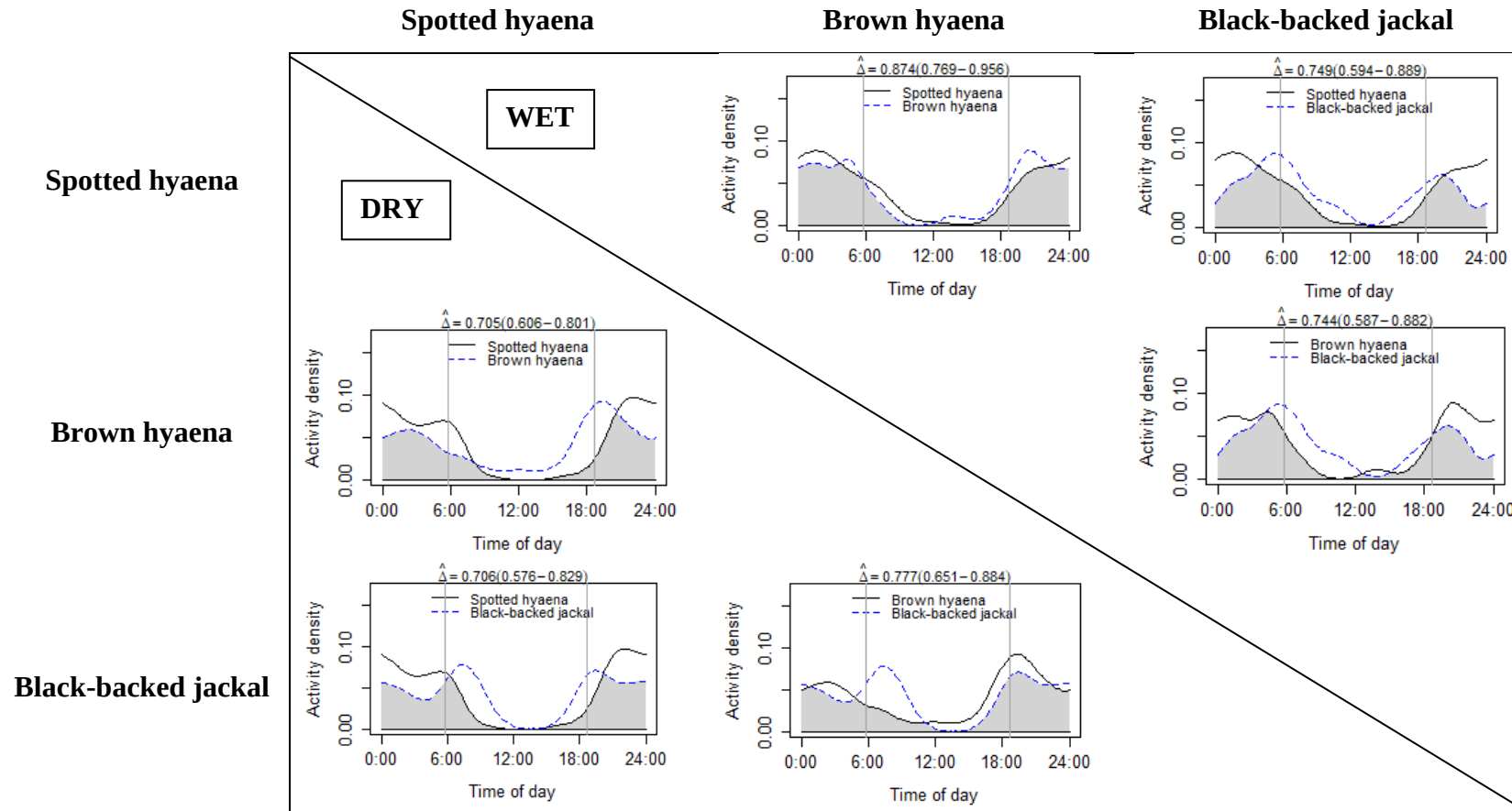


Figure 3.5. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the wet and dry seasons from Madikwe Game Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset during the respective seasons are represented by the solid vertical lines.

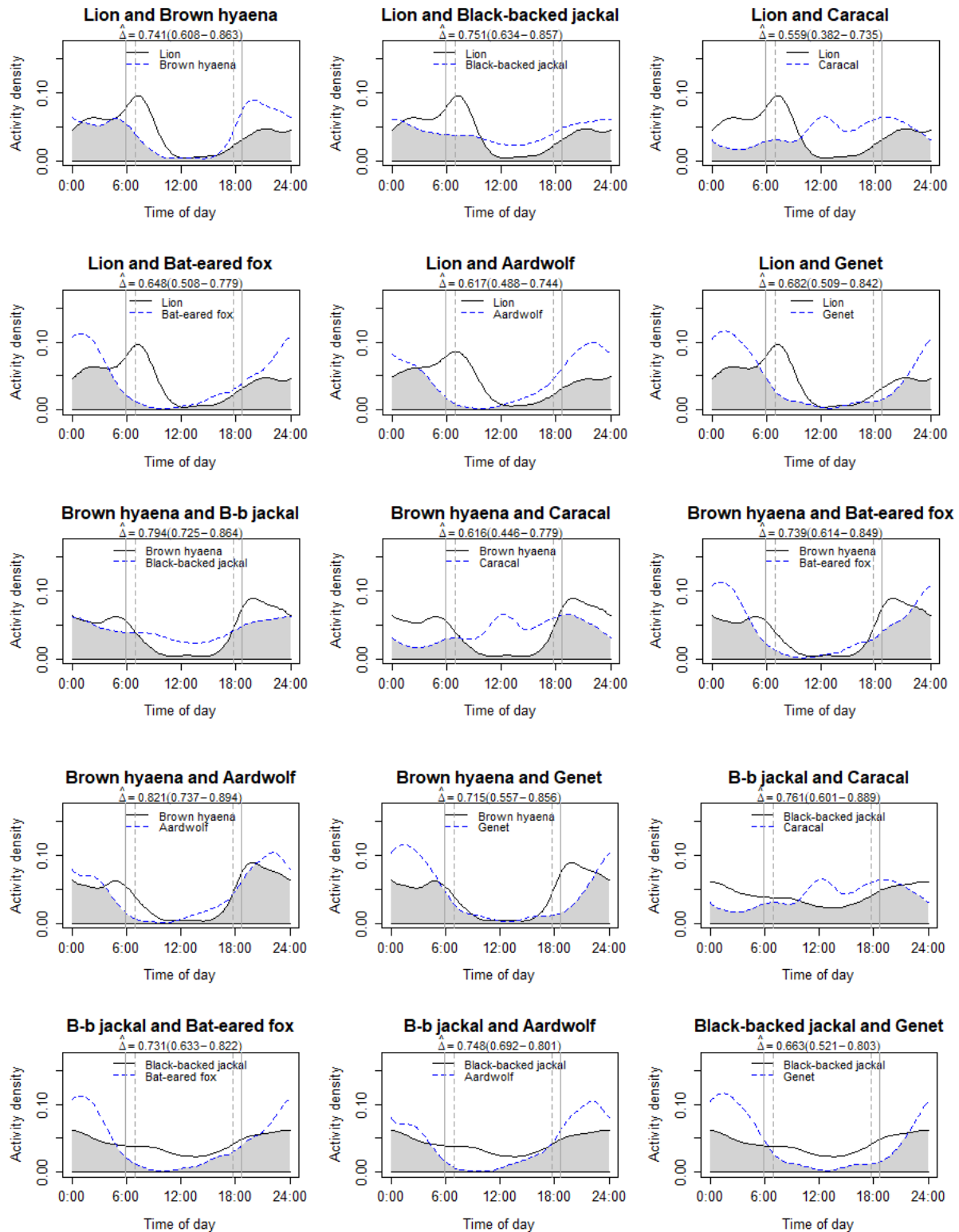
3.4.1.3 Mountain Zebra National Park

Only bat-eared foxes (*Otocyon megalotis*) and small-spotted genets (*Genetta genetta*), bat-eared foxes and aardwolves (*Proteles cristata*), and aardwolves and brown hyaenas had high overlap ($\hat{\Delta} > 0.800$) in their overall activity patterns among all the species-pairs studied in MZNP (Table 3.7, Figure 3.6). The lowest overlap in overall activity patterns among MZNP's carnivore species was centred around the activity of caracals (*Caracal caracal*), where low overlap was observed between caracals and lions, small-spotted genets, bat-eared foxes, and aardwolves ($\hat{\Delta} < 0.590$). The remaining species-pairs all had moderate to high overlap in their overall activity patterns ($0.600 < \hat{\Delta} < 0.800$). However, lions had low overlap ($\hat{\Delta} < 0.280$) in their overall core activity periods with all other species (Table 3.7), whereas their core activity periods had no overlap with that of brown hyaenas, caracals, and aardwolves ($\hat{\Delta} = 0.002$). Black-backed jackals had relatively moderate overlap ($\hat{\Delta} > 0.430$) in their overall core activity periods with most other species, except for lions and caracals ($\hat{\Delta} < 0.350$). Even though bat-eared foxes and aardwolves had moderate to high overlap in their overall activity patterns, there was little overlap in their core activity periods. A similar pattern was observed between bat-eared foxes and brown hyaenas. Among all the species-pairs, aardwolves and brown hyaenas, and bat-eared foxes and small-spotted genets had the highest overlap ($\hat{\Delta} > 0.790$) in overall core activity periods.

Regarding seasonal differences in interspecific activity patterns, the majority of species-pairs had moderate to high overlap ($\hat{\Delta} > 0.650$) in their diel activity patterns during both seasons (Table 3.8, Figure 3.7). However, most species-pairs showed less overlap during the dry seasons than during the wet seasons. Exceptions to this, and thus an increase in overall activity overlap during the dry seasons, were obtained for bat-eared foxes compared to brown hyaenas and black-backed jackals.

Table 3.7. Comparison of temporal activity patterns between carnivores within Mountain Zebra National Park, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Species		Lion	Brown hyaena	Caracal	Black-backed jackal	Aardwolf	Bat-eared fox
A	Brown hyaena	0.741 (0.608-0.863)					
	Caracal	0.560 (0.382-0.735)	0.616 (0.446-0.779)				
	Black-backed jackal	0.751 (0.634-0.857)	0.794 (0.725-0.864)	0.761 (0.601-0.890)			
	Aardwolf	0.617 (0.488-0.744)	0.820 (0.737-0.894)	0.587 (0.422-0.752)	0.748 (0.692-0.801)		
	Bat-eared fox	0.648 (0.508-0.780)	0.739 (0.614-0.849)	0.532 (0.361-0.701)	0.731 (0.633-0.822)	0.828 (0.708-0.933)	
	Genet	0.682 (0.509-0.842)	0.715 (0.557-0.856)	0.452 (0.260-0.647)	0.663 (0.520-0.803)	0.671 (0.515-0.819)	0.839 (0.685-0.962)
B	Brown hyaena	0.002					
	Caracal	0.002	0.393				
	Black-backed jackal	0.213	0.672	0.343			
	Aardwolf	0.002	0.793	0.291	0.641		
	Bat-eared fox	0.225	0.246	0.003	0.546	0.385	
	Genet	0.272	0.125	0.003	0.448	0.228	0.827



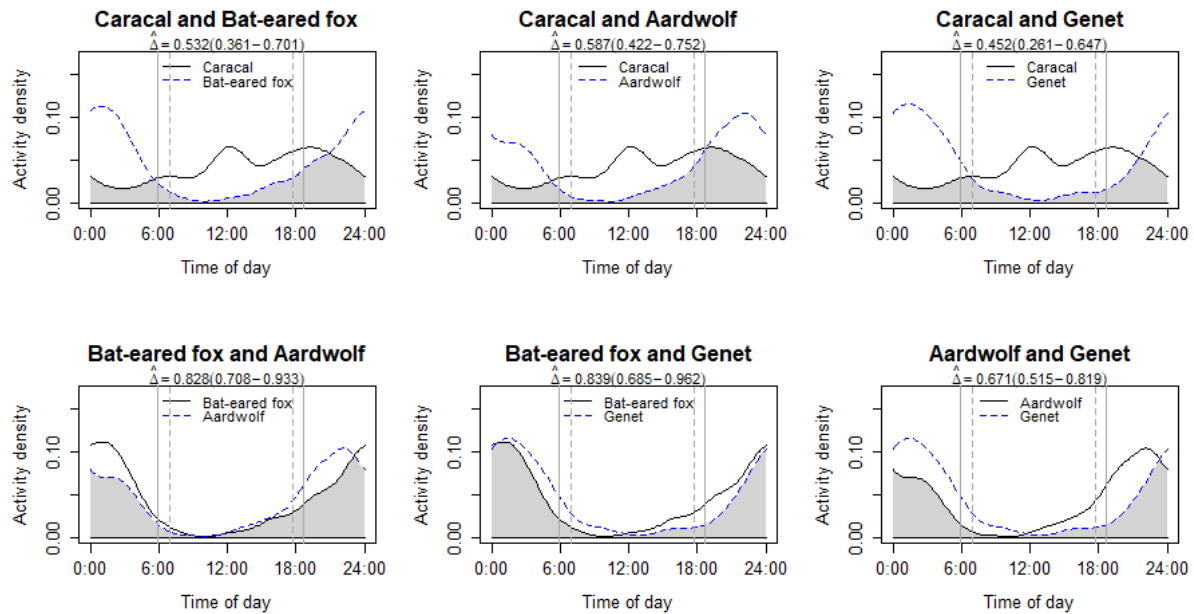


Figure 3.6. Kernel density overlap (shaded area) of diel activity patterns of carnivore species from Mountain Zebra National Park, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the solid vertical lines during wet seasons, and stippled vertical lines during dry seasons.

