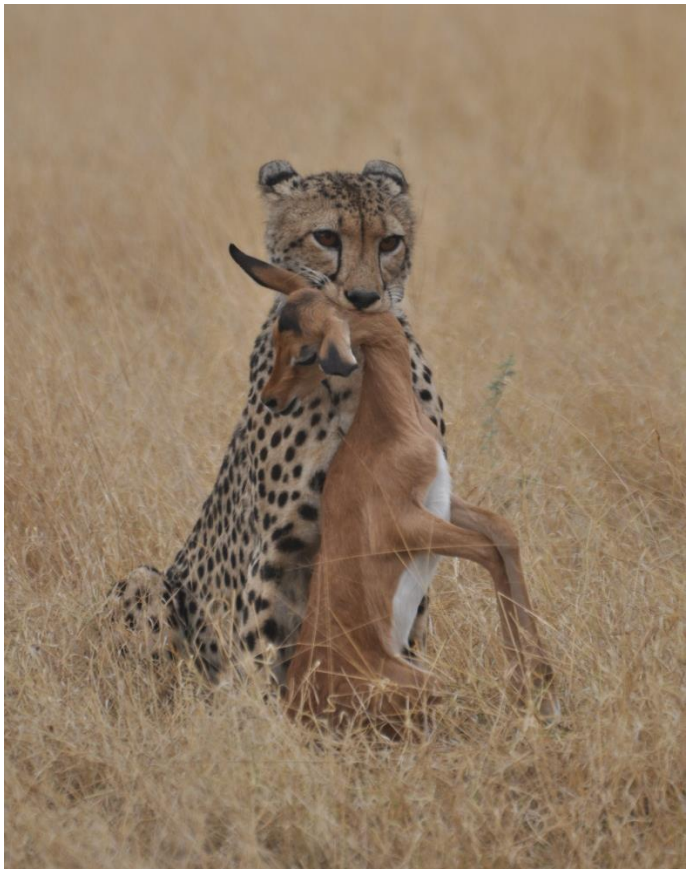
Niche Segregation by Cheetahs (*Acinonyx jubatus*) as a Mechanism for Coexistence with Lions (*Panthera leo*) and Spotted hyaenas (*Crocuta crocuta*)



A thesis submitted for the degree of Doctor of Philosophy

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ABSTRACT

Intraguild competition and predation have been recognised as important ecological factors influencing the population dynamics of carnivores. The effects of these interactions are often asymmetrical due to a size-related dominancy hierarchy. However, it has been suggested that competitively subordinate carnivores can minimise the costs of predation and competition through spatial and temporal avoidance. Here I investigate the ecological and behavioural mechanisms by which cheetahs (*Acinonyx jubatus*) coexist with competitively stronger lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). Fieldwork was carried out in the Okavango Delta, northern Botswana, between October 2008 and August 2011. A total of 20 Global Positioning System (GPS) radio-collars were fitted on all known cheetahs (n=6), lion prides (n=5) and spotted hyaena clans (n=6) in the study area (approx. 3 000 km^2). Pre-programmed radio-collars recorded locations and activity continuously for each individual and these data were complemented with direct behavioural observations. Cheetah data were analysed with respect to the temporal and spatial likelihood of encountering lions and spotted hyaenas. Results suggest that the response to the risks posed by other predators is species-specific, habitat-specific and dependent on the immediacy of the risk. Resource partitioning was not the main mechanism for coexistence as cheetahs overlapped extensively with lions and spotted hyaenas in time, space and habitat use. Instead, cheetahs adjusted their spatial distribution in response to immediate risks or adapted their habitat use depending on their vulnerability (e.g. behaviours such as feeding or with differing levels of moonlight at night). In general, cheetah temporal and spatial distribution is a hierarchical process, firstly driven by resource acquisition and thereafter fine-tuned by predator avoidance. In addition, habitat heterogeneity seemed to be key in facilitating coexistence. Understanding the behavioural mechanisms that interacting apex predators adopt to regulate these negative interactions could be crucial to carnivore conservation, especially as human-related habitat loss is forcing species into ever smaller areas.

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To another beautiful day in Africa

List of Acronyms

AIC	Akaike's Information Criterion
AICc	Akaike's Information Criterion corrected for small sample size
CI	Confidence Intervals
GLMM	Generalized Linear Mixed Model
GPS	Global Positioning System
HMM	hidden Markov models
MEM	Mixed Effects Models
MGR	Moremi Game Reserve
NDVI	Normalized Difference Vegetation Index
SEM	Standard Error of the Mean
SPOT	Système Pour l'Observation de la Terre
SVM	Support Vector Machine
TOD	Time Of Day
WMA	Wildlife Management Area

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CONTENTS

ABSTRACT ..... *i*
Acknowledgements ..... *ii*
List of Acronyms ..... *v*
Authors Affiliations ..... *vi*

CHAPTER 1

General introduction **1**

Summary 2

Competition and coexistence *2*
Competition between species 3
Coexistence between species 4

Carnivore coexistence 5
Kleptoparasitism 6
Intraguild predation 6
Consequences of carnivore coexistence 7

Coexistence between sympatric large African carnivores 8

Study area 11

Thesis overview 15

CHAPTER 2

Fear of the dark or dinner by moonlight? Reduced temporal partitioning among large African carnivores **18**

Abstract 19

Introduction 20

Methods 22

Results 25

Discussion 31

Appendix 35

CHAPTER 3

Cracking the code: using machine learning techniques to translate activity into behaviour 38

Abstract 39

Introduction 40

Methods 42

Results 47

Discussion 55

CHAPTER 4

Scaredy-cat? How fear and foraging affect cheetah temporal distribution 58

Abstract 59

Introduction 59

Methods 62

Results 65

Discussion 71

Appendix 75

CHAPTER 5

Risk avoidance in sympatric large carnivores: reactive or predictive? 77

Abstract 78

Introduction 79

Methods 81

Results 86

Discussion 91

Appendix 95

CHAPTER 6

The ecological small print: fine-scale adaptations in relation to risk and habitat use 100

Abstract 101

Introduction 102

Methods 105

Results 109
Discussion 112
Appendix 117

CHAPTER 7

General discussion 121
Synthesis 122
Conservation implications 129
Future research 131
Conclusion 133

REFERENCES 134

APPENDIX I 154

CHAPTER 1

General introduction

Summary

The coexistence of species is a central theme in animal and community ecology as it has implications for a range of ecological processes such as evolution and speciation (McPeek 1996, Morris 2003). Key to coexistence are the behavioural and evolutionary adaptations that minimise negative interactions between species. Whilst behavioural adaptations such as habitat shifting (Creel et al. 2005), increased vigilance (Lima 1987, Périquet et al. 2010) and changes in group-size (Fortin et al. 2009) have frequently been studied in predator-prey systems, comparatively little is known about the behavioural mechanisms by which mammalian carnivores coexist. Unlike predator-prey systems, where the underlying driver is predation, interactions between species within the same trophic level predominantly stems from competition over resources. In both cases negative interactions can significantly reduce population growth, but for carnivores, which naturally occur at low densities, these interactions could lead to reduced population viability and local extinction (Vucetich and Creel 1999, Creel et al. 2001). Understanding the behavioural mechanisms that interacting apex predators adopt to regulate these negative interactions could therefore be a crucial component in carnivore conservation.

The aim of this D.Phil. thesis is to quantify the ecological and behavioural relationships between sympatric, competing carnivores by taking a multi-species approach to investigate the mechanisms that lead to their coexistence.

Competition and coexistence

Central to the theory of coexistence is the need for animals to maximise benefits whilst minimising costs such as predation and competition (Rosenzweig 1981, Lima and Dill 1990). Under an ideal free distribution, where benefits can be maximised without the need of taking costs into account (Fretwell and Lucas 1969), an animal will occupy what is known as its *fundamental niche*. Species

with similar ecological requirements will occupy a similar fundamental niche and will therefore be part of the same trophic level or guild. However, according to Gause's principle of competitive exclusion, no two species can occupy the same niche for prolonged periods of time; competition over shared resources forces species into what is known as their *realised niche* (Hutchinson 1957, Case and Gilpin 1974). At the extremes, the outcomes of competition can either be exclusion or coexistence. Exclusion occurs when competition is severe enough that access to resources by one species is entirely restricted by the presence of a competing species and can lead to (local) extinction. Coexistence, on the other hand, can occur when competition is reduced by means of an evolutionary or behavioural shift towards a different ecological niche (i.e. resource partitioning) (Pianka 1974, Schoener 1974a). These behavioural adaptations will however depend on the degree and type of competition.

Competition between species

Competition can be split into two categories: exploitation competition and interference competition (Miller 1967). Exploitation competition is the indirect competition whereby a limited resource is exploited by one species thereby limiting availability to other species (Miller 1967, Levine 1976). In this case there is no direct confrontation and the degree of competition is directly related to the abundance of resources, increasing when resources are limited. Interference competition is the antagonistic interaction between species whereby one species attempts to free resources by direct harassment, predation, kleptoparasitism, poisoning or intimidation and can occur whether resources are limited or not (Miller 1967, Case and Gilpin 1974). Unlike exploitative competition, interference competition is not necessarily density-dependent and can therefore continue to reduce population growth at low densities, increasing extinction probabilities (Keddy 2001).

Simple competition models suggest that, despite the potential adverse effects of competition, species can coexist if the cost and benefits to the species involved are equivalent. Competition is,

however, rarely symmetrical as differences in traits will allow the dominant species to outcompete the subordinate species resulting in a competitive hierarchy within a community (Maynard-Smith and Parker 1976, Keddy 2001). Competitive asymmetry is more prominent when there is competition *between* species (interspecific) rather than *within* species (intraspecific) as there will be greater differences in life-history and behavioural traits (Maynard-Smith and Parker 1976, Keddy 2001). Generally, competition by the dominant species has impacts on the distribution, density and behaviour of the subordinate species. Individuals of the subordinate species might, for example, be confined to dimensions of the ecological niche where interactions with dominant species are minimised (competition refuges) (Case and Gilpin 1974, Durant 1998).

Pitfalls

The presence and effects of competition, especially exploitation competition, are notoriously difficult to quantify. The behavioural effects of competition are most conclusively determined by either the introduction or removal (natural or experimental) of competing species (Schoener 1983, Kotler et al. 1993, Harrington et al. 2009). Without such an experimental setup the ecological effects of competition remain hypothetical. Despite this, ecological and behavioural relationships can be explained by, rather than giving evidence for, competition. Understanding these behavioural relationships between species can give an insight into the mechanisms that allow species to coexist.

Coexistence between species

Coexistence between ecologically similar species can occur when competition is minimised through either morphological or behavioural adaptations (Schoener 1974a, Grether et al. 2009). Convergence of morphological traits can reduce competition over similar resources such as food or mates through, for example, disparity in dentition (Dayan et al. 1989, Davies et al. 2007), acoustic signals (Kirschel et al. 2009) and pigmentation (Anderson and Grether 2010). Competition can also be

minimised through behavioural adaptations within one or multiple dimensions of the ecological niche, the most important being food sources, space or time (Schoener 1974a, Linnell and Strand 2000). For example, competing species can avoid each other by being active at different times of day. In smaller mammals this has repeatedly been demonstrated in experimental studies where the competitively dominant species was removed or introduced, resulting in obvious shifts in activity patterns of the competitively subordinate species (Kronfeld-Schor and Dayan 2003, Harrington et al. 2009). For instance, Harrington et al. (2009) found that, in the absence of competitors mink (*Neovison vison*) were predominantly nocturnal but shifted to being diurnal when otters (*Lutra lutra*) and polecats (*Mustela putorius*) were introduced. Similarly, species can avoid each other spatially. Competing species can completely exclude each other from a given area, as has been seen in a study of red foxes (*Vulpes vulpes*) and arctic foxes (*Alopex lagopus*) (Hersteinsson and Macdonald 1992, Tannerfeldt et al. 2002) or they could avoid each other through differential habitat-use or by selecting areas that attract fewer competitors (Durant 1998, Loveridge and Macdonald 2003). In the latter two cases it is believed that a spatially heterogeneous environment is the key to coexistence by providing 'competition refuges' (Chesson 1986, Durant 1998). However, the use of spatial and temporal refuges could mean that species have to use habitats or be active at times of day that are sub-optimal for their ecological requirements. This has repeatedly been demonstrated in the context of optimal foraging theory suggesting that decreased foraging efficiency due to sub-optimal conditions could have a detrimental effect on growth and survivorship (Sih 1980, Kotler et al. 1993, Wirsing et al. 2007).

Carnivore coexistence

Like other species that are ecologically similar, carnivores can be in indirect competition with each other, most notably over prey resources. For example, in Idaho where wolves (*Canis lupus*) and cougars (*Puma concolor*) occur in sympatry, elk (*Cervus elephus)* made up 77% and 73% of their

respective diets (Husseman et al. 2003). Similarly, extensive dietary overlap was noted between the larger members of the African carnivore guild (Hayward and Kerley 2008). Carnivores exploiting the same prey base will be similarly influenced by the behaviour and spatial distribution of common prey and therefore use similar areas or hunt at similar times (Karanth and Sunquist 2000, Hayward and Slotow 2009). Overlap in space and time by competing carnivores increases the chances of interference competition (Palomares and Caro 1999, Karanth and Sunquist 2000). Two forms of interference competition characteristic of the carnivore guild are kleptoparasitism and intraguild predation (Palomares and Caro 1999, Caro and Stoner 2003).

Kleptoparasitism

Kleptoparasitism refers to the parasitic theft of a resource, which in the case of carnivores are captured prey. Individuals are more likely to kleptoparasitise when the net energetic benefit is higher than that of hunting live prey, particularly when the individual that is being stolen from is weaker and the success of kleptoparasitism is higher (Creel 2001). The individual stolen from is negatively impacted by kleptoparasitism, not only because a direct encounter can result in injury, but also because they have to expend additional energy to compensate for the loss, thereby increasing foraging costs. Kleptoparasitism by larger, dominant guild members could therefore be particularly detrimental for smaller species, such as the African wild dog (*Lycaon pictus*), whose hunting techniques are believed to be energetically costly (Gorman et al. 1998).

Intraguild predation

Hostile interactions between carnivores are not uncommon and can be particularly intense due to their behavioural and morphological adaptations for killing (Palomares and Caro 1999, Keddy 2001). When the outcome of these encounters is fatal it is referred to as intraguild predation. Intraguild predation is seen as an exceptional case of interference competition as the killer species benefits indirectly through the freeing of resources by removing potential competitors (Case and Gilpin 1974) rather than directly through consumption (Kotler and Holt 1989). Intraguild predation is almost

exclusively found in the carnivore guild and has been recorded in up to 97 pairs of carnivores, occurring most frequently when there is a high degree of dietary overlap (Holt and Polis 1997, Palomares and Caro 1999, Donadio and Buskirk 2006).

Consequences of carnivore coexistence

In cases of competitive dominance among species, these negative interactions are believed to be partially responsible for the rarity and slow recovery of subordinate species (Vucetich and Creel 1999, Linnell and Strand 2000, Caro and Stoner 2003). For example, the density of African wild dogs is negatively correlated with the density of the competitively dominant lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) (Creel and Creel 1996), while coyote (*C. latrans*) abundance is limited by interactions with wolves (*C. lupus*) (Berger and Gese 2007). Interactions of this sort have always occurred in natural communities and therefore are not in themselves a cause for conservation concern. The problem arises when they occur, or their frequency changes, as a consequence of anthropogenic changes in the environment (Dickman 1996) leading to radical shifts in community dynamics (Fortin et al. 2005) and possibly extinction. For example, human-induced habitat fragmentation is forcing species into ever smaller areas, which can result in an increase in negative interactions between species (Creel et al. 2001). This could in turn result in competitively subordinate species making use of competition refuges outside protected areas (van der Meer et al. 2011, Cozzi et al. 2013), thereby increasing the risk of coming into conflict with humans (Woodroffe and Ginsberg 1998). This is of particular concern for competitively subordinate carnivores, such as African wild dogs and cheetahs (*Acinonyx jubatus*) that already occur at relatively low densities (Linnell and Strand 2000, Creel et al. 2001). Understanding the behavioural and ecological mechanisms by which carnivores manage negative interactions could therefore be crucial for carnivore conservation (Creel et al. 2001).

The behavioural mechanisms by which carnivore species coexist can be expected to vary depending on differences in morphology and behaviour, the intensity of competition and the availability of

resources. Black-backed jackals (*C. mesomelas*) in Zimbabwe showed a strong overlap in diet, intermediate overlap in space but almost complete avoidance in time with side-striped jackals (*C. adustus*) (Loveridge and Macdonald 2003) whereas tigers (*P. tigris*) and leopards (*P. pardus*) in India showed little overlap in diet but overlapped extensively in time and space (Karanth and Sunquist 2000). For the larger members of the African carnivore guild, knowledge of the mechanisms of coexistence is limited.