Similar seasonal patterns were observed for core activity overlap among MZNP's carnivores, with most species-pairs showing a decrease in overlap during the dry seasons (Table 3.8). Bat-eared foxes had low core activity overlap with brown hyaenas during both the wet and dry seasons ($\hat{\Delta} < 0.130$), with almost no overlap during the wet seasons. The most noticeable seasonal difference in core activity overlap among MZNP's carnivores was between aardwolves and bat-eared foxes, which saw an 86% decrease during the dry seasons, from a moderate overlap during the wet season to almost none during the dry season.

Brown hyaenas, black-backed jackals, and aardwolves, had high overlap in both diel activity patterns and core activity periods during MZNP's hottest months, while there was a noticeable decrease during the coldest months (Table 3.9, Figure 3.8). Still, brown hyaenas and aardwolves had very high overlap in their core activity periods during MZNP's hottest and

coldest months, separately; both species peaked in activity around midnight during the hottest months and shortly after dusk during the coldest months of the year (Figure 3.8).

Table 3.8. Comparisons of diel activity patterns between carnivores during the wet and dry seasons within Mountain Zebra National Park, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Season	Species	Brown hyaena	Black-backed jackal	Aardwolf
A	Black-backed jackal	0.824 (0.731-0.909)		
	Aardwolf	0.784 (0.673-0.882)	0.742 (0.667-0.815)	
	Bat-eared fox	0.668 (0.495-0.822)	0.664 (0.518-0.800)	0.791 (0.631-0.925)
	Black-backed jackal	0.721 (0.609-0.822)		
	Aardwolf	0.645 (0.481-0.790)	0.654 (0.559-0.749)	
	Bat-eared fox	0.716 (0.549-0.857)	0.707 (0.585-0.824)	0.659 (0.492-0.816)
B	Black-backed jackal	0.595		
	Aardwolf	0.506	0.645	
	Bat-eared fox	0.030	0.507	0.461
	Black-backed jackal	0.399		
	Aardwolf	0.610	0.468	
	Bat-eared fox	0.128	0.483	0.063

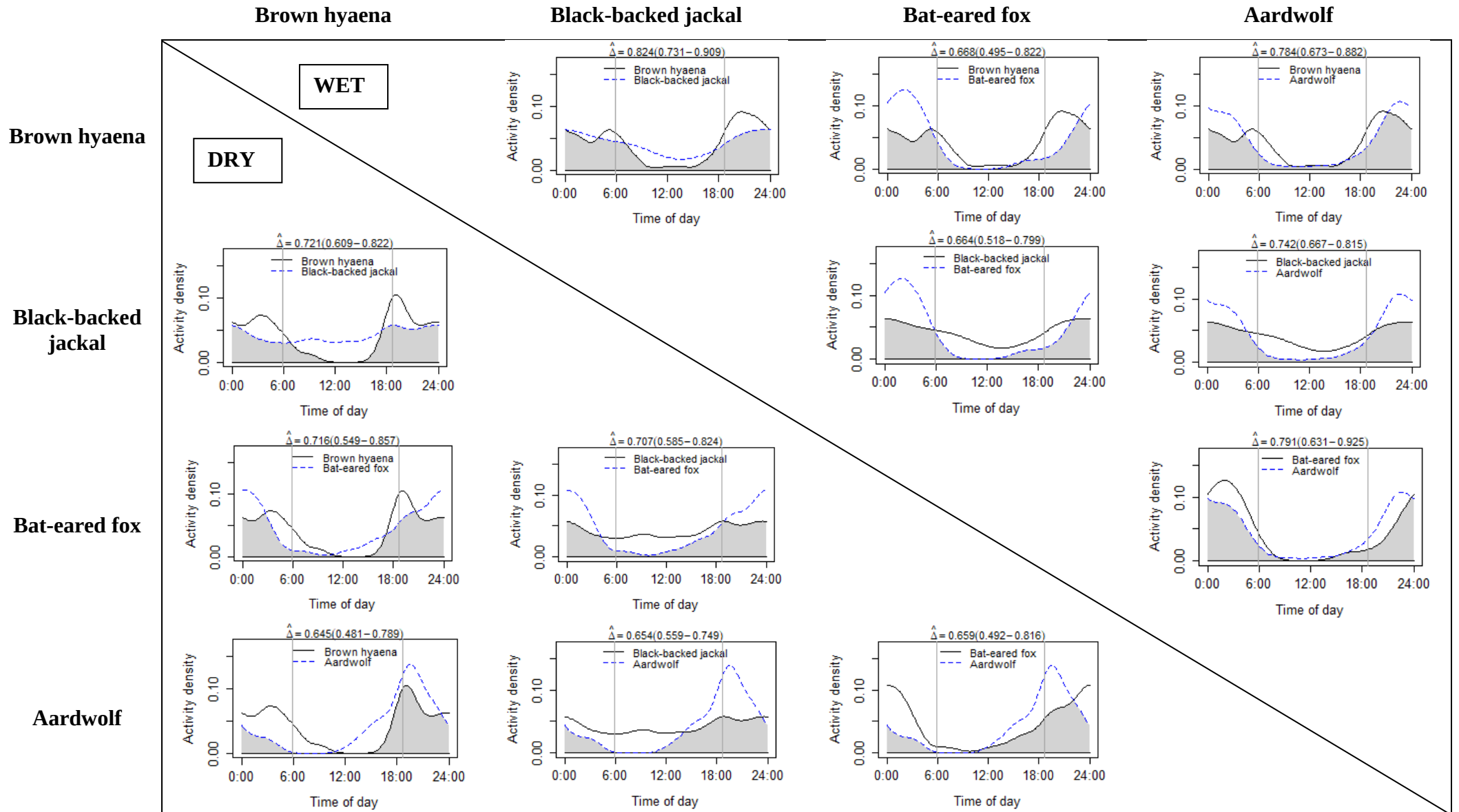


Figure 3.7. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the wet and dry seasons from Mountain Zebra National Park, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset during the respective seasons are represented by the solid vertical lines.

Table 3.9. Comparisons of diel activity patterns between carnivores during the hottest (January and February) and coldest (June, July, and August) months of the year within Mountain Zebra National Park, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

	Species	Brown hyaena	Black-backed jackal
A	Black-backed jackal	0.814 (0.671-0.932)	
	Hottest		
	Aardwolf	0.879 (0.733-0.994)	0.738 (0.627-0.839)
	Black-backed jackal	0.675 (0.521-0.813)	
Coldest	Aardwolf	0.645 (0.460-0.808)	0.561 (0.458-0.663)
B	Black-backed jackal	0.694	
	Hottest		
	Aardwolf	0.911	0.637
	Black-backed jackal	0.550	
Coldest	Aardwolf	0.820	0.421

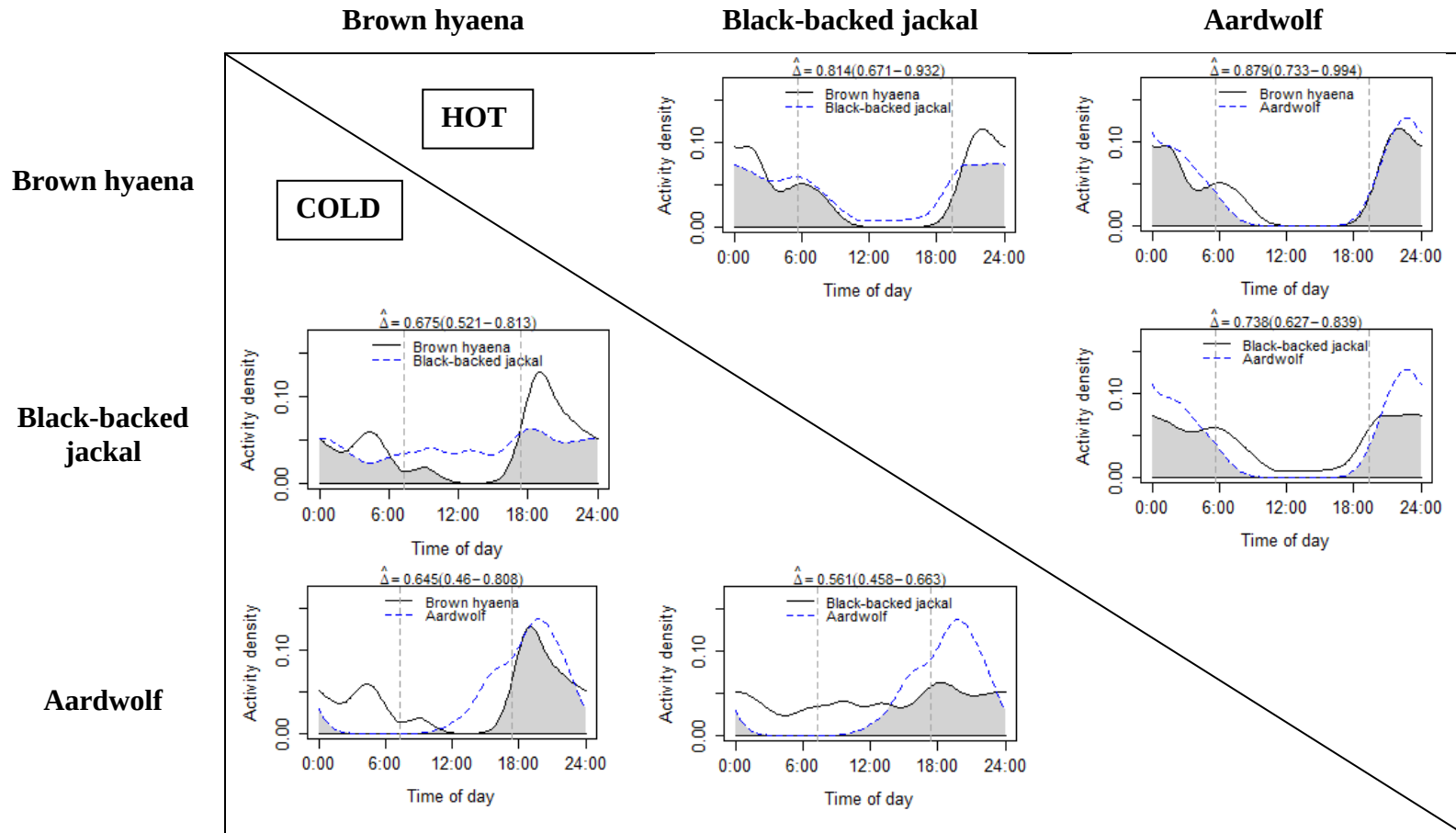


Figure 3.8. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the hottest and coldest months of the year from Mountain Zebra National Park, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the stippled vertical lines.

3.4.1.4 Tswalu Kalahari Reserve

Over the entire study period, the majority of carnivore species-pairs within TKR had high overlap ($\hat{\Delta} > 0.800$) in their diel activity patterns (Table 3.10, Figure 3.9). Only aardwolf associated species-pairs showed moderate overlap ($\hat{\Delta} > 0.690$), with the lowest overlap observed between aardwolves and both black-backed jackals and brown hyaenas. The majority of TKR's species-pairs had relatively high overlap ($\hat{\Delta} > 0.500$) in their overall core activity periods (Table 3.10). Brown hyaenas and aardwolves had the least amount of overlap in core activity periods, while bat-eared foxes and Cape foxes (*Vulpes chama*), and black-backed jackals and Cape foxes had the most. Aardwolves peaked in activity prior to the start of the brown hyaena's core activity period (Figure 3.9).

During both the wet and dry seasons, all species-pairs had high ($\hat{\Delta} > 0.800$) overlap in diel activity patterns (Table 3.11, Figure 3.10). Despite having very similar temporal activity patterns for the majority of the time, a noticeable decrease in overlap, both of diel activity and core periods, were observed during the dry season between bat-eared foxes and Cape foxes. In contrast, bat-eared foxes and black-backed jackals had substantially more overlap in their diel activity patterns during the dry season than the wet season, when core activity overlap increased from a moderate $\hat{\Delta} = 0.474$ to a high overlap of $\hat{\Delta} = 0.857$ (Table 3.11). All other species-pairs experienced slight differences in their core activity overlap between wet and dry seasons.

Only bat-eared foxes and black-backed jackals recorded more than 20 photo-captures during TKR's hottest and coldest months, respectively. During both periods of seasonal extremes, these species' activity patterns had moderate to high overlap (Table 3.12, Figure 3.11). In addition, the two species also had relatively similar core activity periods during both periods (Table 3.12).

Table 3.10. Comparison of temporal activity patterns between carnivore species within Tswalu Kalahari Reserve, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Species		Brown hyaena	Black-backed jackal	Aardwolf	Bat-eared fox	Cape fox
A	Black-backed jackal	0.834 (0.745-0.911)				
	Aardwolf	0.711 (0.541-0.864)	0.691 (0.535-0.836)			
	Bat-eared fox	0.839 (0.741-0.921)	0.860 (0.792-0.921)	0.805 (0.639-0.925)		
	Cape fox	0.887 (0.777-0.970)	0.881 (0.785-0.957)	0.749 (0.572-0.900)	0.891 (0.786-0.971)	
	African wildcat	0.847 (0.724-0.948)	0.836 (0.713-0.936)	0.764 (0.583-0.914)	0.822 (0.697-0.921)	0.885 (0.751-0.985)
B	Black-backed jackal	0.600				
	Aardwolf	0.223	0.529			
	Bat-eared fox	0.433	0.790	0.729		
	Cape fox	0.455	0.815	0.672	0.891	
	African wildcat	0.388	0.540	0.592	0.555	0.570

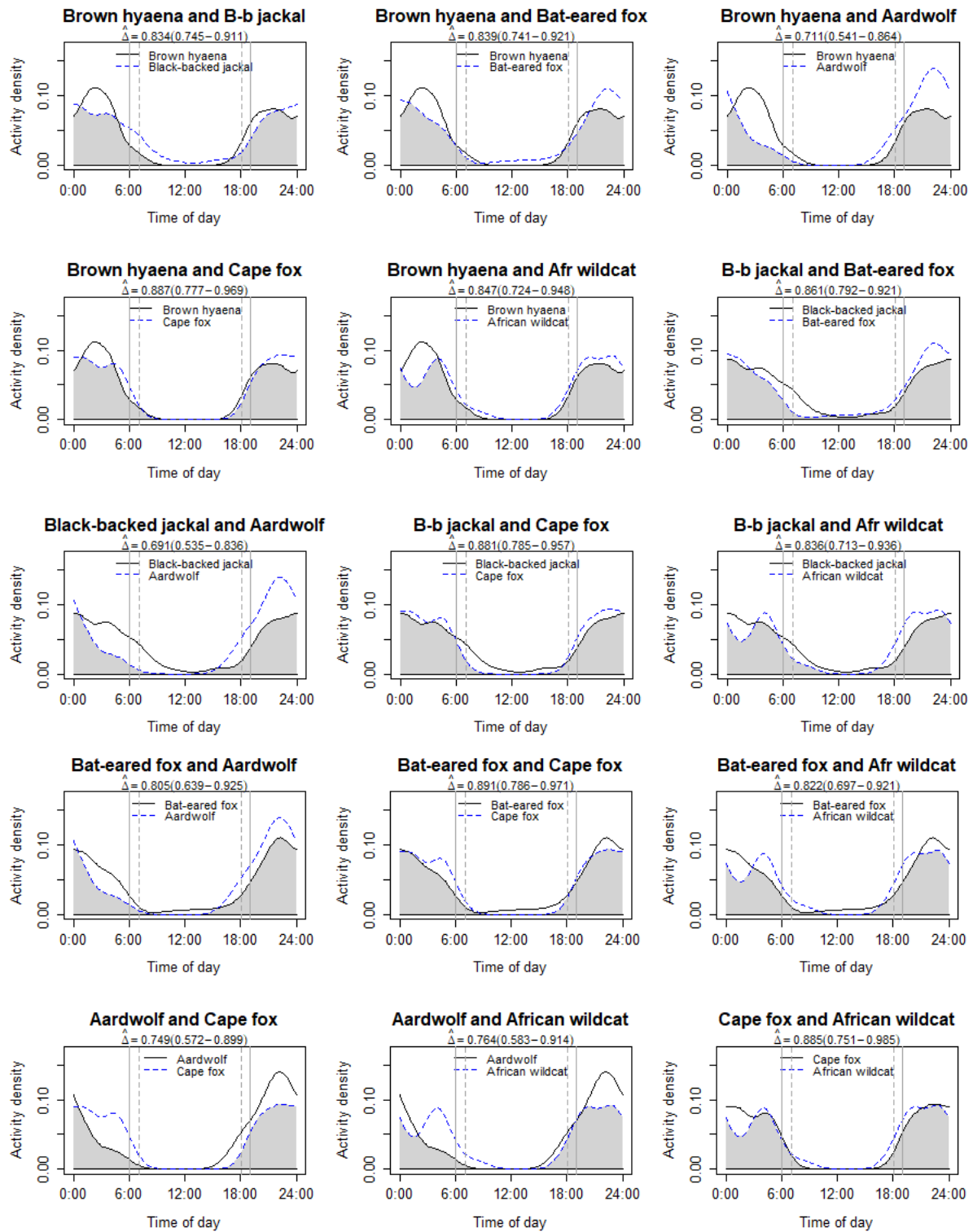


Figure 3.9. Kernel density overlap (shaded area) of diel activity patterns of carnivore species from Tswalu Kalahari Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the solid vertical lines during wet seasons, and stippled vertical lines during dry seasons.

Table 3.11. Comparisons of diel activity patterns between carnivores during the wet and dry seasons within Tswalu Kalahari Reserve, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

Season	Species	Brown hyaena	Black-backed jackal	Bat-eared fox
A	Black-backed jackal	0.850 (0.741-0.939)		
	Wet	Bat-eared fox	0.850 (0.731-0.941)	0.837 (0.743-0.919)
		Cape fox	0.860 (0.692-0.983)	0.826 (0.666-0.950)
				0.933 (0.796-1.000)
	Dry	Black-backed jackal	0.801 (0.684-0.899)	
		Bat-eared fox	0.812 (0.684-0.914)	0.875 (0.789-0.950)
		Cape fox	0.852 (0.696-0.968)	0.814 (0.671-0.930)
B	Black-backed jackal	0.560		
	Wet	Bat-eared fox	0.381	0.474
		Cape fox	0.353	0.474
				0.907
	Dry	Black-backed jackal	0.520	
		Bat-eared fox	0.390	0.857
		Cape fox	0.424	0.420
				0.381

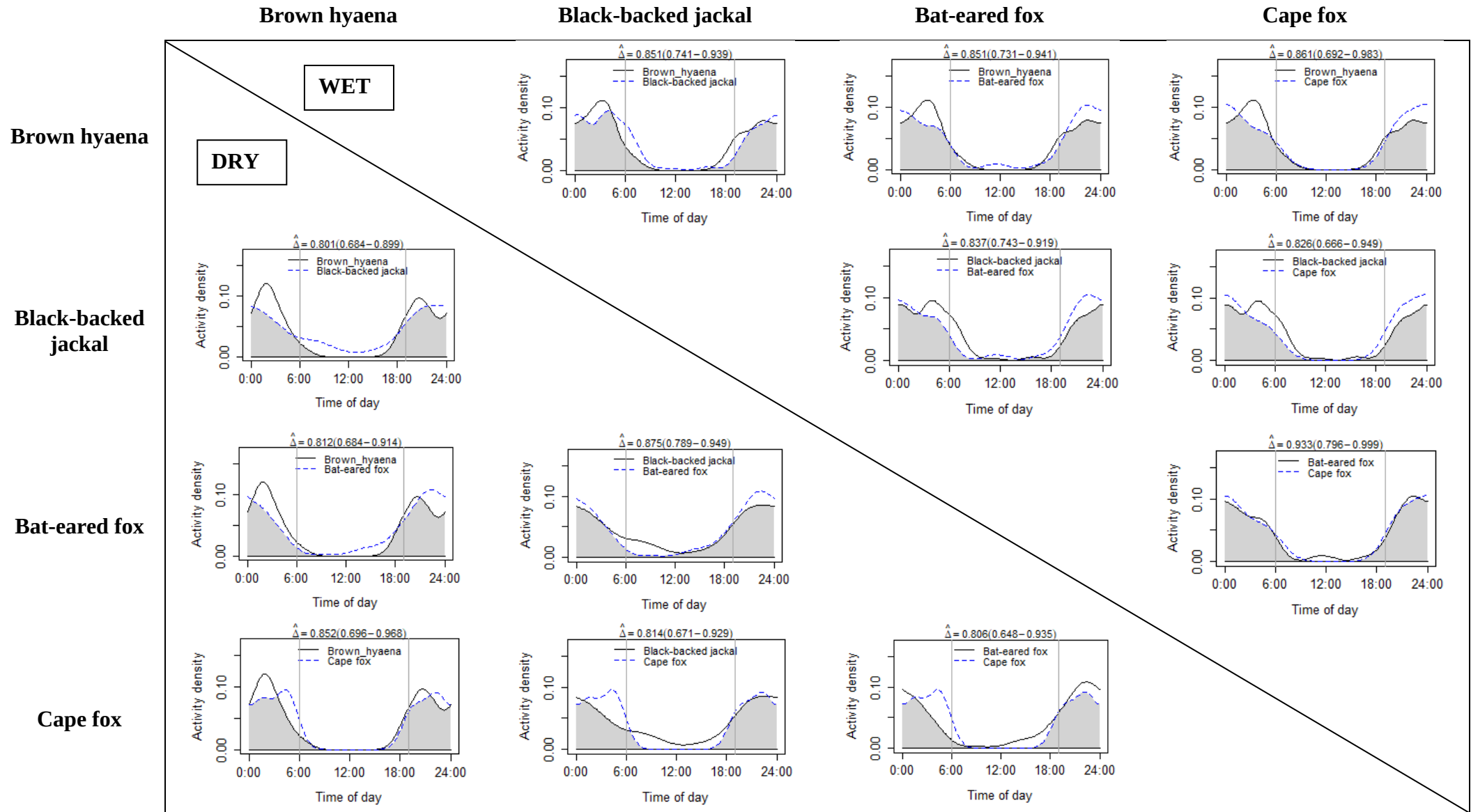


Figure 3.10. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the wet and dry seasons from the Tswalu Kalahari Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset during the respective seasons are represented by the solid vertical lines.

Table 3.12. Comparisons of diel activity patterns between carnivores during the hottest (December, January, and February) and coldest (June and July) months of the year within Tswalu Kalahari Reserve, South Africa. A: Coefficient of overlap, $\hat{\Delta}$ (95% CI), in diel activity patterns. B: Coefficient of overlap ($\hat{\Delta}$) in the core activity periods (50% isopleths).