Coexistence between sympatric large African carnivores

The intact large carnivore guild throughout most of sub-Saharan Africa would typically consist of five species: African wild dogs, leopards, cheetahs, lions and spotted hyaenas. Ranges of the latter three species, which comprise the focal subjects of this thesis, overlap extensively (Figure 1.1). Within these overlapping areas cheetah densities are negatively correlated with lion and spotted hyaena densities (Caro 1994, Laurenson 1995). For example, in Serengeti National Park, Tanzania, where lion and spotted hyaena numbers are high, cheetah densities are low (Laurenson 1995), whereas on the Namibian farmlands where lion and spotted hyaena have been eradicated, the cheetah population is thriving (Marker et al. 2003). In addition, Kelly et al. (1998) found that the reproductive success of cheetahs was lower during periods of high lion abundance than during periods of relatively lower lion abundance. This negative relationship is mainly due to the fact that cheetahs are competitively subordinate to lions and spotted hyaenas. This is attributable to their smaller body size and the fact that, unlike lions and spotted hyaenas which form large social groups, their social system is defined primarily by solitary individuals and relatively small social groups (Durant 1998, Table 1.1).

Table 1.1: Comparison of life-history traits and behaviour between the competitively subordinate cheetahs and the more dominant lions and spotted hyaenas.

	Cheetah (*Acinonyx jubatus*)	Lion (*Panthera leo*)	Spotted Hyaena (*Crocuta crocuta*)
Body size:			
- Males	41.4 ± 5.4 kg [a (mean ± SD)]	189.6 kg (150.0-225.0 kg) [b (mean and range)]	45-62 kg [c (range)]
- Females	35.9 ± 5.3 kg [a (mean ± SD)]	103.8 kg (83.0-165.0 kg) [b (mean and range)]	55-82.5 kg [c (range)]
Litter size	1-6 cubs [c]	2-4 cubs [c]	1-2 cubs [c]
Social structure	Mixture of both solitary and social behaviour. Females are often found alone, unless with dependent cubs whilst males are either solitary or in a coalition [a].	A fission-fusion society with prides of 3-10 adult females, their dependent offspring and a coalition of 2-3 adult males [c].	Clans range from 5-80 individuals. They exhibit a female-dominated hierarchy where rank is usually inherited from the mother [c].
Home-range size	Namibia (north-central farmlands): female (2 161 km^2), male (1 490 km^2) [d] Serengeti Plains: female (833 km^2), male (777 km^2) [a] Kalahari Gemsbok NP: female (320 km^2), male (125 km^2) [e] Kruger NP: female (170 km^2), male (180 km^2) [f] This study area: female (900 km^2), male (507 km^2) [m].	20-500 km^2 depending on pride size and prey abundance [c]. Kgalagadi Transfrontier Park (266-4532 km^2) [g]. Hwange NP: female (293 ± 210 km^2), male (324 ± 190 km^2) [h]. This study area: 276.62 ± 62.74 km^2 (s.e.m.) [m].	Wide variation from 40 km^2 to 1000 km^2 [c]. Kenya and Tanzania 30 – 60 km^2 [l] This study area: 193.89 ± 31.16 km^2 (s.e.m.) [m].
Hunting strategies	High speed cursorial hunter – rarely scavenge	Stalk and ambush hunter – occasionally scavenge	Cursorial hunter – regularly scavenge
Main prey species	Prefer the most abundant prey species with a body mass range of 10-56 kg, including impala, blesbok, springbok, duiker and warthog [a, i]. This study area: impala account for 79% of their total diet [m].	Large prey within the body mass range of 190-550 kg, but do occasionally eat smaller prey [n]. Prey preferences reported in Hwange NP: buffalo 30-35%, kudu 11-24%, giraffe 8-10%, elephant 5-7% [j]. This study area: zebra account for 37% and impala for 17% of their total diet [m].	Scavenge opportunistically and hunt medium-sized (12-80 kg) and large (>80 kg) prey. No preference for any one species, but prey commonly on impala, bushbuck, springbok, gemsbok and kudu [k, o].

References: [a] (Caro 1994), [b] (Smuts et al. 1980), [c] (Macdonald 2001), [d] (Marker et al. 2008), [e] (Mills 1998), [f] (Broomhall et al. 2003), [g] (Funston et al. 2001a), [h] (Davidson et al. 2011), [i] (Hayward et al. 2006), [j] (Loveridge et al. 2006), [k] (Hayward 2006), [l] (Woodroffe and Ginsberg 1998), [m] (F. Broekhuis, unpublished data), [n] (Hayward and Kerley 2008), [o] (Mills 1990)

Because cheetahs, lions and spotted hyaenas are ecologically similar there is a significant degree of dietary and spatial overlap suggesting a potential for competition (Schaller 1972, Mills and Biggs 1993, Caro 1994, Table 1.1). The presence and effect of exploitation competition is hard to quantify but interference competition seems to have a significant, quantifiable impact on cheetahs. For example, in the Serengeti, cheetahs rarely defend their kills from kleptoparasitism, losing up to 12.9% of their kills, of which 78% were taken by spotted hyaenas and 15% by lions (Hunter et al. 2007b). In addition, juvenile mortality was found to be extremely high with only 5% of the cubs reaching independence. The major cause for this high mortality was reportedly predation, comprising up to 73% of all cub deaths. Of the total mortality, 78.6% was caused by lions and 12.2% by spotted hyaenas (Laurenson 1994).

The global cheetah population is rapidly dwindling and with less than 10 000 individuals left in the wild, cheetahs are vulnerable to extinction (Nowell and Jackson 1996, Creel et al. 2001). As interactions with lions and spotted hyaenas are recognised as potential factors that could accelerate the rate of extinction (Creel et al. 2001) a few studies have attempted to quantify the behavioural mechanisms by which cheetah minimise interactions with lions and spotted hyaenas (Durant 1998, 2000b, a). Mechanisms for coexistence can arise from both evolutionary and contemporary behavioural adaptations (Schoener 1974b, Kronfeld-Schor and Dayan 2003). Evolutionarily cheetah are believed to have become diurnal to avoid nocturnal lions and spotted hyaenas (Hayward and Slotow 2009) and become grassland specialists to avoid lions who tend to use denser habitat types to facilitate their ambush-hunting technique (Eaton 1974, Macdonald 1992). While evolutionary adaptation is difficult to prove, studies have observed contemporary behavioural adaptations by cheetahs in response to a perceived risk of encountering lions and spotted hyaenas (Durant 2000b, a, Hunter et al. 2007b). For example, cheetahs were less likely to hunt and more likely to move when lion roars were played in close proximity (Durant 1998, 2000a). Cheetahs also avoided areas with high numbers of prey, where lions and spotted hyaenas were more likely to be present, selecting for areas with low and intermediate prey densities (Durant 1998).

Despite these studies, the mechanisms by which cheetahs, lions and spotted hyaenas coexist are still poorly understood (Durant 1998, Mills et al. 2004, Bissett and Bernard 2007) mostly due to the fact that fine-scale quantitative analyses are scarce. For example, studies investigating temporal partitioning have not documented the activity of individuals that are present in the same area (Hayward and Slotow 2009). Similarly, studies investigating spatial avoidance have come from the Serengeti ecosystem, a homogenous ecosystem dominated by grassland making it impossible to look at the importance of habitat heterogeneity in carnivore coexistence. The research reported in this thesis aims to fill these gaps by conducting the research in an environmentally heterogeneous area where all three carnivores occur sympatrically (Figure 1.1).

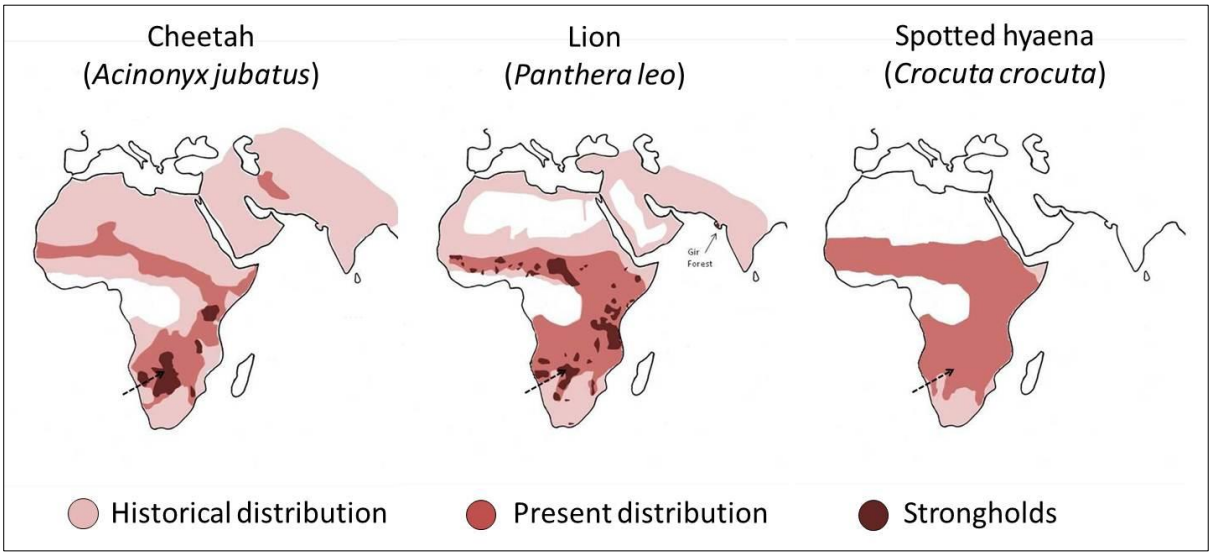


Figure 1.1: Present and historic distributions of cheetahs, lions and spotted hyaenas. The arrows indicate the study area in the Okavango Delta, northern Botswana. Figures adapted from Macdonald (2001), courtesy of G. Cozzi.

Study area

The study was conducted on the periphery of the Okavango Delta, a permanent inland delta situated in the northern part of Botswana, which was listed as a Ramsar site in 1997 (Figure 1.2). The core study site (19°31'S, 23°37'E; elevation ca. 950m) encompasses an area of approximately 2 700 km^2 which includes the southern part of the Moremi Game Reserve and the adjacent Wildlife Management Areas (WMAs) (McNutt 1996, McNutt and Silk 2008, Figure 2.1).

Habitat composition

The study area lies in a semi-arid ecosystem characterised by five distinct transitional habitat types; *Colophospermum mopane* woodland, mixed forest dominated by *Acacia spp*. (*A. erioloba* and *A. tortilis*), riparian woodland, open grasslands and floodplains created by the extremities of the Okavango Delta (McNutt 1996). The different habitat types are classified as follows:

1. Swamp – moist and seasonally flooded open grasslands usually along a river course characterised by sedges and grass species *Panicum repens* and *Cynodon dactlyon*
2. Grassland – including former floodplains, are characterised by open shrubbed grassland dominated by grass species *C. dactylon*, *Chloris virgata* and *Eragrostis spp*.
3. Mixed woodland – predominately characterised by *Acacia spp.* with a grassy understory consisting of *C. dactylon*, *Panicum spp.* and *Eragrostis spp.*
4. Mopane – woodland characterised by *C. mopane* shrubs and trees
5. Riparian – tall open mixed woodland located on riverine or historic riverine areas characterised by *A. nigrescens* and *Combretum imberbe* trees

The dense *C. mopane* forest covers the majority of the Northern and North-Eastern sections of the study area and makes up 48% (629 km^2) of the total core area (Figure 1.2). The habitat in the Western part is influenced by the Gomoti River, a primary distributary of the Okavango Delta and is characterised by seasonal floodplains and grasslands interspersed with islands of mixed Acacia woodland and riparian vegetation. In the Southern and South-Eastern section the habitat is a heterogeneous mosaic of grassland, mixed *Acacia* woodland and *C. mopane* woodland. In the study area, floodplains account for 7% (96 km^2), grassland for 19% (255 km^2), mixed Acacia woodland for 22% (295 km^2) and riparian for 3% (45 km^2) of the total core area.

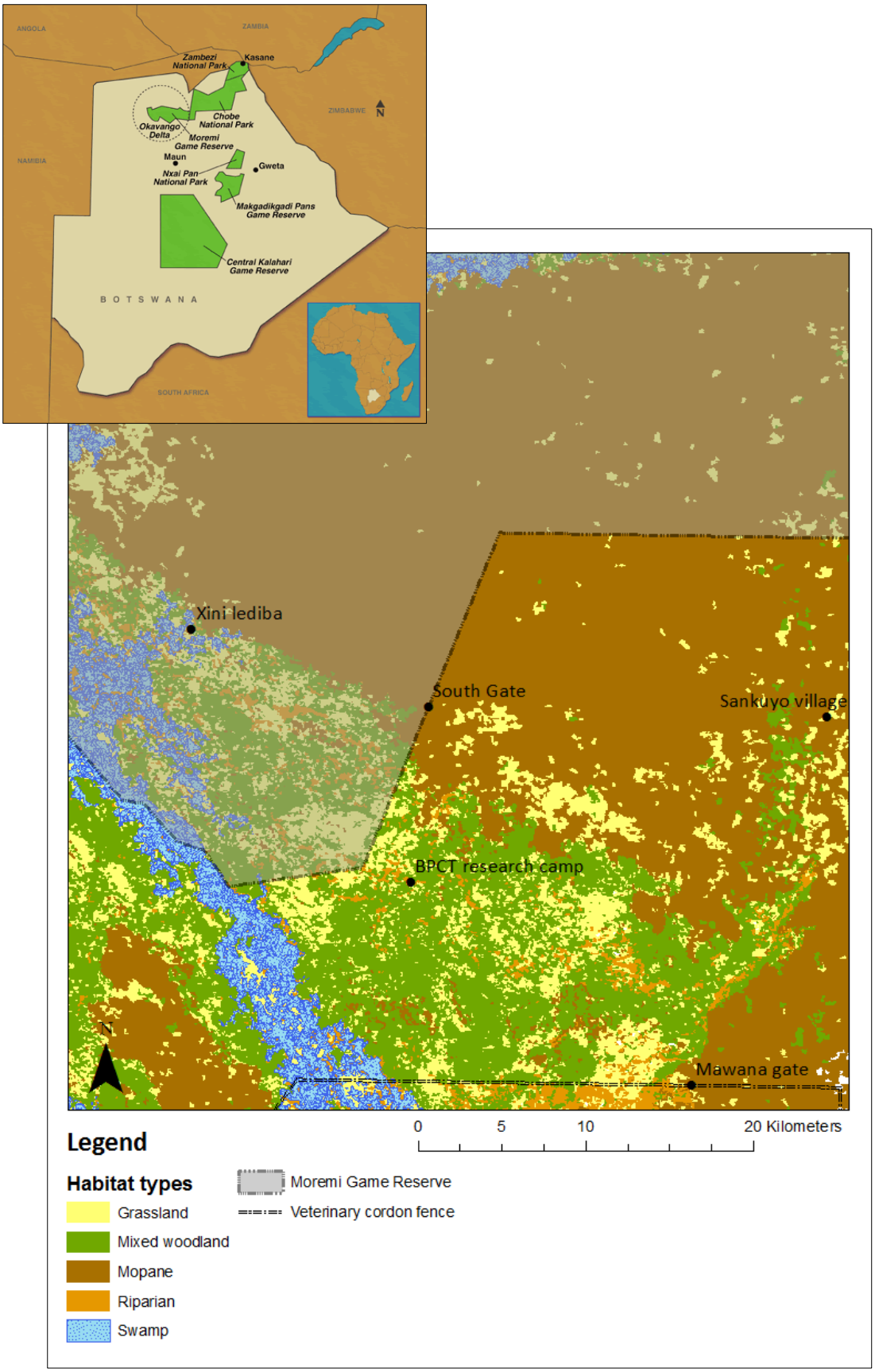


Figure 1.2: Map of the study area. The map in the top left corner shows the study area in relation to the rest of Botswana and the main map shows the core area including five main habitat types.

Rainfall and water sources

Water availability is dependent on both seasonal rainfall and annual floods. The majority of the annual precipitation (300-600 mm) falls during the summer months (October-March) which are then followed by the dry winter months (April-September) (Mendelson et al. 2010, Bartlam-Brooks et al. 2011). In addition to the rains, the Okavango Delta floods once a year when the floodwater from the South-eastern Angolan highlands makes its way along the Okavango River. The floods are out of synchrony with the rains, reaching the lower part of the Okavango Delta during the dry winter season, peaking at the periphery of the Okavango Delta between August and September and gradually reaching a low in the wet summer months (McNutt 1996, McCarthy et al. 2003). As a result of the floods, parts of the study area are divided into permanent swamp and seasonal floodplain. Due to the scarcity of water in Botswana, both the permanent swamps and the seasonal floodplains are an important resource for the wildlife population.

Human impact

Although the Okavango Delta is an important water source in Botswana, it is relatively sparsely populated, with the exception of the Western and Southern margins. This is due to the historic occurrence of tsetse flies (*Glossina morsitans*), carrying trypanosomiasis, and the construction of a veterinary cordon fence (Figure 1.2) restricting the farming of cattle, a major livelihood for the local population (ODMP 2008). The combination of the perennial waters and the low human impact factor gives rise to a relatively healthy ecosystem with stable wildlife populations.

Carnivore community

Botswana is one of the remaining strongholds for the rapidly dwindling cheetah population (Nowell and Jackson 1996). Whilst Botswana is believed to accommodate almost 20% of the global cheetah population, most research has focused on the agricultural regions and not in protected areas where cheetahs have the potential to interact with lions and spotted hyaenas (Klein 2007). In the entire

Okavango Delta, an area of approximately 14 750 km^2, there are believed to be about 52 individual cheetahs (minimum estimate = 22 individuals, maximum estimate = 83 individuals)(ODMP 2006). Figures for lions and spotted hyaenas are currently unknown. The area where this study took place (approx. 2 700 km^2) has an intact guild of large carnivores consisting of the intensively studied African wild dog and relatively unknown populations of cheetahs, lions and spotted hyaenas, making it an ideal area to study the interaction between carnivore species in a relatively pristine ecosystem. During the three years of fieldwork I managed to collect data on all the known individual cheetahs (n=6), lion prides (n=5) and spotted hyaena clans (n=6) in the study area.

Prey species

The study area has a sedentary prey base including a variety of herbivore species ranging from the small ungulates like steenbok (*Raphicerus campestris*), warthog (*Phacochoerus africanus*) and impala (*Aepyceros melampus*) to the larger species including African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*) and African elephant (*Loxodonta africana*).

Thesis overview

Chapter 2: Fear of the dark or dinner by moonlight? Reduced temporal partitioning among large African carnivores

In this chapter we investigate the temporal partitioning of cheetahs with lions and spotted hyaenas. The analysis of activity patterns, based on data from radio-collars, revealed an unexpectedly high degree of temporal overlap which was mainly due to the extensive and previously undescribed nocturnal activity of cheetahs. In addition, their nocturnal activity fluctuated with the lunar cycle and was primarily constrained by moonlight availability rather than by the nocturnal activity of lions and spotted hyaenas. These results indicate that the benefits of being active on moonlit nights offset the risks of encountering nocturnal predators and competitors. Whether this is the case is explored in Chapter 3. A modified version of this chapter has been published in *Ecology*.

Chapter 3: Cracking the code: using machine learning techniques to translate activity into behaviour

In this chapter we use machine learning techniques to transform the activity data collected by the radio-collars into behavioural categories based on behavioural data collected in the field. We focus on three fundamental behaviours: feeding, moving and resting and give an example of how this type of classified data can be used to investigate animal behaviour. A slightly modified version of this chapter has been published in *PLoS ONE*.

Chapter 4: Scaredy-cat? How fear and foraging affect cheetah temporal distribution

In this chapter we use the classified data from Chapter 3 to test the hypothesis in Chapter 2 that the temporal distribution of behaviour, in particular foraging, of a competitively subordinate carnivore is driven by maximisation of resource acquisition rather than predator avoidance. The results suggest that cheetahs are more plastic in their behaviour than was previously thought and that, within the constraints of their evolutionary adaptations, the temporal distribution of their behaviour is driven by resource acquisition rather than predator avoidance. This chapter has been submitted to *Animal Behaviour*.

Chapter 5: Risk avoidance in sympatric large carnivores: reactive or predictive?

The focus of this chapter is the spatial aspect of avoidance. I tested whether cheetahs' spatial response to encountering lions or spotted hyaenas is either reactive or predictive. Cheetahs generally selected for habitats and areas that were intensively used by lions and spotted hyaenas, however, if there was an immediate risk of encountering lions, cheetahs tended to be further away than expected, apart from when they were in mixed woodland. This suggests that not only is cheetah spatial distribution a reactive, rather than a predicate response, but it also indicates that

habitat heterogeneity is an important factor in carnivore coexistence. A slightly modified version of this chapter has been published in *Journal of Animal Ecology*.

Chapter 6: The ecological small print: fine-scale adaptations in relation to risk and habitat use

The aim of this chapter was to tie up the loose ends of the previous chapters by taking a more fine-scale approach to investigate the ecological and behavioural mechanisms that cheetahs adopt to facilitate coexistence with competitively more dominant carnivores. More specifically we investigate whether habitat-use by cheetahs is influenced by their behaviour and whether this varies according to the level of both the temporal and spatial risk of encountering lions.

Chapter 7: General discussion

The concluding chapter summarises and discusses the results from Chapters 2-6 and puts them into a global context.

Appendices

Appendix I – This manuscript uses the data and analyses used in Chapter 2 in combination with similar data on African wild dogs to investigate the temporal behaviour of competitively subordinate carnivores in relation to that of more dominant carnivores. This manuscript has been accepted for publication by *Ecology***.**

CHAPTER 2

Fear of the dark or dinner by moonlight? Reduced temporal partitioning among large African carnivores

A modified version of this chapter has been published in *Ecology*

Abstract

Africa is home to the last intact guild of large carnivores, providing a unique opportunity to investigate mechanisms of coexistence among large predator species. Strong asymmetric dominance hierarchies typically characterise guilds of large carnivores, but despite this asymmetry, competitively subordinate species may persist alongside their stronger counterparts through temporal partitioning of habitat and resources. In the African large carnivore guild, the competitively subordinate cheetahs are routinely described as diurnal and crepuscular. These activity patterns have been interpreted to result from the need to avoid encounters with the stronger, nocturnal lions and spotted hyaenas. However, the idea that diel activity patterns of carnivore species are strongly shaped by competition and predation has recently been challenged by new observations. We therefore investigated the daily activity patterns and temporal partitioning for cheetahs, lions and spotted hyaenas by fitting radio-collars that continuously recorded their activity. Analysis of activity patterns revealed an unexpected high degree of temporal overlap among the three species which was mainly due to the extensive and previously undescribed nocturnal activity of cheetahs. Cheetahs' nocturnal activity accounted for up to 40% of their diel activity budget and was positively correlated to the amount of moonlight available. In contrast, the nocturnal activity patterns of lions and spotted hyaenas were unaffected by moonlight and remained constant over the lunar cycle. The results suggest that other ecological factors such as optimal hunting conditions have shaped the diel activity patterns of competitively subordinate, large predators. We suggest that the benefits of being active on moonlit nights must therefore offset the risks of encountering nocturnal predators and competitors.

Introduction

Intraguild competition and predation have been recognised as important ecological factors influencing the population dynamics of carnivores (Palomares and Caro 1999, Linnell and Strand 2000, Caro and Stoner 2003). Large predators in extant and extinct guilds are known to compete for similar prey species, despite the variation in body size among guild members (Sinclair 2003, Radloff and Du Toit 2004). This body-size variation has led to strong interspecific dominance hierarchies, resulting in larger members of the guild dominating the smaller ones (Rosenzweig 1966, Maynard-Smith and Parker 1976, Polis and Holt 1992, Palomares and Caro 1999). Lions and spotted hyaenas are, for example, known to kill cheetah cubs, steal their food and exclude them from prey-rich areas, whereas cheetahs have little or no influence on the larger members of the guild (Laurenson 1995, Laurenson et al. 1995, Durant 1998). Costly interactions with competitively dominant species could be responsible for the general rarity of competitively subordinate predator species (Palomares and Caro 1999, Caro and Stoner 2003) and may push some species to the edge of extinction (Vucetich and Creel 1999). Understanding the relationships among the members of a guild is particularly important for large carnivores as they tend to be extinction-prone, due to low population densities and low reproductive rates (Purvis et al. 2000). Furthermore, human related habitat loss and fragmentation are forcing carnivores to inhabit ever-smaller areas, increasing the frequency of antagonistic interactions and hence potentially accelerating extinction rates (Creel et al. 2001, Caro and Stoner 2003).

It has been suggested that smaller, competitively subordinate species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources (Pianka 1974, Schoener 1974a, Durant 1998, Linnell and Strand 2000, Harrington et al. 2009). Temporal partitioning as a mechanism to reduce competition or predation has been suggested, for example, between predators and prey (Sih 1980, Kotler et al. 1993, Ziv et al. 1993). Accordingly, it is widely

accepted that lions and spotted hyaenas have strongly shaped the temporal niche of cheetahs (Caro 1994). In particular, the previously described diurnal and crepuscular activity pattern of cheetahs has commonly been interpreted as a behavioural adaptation to avoid encounters with the predominantly nocturnal lions and spotted hyaenas (Hayward and Slotow 2009).

Direct field evidence for temporal partitioning in African large carnivores is, however, lacking, and there has been no detailed study of activity patterns conducted simultaneously on sympatric species. In the only published paper investigating the temporal partitioning between African large carnivores, Hayward and Slotow (2009) conclude that "top-down effects appear to drive temporal partitioning within the [African] large-predator guild" and that "the remaining members of the guild probably evolved to become active in periods that limit their potential for interaction with lions". In fact, anecdotal observations (Schaller 1972, Creel and Creel 2002) and a more recent study (Rasmussen and Macdonald 2012) suggest that light availability at night may influence activity patterns of diurnal carnivores, and that nocturnal activity may be more pronounced than previously thought, thus questioning the real role of lions and spotted hyaenas in influencing the activity patterns of competitively subordinate species.

While a critical test of the temporal partitioning hypothesis would involve removing the competitively dominant predators and looking for a change in the behaviour of the competitively subordinate species, such a study is clearly impractical. Instead, a detailed study of activity patterns was carried out to test whether the activity patterns of cheetahs are primarily shaped by light availability, rather than by avoidance of lions and spotted hyaenas. To do this, radio-collars equipped with activity sensors were attached to individual cheetahs, lions and spotted hyaenas. First, we investigated how activity was distributed throughout the 24-hour cycle for all species. Second, we tested if the nocturnal activity patterns were correlated with moonlight availability: a strong positive relationship would suggest that light availability plays an important role in determining activity at

night. Third, we investigated whether for cheetahs there were trade-offs in activity during different periods of the 24-hour cycle. Specifically, we investigated whether increased nocturnal activity resulted in reduced activity on the following day. Trade-offs in activity within the 24-hour cycle would suggest that, when moonlight is sufficient, competitively subordinate predators shift their diurnal activities to the night hours, despite the risk associated with a higher likelihood of encountering more dominant members of the guild.

Methods

Field work

Radio-collars equipped with sensors (VECTRONIC Aerospace GmbH, Germany) designed to record activity data (see below for more details) were fitted to the study animals (following Kock et al. 2006) by a registered veterinarian in compliance with Botswana law. After immobilisation, the collared individuals safely re-joined their group showing no signs of distress. Between 2008 and 2010 we monitored the activity of a total of six individual cheetahs (two males and four females), six lions in five prides and six spotted hyaenas in five clans. The collared individuals ranged over an area of approximately 2 720 km^2 with their territories largely overlapping**.** Throughout the duration of the study, at least two individuals of each species were collared at any time. However, no more than one individual per social group was collared at any given time to avoid data duplication owing to the collective movement of group members. Activity data were recorded for a mean of 329 days for cheetahs (range: 217–472 days); 416 days for lions (range: 328–486 days) and 432 days for spotted hyaenas (range: 310–587 days).

Subdivision of a 24-hour cycle

To investigate activity patterns, each 24-hour cycle was divided into five periods: night, morning twilight, morning, afternoon and evening twilight. These periods reflect the main activity periods for

cheetahs (day and twilight) and for lions and spotted hyaenas (night and twilight) as currently described in the literature (Caro 1994, Hayward and Slotow 2009). Night stretched between the astronomical dusk and dawn, when the sun was 18° below the horizon and sunlight contribution to overall luminosity was nil (http://aa/usno.navy.mil/). The morning twilight started at dawn and ended at sunrise; the evening twilight started at sunset and ended at dusk. The day lasted from sunrise to sunset and the division between morning and afternoon occurred around noon each day (Appendix 2.1). The night was further divided into seven periods; three periods before midnight, one period across the midnight hour and three periods after midnight. Each period (apart from the midnight period) had an exact duration of 1.2 hours and was therefore directly comparable to the duration of the morning and afternoon twilight periods. Because the overall night length slightly changes over time, we had to adjust the length of the period spanning midnight, which therefore varied slightly in length (± 30 minutes).

Light availability and environmental factors

Moonlight intensity, the main predictor variable, was taken as a measure of light availability at night and was defined as the percentage of the lunar disc illuminated (http://aa/usno.navy.mil/). Full moon nights and new moon nights were defined when respectively ≥ 95% and ≤ 5% of the lunar disc was illuminated, giving 4–5 full moon and 4–5 new moon nights per lunar cycle. First quarter and third quarter moon (i.e. half of the moon visible from the Earth's surface) were defined when the percentage of the lunar disc illuminated was between 45% and 55% and are referred to as half-moon waning and half-moon waxing. Since cloud cover reduces available moonlight during the rainy season, only data collected during the dry season (April–October) when cloud cover was negligible were considered. Because temperature has been shown to influence activity patterns of carnivore species (Theuerkauf 2009), this was included as a covariate in the statistical models. For each day, average temperatures for the five periods of the 24-hour cycle were calculated using the data

recorded at 15 minute intervals by a fixed weather station (http://www.jacanaent.com/Weather.htm).

Data analysis

The activity data for the analyses were systematically collected by radio-collars, equipped with two motion sensors, attached to the study animals. The two motion sensors continuously recorded activity bursts and summed them over 5 minute intervals; a raw data point consisted of the number of activity bursts/5 minutes making the data continuous, not categorical. To account for pseudo-replication, we averaged, for each day, the activity data recorded by each collar over the five periods of the 24-hour cycle. The resulting dataset consisted of one activity value for night, morning twilight, morning, afternoon and evening twilight, for each day and for each individual. Study animals were followed during the day-time and the observed behaviour was matched with the data collected by the collars at the time of observation. Resting animals usually showed activity levels of about 5–15 counts/5 minutes depending on the species.

For each species, mean activity values were calculated for each period of the 24-hour cycle during full-moon and new-moon days, as well as mean activity values for the seven periods of the night during full-moon, half-moon (waning and waxing) and new-moon days. Periodicity in the nocturnal activity was analysed using Fourier spectral analysis, performed using the statistical software R (R Development Core Team 2012). The Fourier algorithm isolates the period of a sinusoidal waveform (e.g. Polansky et al. 2010), and was applied to nocturnal activity values of each individual separately. Because Fourier analysis does not reveal the directionality and strength of the relationship between variables, the nocturnal activity was further analysed using linear mixed effects models, performed using the statistical software GenStat (VSN International 2010), with moonlight intensity as an explanatory variable. Nocturnal activity, the response variable, was log-transformed to meet the assumptions of normality and homoscedasticity. Animal identity was treated as a fixed effect; night

temperature and activity during the previous day-time were entered as covariates; moon cycles and days nested within moon cycles were treated as random effects. A first-order auto-regressive error structure was included when necessary, based on diagnostic plots of residuals.

To further investigate the effects of nocturnal activity on activity levels the following day and to understand how activity was partitioned across the 24-hour cycle, we constructed four additional mixed effects models with, respectively, morning twilight activity, morning activity, afternoon activity and evening twilight activity as response variables. The activity variables were log-transformed to meet the assumptions of normality and homoscedasticity. For each model, animal identity, moonlight intensity, activity during the previous periods of the 24-hour cycle (e.g. morning twilight activity when analysing morning activity) and temperature of the respective period were treated as fixed effects. For both models, moon cycles and days nested within moon cycles were treated as random effects. Model simplification started from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2011).

Results

The nocturnal activity of cheetahs made up 25.6 ± 3.5 % of their overall diel activity budget, a high value for a species currently described as diurnal and crepuscular. In contrast, for lions and spotted hyaenas nocturnal activity made up 60 ± 2.7 % and 67.9 ± 2.6 % of their respective activity budgets (Table 2.1). In addition, roughly half of cheetahs' total activity (43.8 ± 1.9 %; Table 2.1) was carried out during the main activity periods of lions and spotted hyaenas (night and twilight). This rather extensive and unexpected overlap between the activity patterns of the subordinate and the dominant carnivores is inconsistent with the idea of strict temporal partitioning.

Table 2.1: Percentage (± s.e.m.) of activity during the five periods of the 24-hour cycle over an entire lunar cycle and for two different phases of the lunar cycle. 'Partial overlap' is the sum of the activities recorded during the three periods of major lion and spotted hyaena activity, as described in the literature (night, morning twilight and evening twilight) and shows how much of cheetah diel activity takes place during times of overlapping activity with lions and spotted hyaenas.