		Species	Black-backed jackal
A	Hottest	Bat-eared fox	0.737 (0.555-0.897)
	Coldest	Bat-eared fox	0.772 (0.632-0.899)
B	Hottest	Bat-eared fox	0.594
	Coldest	Bat-eared fox	0.696

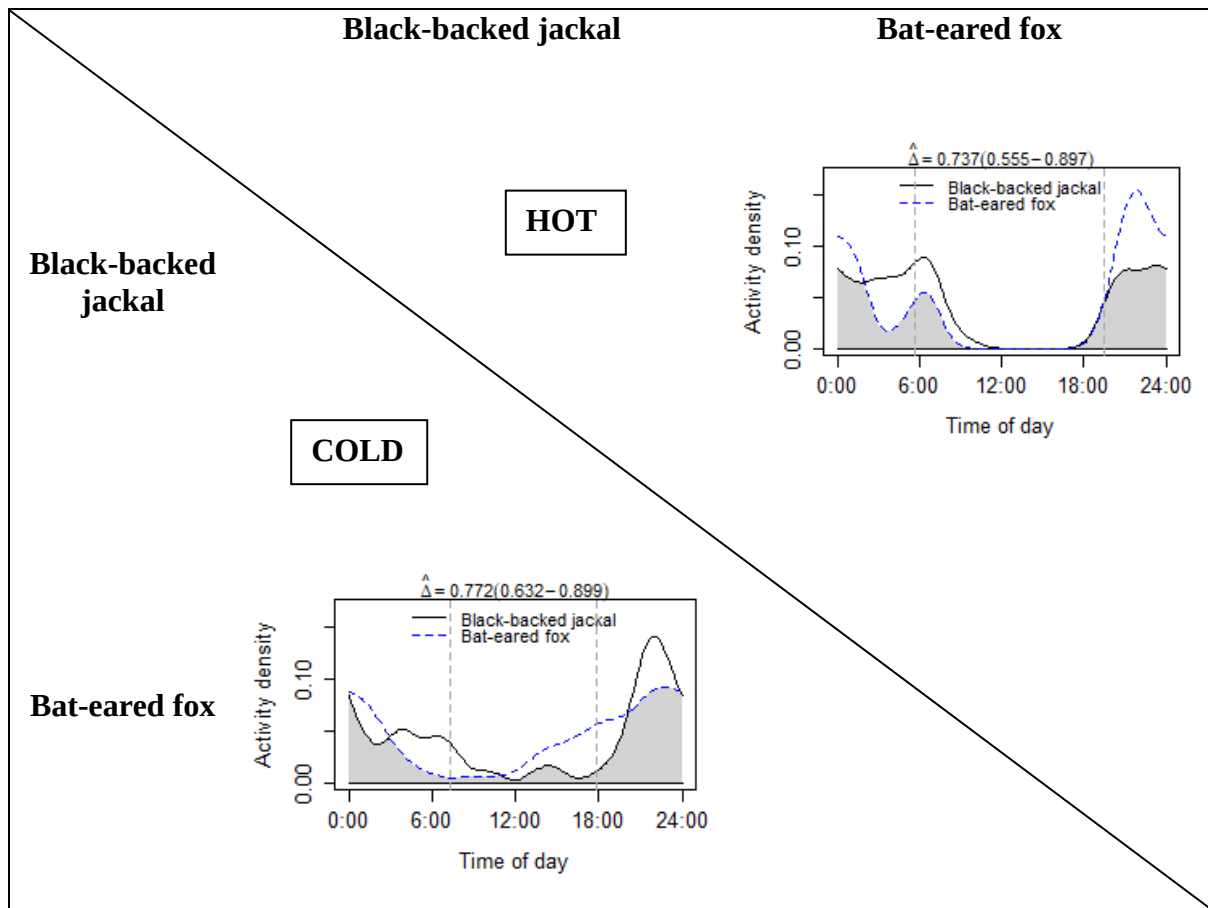


Figure 3.11. Kernel density overlap (shaded area) of carnivore species' diel activity patterns during the hottest and coldest months of the year from the Tswalu Kalahari Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the stippled vertical lines.

Only brown hyaenas (55 detections in Korannaberg and 30 in Lekgaba), black-backed jackals (151 detections in Korannaberg and 83 in Lekgaba), and bat-eared foxes (240 detections in Korannaberg and 20 in Lekgaba) recorded enough detections to have their species-specific diel activity patterns compared between the two sections. Species-specific overlap in diel activity patterns for brown hyaenas ($\hat{\Delta}_1 = 0.848$, 95% CI = 0.706–0.961), black-backed jackals ($\hat{\Delta}_4 = 0.939$, 95% CI = 0.857–1.000), and bat-eared foxes ($\hat{\Delta}_1 = 0.855$, 95% CI = 0.710–0.964) were

high when each of the species' diel activity patterns were separately compared between the Lekgaba (lions present) and the Korannaberg sections (lions absent) of TKR (Figure 3.12).

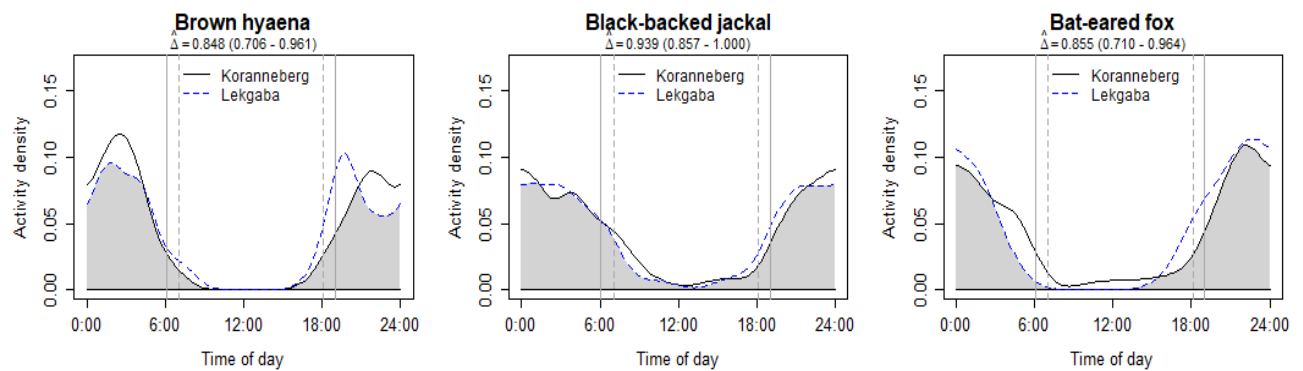


Figure 3.12. Kernel density overlap (shaded area) of species-specific diel activity patterns of carnivore species from the two sections, Korannaberg (lions absent) and Lekgaba (lions present), of Tswalu Kalahari Reserve, South Africa. Overlap is numerically represented by the coefficient of overlap, $\hat{\Delta}$ (95% CI). Times of sunrise and sunset are represented by the solid vertical lines during wet seasons, and stippled vertical lines during dry seasons.

3.4.2 Fine-scaled temporal partitioning

Only 12 species-pairs across all four protected areas obtained enough proximate photo-captures within seven days of the reference encounter (> 20) to be included in the analysis (Table 3.13).

Table 3.13. The number of paired camera trap detections of a carnivore species with the nearest detection of another carnivore species (proximate detection) at the same camera trap station from four South African protected areas.

Site	Species-pair	Total proximate	Proximate detections
		detections	within 7-day interval
APNR	Lion-spotted hyaena	161	102

	Spotted hyaena - leopard	230	136
	Spotted hyaena - African civet	112	60
MGR	Spotted hyaena - brown hyaena	96	40
	Spotted hyaena - black-backed jackal	51	20
	Brown hyaena - black-backed jackal	70	24
MZNP	Brown hyaena - black-backed jackal	96	71
	Brown hyaena - aardwolf	64	45
	Black-backed jackal - aardwolf	170	145
	Black-backed jackal - bat-eared fox	65	43
TKR	Brown hyaena - black-backed jackal	50	27
	Black-backed jackal - bat-eared fox	92	60

APNR = Associated Private Nature Reserves, MGR = Madikwe Game Reserve, MZNP = Mountain Zebra National Park, TKR = Tswalu-Kalahari Reserve.

Despite most species-pairs showing signs of spatiotemporal aggregation due to high proportional p-values within APNR, none were statistically significant (Figure 3.13a). Spotted hyaenas had 21.7%, 17.0%, and 14.3% of their proximate detections occurring within 24 hours of lion, leopard, and African civet reference detections, respectively. Lions and spotted hyaenas had the highest proportional p-value, with a median observed interval between proximate and reference detections of 1.75 days. Even though a high number of proximate detections were available between lions and leopards ($N = 94$), not enough occurred within seven days and were therefore not included in the analysis.

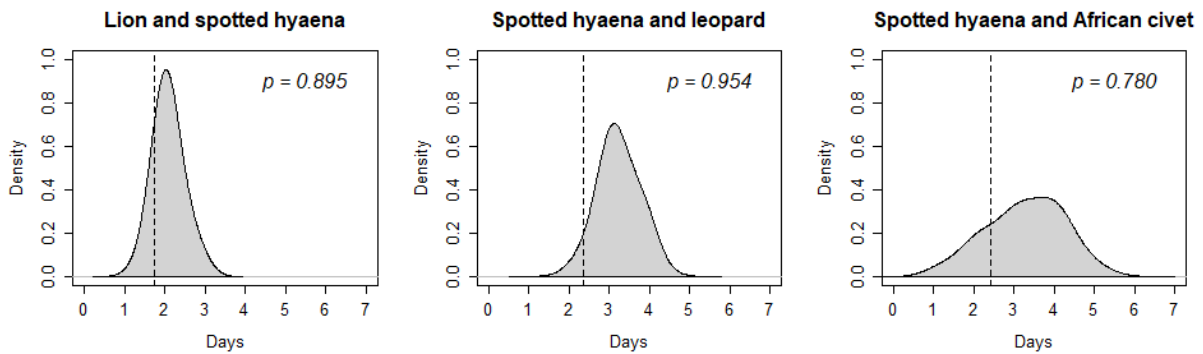
Within MGR, only spotted hyaenas and brown hyaenas showed indications of significant spatiotemporal attraction (Figure 3.13b). Spotted hyaenas had 12.5% of their proximate detections within 24 hours of brown hyaena reference detections. Although not statistically significant, spotted hyaenas and black-backed jackals had a low proportional p-value, with the

highest observed median time of 3.62 days and only 3.92% of the spotted hyaena proximate detections occurring within 24 hours of the black-backed jackal reference detections. Furthermore, brown hyaenas and black-backed jackals showed no significant relative avoidance or attraction behaviour within MGR.

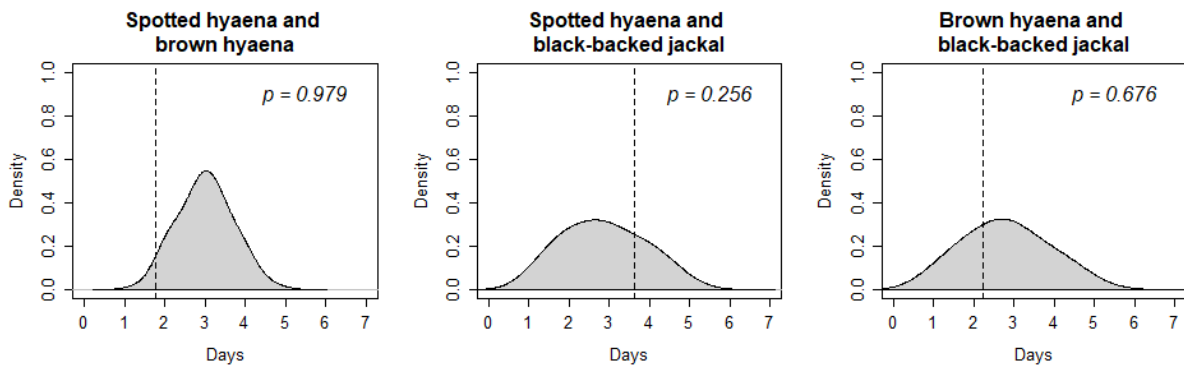
Except for brown hyaenas and aardwolves, all species-pairs within MZNP that obtained sufficient relative photo-captures showed indications of significant spatiotemporal attraction (Figure 3.13c). Brown hyaenas and black-backed jackals, black-backed jackals and aardwolves, and black-backed jackals and bat-eared foxes had 44.8%, 38.2%, and 33.8% of their total proximate detections within 24 hours of the reference detections, respectively. As a result, the median time interval between proximate and reference detections within the 7-day relevance period was low for all three species-pairs. The shortest median was between black-backed jackals and aardwolves, with 50% of the relevant proximate detections occurring in less than 0.98 days. Despite a high proportional p-value and a relatively high percentage of proximate detections within 24 hours (21.9%), brown hyaenas and aardwolves did not show significant indications of fine-scaled attraction. Within the 7-day relevance period, this species-pair also had the longest median value (1.91 days) of the time interval between proximate and reference detections.

Only two species-pairs from TKR, namely brown hyaenas and black-backed jackals, and black-backed jackals and bat-eared foxes, obtained more than 20 proximate detections during the 7-day relevance period and were thus included in the analyses (Figure 3.13d). In terms of fine-scaled spatiotemporal behaviour, neither of these species-pairs obtained significant proportional p-values. However, brown hyaenas and black-backed jackals displayed higher proportional p-values and more proximate detections within 24 hours of the reference detections (22.0%) compared to black-backed jackals and bat-eared foxes. Black-backed jackals and bat-eared foxes had 16.3% of proximate detections within 24 hours of the reference detections.

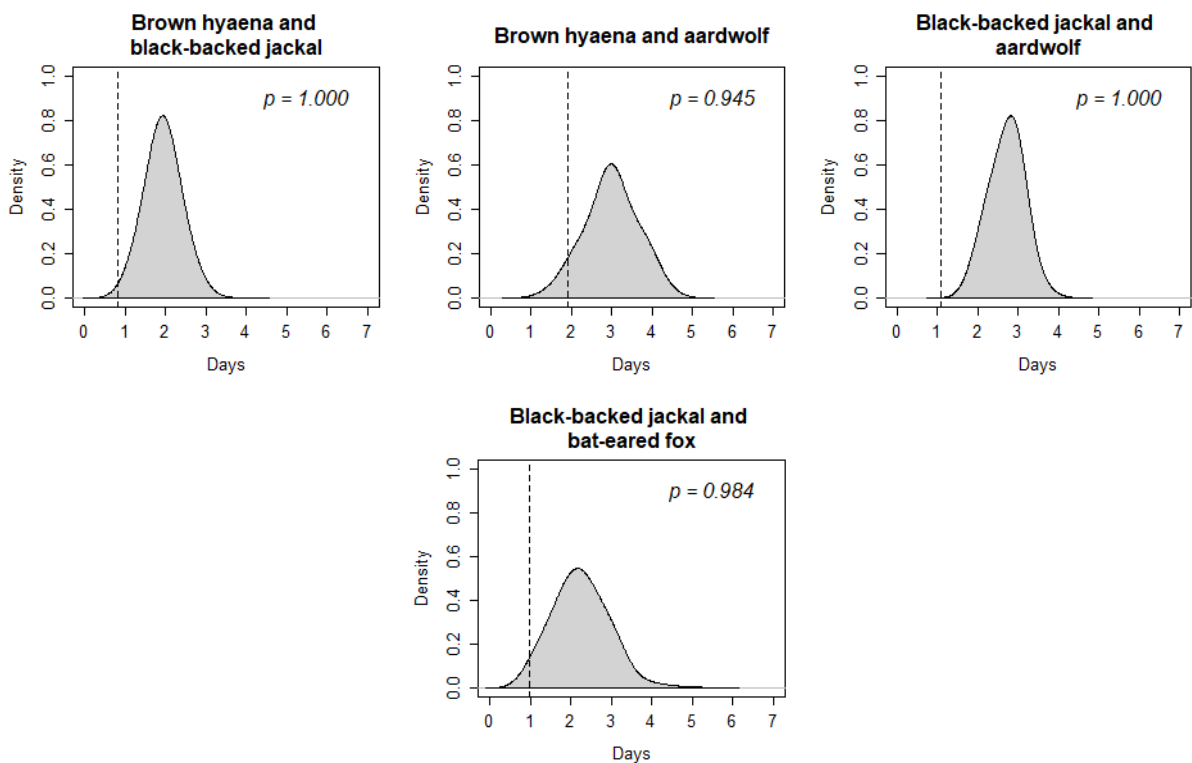
a) Associated Private Nature Reserves



b) Madikwe Game Reserve



c) Mountain Zebra National Park



d) Tswalu Kalahari Reserve

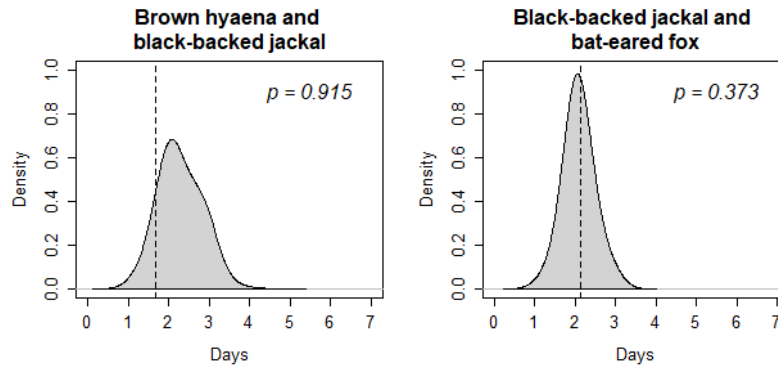


Figure 3.13. Relative fine-scaled spatiotemporal behaviour of carnivore species within four South African protected areas. The shaded density distribution represents 1000 randomised medians of time between reference and proximate detections, whereas the vertical stippled line represents the median observed time between reference and proximate detections. The p -value shows the proportional number of randomised medians greater than the observed median.

3.5 Discussion

In this study, the daily activity patterns of South African Carnivora species were compared to investigate temporal partitioning as a potential avoidance mechanism used to reduce encounters with more dominant carnivores. However, most species-pairs (63%) across all combinations and sites in this study showed no clear indications of using temporal avoidance behaviour as a strategy to coexist with a potential risk-associated, dominant species. There exists a trade-off in subordinate carnivores between resource acquisition and risk associated with sympatric predators (Linnell and Strand 2000), with the former likely outweighing the latter in most cases in this study. This is a viewpoint shared by many previous studies on African carnivores, in which hunting success is said to be prioritized over the possibility of encountering dominant

predators (Cozzi et al. 2012, Miller et al. 2018, Evers et al. 2022). Müller et al. (2022), for example, found no clear temporal segregation of leopard and caracal diel activity patterns in the Cederberg region of South Africa's Western Cape, but concluded that these species are more likely to coexist through spatial and dietary partitioning. Mugerwa et al. (2017) showed that leopards in Zimbabwe's Bulyebe Valley Conservancy do not avoid lions through temporal partitioning of diel activity patterns, but prioritize resource acquisition through improved hunting success. The findings of this study support the idea that leopards use strategies other than temporal partitioning to coexist with other large carnivores. One such method is the characteristic caching behaviour of leopards, in which they hoist prey carcasses into trees to avoid kleptoparasitic losses, lending support to the kleptoparasitism-avoidance hypothesis (MacDonald 1976, Balme et al. 2017a).

The preference for nocturnal activity patterns observed in many large carnivores is attributed to improved concealment due to low light conditions and avoidance of thermal stress experienced during daytime-high ambient temperatures (Miller et al. 2018). This generally leads to increased hunting success. Furthermore, Greco et al. (2021) rejected the hypothesis that the temporal activity patterns of carnivores are dictated by apex predator avoidance, instead attributing it to optimal niche utilisation and prey acquisition (i.e., hunting and foraging behaviour). A lack of temporal avoidance behaviour is not restricted to large carnivores, but has also been reported in mesopredators and small carnivores (Mills et al. 2019, Vissia and van Langevelde 2022). For example, Comley et al. (2020b) stated that negative influences exerted on mesopredators by larger, more dominant carnivores are an exception, rather than a commonly observed rule. Disregarding inferences about honey badger and caracal behaviour due to low sample sizes, the findings of this study support the statement made by Comley et al. (2020b), as clear patterns of temporal partitioning with dominant species were rarely observed among mesopredators. For example, APNR's African civets showed no evidence of temporally

avoiding larger and more dominant carnivores, and only a few dominant species were possibly avoided on a finer temporal scale by bat-eared foxes and black-backed jackals. Furthermore, the presence of lions within the Lekgaba section of TKR had no effect on the activity patterns of brown hyaenas, black-backed jackals, and bat-eared foxes.

Furthermore, Ramesh et al. (2017) showed that smaller carnivores (e.g., large-spotted genets and striped polecats) rarely use temporal partitioning to avoid large carnivores (i.e., leopards and spotted hyaenas). The findings of this study support this; for example, the daily activity patterns of TKR's Cape foxes were unaffected by the temporal activity of larger or more dominant carnivore species. The lack of temporal avoidance observed for subordinate carnivores has also been reported outside of Africa, such as between leopards (*P. p. fusca*) and Asiatic lions (*P. l. persica*) in India's Gir Forest (Chaudhary et al. 2020), and for red foxes (*Vulpes vulpes*) in and Iberian lynxes (*Lynx pardinus*) in southwestern Europe (Monterroso et al. 2014a). The current study's findings suggest that bat-eared foxes are likely to encounter black-backed jackals regularly, partly due to a lack of temporal avoidance behaviour. The two species had a high overlap in their diel activity patterns and core activity periods, displayed significant evidence of spatiotemporal aggregation in MZNP, and recorded high detection frequencies. In TKR, the core activity periods of bat-eared foxes and black-backed jackals were even more similar during the dry seasons, recording nearly 86% overlap compared to the wet seasons. Regardless of potential spatial avoidance, bat-eared foxes are thus very likely to encounter black-backed jackals during the TKR's dry seasons and coldest months of the year. According to Kamler et al. (2017), bat-eared foxes have significantly larger group sizes during the dry seasons in Benfontein Game Reserve in the Northern Cape, South Africa. This was proposed as a possible response of bat-eared foxes to increased temporal overlap with black-backed jackals in the reserve (Kamler et al. 2017). In addition, Kamler et al. (2013) reported that the activity patterns of bat-eared foxes are more likely influenced by the activity patterns

of their dominant prey species, *Hodotermes* termites, rather than the activity of a common risk species, black-backed jackals. As a result of the aforementioned, it is possible that bat-eared foxes in the TKR's dry seasons and colder months may either increase their group sizes in response to increased temporal overlap with black-backed jackals, or, conversely, are able to be more active during similar periods with black-backed jackals due to larger group sizes that may better defend themselves against the threat posed by the jackals; however, further research is needed to confirm this. Furthermore, black-backed jackals pose a significant threat to Cape foxes and will kill them in territorial defence, leading to the suppression of Cape fox populations (Kamler et al. 2013, Kamler and MacDonald 2014). TKR's Cape foxes, on the other hand, showed no evidence of temporally avoiding black-backed jackals via partitioning of their diel activity patterns in this study. This contradicts previous findings (Kamler et al. 2012, Edwards et al. 2015).

It is important to recognize that a lack of clear temporal avoidance behaviour among a carnivore species-pair does not imply a lack of competition or risk, but that encounters with the dominant species may be low enough to be considered negligible. Furthermore, it is acknowledged that other methods of avoidance, such as spatial or dietary partitioning, may be used by carnivores to facilitate coexistence. True frequencies of encounters between carnivores are nearly impossible to discern using camera trapping methods, particularly for elusive and cryptic species, and thus require finer-scaled continuous data collection methods such as GPS collaring and direct observations. Knowledge of site-specific carnivore densities is also important because low densities result in few encounters, which may make temporal avoidance negligible (Romero-Muñoz et al. 2010, Cozzi et al. 2012, Edwards et al. 2015, Mills 2015, Müller et al. 2022). As the densities of the respective species increase, so will the number of encounters between them (Creel et al. 2001). This was apparent in the evidence of significant spatiotemporal aggregation between MZNP's aardwolves and black-backed jackals.

Documented cases of aardwolves being attacked and killed by black-backed jackals are lacking in the literature (Curveira-Santos et al. 2022). There is also a negligible overlap in their diets (Klare et al. 2010). Therefore, it can only be assumed that this aggregation was due to the high detection frequency of black-backed jackals in the park, which resulted in short time intervals between subsequent relative detections of the two species, rather than either species benefiting from being attracted to the other. Information on site-specific densities would improve the reliability and comprehension of carnivores' relative temporal activity patterns and the relevance of associated avoidance behaviour.

The potential for competition between specific carnivore species is also important when determining possible temporal avoidance behaviour (Caro and Stoner 2003). Even though competition between most sympatric carnivores is theoretically acknowledged, it should be empirically confirmed through direct observations such as aggressive interactions and interspecific killings. For instance, interspecific killings have been documented among specific species (Palomares and Caro 1999), but these events may be rare enough to be considered negligible. For example, aardwolves have rarely been observed as victims of aggressive interactions and have no dietary overlap with more dominant carnivores (Curveira-Santos et al. 2022); thus, avoidance may not be necessary. Overall, published studies overlook documented cases of intraguild aggression among carnivores and focus on theoretical research and assumptions (Curveira-Santos et al. 2022). There is a clear need for documented cases of antagonistic interactions between carnivores in the scientific literature. This will increase the relevance and reliability of theoretical findings and inferences regarding interspecific competition among carnivores. Nonetheless, due to their opportunistic predatory behaviour, hypercarnivorous felids such as lions, leopards, and caracals are responsible for most intraguild killings (Donadio and Buskirk 2006, Curveira-Santos et al. 2022). Among the hypercarnivorous felids in this study, only lion activity forced indications of fine-scaled temporal avoidance

behaviour in subordinate species. In addition, clear temporal partitioning was observed between caracals and both aardwolves and bat-eared foxes; however, this partitioning cannot be confidently attributed to avoidance behaviour due to a low sample size for caracals in MZNP.

Furthermore, in addition to their small body size, genets' semi-arboreal and cryptic behaviour may be evolutionary adaptations that allow them to avoid encounters with larger carnivores while remaining active during similar periods of the day (Maddock and Perrin 1993, Pereira et al. 2012). It is also stated that carnivore species with minor differences in relative body size rarely engage in aggressive interactions (Donadio and Buskirk 2006). For example, antagonistic behaviour and aggressive interactions are rarely, if ever, observed between aardwolves and sympatric bat-eared foxes, where they appear to barely notice each other's presence upon encounter (Bothma and Nel 1980, Waser 1980). Furthermore, although Jumbam (2019) observed bat-eared foxes chasing Cape foxes away from food sources regularly, the presence of bat-eared foxes is most likely not regarded as a threat by Cape foxes. Kamler et al. (2012) found no considerable dietary overlap between the two sympatric fox species and showed that, due to a lack of aggression during encounters, they do not recognise each other as a noticeable threat to either adults or young. Therefore, avoidance behaviour between Cape foxes and bat-eared foxes is highly unlikely and was not observed in this study as both fox species had very similar daily activity patterns.