		Cheetah	Spotted hyaena	Lion
Overall	Night	25.6 ± 3.5	67.9 ± 2.6	60.0 ± 2.7
	Morning twilight	9.9 ± 1.4	8.1 ± 0.8	7.4 ± 0.7
	Morning	34.3 ± 2.1	10.4 ± 1.7	16.3 ± 1.4
	Afternoon	21.9 ±1.5	5.0 ± 1.1	9.3 ± 1.8
	Evening twilight	8.3 ± 0.7	8.6 ± 0.5	7.9 ± 0.8
	Partial overlap	**43.8**	**84.6**	**75.3**
Full moon	Night	39.7 ± 4.4	66.7 ± 2.3	57.7 ± 4.0
	Morning twilight	7.1 ± 1.6	9.3 ± 0.4	7.7 ± 0.5
	Morning	28.1 ± 2.1	10.5 ± 1.7	16.9 ± 2.1
	Afternoon	17.2 ± 1.0	4.9 ± 1.2	9.8 ± 2.0
	Evening twilight	7.8 ±0.7	8.6 ± 0.6	8.0 ± 0.9
	Partial overlap	**54.6**	**84.6**	**73.4**
New moon	Night	13.8 ± 2.4	67.7 ± 2.9	60.9 ± 2.4
	Morning twilight	12.3 ± 1.2	7.6 ± 1.3	7.4 ± 0.8
	Morning	40.1 ± 2.0	10.8 ± 1.6	14.5 ± 1.4
	Afternoon	24.7 ± 1.8	5.0 ± 1.1	9.2 ± 1.4
	Evening twilight	9.1 ± 0.7	8.9 ± 0.5	8.0 ± 0.8
	Partial overlap	**35.2**	**84.2**	**76.3**

Mean activity values over the five periods of the 24-hour cycle (night, morning twilight, morning, afternoon and evening twilight) showed significant differences between full moon days and new moon days for cheetahs but not for lions and spotted hyaenas (Figure 2.1, Table 2.1). This suggests that the activity pattern of cheetahs changes over a lunar cycle, while the activity pattern of lions and spotted hyaenas remains constant and is thus uncoupled from the phases of the moon (Figure 2.1, Table 2.1). On full moon days, 39.7 ± 4.4 % of the total diel activity of cheetahs occurred at night while this figure dropped to approximately 13.8 ± 2.4 % during new moon days (Table 2.1). In contrast, the night time activity of lions and spotted hyaenas did not change between the different phases of the lunar cycle (Table 2.1).

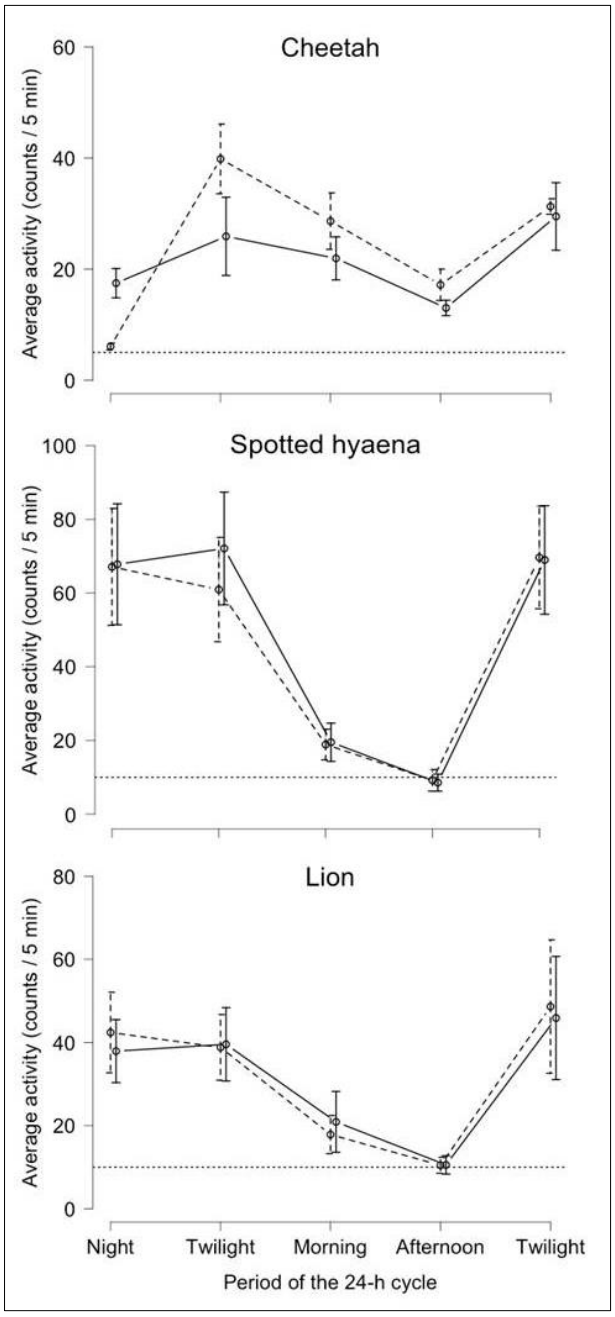


Figure 2.1: Average activity values during five periods of the 24-hour cycle for full moon days (solid lines) and new moon days (dashed lines). Error bars represent standard errors of the mean. Connecting lines between mean values have been added for visualization purposes. The horizontal dotted line shows the inactivity threshold.

The Fourier spectral analysis showed that the nocturnal activity of five out of six cheetahs exhibited a main period of 30.45 ± 0.49 days (Figure 2.2), while one individual (#3) showed little signature at this wavelength (Figure 2.3). In contrast, the nocturnal activity of lions and spotted hyaenas showed

no relationship with the lunar cycle, although they exhibited shorter activity cycles of a few days (Figure 2.2). A fine-scale investigation of the night-time activity between different phases of the lunar cycle showed that cheetahs adjusted their nocturnal behaviour according to the presence of the moon in the sky. For example, during a waning moon, when the moon is in the sky during the first half of the night, cheetahs were highly active during the hours preceding midnight (Appendix 2.2). With sufficient moonlight, the night activity levels of cheetahs were comparable to activity levels exhibited during the morning twilight on full moon days (compare Figure 1 with Appendix 2.2). In contrast, the activity of lions and spotted hyaenas was not related to the presence of the moon in the sky and remained generally constant during the night. This further supports the prediction that moonlight intensity, rather than the activity of lions and spotted hyaenas, is a major driver influencing the nocturnal activity of cheetahs.

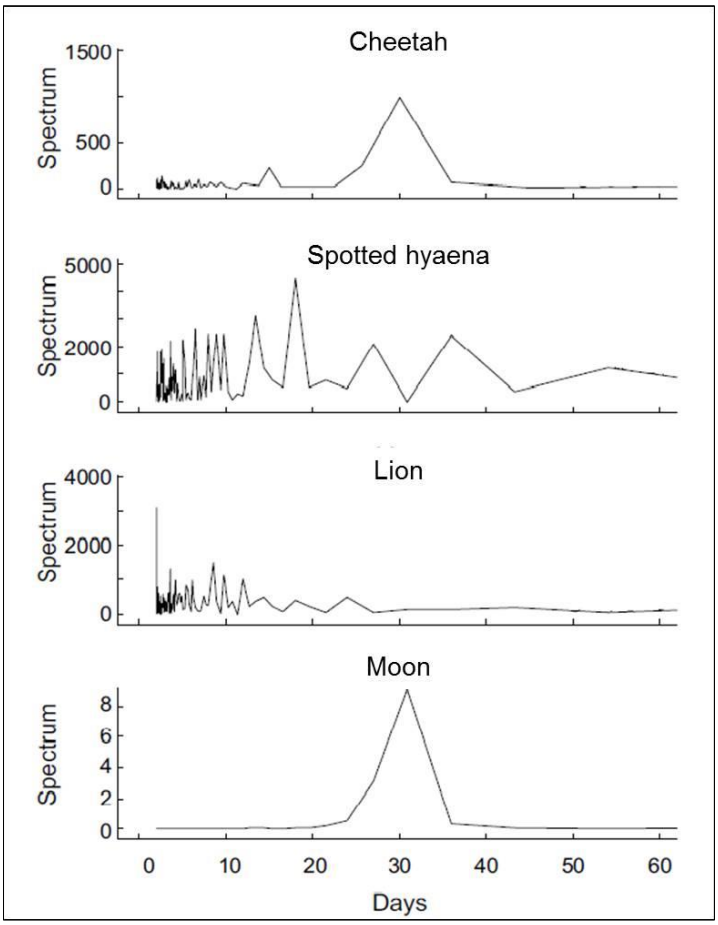


Figure 2.2: Spectrogram showing periodicity in the nocturnal activity pattern of a typical cheetah, spotted hyaena and lion. Activity data recorded by the collars were averaged per night and investigated using Fourier spectral analysis. For comparison the spectrogram of the moon is shown. While the activity of cheetahs show a main period of 30 days (similar to the period of the lunar cycle), the activity of spotted hyaenas and lions show cyclicity every few days.

In the linear mixed effects models, the nocturnal activity of lions and spotted hyaenas showed no relationship with moonlight intensity, despite reports that the hunting success of lions increases when the moon is absent or obscured by clouds (Funston et al. 2001b, Packer et al. 2011). In contrast, there was a strong positive relationship between cheetah nocturnal activity and moonlight intensity ($F_{1,981}$ = 164.02, $p < 0.001$) although one male (#3) showed consistently high levels of activity at night (interaction term individual by moonlight: $F_{5,981}$ = 6.38, $p < 0.001$) (Figure 2.3). For cheetahs, the total diel activity remained roughly constant over a lunar cycle and hence showed no

relationship with moonlight intensity ($F_{1,980}$ = 1.37, p = 0.24). This suggests that cheetahs trade-off and partition nocturnal and diurnal activity according to available moonlight.

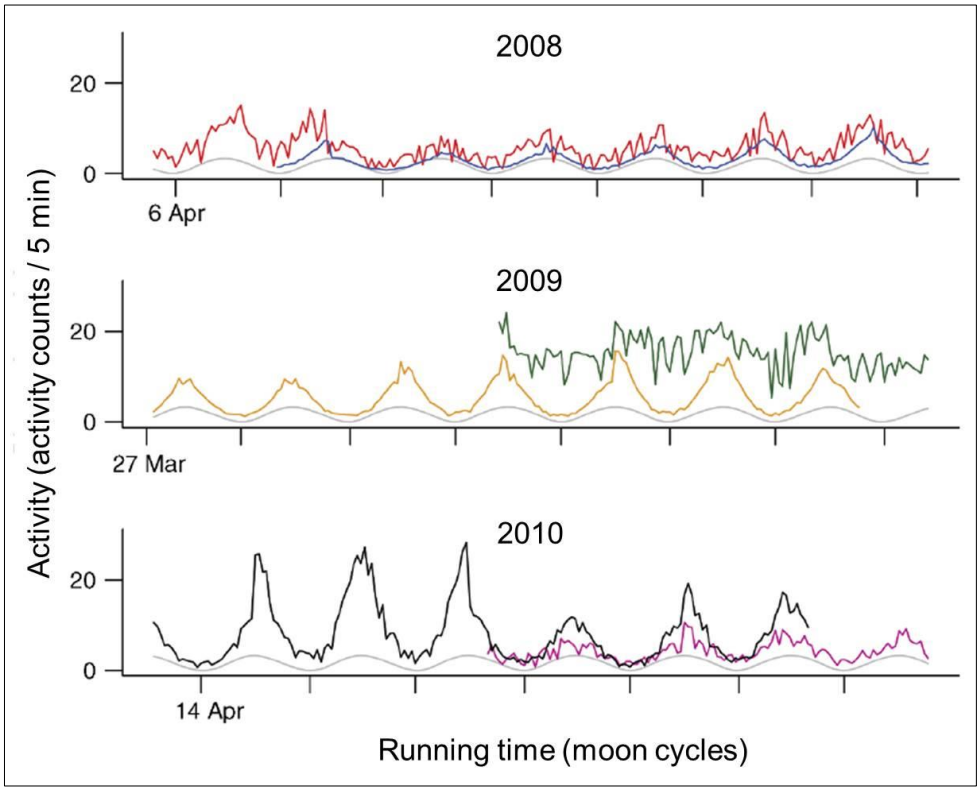


Figure 2.3: Fitted values from mixed effects models showing the nocturnal activity patterns of cheetahs (n = 6) during the dry season in three consecutive years. Each colour represents a different individual. Variation in moonlight intensity is depicted for comparison in each panel (grey line; not to scale) and highlights the strong positive relationship between cheetah activity and moonlight availability. One cheetah (#3, light green) shows consistently high nocturnal activity (2nd panel).

To further investigate this suggestion and understand how diel activity was partitioned, additional analyses were carried out for each period of the 24-hour cycle. For cheetahs, high levels of moonlight intensity negatively influenced the activity during each period of the following day, with the exclusion of the evening twilight activity of cheetahs (all p-values < 0.001: Appendix 2.3). After correcting for differences in activity due to differences in moonlight intensity, we found that levels of activity in adjacent periods showed a positive relationship; hence it seems that, once active, cheetahs remain active over long periods (Figure 2.1 and Appendix 2.3). In addition, temperature

only had a negative influence on activity during the hottest part of the day (i.e. morning and afternoon periods) (Appendix 2.3).

Discussion

In contrast to previous studies suggesting a high degree of temporal partitioning among African large predators (Hayward and Slotow 2009) this study revealed extensive temporal overlap. This was mainly due to the unexpected nocturnal activity of cheetahs – a species previously regarded as diurnal – and the partly diurnal habits of lions and spotted hyaenas. In addition cheetahs' nocturnal activity correlated with the lunar cycle: with sufficient moonlight, they were considerably more active at night as nocturnal activity constituted almost half of the total diel activity on full moon days. It therefore seems that activity patterns of these competitively subordinate species are primarily constrained by light availability, rather than by the activities of the larger, dominant species. These findings support the idea that at the diel level temporal niche partitioning may be a relatively rare event (Schoener 1974b).

These results conflict with those from the meta-analysis carried out by Hayward and Slotow (2009) who concluded that available studies did not support nocturnal behaviour for cheetahs. However, the authors used data from different sites that had been collected opportunistically using a range of different methodologies for different species. In addition, they often assumed that the timing of sunrise and sunset were constant through the year and along a latitudinal gradient. These assumptions can lead to incorrect conclusions, as pointed out by Nouvellet et al. (2012). Although the results are not consistent with the hypothesis that activity patterns of dominant competitors have been the main driver in shaping the temporal niches of cheetahs, we nonetheless acknowledge that lions and spotted hyaenas pose a real threat (Laurenson 1995, Mills and Gorman 1997, Gorman

et al. 1998). Cheetahs, for example, exhibited short-term behavioural modifications, such as reduced hunting activity, in response to the presence of lions and spotted hyaenas (Durant 2000a).

Only cheetahs showed nocturnal activity patterns that were correlated with the availability of moonlight while the nocturnal activity of spotted hyaenas and lions did not vary over the lunar cycle. This raises the question of why good light is a key requirement for activity in cheetahs but not in lions and spotted hyaenas. Cheetahs hunt small and medium-sized ungulates, such as impala (*Aepyceros melampus*) usually by conducting high-speed chases that can reach speeds of over 100 km/hour. Such chases are inherently risky and good light conditions, and therefore sufficient visibility (i.e. during the day and on moonlit nights), are likely to be essential to maintain contact with the prey, avoid fatal injuries and increase hunting success (Schaller 1972, Caro 1994, Rasmussen and Macdonald 2012). This cursorial hunting technique is in contrast to the ambush hunting technique of lions, whose success increases when the moon is absent or obscured by clouds (Funston et al. 2001b, Packer et al. 2011). Different foraging strategies may thus explain the different activity patterns among the species of the guild, and stress the evolutionary importance of bottom-up forces (e.g. prey acquisition) in shaping the behaviour of large carnivores.

If lions and spotted hyaenas pose a threat to cheetahs, why do they not completely avoid nocturnal activity? One possibility is that they must take every opportunity to catch prey and that they cannot afford to miss exploiting nights with sufficient moonlight. Thus, cheetahs may have evolved to respond to short-term visual, auditory and olfactory cues, e.g. fleeing on hearing lion calls, to avoid potentially dangerous situations, rather than completely avoiding being active at night. Cheetahs did not show any cyclical pattern in their total diel activity over the course of a lunar cycle, suggesting that nocturnal activity was not a strategy to increase the overall activity budget. We therefore assume that the benefits of nocturnal activity offset the risks of encountering night-active predators and competitors. Indeed, we might expect hunting success to be higher at night because prey

animals have a reduced chance of spotting predators under dim light conditions. For example, it is known that hunting success in cheetahs is higher when they can stalk undetected very close to intended prey (FitzGibbon and Fanshawe 1988, Hilborn et al. 2012) and that wolves (*Canis lupus*) are almost twice as successful when hunting on moonlit nights (Theuerkauf et al. 2003). To the contrary, the high levels of activity during early mornings that followed moonless nights, when activity was limited, suggest a behavioural response to an increasing hunger risk.

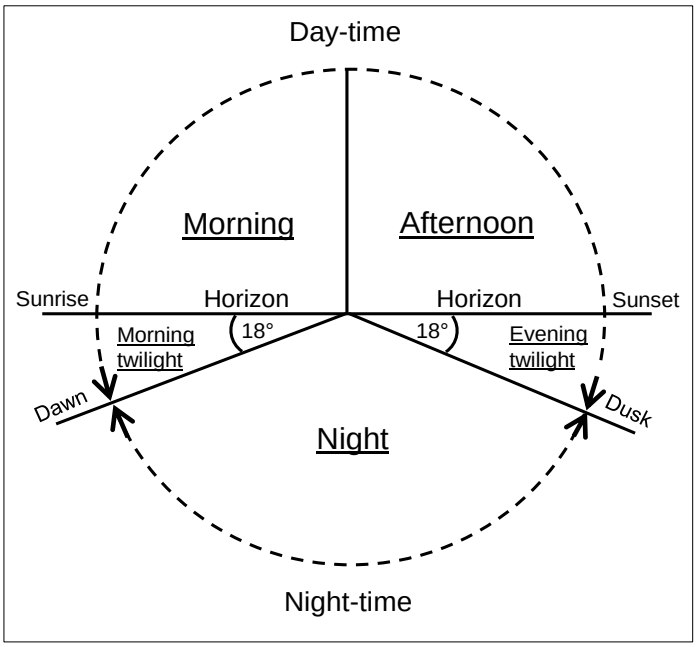
The influence of moonlight on the hunting behaviour of predator species has been widely described for nocturnal species (Horning and Trillmich 1999, Lang et al. 2006), and our results suggest that moonlight can equally influence (allegedly) diurnal species. Understanding and quantifying the energetic budget of single species based on patterns of activity is beyond the scope of this study; nevertheless, on the basis of our findings, it is evident that cheetahs have more time to fulfil their energetic requirements than just a few hours in the morning and in the late afternoon as currently assumed. Further research is thus required to understand the role of each period of the 24-hour cycle for the diel energetic budget as compared to the diel activity budget.

Our findings suggest that the temporal niches of competitively subordinate large predator species are only moderately shaped by the need to avoid predation and competition (Lima and Dill 1990, Theuerkauf 2009). This is in contrast to findings at other trophic levels, for example, in guilds of herbivore species (Sinclair et al. 2003, Chesson and Kuang 2008). Competitively subordinate large predators must trade off the risk of encountering dominant species against the risk of starvation (e.g. Lima 1988, Roth II and Lima 2007) and competitively subordinate large predators appear to be mainly “starvation driven”. The well-documented positive relationship between the distribution and density of prey species and their predators (e.g. Carbone and Gittleman 2002) further suggests a tight causal association between bottom-up forces and communities of large predators. Additional research in ecosystems characterised by different densities of competitors and prey species will be

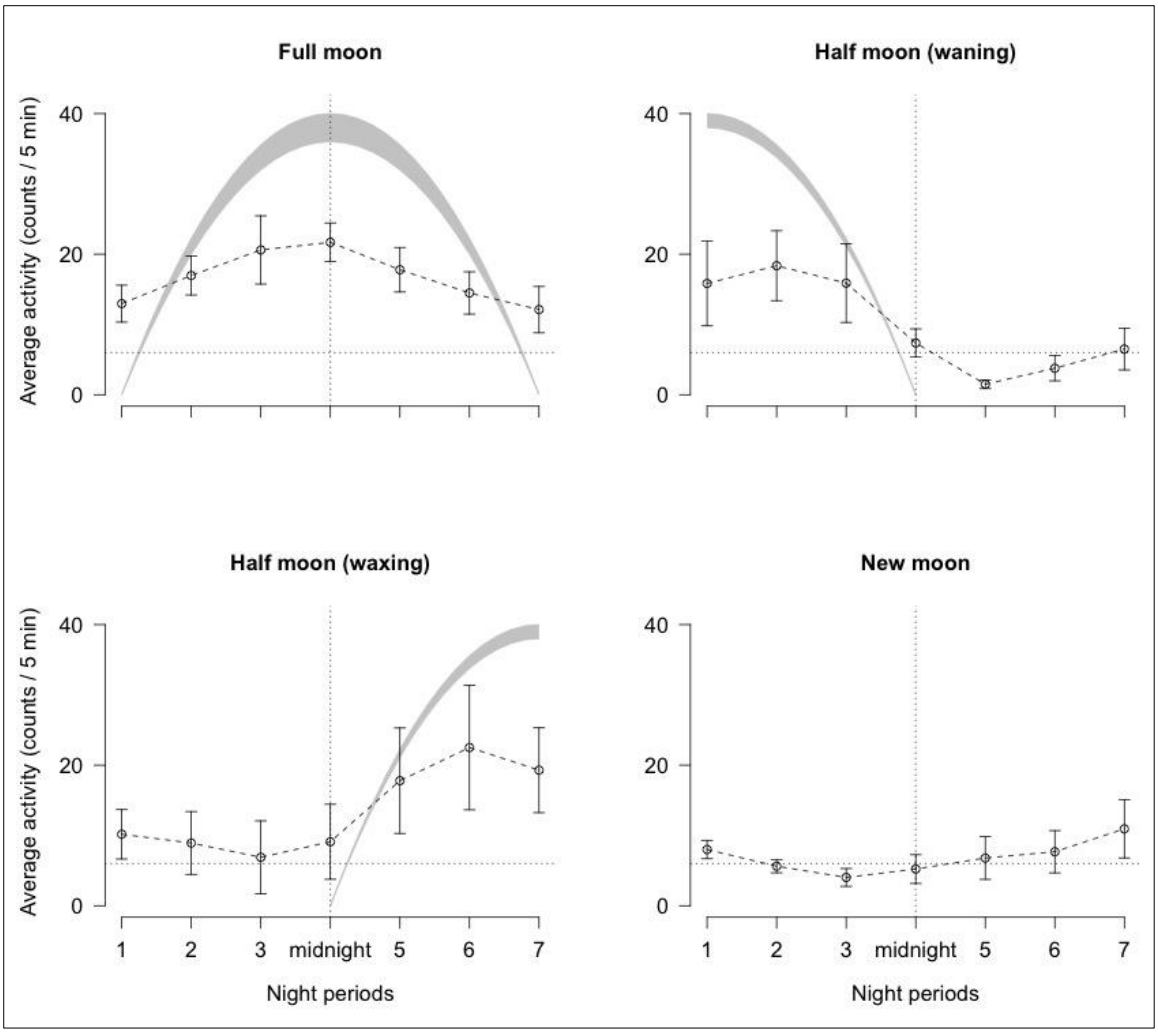
necessary to better understand the role of top-down and bottom-up forces in shaping animal communities and facilitating coexistence. In contrast to herbivores, large carnivores must invest a lot of energy finding and catching food, as prey are widely scattered, often rare and difficult to catch, and hunting is energy-intensive, time-consuming and often unsuccessful (e.g. Carbone et al. 1999). Given the relative difficulty of catching a meal versus the relatively low likelihood of encountering a dominant species (large predators live at relatively low densities (Carbone and Gittleman 2002)), we conclude that, on moonlit nights, cheetahs prioritise hunting opportunities and success over the need to avoid being hunted and over the possibility of losing their kill. In conclusion, it appears that under favourable light conditions, the benefits of nocturnal activity outweigh the costs of encountering stronger competitors and predators.

Appendix

Appendix 2.1: Division of a 24-hour cycle into five periods: morning twilight, morning, afternoon, evening twilight and night. Night-time spanned between the astronomical dusk and the astronomical dawn (sun 18° below the horizon) on the consecutive day. The only source of light during night-time is provided by the moon and the stars. Exact times were obtained from http://aa.usno.navy.mil/.



Appendix 2.2: Detailed night-time activity pattern during four phases of the lunar cycle (full moon, half-moon waning, half-moon waxing and new moon) for cheetahs in the Okavango Delta, Botswana.



Appendix 2.3: Mixed effects models to investigate how cheetah activity in a given period of the 24-h cycle is influenced by the activity during previous periods. For each case, the best (final) model is given, as well as the effect of each explanatory variable on the response (positive (+), or negative (-) effect), F- values (F), p-values (p), numerator and denominator degrees of freedom (ndf, ddf). Interactions between explanatory variable are expressed by ' **:** '.

Morning.twilight.activity ~ Individual+Moon+Night.activity+Individual:Moon

	Ind	Moon	Night	Ind:Moon
effect:		(-)	(+)	
p =	< 0.001	< 0.001	0.008	< 0.001
F =	21.29	57.59	7.10	6.51
ndf,ddf =	5,69	1,623	1,983	5,793

Morning.activity ~ Individual+Moon+Morning.twilight.activity+Temperature+ Individual:Moon+Individual:Morning.twilight.activity

	Ind	Moon	Mtwl	Temp	Ind:Moon	Ind:Mtwl
effect:		(-)	(+)	(-)		
p =	< 0.001	< 0.001	< 0.001	< 0.001	NS	< 0.001
F =	9.08	53.22	378.38	17.55		10.91
ndf.,ddf. =	5,62	1,580	1,991	1,54		5.983

Afternoon.activity ~Individual+Moon+Morning.activity+Temperature+ Individual:Morning.activity+Moon:Morning.activity+Moon:Temperature

	Ind	Moon	Morn	Temp	Ind:Morn	Moon:Morn	Moon:Temp
effect:		(-)	(+)	(-)		(+) (-)	(-)
p =	< 0.001	< 0.001	< 0.001	0.021	< 0.001	0.047	0.004
F =	7.74	38.54	306.29	5.60	4.49	3.96	8.14
ndf,ddf =	5,60	1,990	1,996	1,67	5,993	1,989	1,997

Evening.twilight.activity ~ Individual+Moon+Afternoon.activity+Temperature+ Individual:Moon+Individual:Afternoon.activity

	Ind	Moon	After	Temp	Ind:Moon	Ind:After
effect:			(+)	(+)		
p =	< 0.001	NS	< 0.001	0.043	NS	0.021
F =	23.73		143.43	5.98		2.72
ndf,ddf =	5,12		1,172	1,7		5,185

CHAPTER 3

Cracking the code: using machine learning techniques to translate activity into behaviour

A modified version of this chapter has been published in *PLoS ONE*

Abstract

Data from data-loggers provide biologists with an opportunity to study behaviour in a previously unknown level of detail and accuracy. Whilst continuously recorded data can give new insights into animal ecology, these data can be even more valuable when the resulting large volumes of raw data are reliably translated into actual behaviour. We propose a new method, based on machine learning techniques, for the analysis of a combination of continuous data from data-loggers and a sampling of contemporaneous behavioural observations. This was done by applying a Support Vector Machine and a hidden Markov model that allowed us to classify an animal's behaviour using a small set of field observations to calibrate continuously recorded activity data. This method classified animal behaviour over extended periods of time and at times when observations were difficult or impossible to come by. We demonstrate the usefulness of the method by applying it to data from six free-ranging cheetahs (*Acinonyx jubatus*) in the Okavango Delta, Botswana. Cumulative activity data scores were recorded every five minutes by accelerometers embedded in Global Positioning System (GPS) radio-collars fitted on the cheetahs for an average of one year. Direct behavioural observations for each of the six cheetahs were conducted in the field for comparatively short periods of time. Using this approach we were able to classify each five minute activity score into a set of three key behaviours: feeding, moving and resting, creating a continuous behavioural sequence for the entire period for which the collars were deployed. Evaluation of our classifier with cross-validation shows the accuracy to be 83 - 94%, but that the accuracy for individual classes was reduced with decreasing sample size of direct observations. We give examples of how these processed data can be used to study animal behaviour. Whilst we applied our methods to data from cheetahs, the approach can, in principle, be applied to any animal as long as both observations and sensor measurements are available.

Introduction

Advances in technology allow biologists to collect large amounts of high resolution data without the need to be physically present (Tomkiewicz et al. 2010). This has the potential to give researchers a unique insight into aspects of animal behaviour and ecology that have, in the past, been more restricted due to environmental conditions and animal behaviour (e.g. Guilford et al. 2009, Hart et al. 2010a). Despite the popular use of this technology, the use of these data are still limited. For example, accelerometers quantifying animal movement, allow us to investigate behavioural patterns and states through changes in activity (e.g. Hart et al. 2010b). However, to date, most studies have used simple data oriented methods of analysis: for example, threshold-based detection of active/inactive states (Gottardi et al. 2010) or classification into slightly richer behavioural states (Laich et al. 2008, Shepard and Halsey 2008). These techniques have often been used in marine systems where the animals in question are near to impossible to follow and observe (Hart et al. 2010b).

Despite the fact that these techniques have given a valuable insight into behaviours such as underwater foraging in free-living penguins (Hart et al. 2010a) and swimming and diving in marine mammals and birds (Yoda et al. 1999, Hart et al. 2010b) it is hard to draw robust conclusions about actual behaviour from such analysis. Combining the data from data-loggers with behavioural observations from the field provides a powerful tool to investigate animal behaviour that is based on actual behaviour rather than purely on activity values and arbitrary thresholds. Admittedly, this would be difficult to achieve for most marine animals, but it is certainly feasible in terrestrial systems where animals are easier to observe. Whilst the translation of activity values into actual behavioural states has been done for domesticated and captive animals (Watanabe et al. 2005, Moreau et al. 2009) this, to the authors knowledge, has never been accomplished for free-ranging, terrestrial mammals. Generally, collecting large amounts of behavioural data on wild animals and several individuals simultaneously can be difficult and extremely time consuming. By combining

technology with field observations, large amounts of behavioural data can be collected in a relatively short space of time. With these data we can start to address more detailed behavioural questions which are extremely valuable especially for elusive, far-ranging species that do not occur in high densities and can often not be monitored continuously. The main difficulty that needs to be overcome with this approach is the processing of the data, as the databases are typically too vast to be processed by hand and therefore needs to be automated. We fill this gap by using machine learning techniques to translate activity data, recorded by radio-collars fitted on free-ranging animals, into actual behaviours.

In this study, we used commercially available radio-collars that were equipped with accelerometers that recorded the animals' acceleration on two different axes. In the past, accelerometers have been used to sense movement to estimate energy expenditure and create simple activity diaries (e.g. Wilson et al. 2008). The processing of such signals can range from simple estimates of peak value or magnitude to average values over time. The radio-collars that we used combined two dimensional accelerometer data over a five minute period to form a value between 0 and 255; little additional information was available about the nature of the algorithm used for data reduction. We were interested in whether such a simple signal can be used to differentiate between different behaviours and address this challenge using machine learning techniques (Bishop 2008). Our method is based on a Support Vector Machine (SVM) which is a popular and powerful method for classification (Shawe-Taylor and Cristianini 2004). As the SVM does not consider temporal information, we post-processed the SVM results with a hidden Markov model (HMM) to introduce dependencies over time. This method classifies the recorded activity into a sequence of behaviours that can be post-processed to address scientific questions on animal behaviour. We also illustrate that only a relatively small number of behavioural observations are required for a robust analysis, ideal for animals that are difficult to monitor. To validate the approach, and to show its potential, we applied the method to an activity dataset from six free-ranging cheetahs (*Acinonyx jubatus*).

Cheetahs are one of Africa's large carnivores and with fewer than 10 000 individuals left in the wild they are classified as vulnerable by the IUCN (IUCN 2012). Cheetahs are predominantly solitary and with home-ranges anywhere between 200 and 2000 km^2 (Caro 1994, Marker et al. 2008) making them difficult to locate and therefore making it impossible to obtain large amounts of behavioural data in a short period of time. In addition, behavioural observations are limited in areas, such as where this study was conducted, where visibility is restricted by vegetation. Our technique allows us to extrapolate behavioural data for several individuals simultaneously that can then be used to explore different behavioural states, in this case feeding, moving and resting.

Methods

Data collection

Between 2008 and 2011, six cheetahs (two males and four females) were fitted with Global Positioning System (GPS) radio-collars (VECTRONIC Aerospace GmbH, Germany). A Botswana registered veterinarian was responsible for the immobilisation procedures needed to fit the GPS radio collars and typically used a combination of Ketamine and Medetomidine for the immobilisations (Kock et al. 2006). The radio-collars were embedded with bi-axial accelerometers that recorded both the forward-backwards and sideways movement every five minutes for the entire time that the collars were deployed. The collars were deployed for an average of 332 days (range: 276 – 373 days). In addition to the activity measurements that were recorded by the collars, behavioural observations were collected in the field for each of the six cheetahs independently. Behavioural observations were obtained by continuously following each collared individual in a vehicle for a minimum of one hour on any given day. During the periods of observation three behavioural states were recorded: resting, moving and feeding. Each time the focal animal changed its behavioural state, the exact time was recorded using a handheld GPS device (Garmin eTrex HC; Garmin, Olathe, Kansas, USA). An average of 31 hours ± 8 hours (mean ± s.e.m.; range: 21hr 59min - 40hr 49min) of behavioural observations were recorded for each individual. These behavioural

observations were then synchronised with the activity data from the collars to give the labelled dataset. This resulted in an average of 332 ± 78 labelled data points per individual (mean ± s.e.m.; range: 241 - 447 data points). Of this labelled dataset, we only used labelled data points that were dominated by one discrete behaviour during the 5 minute interval, for example, we excluded data points where, in the 5 minutes, an animal was both feeding and mobile. The number of labelled data points used can be found in Table 3.1.

The classifier

We used a Support Vector Machine (SVM) in combination with a hidden Markov model (HMM) approach to classify cheetah behaviour over a long period of time based on activity measurements and a small set of labelled data. We trained the SVM to predict three different behavioural categories: feeding, moving and resting. We applied the SVM independently to each activity value and then applied the classifier to the full activity sequence giving us a sequence of predicted behaviours. Unfortunately, the classifier does not take temporal information into account. This can lead to "obvious" misclassifications such a: we observe a long sequence of resting behaviour surrounding a single feeding data point. Such misclassifications can, however, be eliminated by incorporating an understanding of the likely temporal behaviour of the animals. We included temporal information by "smoothing" the behavioural sequence with the help of an HMM approach. Here we give some background information on the SVM and the HMM approach and discuss the extent to which we can validate the predicted behavioural sequence.