However, some species-pairs in this study displayed clear indications of potential temporal avoidance behaviour. This revolved around the highly crepuscular behaviour of APNR's African wild dogs, and the increased diurnal activity of MZNP's caracals due to their cathemeral behaviour. According to Hayward and Slotow (2009), top-down effects, i.e., competition and threat posed by top predators, are the primary determinants of temporal partitioning observed in subordinate carnivores, especially among species of the large predator guild. African wild dogs are vulnerable to interference competition from larger and more

dominant carnivores such as spotted hyaenas and, in particular, lions (Mills and Gorman 1997, Jackson et al. 2014, Swanson et al. 2014, Dröge et al. 2017, Davies et al. 2021, Goodheart et al. 2022). As a result, African wild dogs may have undergone forced evolutionary adaptations for activity preferences during crepuscular periods. It is also worth noting that African wild dogs are more likely to avoid lions compared to avoiding spotted hyaenas (Darnell et al. 2014). If a larger relative group size is present, African wild dogs can dominate encounters with spotted hyaenas (Creel and Creel 1996, Darnell et al. 2014). Schuette et al. (2013) also attributed the use of temporal partitioning by subordinate carnivores in Kenya's southern Rift Valley as a response to competition exerted by more dominant species. Small carnivores have been stated to rely on temporal avoidance to coexist with larger predators, especially lions (Comley et al. 2020b).

It is important to note that carnivore species-pairs that behaviourally conform to a similar temporal niche classification at the population level (e.g., nocturnal) will have high temporal overlap values when diel activity patterns are compared. However, temporal avoidance may still be used by carnivores to coexist. This necessitates finer-scaled temporal comparisons of their diel activity patterns to discern temporal partitioning. Most of the species-pairs that displayed possible temporal avoidance behaviour in this study were predominantly nocturnal, and thus likely relied on finer-scaled temporal partitioning via adaptations to their temporal activity peaks and core activity periods to facilitate coexistence. This allows species to still be active when hunting success is greatest, while minimising or reducing the risk of encounters with dominant species, which may therefore be less costly to manage than large-scaled avoidance. For example, brown hyaenas are scavenging specialists and should, therefore, be facilitated by the presence of larger carnivores such as lions in an area as they benefit from eating the remains of their kills (Mills 1989, Slater and Muller 2014, Mills 2015, Comley 2016, Bashant et al. 2020). However, brown hyaenas use fine-scaled temporal avoidance to avoid

direct interactions and as a result likely being killed by these dominant predators (Owens and Owens 1978, Mills and Mills 1982, Bashant et al. 2020) by peaking in activity at different times than lions. In MGR and MZNP, brown hyaenas had comparatively moderate overlap in their activity patterns with lions, but the two species' core activity periods were completely different. These brown hyaenas showed less activity during periods when lions were most active, therefore facilitating coexistence. This study also found fine-scaled avoidance behaviour in two facultative scavengers; MGR's black-backed jackals peaked in activity before and after spotted hyaena activity peaks.

Many previous studies attribute temporal avoidance among carnivores to finer-scaled behavioural partitioning of, for instance, peak activity periods, in attempts to facilitate coexistence (Lewis et al. 2015, Swanson et al. 2016, Searle et al. 2021, Müller et al. 2022). For example, Marinho et al. (2020) showed that mesocarnivores in the Caatinga dry forests in north-eastern Brazil rely on finer-scaled partitioning of their peak activity periods to coexist. Vissia and van Langevelde (2022) emphasized that, due to African carnivores' widespread nocturnality, asynchronization of peak activity periods is a crucial behavioural adaptation that allows the continent's carnivore species to coexist. On Namibian farmlands, Edwards et al. (2015) also observed finer-scaled temporal partitioning of carnivores at frequently visited water sources. Furthermore, Easter et al. (2020) showed that fine-scaled temporal partitioning is a method also used by small carnivores such as genets, civets, and mongooses to facilitate coexistence. This leads to the hypothesis that carnivores rely more on reactive avoidance of dominant predators than predictive behavioural adjustments, as was revealed by Broekhuis et al. (2013) regarding cheetahs in the Serengeti National Park, and by Mills et al. (2019) for smaller carnivores such as civets in the presence of African golden cats (*Caracal aurata*). Confirming a preference for reactive avoidance among carnivore species will require finer-

scaled data collection and analysis, which cannot be accomplished using only camera trapping networks.

Furthermore, fine-scale data collection methods such as GPS tracking may reveal behavioural variation among individuals of a species. For example, specific spotted hyaena individuals may exhibit increased risk-taking behaviour and thus be less likely to avoid encounters with lions (Watts et al. 2010). This may explain why there was no statistically significant evidence of fine-scaled spatiotemporal avoidance or aggregation between APNR's lions and spotted hyaenas, even though a large proportion of spotted hyaena photo-captures were within one day of lion photo-captures. This could also imply possible situational fine-scaled attraction related to predation events, in which hyaenas benefit from scavenging opportunities provided by lions (Watts et al. 2010).

Fine-scaled spatiotemporal avoidance, or reactive avoidance (Broekhuis et al. 2013), is an important component of carnivore coexistence. This study, in congruence with many previous studies (Broekhuis et al. 2013, Cusack et al. 2017, Karanth et al. 2017, Niedballe et al. 2019, Paúl et al. 2020, Searle et al. 2021), advocates for the inclusion of fine-scaled analyses of potential carnivore avoidance behaviour in future studies. Attention should be given to the formulation of reliable fine-scaled spatiotemporal analysis methods and the associated data collection procedures that will result in sufficient sample sizes.

Seasonal considerations are also important when comparing the daily activity patterns of competing carnivore species (Greco et al. 2021, Vilella et al. 2020). In this study, a relatively common trend was observed in which the temporal overlap between species was noticeably lower during the dry seasons compared to the wet seasons, as well the coldest compared to the hottest months of the year. This trend has also been reported recently by Finnegan et al. (2021) within a carnivore assemblage in the Brazilian Pantanal, and by Vissia and Van Langevelde (2022) among carnivores in Botswana's central Tuli region. This decrease in temporal overlap

during the dry season could be due to increased competition among species as resources become less available and more concentrated in specific areas (Finnegan et al. 2021, Vissia and van Langevelde 2022). Despite having high overlap in their overall diel activity patterns in this study, seasonality in temporal overlap was evident between aardwolves and bat-eared foxes, with less overlap in diel activity during the dry seasons compared to the wet seasons. Furthermore, during the dry seasons, the two species had very little overlap in their core activity periods, with aardwolves peaking in activity before bat-eared foxes. This could indicate finer-scaled partitioning of resources and time between the two species during the dry seasons due to diet overlap in terms of foraging for *Hodotermes* termites which may result in increased competition. In response, aardwolves forage for termites earlier in the night than bat-eared foxes during MZNP's colder months, lowering the risk of losing access to a termite colony.

In this study, a number of species-pairs displayed noticeable differences in temporal overlap between the wet and dry seasons, as well as the hottest and coldest months of the year in the respective protected areas. For example, MGR's lions and spotted hyaenas had noticeably different diel activity patterns, suggesting that competition and the potential for avoidance behaviour is evident within the reserve. This could be due to the high spotted hyaena density within MGR (Honiball et al. 2021), which results in a shift in dominance, where higher spotted hyaena abundance and larger clan sizes may cause lions to temporally avoid periods of increased spotted hyaena activity in an attempt to reduce competitive interactions (Lehmann et al. 2017). This, however, cannot be verified and thus necessitates additional research. In more detail, double the number of MGR's lion photo-captures were recorded during the dry season compared to the wet season. Furthermore, strong indications of possible avoidance behaviour by diel activity partitioning were observed during APNR's dry seasons when the two species had contrasting activity peaks. This difference was even more prominent during APNR's coldest months of the year. As a result, avoidance behaviour caused by potential increased

competition between lions and spotted hyaenas may be much more evident during the dry seasons and winter months, which may have resulted in the indications of temporal segregation between spotted hyaenas and lions in MGR. This trend is supported by Périquet et al. (2021).

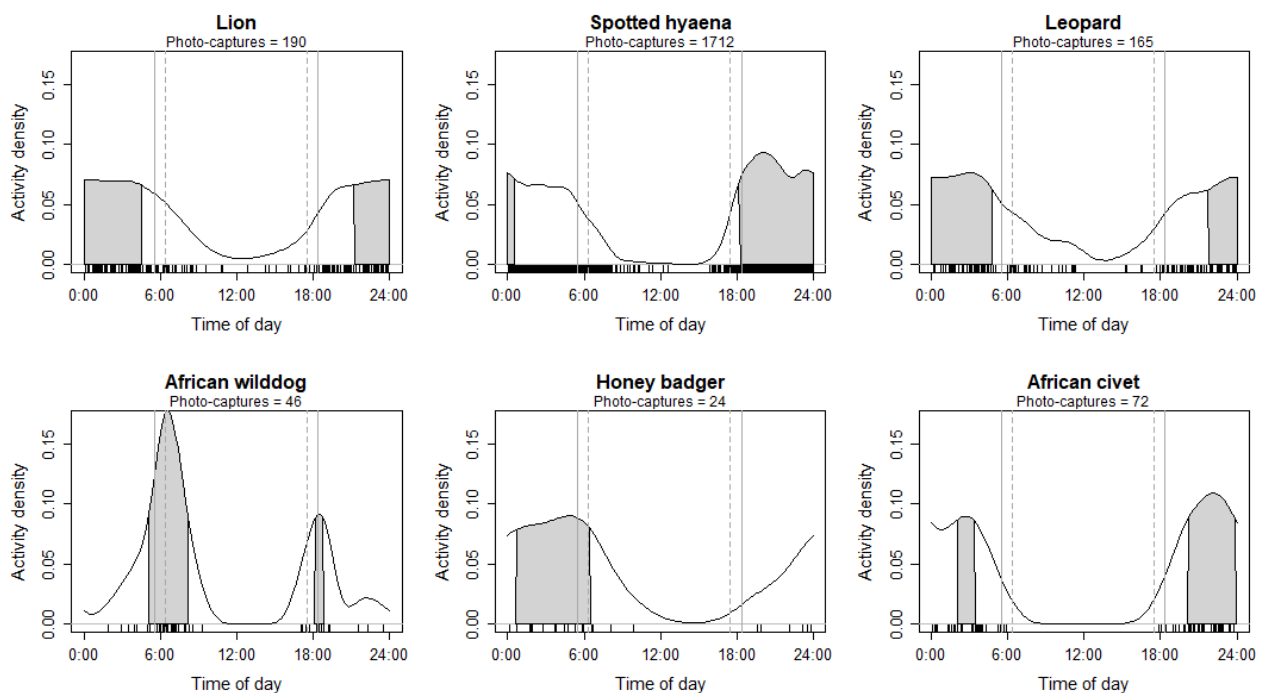
A thorough understanding of the temporal synecology of carnivores could aid in improving future conservation strategies that would require careful management interventions (Ritchie and Johnson 2009, Karanth et al. 2017). For instance, as climate change will likely result in rising local temperatures, understanding the behavioural adaptations of carnivores such as critically endangered African wild dog populations is crucial (Rabaiotti and Woodroffe 2019). In response to high daytime temperatures, African wild dogs become more nocturnal during moonlit nights (Cozzi et al. 2012). Therefore, if days with extremely high daytime temperatures become more common, African wild dogs may be forced to risk increased encounters with dominant carnivores such as lions and spotted hyaenas by becoming more nocturnal. It is thus imperative that the temporal behaviour of African wild dog populations is closely monitored, as increased bouts of unusual nocturnality may be indicative of stress experienced. Therefore, conservation strategies regarding African wild dogs could consider changes in their temporal behaviour as a proxy for potential hunting success. This may reveal forced adaptations detrimental to the population, such as increased susceptibility to kleptoparasitic events and intraguild killings, which would necessitate vital management interventions. It is also imperative that future research be conducted on the morphological adaptations that may limit African wild dogs from becoming more nocturnal, as this is severely lacking in the literature.