Support Vector Machine - The SVM is a popular method for learning classifiers as it is robust and fast (Shawe-Taylor and Cristianini 2004). In the following, we explain the central concept of the SVM to illustrate the operation of the method. In general, a classification problem consists of a set of input vectors $x_1, \ldots, x_n$ and a set of corresponding labels $y_1, \ldots, y_n$. In the simplest case, there are two classes and the labels are binary {-1, +1}. For simplicity, assume that our inputs are 2-dimensional and that we can separate the two classes in the input space with the help of lines (i.e. there exists a

line such that all the positive examples are on one side and all the negative examples on the other). Usually, many different lines are able to separate the two classes so one needs to be able to distinguish which of these lines would be the best choice. The SVM is a so-called large margin method as it finds the specific line that maximises the margin from the line to the two classes. In other words, it maximally separates the two classes. Intuitively this is a good choice as the classifier is robust against new data points that lie slightly outside the observed class boundaries. Besides this intuition there are formal guarantees for the performance of an SVM (Shawe-Taylor and Cristianini 2004) and the SVM has been shown to be very robust in various applications. SVMs rely on the so-called *kernel-trick* to increase the separation between classes. The kernel-trick makes use of a kernel $k(x, y)$ that measures similarities between elements x and y and needs to fulfil certain properties to be applicable (it needs to be positive semi-definite). A frequently used kernel is the Gaussian kernel:

$$k(x, y) = \exp(-\sigma \|x - y\|^2)$$

where σ is a hyper-parameter and $\|\cdot\|$ the Euclidean norm. Using the Gaussian kernel implies that the data is embedded in an infinite dimensional space and all operations are applied in this space. In our application, the input elements were 2-dimensional vectors representing aggregated 2D accelerometer readings, and we had three classes of behaviour: resting, moving and feeding. We trained three classifiers, one for each class: the positive examples were the elements x_i with the correct behaviour and negative examples were the elements with one of the remaining two behaviours. In addition to the Gaussian kernel we used the SVM package from Chapelle (2007) for our experiments. For each cheetah we used all available labelled data for training and applied it to the whole set of activity measurements of that cheetah. The number of training data points and sample sizes can be found in Table 3.1.

Hidden Markov model - We smoothed the classification sequence with the help of a HMM approach. This requires that the SVM output includes a probability value for how certain the predicted class is.

A standard approach for obtaining this is to apply the logistic function to the distance from the hyper-plane (Platt 1999). The logistic function is:

$$f(x) = \frac{1}{1 + \exp(-x)}$$

The value of f is between 0 and 1 and can thus be interpreted as a probability. We applied the logistic function to the three trained classifiers which resulted in three sequences $\hat{p}_f(t)$, $\hat{p}_m(t)$ and $\hat{p}_r(t)$. From these we generated probabilities that the behaviour is feeding at time $(p_f(t))$, moving $(p_m(t))$ or resting $(p_r(t))$ given the observation $o(t)$ in the following way:

1. The animal can only be in one behavioural state at any given time t and hence the other two behaviours should not be present. This leads us to use:

$$\tilde{p}_f(t) := \hat{p}_f(t)\big(1 - \hat{p}_m(t)\big)\big(1 - \hat{p}_r(t)\big),$$

$$\tilde{p}_m(t) := \hat{p}_m(t)\Big(1 - \hat{p}_f(t)\Big)\big(1 - \hat{p}_r(t)\big),$$

$$\tilde{p}_r(t) := \hat{p}_r(t)\Big(1 - \hat{p}_f(t)\Big)\big(1 - \hat{p}_m(t)\big).$$

2. We normalised the values from the first step such that they sum to unity for each time step t, i.e.

$$p_f(t) := \frac{\tilde{p}_f(t)}{N\,(t),}\;\; p_m(t) := \frac{\tilde{p}_m(t)}{N\,(t),}\;\; p_r := \frac{\tilde{p}_r(t)}{N\,(t),}$$

where

$$N\,(t) \coloneqq\; \tilde{p}_f(t) + \;\tilde{p}_m(t) \;+\; \tilde{p}_r(t)$$

(eq. 1)

We constructed a HMM with three states that encode the three behaviour classes (Rabiner 1989). We interpreted the three sequences p_f, p_m and p_r as the conditional probabilities $p\big(s_f\,(t)\big|o(t)\big), p\big(s_m(t)\big|o(t)\big), p(s_r(t)|o(t))$ that the behaviour is feeding, mobile or resting at time t given the observation $o(t)$. For our algorithm we calculated the likelihoods using Bayes rule (Bishop 2008). If prior knowledge about the probabilities for certain observations or the probabilities for certain states is known then it can be exploited here. However, in our experiments we had no

prior knowledge and therefore used uniform distributions. To determine these likelihoods it was necessary to define a transition model for the states. For this, we used:

$$P := \begin{pmatrix} p_{ff} & (1 - p_{ff})/2 & (1 - p_{ff})/2 \\ (1 - p_{mm})/2 & p_{mm} & (1 - p_{mm})/2 \\ (1 - p_{rr})/2 & (1 - p_{rr})/2 & p_{rr} \end{pmatrix},$$

where P_{ij} is the probability of transitioning from state i to state j with state 1 being feeding, state 2 moving and state 3 resting. Our motivation for this form is that we expect the current behaviour to continue with high probability (e.g. resting) and expect the behaviour to change with a lower probability. We used the same probabilities to switch to either of the two alternative behaviours (e.g. from resting to moving or feeding) to keep the number of parameters small. Our main interest in using this smoothing is to rule out single events, like feeding in longer sequences of resting behaviour. We expected that the smoothing should be relatively robust to the particular choice of values p_{ff}, p_{mm} and p_{rr}, so long as they were sufficiently high. We used values of p_{ff} = 0.8 and p_{mm}, p_{rr} = 0.9 as feeding is likely to be shorter than stationary or mobile behaviour. We analysed the effect of changing p_{ff} and robustness results can be found in the next section. Note that the choice of this value implies an expected length of time each state is maintained before a transition is made to a new state. The value of 0.8 corresponds to one hour twenty minutes, a value that agrees in magnitude with our observations of feeding. The value 0.9 corresponds to seven and a half hours and is at the upper end of what we would expect for stationary or mobile behaviour - refining the parameter up to the second decimal digit might lead to slight improvements, but we decided, in this case, that parameter tuning to this extent was a second order improvement. We also specified the initial probabilities for the three behavioural states. We used $p_f(0) = p_m(0) = p_r(0) = 1/3$. Given P and the likelihoods $p(s_f(t)|o(t)), p(s_m(t)|o(t)), p(s_r(t)|o(t))$ we used the Viterbi algorithm to calculate the most probable state sequence (Rabiner 1989).

Test-set performance and parameter robustness

We evaluated the performance of the method based on the recorded data and in terms of robustness of the parameters of the Markov chain. The performance of the method was assessed with the help of cross-validation: our training data consists of multiple time-delimited segments of observations of the cheetah, e.g. the cheetah was observed on Monday from 13:00 to 15:00 then again on Friday from 10:00 to 11:00 etc. We used each of these segments as a validation set and the remainder of the data as training data for the method. We then evaluated the performance on this validation set and we averaged the performance over all possible training-validation set combinations. The resulting percentage of correct classification is shown in Table 3.1. In addition, we evaluated the sensitivity of the results to parameter changes in the Markov chain. For this we measured the log evidence over the same segments that we used for the cross-validation. The evidence can be calculated by summing the likelihoods of all possible paths in the HMM. Like the likelihood, the evidence can be calculated efficiently through recursion:

$$e_{t+1}(j) = \sum_{i \leq 3} e_t\,(i) P_{ij} P(o(t+1)|s(t+1) = j$$

The initial value for the sequence of es is

$$e_1(i) \;=\; p_i(0) P(o(1)|s(1) \;=\; i\,)$$

and the probabilities $P(o(t)|s(t) \;=\; j)$ are again the values from the SVM (eq. 1).

Results

We developed a SVM-based classifier that allowed us to classify behaviour of animals over a long period of time based on activity measurements and a small set of labelled data. The results indicate that for our method it is crucial to have enough characteristic data for the different classes of behaviour. Here we give an example of the classified data of two individuals, male M1 and female F3 (Figure 3.1). The top row are the plots for the performance of the SVM classifier whilst the bottom row shows the performances of the combined SVM and HMM classifier for M1 (left) and F3 (right).

For M1 the classifier achieved a high performance and one can observe that the HMM does not change the classifier region fundamentally but labels single data points differently compared to the pure SVM classifier. For F3 the classifier achieved weaker performance possibly because there was less observational data available, in particular for feeding (Table 3.1). The feeding region based on the SVM classifier in the F3 plots looks significantly different from M1. In addition, the HMM changes the shape of the feeding region significantly and makes the F3 plot more similar to the M1 plot.

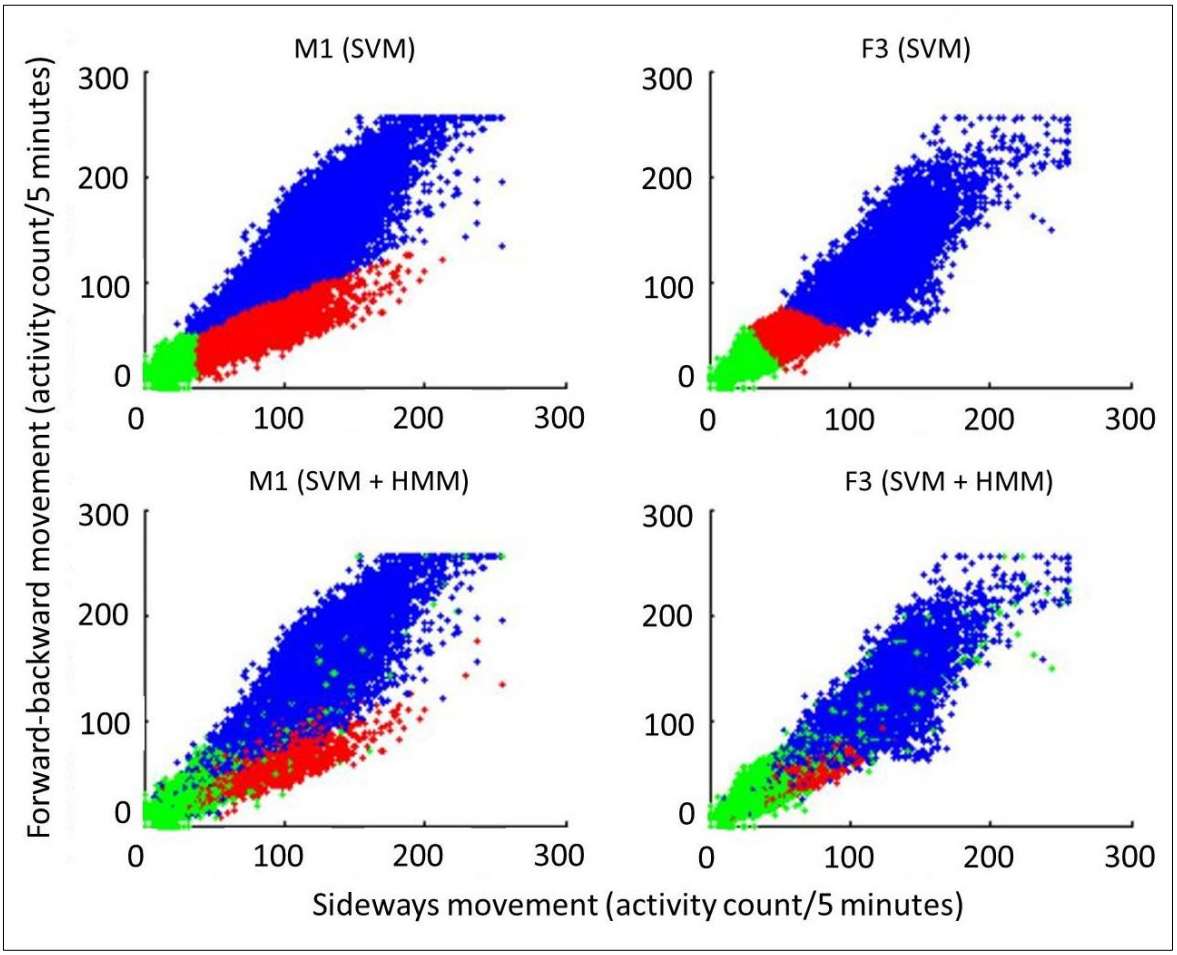


Figure 3.1: The figure shows the data for two cheetahs (male M3 (left) and female F3 (right)). The graphs in the top row show the different classes of behaviour using SVM. The graphs in the bottom row show the different classes of behaviour using the post-processed SVM classifier (SVM+HMM). Green = resting, blue = moving and red = feeding.

Evaluation

We evaluated our method in two different ways: 1) we estimated the classification performance with a leave-one-out cross validation; 2) we tested the dependency of the HMM performance on a critical parameter. The number of training data points, cross-validation results and resulting sample sizes are shown in Table 3.1.

Table 3.1: Number of labelled data points and the cross-validation of the combined SVM and HMM method for each of the six radio-collared cheetahs. The true positives are the percentages with which the three different behaviours were detected correctly whereas the false positives are the percentages with which behaviours were falsely classified as one of the other behaviours.

	Individuals	M1	M2	F1	F2	F3	F4
Number of labelled data points	Feeding	100	46	58	42	31	47
	Mobile	99	76	61	97	81	83
	Resting	153	268	122	139	171	317
	Total	352	390	241	278	283	447
True positives	Overall	94%	92%	91%	94%	84%	90%
	Feeding	93%	52%	95%	100%	23%	66%
	Mobile	97%	87%	74%	91%	75%	69%
	Resting	93%	100%	98%	95%	99%	99%
False positives	Feeding	2%	2%	5%	0%	6%	0%
	Mobile	9%	24%	0%	7%	21%	2%
	Resting	7%	5%	16%	6%	16%	13%
Number of predicted data points	Feeding	4 089	4 504	2 790	2 948	1 862	2 409
	Mobile	22 511	16 274	13 072	7 306	9 413	10 752
	Resting	87 702	74 150	83 328	68 179	68 590	92 852
	Total	114 302	94 928	100 233	78 434	79 865	106 013

The true positives for all the behaviours combined show that the method used accurately classified 83% - 94% of the data points. The true positives for the individual behaviours show that the performance is dependent on the number of observations available for each of the different classes. In particular, one can observe that the feeding accuracy can be low if there are too few feeding observations (~50). The false positives are the percentage of data points that were falsely classified as one of the other behaviours e.g. feeding instead of moving. The probability for missing a whole sequence is p^n, where p is the probability of an error and n the length of the event. For example, female F3 has the worst feeding performance, which results in an error rate of around 78% per data

point. If feeding takes one hour then we have 12 data points and the chance of missing it is 0.78^{12} = 0.05 if we assume the observations are independent. In this worst case we have 5% possibility of missing an average length feeding event completely.

Beside the cross-validation we tested the sensitivity of the classifier to the HMM parameter $p_{ff} \cdot p_{ff}$. This is the most interesting parameter of the three HMM parameters as we have few feeding observations for some individuals and because feeding times are in a range that could potentially be covered by a large portion of the parameter space. We would expect feeding to lie in the range from 2-3 data points (that is 10-15 minutes; e.g. a small kill) up to 24-36 data points (2-3 hours; e.g. a big kill). This corresponds roughly to parameters p_{ff} = 0.5 and p_{ff} = 0.85. In contrast, for moving and resting we would expect parameters in the range of 0.8 – 0.9. We measured the sensitivity with the help of the Bayesian evidence for our model, that is the probability under our model that we observe certain observations. As in the cross-validation here we also used a leave-one-out approach: we trained the SVM on all but one set of data points, determined the evidence on the omitted set, and repeated that for each set (Figure 3.2).