To conclude, this study suggests that the daily activity patterns of most South African species of the Carnivora order are more likely influenced by environmental factors (e.g., temperature constraints) and bottom-up forces (e.g., prey availability and hunting success) than top-down suppression due to competition and risk associated with more dominant carnivore species. However, possible indications of temporal partitioning between dominant and subordinate

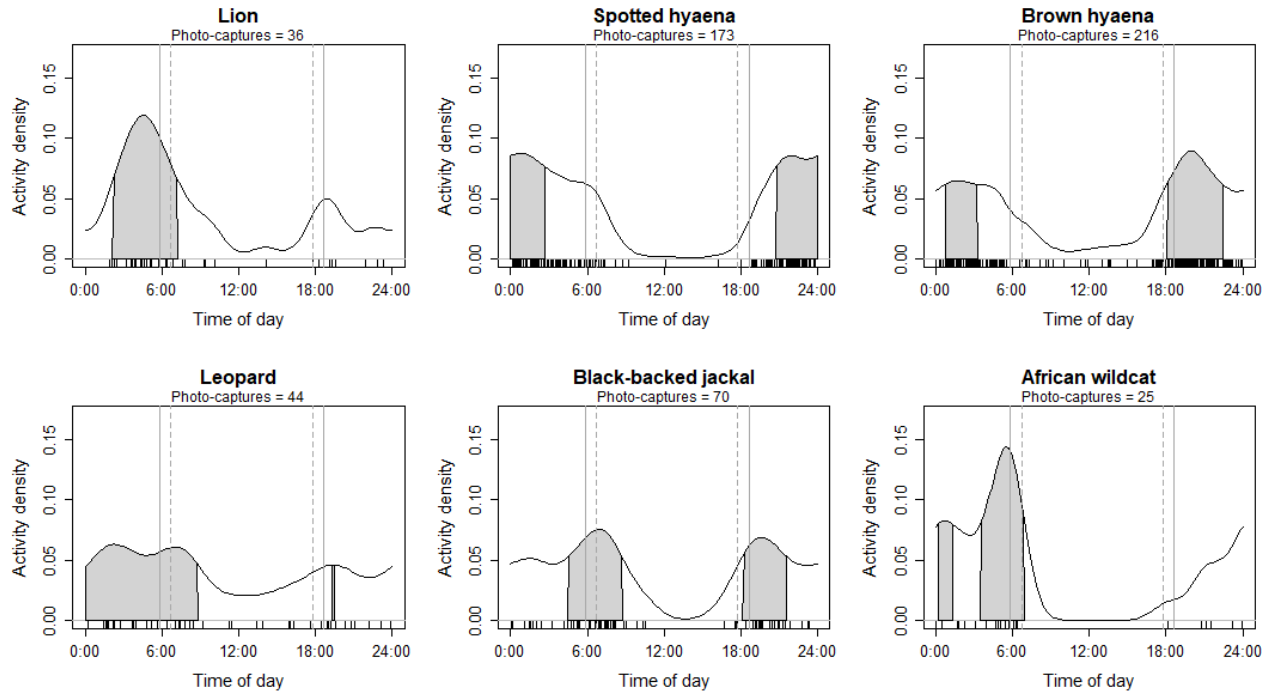
carnivores as an avoidance mechanism are more likely to manifest as finer-scaled behavioural adjustments that require appropriate methods to discern. It is also suggested that future studies should incorporate various data collection methods to determine temporal avoidance behaviour in carnivores, such as camera trapping networks accompanied by selective radio or GPS collaring of individuals, as well as personal observations by researchers, wildlife managers, and field staff. This will improve the reliability of inferences regarding temporal avoidance behaviour and present data on interspecific interactions such as aggressive encounters and intraguild killings that may direct reason to temporal partitioning. Furthermore, additional information such as site-specific densities and diets of carnivores would significantly improve the reliability and comprehension of their temporal synecology.

3.6. Supporting information

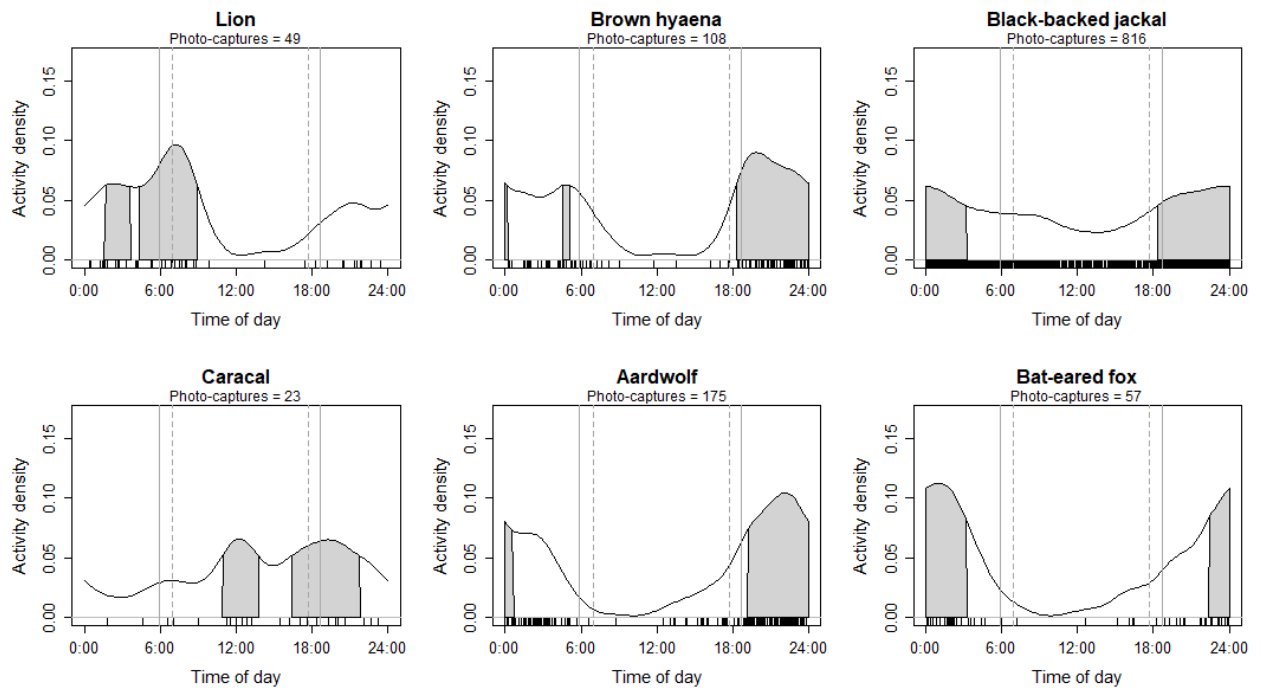
a) Associated Private Nature Reserves

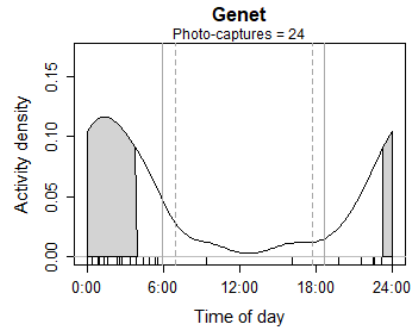


b) Madikwe Game Reserve



c) Mountain Zebra National Park





d) Tswalu Kalahari Reserve

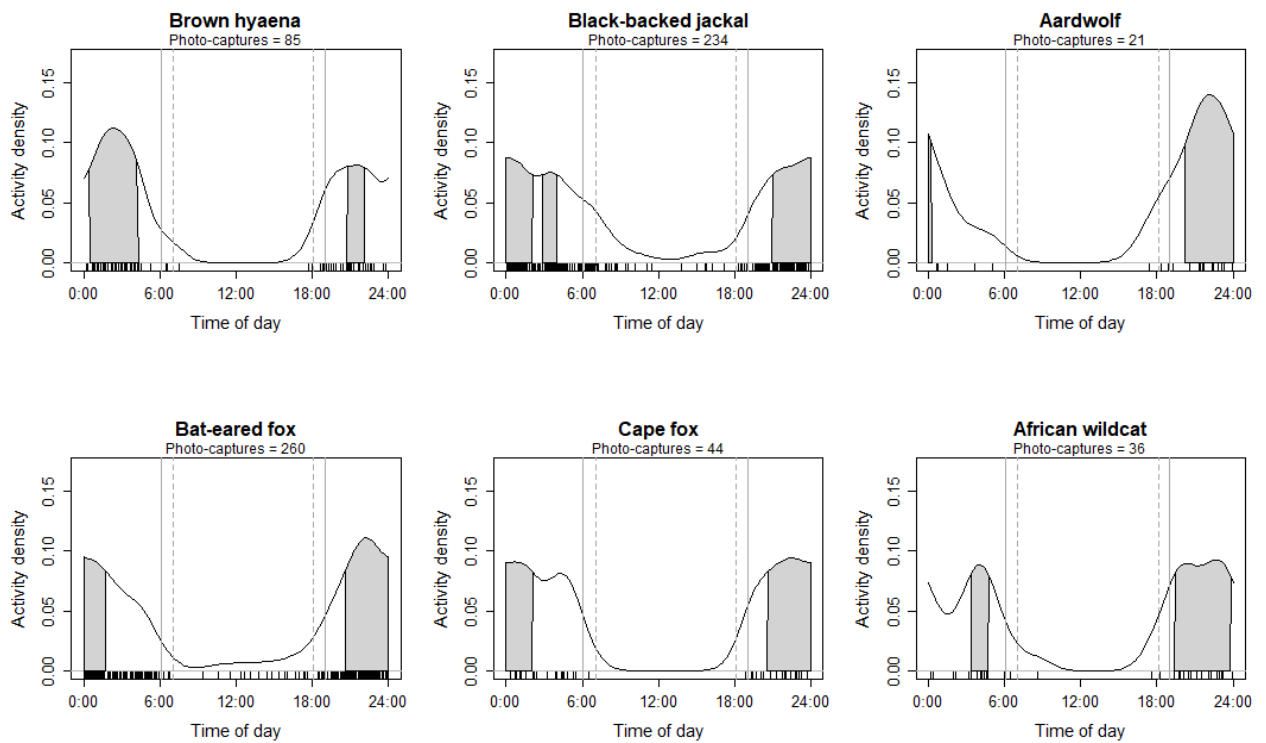


Figure S3.1. Kernel density graphs of the diel activity patterns of Carnivora species from four protected areas in South Africa. Sunrise and sunset within each protected area are represented by solid vertical lines for wet seasons and stippled vertical lines for dry seasons. Shaded areas represent the core (50% isopleths) activity range.

CHAPTER 4

General conclusions

This thesis set out to identify interspecific spatial and temporal avoidance behaviour and its associated hypotheses within carnivore communities in four South African protected areas.

Chapter 2 demonstrated that most South African carnivore species do not avoid large-scale areas occupied by risk-associated species. The cost of avoiding dominant species in space-restricted fenced areas may be too deleterious to the fitness of a subordinate species. Therefore, factors such as resource acquisition, intraspecific territoriality, and fine-scaled reactive avoidance are presumed to outweigh the need for large-scaled spatial avoidance of dominant risk-associated carnivore species (see Broekhuis et al. 2013, Swanson et al. 2016).

Similarly, chapter 3 demonstrated that most subordinate South African carnivore species are unlikely to avoid the temporal activity patterns of more dominant species at the population level. If avoidance is required, it is more likely to manifest as fine-scaled avoidance of peak or core activity periods. However, due to the rarity of temporal avoidance behaviour revealed in chapter 3, results from this study suggest that the diel activity patterns of most South African Carnivora species are more likely to be influenced by temperature constraints and bottom-up forces such as hunting success than top-down forces in the form of competition suppression by more dominant species.

It was predicted in this study that potential avoidance behaviour would be more prevalent among carnivore species with intermediate relative body size differences due to the hypothesised rarity of antagonistic encounters among carnivore species with large relative body

size differences (Donadio and Buskirk 2006, Curveira-Santos et al. 2022). Partitioning and the potential for spatial or temporal avoidance behaviour were more common among species with intermediate differences in body sizes. For example, MZNP's black-backed jackals (*Lupulella mesomelas*) and caracals (*Caracal caracal*) showed signs of spatial avoidance behaviour, and aardwolves (*Proteles cristata*) and bat-eared foxes (*Otocyon megalotis*) in MZNP and TKR showed signs of spatial and temporal avoidance behaviour. Species-pairs with large differences in relative body sizes had fewer instances of clear avoidance behaviour. For example, APNR's African civets (*Civettictis civetta*) did not show any signs of avoiding species from the large predator guild (i.e., lions *Panthera leo*, leopards *Panthera pardus*, and spotted hyaenas *Crocuta crocuta*), and TKR's Cape foxes (*Vulpes chama*) did not avoid black-backed jackals. This study thus found support for the prediction that avoidance behaviour associated with risk and interspecific competition is most prevalent among carnivore species with intermediate differences in relative body sizes. However, caution is advised against generalisation based on this hypothesis as exceptions were found. For example, black-backed jackals potentially used finer-scaled temporal partitioning to avoid encounters with the markedly larger spotted hyaenas and TKR's bat-eared foxes appear to avoid species from large predator guild (e.g., lions and brown hyaenas *Hyaena brunnea*).

Furthermore, this study hypothesized that subordinate carnivore species would avoid hypercarnivorous felids like lions, leopards, and caracals more than other carnivores due to their opportunistic predatory behaviour, which leads to these felids being responsible for most intraguild killings (Donadio and Buskirk 2006, Curveira-Santos et al. 2022). However, results from this study does not provide a clear distinction in the prevalence of avoidance behaviour between hypercarnivorous felids and other carnivore species such as hyaenas and black-backed jackals. However, lions appear to have an effect on the core activity period of many subordinate carnivore species, and lion-associated species-pairs obtained the lowest spatial overlap within

MZNP. Therefore, this study does not provide clear support to the hypothesis that subordinate carnivores would more likely avoid hypercarnivorous felids than other dominant carnivores. In addition, this study does not provide support to the prediction that carnivores of all body sizes that are considered subordinate to leopards will show signs of avoiding leopards spatially or temporally. APNR's African civets, and MGR's brown hyaenas, black-backed jackals, and African wildcats (*Felis silvestris lybica*) did not appear to avoid leopards spatially or temporally, at least not on the scale conducted in this study. This study, therefore, suggests that subordinate carnivores will be more inclined to avoid the core activity periods and territories of lion prides than solitary leopards.

This study also demonstrated that potential avoidance behaviour is not limited to the larger carnivore species, but may also, in rare instances, manifest among the smaller species such as Cape foxes, bat-eared foxes, black-backed jackals and aardwolves. For example, aardwolves and bat-eared foxes, even though interspecific killings have never been recorded, show evidence of avoidance behaviour in both MZNP and TKR, with the most likely cause being an overlap in diet during the dry seasons (Williams et al. 1997, Kamler et al. 2013). Intraguild killings and aggression are less common among the smaller carnivore species (Curveira-Santos et al. 2022); thus, diet partitioning likely plays a major role in interspecific competition. Because species diets were not analysed and the evident importance is highlighted among many species-pairs, this study advocates that dietary aspects of carnivore species are included into future analyses of interspecific competition and avoidance behaviour.

It was hypothesised in this study that indications of interspecific avoidance behaviours among South African carnivores will vary with the different climatic seasons and to different degrees depending on the temporal scale considered. Seasonality in avoidance behaviour was evident in this study, and as a result, clear support for the hypothesis is provided. MGR's black-backed jackals had markedly more spatial overlap with spotted and brown hyaenas during the dry

compared to wet seasons; therefore, black-backed jackals may rely more on scavenging opportunities during the dry seasons. Furthermore, a relatively common trend was observed in which the temporal overlap between species was noticeably lower during the dry seasons compared to the wet seasons, as well the coldest compared to the hottest months of the year. This decrease in temporal overlap during the dry season could be due to increased competition among species as resources become less available and more concentrated in specific areas (Finnegan et al. 2021, Vissia and van Langevelde 2022). MGR's lions and spotted hyaenas had noticeably different diel activity patterns, suggesting that competition and the potential for avoidance behaviour is evident within the reserve. However, double the number of MGR's lion photo-captures were recorded during the dry season compared to the wet season. Furthermore, strong indications of possible avoidance behaviour by diel activity partitioning were observed during APNR's dry seasons when the two species had contrasting activity peaks. This difference was even more prominent during APNR's coldest months of the year. As a result, avoidance behaviour caused by potential increased competition between lions and spotted hyaenas may be much more evident during the dry seasons and winter months, which may have resulted in the indications of temporal segregation between spotted hyaenas and lions in MGR. This trend is supported by Périquet et al. (2021). Seasonality is frequently overlooked in studies concerning the diel activity patterns and interspecific temporal overlap of carnivores. Therefore, it is advised that future studies should not only include multi-seasonal data and comparisons, but also attempt to maintain an equal balance of detections from each respective season, as was seen in MGR's lions in this study. It is also important to consider the scale at which seasonal comparisons are made. This was evident in this study as APNR's leopards showed no indications of temporally avoiding lions during the wet and dry seasons. However, possible fine-scaled avoidance by partitioning core activity periods was apparent during APNR's hottest and coldest months of the year. Taking into account seasonality at high latitudinal regions when

considering the interspecific relationships of carnivores is important and encouraged and should receive more focus in future research studying similar aspects of carnivore community ecology.

This study also predicted that carnivores in open environments (i.e., MZNP and TKR) would rely more on interspecific spatial avoidance behaviour, whereas carnivores in regions with denser vegetation (i.e., APNR and MGR) would rely more on temporal avoidance behaviour. The results from this study provide partial support to this prediction as none of the species-pairs in APNR and MGR displayed any apparent signs of interspecific spatial avoidance behaviour; however, no evidence was found that temporal avoidance behaviour is more prevalent in regions of denser vegetation. Carnivore species-pairs in MZNP and MGR had lower temporal overlap values, whereas carnivore species-pairs in APNR and TKR had higher overlap values. It is, therefore, advised that future research be conducted on the effect of vegetation density on interspecific avoidance strategies of carnivore species in South Africa.

Most of the species assessed in this study were predominantly active at night (i.e., between dusk and dawn). As a result, evidence of temporal partitioning in this study mostly manifested as fine-scaled asynchronization of core activity periods. The results from chapter 3, therefore, satisfy the prediction that interspecific temporal avoidance behaviour among South African carnivores will more likely be expressed as finer-scaled asynchronization of their core activity periods than complete avoidance throughout the 24-hour diel period. For example, MGR and MZNP's brown hyaenas had moderate overlap in their diel activity patterns with lions, but the two species' core activity periods were completely different. These brown hyaenas showed less activity during periods when lions were most active, therefore facilitating coexistence. This study also found fine-scaled avoidance behaviour in two facultative scavengers; MGR's black-backed jackals peaked in activity before and after spotted hyaena activity peaks. Finer-scaled temporal avoidance of core activity periods allows species to remain active when hunting success is highest while reducing the risk of encounters with dominant species, which may be

less costly to manage than total avoidance. This study recommends that future research on temporal avoidance behaviour should take into account finer-scaled avoidance of, for example, core activity periods.

In greater detail, lions appear to have some spatial affinity for areas regularly used by their preferred prey species and are more active in the early mornings during the colder and drier periods of the year. This resulted in some temporal differences in activity patterns with spotted hyaenas, their main competitor species, during APNR's dry season and coldest months of the year, and MGR's dry seasons. Therefore, if lions are to avoid spotted hyaenas, particularly during the dry seasons, they are more likely to shift periods of activity than avoid areas used more regularly by spotted hyaena clans.

Spotted hyaenas do not appear to use temporal or spatial means of avoiding lions and may benefit from occupying similar areas and temporal niches to improve resource acquisition (Watts et al. 2010, Périquet et al. 2015). They do, however, show signs of using different vegetation types to lions in KNPR, with a slight preference for the Mopaneveld vegetation over the Granite Lowveld that lions prefer. This supports findings by Kushata et al. (2017), who showed that spotted hyaenas prefer to rest during the day in areas that are thicker in vegetation (i.e., woodland) that provide more refuge and would avoid resting in areas closer to lions. Furthermore, the presence of lions in an area appears to have an effect on the denning behaviour of spotted hyaenas (Périquet et al. 2016), which could have been the reason for the moderate spatial-use differences and habitat selection in KPNR. Therefore, spotted hyaenas are unlikely to avoid other large carnivore species, and may even be attracted to their presence and activity as they benefit from kleptoparasitic and scavenging opportunities (Henschel and Skinner 1990, Hayward 2006).

Similarly, leopards are also unlikely to avoid other large carnivore species via spatial and temporal partitioning and may rather rely on reactive responses and caching behaviour to avoid

interactions with species such as spotted hyaenas and lions (Balme et al. 2017a, Miller et al. 2018).

Only the temporal behaviour, and not spatial behaviour, of African wild dogs (*Lycaon pictus*) was analysed due to scarcity of detections; however, their strict crepuscularity may indicate avoidance behaviour, particularly of lions in the APNR.

Brown hyaenas appear to rely only on finer-scaled temporal avoidance of apex predators' peak activity periods to reduce encounters. Being scavenging specialists (Slater and Muller 2014, Comley 2016), brown hyaenas benefit from closely coexisting with other predators and, therefore, spatial avoidance would be detrimental.

Small sample sizes of elusive yet important species, such as honey badgers (*Mellivora capensis*) and caracals, prevented reliable and robust inferences. However, caracals in MZNP were more diurnal (i.e., cathemeral) than was expected and this resulted in potential indications of caracals avoiding the activity patterns of MZNP's lions. Caution is advised against using these results obtained for caracals and honey badgers in this study due to the low number of detections. It is, therefore, advised that future studies looking into the activity patterns of carnivore species should aim for more detections than was considered in this study.

Much variation in temporal and spatial behaviour was observed for black-backed jackals, owing to their behavioural adaptability and generalist nature. Apart from potential fine-scaled avoidance of MGR's spotted hyaenas via partitioning of peak activity periods, they are unlikely to use spatial and temporal avoidance of larger carnivore species and may even be attracted to their movements when scavenging is relied upon for sufficient food intake.

African civets in APNR and KPNR do not avoid large carnivore species via spatial or temporal means. Further research is needed on this; however, it is speculated here that their elusive

nature, potentially low abundances, and cryptic nature leads to avoidance of large carnivores being negligible as encounter rates between them and the large predators are probably very low.

The movements of aardwolves appear to be centred around termite activity and availability, and not predator avoidance. Being highly specialised feeders, they cannot afford to avoid areas or miss the opportunity to forage for active termites and, therefore, avoidance of larger carnivores may be too costly. However, their relationship with bat-eared foxes seems important as the two species potentially avoid areas used by the other, mainly through vegetation type preferences, and by avoidance of activity patterns, particularly during South Africa's dry seasons.

Bat-eared foxes display considerable flexibility in behaviour. For instance, they may avoid encounters with TKR's brown hyaenas by spatial partitioning and preferring different vegetation types, whereas they show signs of temporally avoiding the core activity periods of MZNP's brown hyaenas without any indications of spatial avoidance. In addition, they potentially avoid areas regularly used by black-backed jackals in MZNP, particularly during the dry seasons. Therefore, the spatial and temporal behaviour of bat-eared foxes is complex and requires careful investigation before assumptions are made, or behaviour is generalised.

African wildcats do not avoid the temporal activity patterns of larger, more dominant species, and do not avoid areas used by black-backed jackals. Therefore, it can be suggested that the cryptic behaviour and likely low abundances of African wildcats mean that they can rely on reactive avoidance responses due to potentially rare encounters with dominant carnivores.

Cape foxes are unlikely to avoid mesocarnivore species in TKR as they showed similarity in both spatial and temporal behaviour. They potentially avoid areas used by TKR's brown hyaenas; however, this is more likely attributed to habitat and vegetation type preferences than actual avoidance behaviour. Therefore, Cape foxes also likely rely on reactive responses to the presence of dominant species if avoidance is necessary.

MZNP's small-spotted genets (*Genetta genetta*) had overall low spatial overlap with larger carnivore species; however, given their semi-arboreal nature, it is suggested that this spatial-use differences are consequences of the genets' preferences for thicker vegetation with more trees as opposed to the other carnivores. Genets are strictly nocturnal and are unlikely to use temporal partitioning to avoid encounters with larger predators, but may use the cover of darkness to avoid detection.

Overall, this thesis provides information on the behavioural mechanisms used by carnivores in South African protected areas to coexist with each other. Given the ongoing transition from natural, connected ecosystems in Africa to increasingly fragmented habitats under constant anthropogenic pressure, this thesis demonstrated that carnivore species coexist in fenced, space-restricted protected areas without the need for drastic behavioural adaptations to intraguild competition and risk.

This thesis suggests that future studies examining interspecific avoidance behaviour among African carnivores should consider critical limitations such as the potential for encounters and aggression among specific species, the cost of avoidance, and temporal variation in the need for avoidance (e.g., avoidance only required during hunting events and negligible during periods of rest). This presents a number of potential future research directions:

- Empirical evidence of degrees of antagonism in carnivore species interactions is required.
- What is the potential for encounters between carnivore species, particularly when at low population densities?
- How does vegetation density affect the intraguild avoidance strategies of carnivore species?
- Does intraspecific territoriality outweigh predator and competitor avoidance?

- Are dominant carnivore species a constant threat or does risk and the need for avoidance vary with different actions (e.g., during resting, satiety after a feeding event, or dispersion).
- How much does intraspecific variation in risk taking behaviour influence the avoidance behaviour of carnivore populations?

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