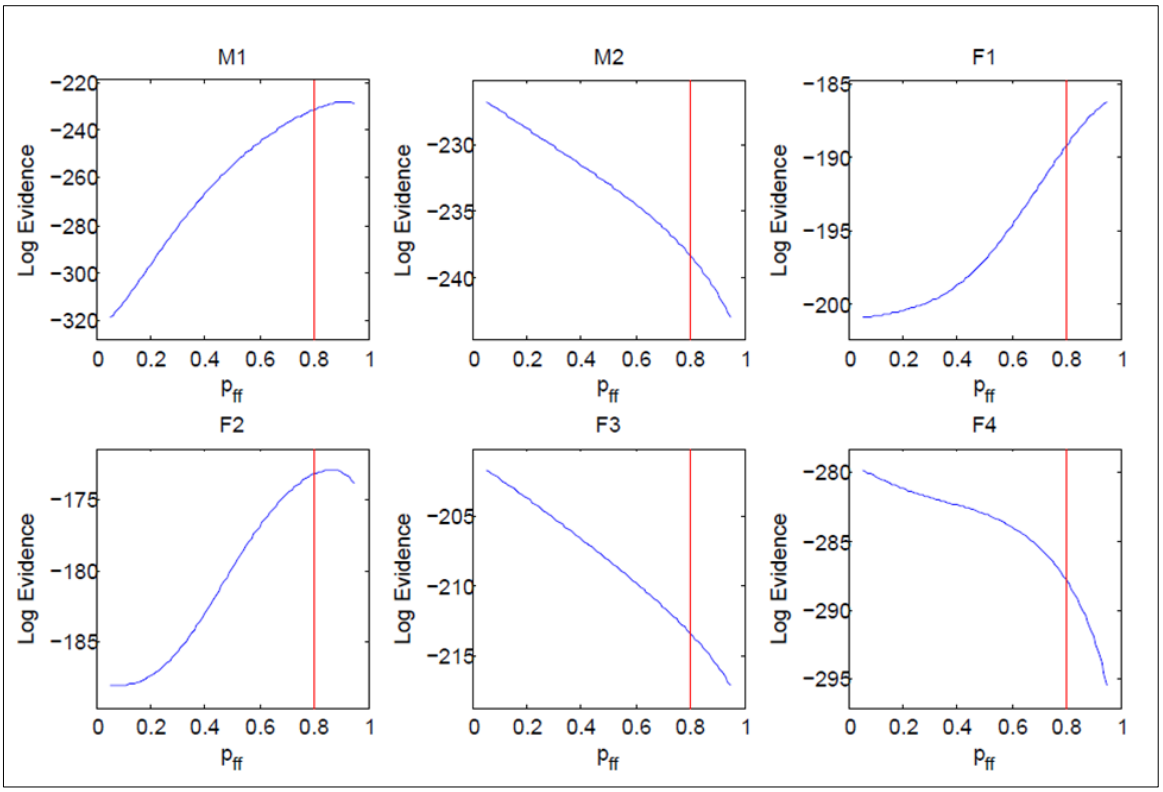


Figure 3.2: The figure shows how robust the method is to changes in the parameter p_{ff}. On the x-axis the parameter p_{ff} is varied and on the y-axis the corresponding evidence is plotted. The red (vertical) line marks the parameter that we used for the experiments in the remainder of this chapter.

The higher the value in the plot, the higher the evidence. The plots show two things: 1) for the three cheetahs for which we have the lowest feeding prediction accuracy as a result of too few feeding observations (male M2 and females F3 and F4) we have evidence plots that peak at 0. So, the overall performance is maximised by ignoring feeding altogether; 2) for male M1 and female F2 we have an optima between 0.8 and 0.9 while female F1 does not peak in the range we tried. In the experiments, we used a single parameter p_{ff} with a value of 0.8 (the red lines) for all six cheetahs to keep the number of parameters in the model small. Increasing p_{ff} to a value slightly higher than 0.8 might improve the performance for individuals M1, F2 and F1 but will decrease the performance for the other three. The conclusion of the experiment is that the evidence indicates whether there are too few observations or, in the case in which we have enough observations, it shows us which average feeding length is best for explaining the data and how sensitive the results are to this parameter.

Cheetah behaviour

Using the classified data for each individual we explored the daily behavioural budgets and the length and frequency of feeding events to illustrate the capabilities of our method and to demonstrate the sort of questions that can be addressed.

We created a daily behavioural budget for each of the six cheetahs by calculating the proportion of each behaviour (feeding, moving and resting) per hour (Figure 3.3). The top plots show the results for the males (M1 and M2) and the remaining plots the results for the females (F1 – F4). All six cheetahs showed a peak in mobile behaviour at around 06h00 – 07h00 in the morning and 17h00 – 18h00 in the evening. There seems to be a difference between sexes as the peaks for males are much higher than those for females. Similarly, males moved more at night compared to females. In general, the six cheetahs were active approximately 16% of the time. Feeding for all six cheetahs occurred mainly between 06h00 and 19h00 with some feeding events during the night. For both male and female cheetahs there were slight peaks in feeding in the morning and evening. Male and female cheetahs seemed to have about the same number of night feeding events, even though males moved more at night.

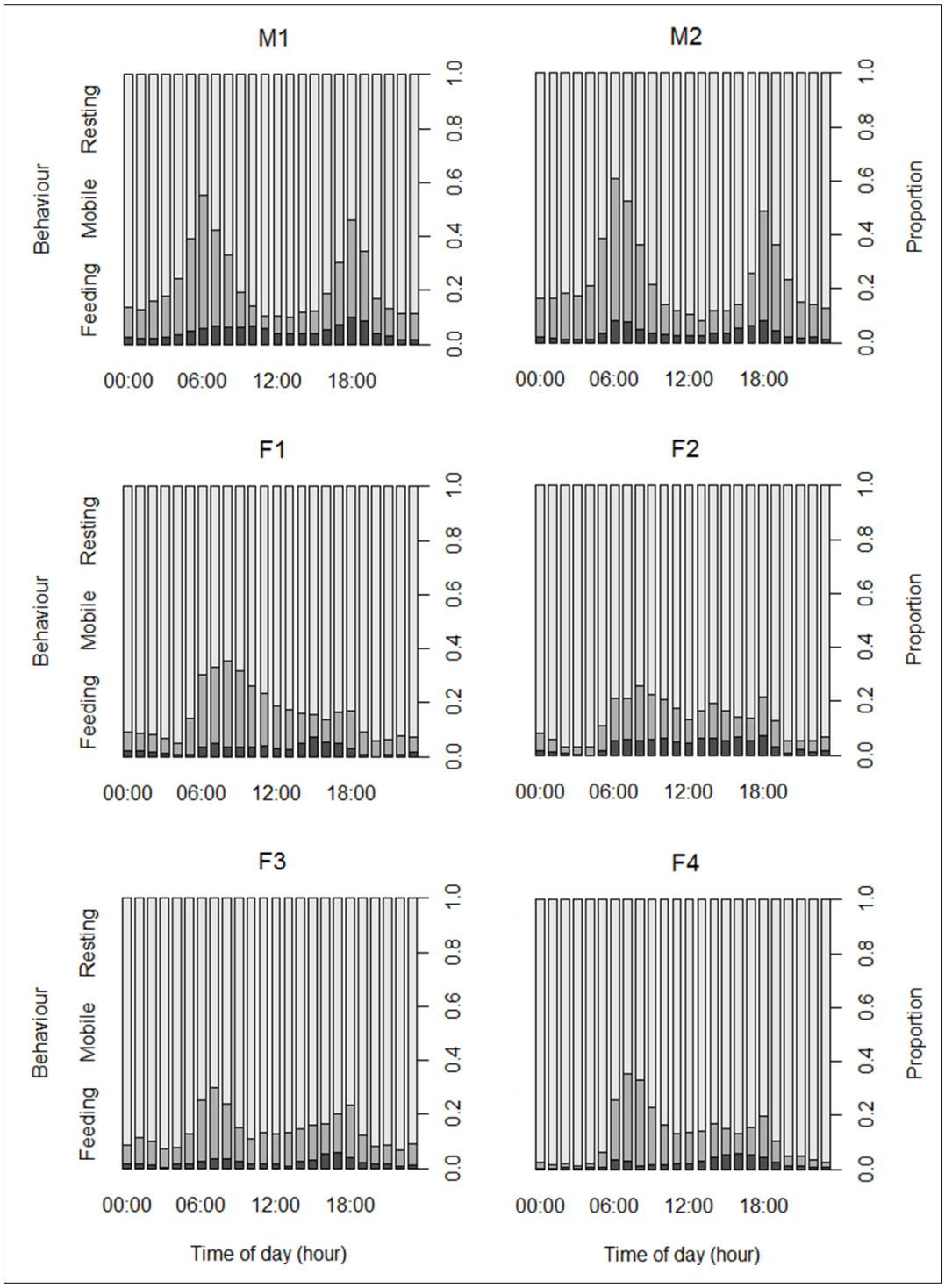


Figure 3.3: The classification of the daily behaviour of the six free-ranging cheetahs in the Okavango Delta, Botswana. The three different behaviours are colour coded dark-grey = feeding, grey = moving and light-grey = resting. The proportion of each behaviour was calculated per hour.

Feeding events were taken as the continuous sequence of classified feeding points and feeding length was the duration of each sequence. The distribution of feeding lengths was similar for all six cheetahs with most feeding events lasting around 20-40 minutes (Figure 3.4).

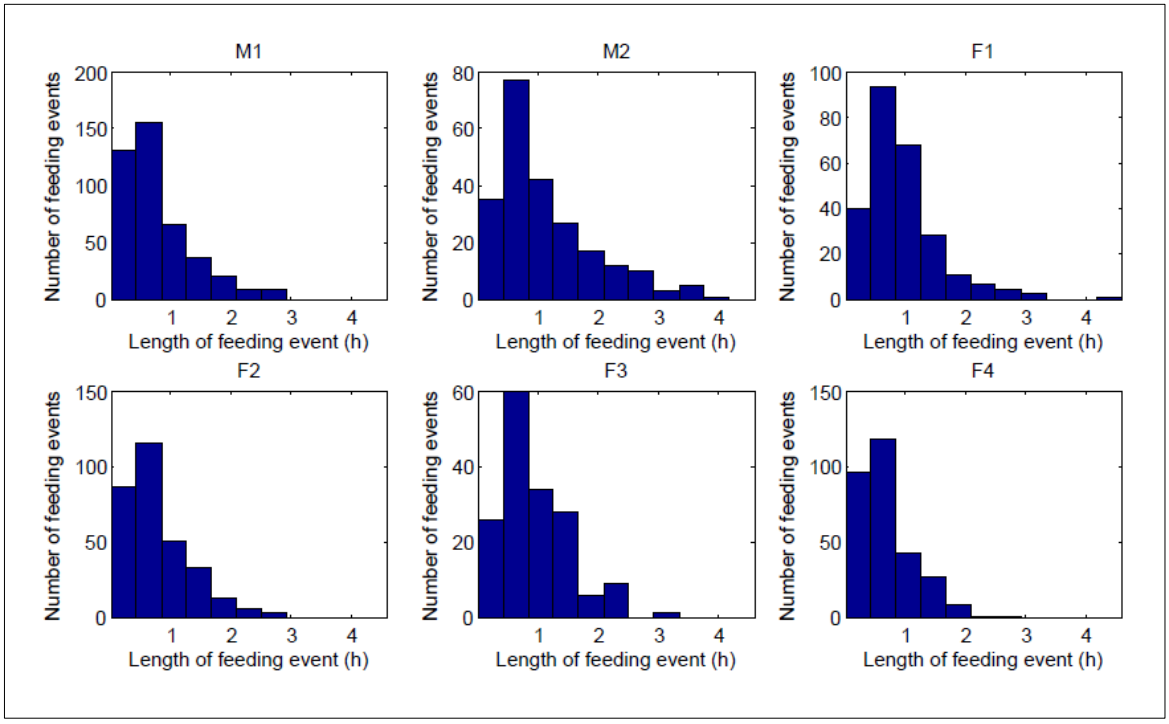


Figure 3.4: Histograms of the length of feeding events for the six individual cheetahs. On the x-axis the length is plotted and on the y-axis the number of events in the data with the respective length.

In addition, we calculated the feeding rate for each individual by measuring the number of days that passed between feeding events. Based on this analysis, all six cheetahs feed on average every second day (Table 3.2).

Table 3.2: The feeding frequency for six free-ranging cheetahs in the Okavango Delta, Botswana.

Individual	M1	M2	F1	F2	F3	F4
Feeding rate (overall)	0.50	0.43	0.46	0.58	0.43	0.45
Feeding rate (wet season)	0.53	0.43	0.43	0.60	0.39	0.38
Feeding rate (dry season)	0.46	0.43	0.49	0.58	0.46	0.54

Discussion

Owing to recent advances in various technologies applied to the study of animal behaviour, biologists can now record high resolution behavioural data over extended periods of time. However, data from long, otherwise unobserved, periods are often insufficient to draw biologically relevant conclusions because meaningful information can be obscured within the vast quantities of accumulated dimensionless data. As a consequence, there is a temptation to make use of *ad hoc* analytical methods. With this work we demonstrated that generally applicable machine learning methods can be used to process and present such accumulations of data to identify specific behaviours. In particular, we applied an SVM together with an HMM to classify activity reliably into three categories: resting, moving and feeding. The result is a continuous recording of behaviour, including periods when direct observations were absent or impossible to obtain. We evaluated our approach with the help of a cross-validation and evidence analysis. The accuracy obtained from these is based on the assumption that the data we used for training is representative of the data from the whole year. This will most likely be the case for large parts of the data as long as there is neither an injury to the animal nor damage to the collar. If there is sporadic behaviour that we did not record during the behavioural observations in the field then it is possible to get systematic misclassifications. For example, all four collared females had cubs and were lairing during part of the data collection. As we had no field observations of the nurturing behaviour of these cheetahs, it is possible that some of this behaviour caused misclassification of other behavioural states. This effect is very typical for experimental studies as it is nearly always the case that we cannot observe animals in all situations.

Our results demonstrate that for our method it is crucial to have enough characteristic data for the different classes of behaviour. The HMM approach does improve the classification but cannot fully account for the initial shortcomings of the SVM classifier. An alternative to our approach of applying an HMM together with an SVM would be to use only an HMM by defining a suitable observation

model and learning the HMM transition model with the help of the Baum-Welch algorithm (Rabiner 1989). A disadvantage of this approach would be that it is not straightforward to make use of the labelled data, i.e. the behavioural observations. Furthermore, as our evidence analysis shows, the Baum-Welch algorithm would, most likely, suppress the feeding state altogether for three of the six cheetahs and thus result in a model that could not be used to study feeding behaviour. A further alternative would be to focus on the SVM side and drop the generative model approach that we pursue. This could be done with the help of structured output learning, similar to Altun et al. (2003). Given the recent development and advancement of technology one can expect that the amount of recorded data will continue to grow as hardware becomes cheaper and recording frequencies increase due to better batteries and less energy consuming sensor devices. Furthermore, with new technology it might be possible that in the near future behavioural observations can be made remotely through recording devices like cameras. Field studies are important either to verify and/or to raise new hypotheses about animal behaviour (Hebblewhite and Haydon 2010). It is important that the data and the data processing methods allow researchers to study or formulate hypotheses by providing insight into animal behaviour.

We give a taster of how these classified data can be used to explore animal behaviour in more detail. For example, by creating a behavioural budget we can see that male cheetahs moved more than females. This is likely due to the fact that the males, unlike females, are territorial and therefore spend more time moving in order to patrol their territory (Caro et al. 1989, Caro 1994). In addition, the results in this chapter correspond with those in Chapter 2 in that cheetahs are seen to be active at night. The resulting hypothesis in Chapter 2 was that at night cheetahs increased their activity with increased moonlight intensity as a result of increased hunting behaviour. Whilst this is likely to be the case, this could not be established with any degree of certainty as there were no behavioural observations to support this. With these data this unexpected behaviour can be explored in more

detail by looking at actual behaviours rather than simple activity values. This will be demonstrated in the subsequent chapters.

In summary, we would like to emphasise that, while we applied our methods to data from cheetahs, the approach is neither restricted to cheetahs nor to the three behaviours described here. In principle, any animal and any behaviour can be studied with this method as long as both observations and sensor measurements are available.

CHAPTER 4

Scaredy-cat? How fear and foraging affect cheetah temporal distribution

Abstract

Animals can adapt the timing of behaviour and activity to maximise resource acquisition whilst minimising the risk of predation and competition. Whilst the temporal distribution of behaviour has frequently been studied in small mammals and a variety of predator-prey systems, it has not previously been documented within the large carnivore guild. Members of a carnivore guild influence each other indirectly through resource competition and directly through competition with behaviours such as kleptoparasitism and intraguild predation. Here, we use a dataset on behaviour from six free-ranging cheetahs (*Acinonyx jubatus*) to investigate whether the temporal distribution of behaviour, in particular foraging, of a competitively subordinate carnivore is driven by maximisation of resource acquisition or by the avoidance of other predators. The behavioural dataset was created by converting activity values recorded by radio-collars fitted on cheetahs into three distinct behavioural states (feeding, mobile and resting) based on behaviours observed in the field. The temporal distribution of these data was analysed in terms of the diel phase (day vs. night) and the amount of moonlight that was available at night. Despite the fact that cheetahs are predominantly diurnal, 45.2% of their mobile and 32.5% of their feeding behaviour occurred at night and these percentages increased with increasing moonlight availability. Results suggest that cheetahs are more plastic in their behaviour than was previously thought and that, within the constraints of their evolutionary adaptations, the temporal distribution of their behaviour is driven by resource acquisition rather than predator avoidance.

Introduction

Activity patterns and the timing of behaviour are influenced by the need to maximise resource acquisition whilst minimising risk of predation or competition (Schoener 1974a, Kronfeld-Schor and Dayan 2003). Through the process of natural selection, patterns of activity are often entrained by the day-night cycles as different levels of light availability require different anatomical, physiological and behavioural adaptations (Daan and Aschoff 1975, Kronfeld-Schor and Dayan 2003). This leads to

species either being active during the day (diurnal) or active at night (nocturnal) (Daan and Aschoff 1975). These adaptations to specific light conditions are, however, not rigid. For example, several studies have shown diurnal species to be active at night when there is sufficient moonlight available (Fernandez-Duque 2003, Rasmussen and Macdonald 2012, Chapter 2). This behavioural adjustment suggests that species can adapt their activity and behaviour in such a way to maximise resource acquisition and minimise the risk of predation and competition. Resource availability and risks both vary over time, and temporal patterns of animal behaviour can therefore be expected to reflect adaptive, if not optimal, cost-benefit responses to such variations (Daan and Aschoff 1975, Lima and Bednekoff 1999, Kronfeld-Schor and Dayan 2003, Kotler et al. 2010). For example, Fenn and Macdonald (1995) showed that the nocturnal Norwegian rat (*Rattus norvegicus*) shifted to being diurnal in order to escape predation by the nocturnal fox (*Vulpes vulpes*) and Harrington et al. (2009) showed a similar shift by mink (*Neovison vison*) in response to the presence of competitively dominant otters (*Lutra lutra*) and polecats (*Mustela putorius*). This plasticity in the timing of activity has often been studied in the framework of optimal foraging theory as foraging species are often at greater risk of predation and interference competition (Lima and Dill 1990, Sih et al. 2000, Kotler et al. 2010). Whilst the timing of foraging behaviour as an anti-predator response has often been studied in birds (Lima and Dill 1990) and small rodents (Kotler et al. 1993, Jones et al. 2001), it has received comparatively little attention for any species of mammalian predator.

Carnivores can have direct negative effects on each other through intraguild competition and predation (Polis and Holt 1992, Holt and Polis 1997) and the adaptive response to these interactions is believed to have shaped the asynchronous behaviour patterns that have been observed amongst sympatric carnivores such as those within the African large carnivore guild (Mills and Biggs 1993, Hayward and Slotow 2009, but see Chapter 2). For example, the predominantly diurnal activity pattern of cheetahs (*Acinonyx jubatus*) is rare among the Felidae and is believed to be an evolutionary adaptation to avoid risks associated with temporal overlap with larger, more competitive, nocturnal carnivores, in particular lions (*Panthera leo*) and spotted hyaenas (*Crocuta*

crocuta) (Durant 1998, Hayward and Slotow 2009). Cheetahs, lions and spotted hyaenas indirectly compete over similar prey resources (Mills and Biggs 1993, Hayward and Kerley 2008); cheetahs however have a competitive disadvantage mainly due to their smaller body size and predominantly solitary nature (Caro 1994). Despite the fact that at night the risk of encountering lions and spotted hyaenas is higher than during the day, recent studies have shown that cheetahs are active at night (Marnewick et al. 2006, Bissett and Bernard 2007, Chapter 2). However, the timing of foraging behaviour in relation to the risk of encountering lions and spotted hyaenas has not yet been investigated in detail. Investigating the temporal distribution of cheetah behaviour and the factors driving and influencing behaviours such as foraging may provide insight into the complex trade-off between resource acquisition and risk avoidance in carnivores.

We investigated the behaviour of a free-ranging population of cheetahs co-occurring with lions and spotted hyaenas in a savannah ecosystem in northern Botswana. The daily behavioural time budgets of six cheetahs were summarised using a combination of direct behavioural observations and continuous cumulative activity scores from data-loggers fitted on each individual cheetah. This method enabled continuous reliable categorisation of cheetah behaviour, including during times when the animals could not be monitored directly. Using these data we investigated the diel composition of three key categories of behaviour; feeding, moving and resting. The goals of this study were to quantify cheetah behaviour and to investigate whether foraging behaviour was driven by maximisation of resource acquisition or by the avoidance of predators. In the context of optimal foraging theory we hypothesised that the need to acquire resources (e.g. foraging behaviour) should counteract the increase in risk associated with temporal overlap during activity peaks of lions and spotted hyaenas. This was tested by first investigating the temporal distribution of different cheetah behaviours and then by investigating the frequency and length of feeding events in relation to temporal variation in light intensity (day/night and lunar cycles). As both lions and spotted hyaenas are predominately nocturnal (Kruuk 1972, Schaller 1972, Hayward and Slotow 2009) the diel phase (day vs. night) was used as a proxy for relative risk.

Methods

Study area

The study was conducted in the Okavango Delta, a permanent inland delta located in northern Botswana. The core study site (19°31'S, 23°37'E; elevation ca. 950m) encompassed an area of approximately 2 720 km^2 including the southern part of the Moremi Game Reserve and the adjacent Wildlife Management Areas (for details see McNutt 1996, McNutt and Silk 2008). The area is characterised by two distinct seasons: a dry, cold winter between April and October and a wet, hot summer between November and March with an annual rainfall of 450-600 mm/year (Mendelson et al. 2010). During the year there is little variation in the number of daylight hours with daylight spanning from 05h40-19h15 during the winter solstice (21st June) and from 04h30-20h20 during the summer solstice (21st December) (http://aa.usno.navy.mil/data/).

Cheetah data

Between October 2008 and July 2011 six free-ranging adult cheetahs (two males and four females) were fitted with GPS (Global Positioning System) radio-collars (VECTRONIC Aerospace GmbH, Germany). A Botswana registered veterinarian was responsible for the immobilisation procedures (following Kock et al. 2006). The GPS radio-collars were equipped with two single axis accelerometers providing quantitative activity data in both the lateral (y-axis) and the anterior-posterior (x-axis) movement. The animals' acceleration on these two axes was continuously recorded 4 times/second and cumulative scores were logged every five minutes for the duration of the study (collars recorded continuously for a mean of 332 days (range: 282 – 381 days)). In addition, behavioural data were collected through direct field observations on an *ad lib* basis from each collared individual throughout collar deployment. Three fundamental behaviour categories were recorded: feeding, moving, and resting. Collared individuals were observed from a research vehicle at a minimum distance of 30 meters.

Data processing

The behavioural data from the field were synchronised with corresponding activity data to create a labelled dataset. The labelled dataset was then used in combination with a Support Vector Machine (SVM) and hidden Markov model (HMM) approach to predict the three behavioural categories (feeding, mobile and resting) for the entire activity dataset. This approach gave an overall accuracy of 83% - 94% (see Chapter 3 for methodologies and Table 4.1 for sample sizes and data validation).

Table 4.1: Number of labelled data points and the cross-validation of the combined SVM and HMM method for each of the six radio-collared cheetahs. The true positives are the percentages with which the three different behaviours were detected correctly whereas the false positives are the percentages with which behaviours were falsely classified as one of the other behaviours.

	Individuals	M1	M2	F1	F2	F3	F4
Number of labelled data points	Feeding	100	46	58	42	31	47
	Mobile	99	76	61	97	81	83
	Resting	153	268	122	139	171	317
	Total	352	390	241	278	283	447
True positives	Overall	94%	92%	91%	94%	84%	90%
	Feeding	93%	52%	95%	100%	23%	66%
	Mobile	97%	87%	74%	91%	75%	69%
	Resting	93%	100%	98%	95%	99%	99%
False positives	Feeding	2%	2%	5%	0%	6%	0%
	Mobile	9%	24%	0%	7%	21%	2%
	Resting	7%	5%	16%	6%	16%	13%
Number of predicted data points	Feeding	4 089	4 504	2 790	2 948	1 862	2 409
	Mobile	22 511	16 274	13 072	7 306	9 413	10 752
	Resting	87 702	74 150	83 328	68 179	68 590	92 852
	Total	114 302	94 928	100 233	78 434	79 865	106 013

The result was that each five minute activity value was assigned a corresponding behavioural state giving a continuous sequence of predicted behaviour for the entire period that the collars were operational. Feeding events were made up of one or more feeding bouts which were defined as a continuous block of feeding data points, not segregated by mobile behaviour (Figure 4.1).

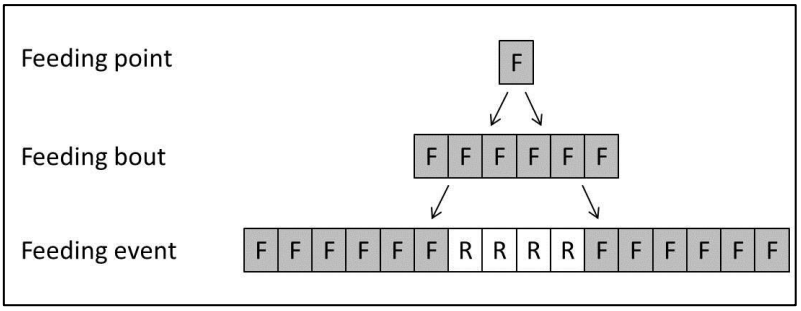


Figure 4.1: Definition of feeding point, feeding bout and feedings events. F = feeding and R = resting. Each compartment represents a five minute interval.

Using a two-stage process this predictive dataset was used to investigate the temporal distribution of cheetah behaviour. First, the entire predictive dataset was used to investigate the proportion of time cheetahs spent in each behavioural state. The second part of the analysis focused on the feeding behaviour of cheetahs as this is when cheetahs are most at risk of kleptoparasitism by lions and spotted hyaenas. The proportion of time cheetahs spent feeding is a function of both the feeding frequency and the length of feeding events. Both these components were investigated in relation to the diel phase (day vs. night), the seasons and the proportion of visible moon (which is a proxy for the amount of moonlight). Data on feeding events were collected by extracting sequences of continuous feeding data points from the entire predictive dataset. Only feeding events that took place exclusively during the day or night were considered for further analysis.

Predictor variables

To determine whether day-night cycles and light availability influenced cheetah behaviour, data on the time of the transition between day and night and data on the phases of the moon cycle were obtained from the United States Naval Observatory (USNO) website (http://aa.usno.navy.mil/data/). Discrimination between day and night was based on the astronomical twilight, which is when the sun is 18° below the horizon. There were therefore three predictor variables: diel phase (categorical with two levels: night and day), season (categorical with two levels: wet and dry) and moonlight intensity (a continuous variable rendering the proportion of the moon that was visible where 0 = new moon and 1 = full moon).

Statistical analysis

The proportion of time cheetahs spent feeding, mobile or resting in relation to the diel phase (day vs. night), season and the moon cycle were analysed separately using Generalized Linear Models (GLM) with a binomial error structure (Warton and Hui 2010). The frequency of feeding events was similarly analysed using GLMs with a binomial error structure. The lengths of feeding events were log transformed to meet the assumption of normality and were then entered as a dependent variable in a linear model. To account for repeated measures, individual cheetahs were entered as a fixed blocking effect (Bolker *et al.* 2009). For the analyses of proportions, 14 *a-priori* candidate models were created for each of the behavioural states including each of the main effects (diel phase, season and moonlight intensity) and their interaction terms. Models were ranked using Akaike Information Criterion corrected for small sample size (AICc). If one model was clearly dominant ($w_i > 0.9$) this was used, otherwise parameter estimates were averaged across the models correcting for model weights (w_i) (Burnham and Anderson 2002). Models and model comparison statistics can be found in the Appendix. Statistical analyses were performed using the statistical software R 2.14.2 (R Development Core Team 2012). Central tendencies are reported as mean ± 95% confidence interval (CI).

Results

Temporal distribution of cheetah behaviour

Cheetahs spent the majority of their time resting (84.5 ± 2.78 %) and only spent a small portion of their time feeding (3.0 ± 3.2 %) or mobile (12.5 ± 2.78 %) (Figure 4.2). However, in contrast to the general understanding of the strongly diurnal behaviour of cheetahs, the results show that 45.2 % of their mobile behaviour and 32.5 % of their feeding behaviour occurred at night (mobile: Z=9.797, $p < 0.001$; feeding: Z=5.138, $p < 0.001$). However, cheetahs still spent a greater proportion of their time resting during the night than during the day (night: 0.942 ± 0.026; day: 0.786 ± 0.023; Z=10.711, $p<0.001$) (Figure 4.2).

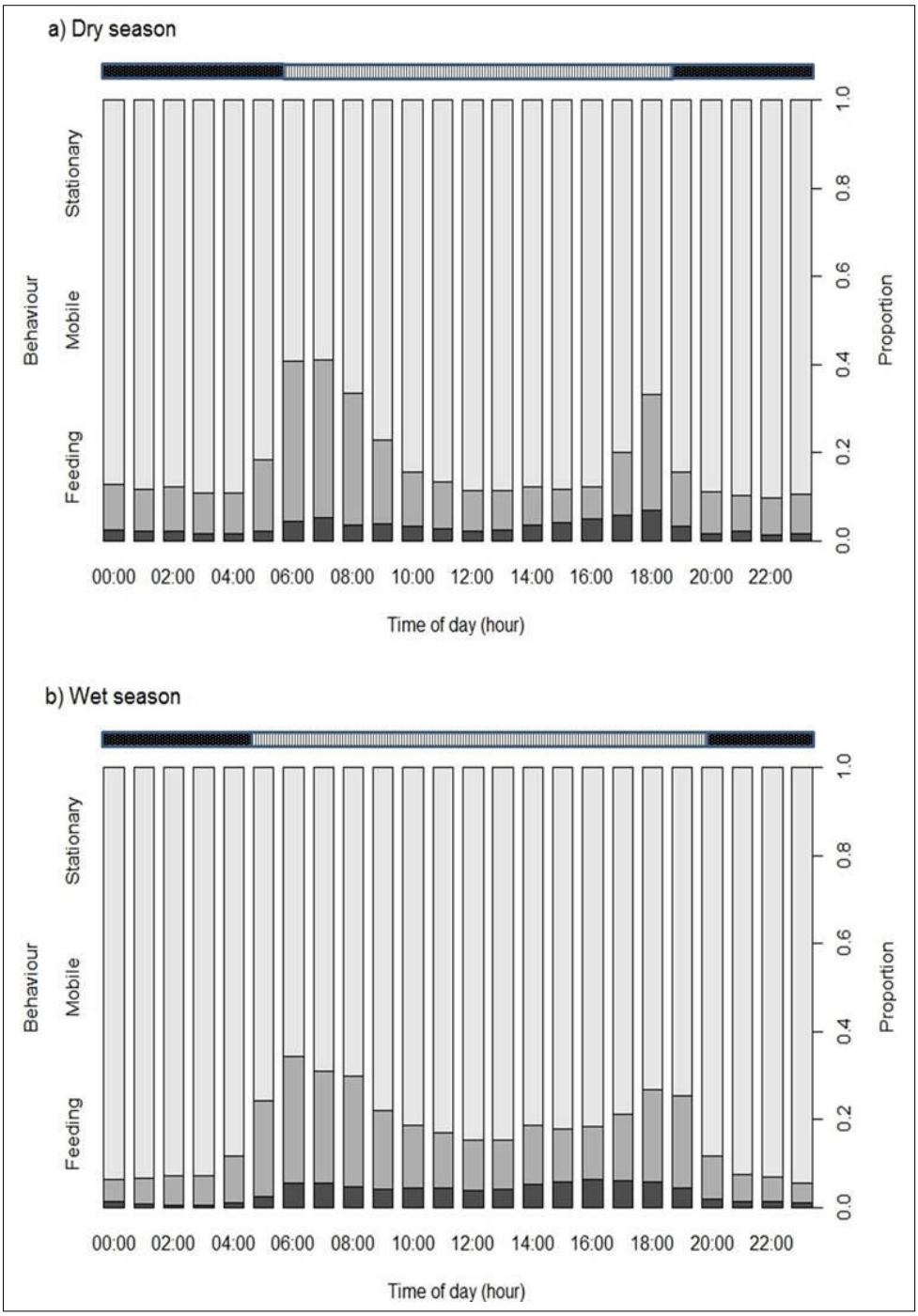


Figure 4.2: Proportion of time cheetahs in northern Botswana (n=6) spent feeding (black), mobile (dark grey) and resting (light grey) in relation to time of day for the a) dry and b) wet season. The bar above the individual figures depicts the day-night length (day=grey, night=black) based on the astronomical twilight on the solstices.

The proportion and temporal distribution of cheetah behaviour was influenced by season. Cheetahs spent a greater proportion of their time feeding during the wet season compared to the dry season (Z=2.424, p=0.015) and there was a significant interaction between the diel phase and season

(*Z*=3.459, p<0.001), suggesting the day-night difference was not the same in the wet and dry seasons. Cheetahs spent less time feeding during the day in the dry season compared to the wet season (day_{dry}: 0.034 ± 0.01; day_{wet}: 0.042 ± 0.005 ; t= 2.238, p=0.027) and more time feeding at night in the dry season compared to the wet season ($night_{dry}$: 0.012 ± 0.00; $night_{wet}$: 0.004 ± 0.003; t= -3.384, p<0.001). Similarly the proportion of time cheetahs were mobile at night was higher in the dry season than in the wet season ($night_{dry}$: 0.031 ± 0.024; $night_{wet}$: 0.005 ± 0.002; t= -2.770, p<0.001) whilst the proportion of time cheetahs were mobile during the day did not differ between seasons (*Z*=0.152, p=0.879) (Figure 4.2). These results suggest that cheetahs actively shift their feeding, and hence foraging, behaviour to the night during the dry season.

Moonlight intensity had no influence on the proportion of time spent feeding (Figure 4.3a) but did influence the proportion of time for which cheetahs were mobile (Figure 4.3b). Higher levels of moonlight were linked to a significant increase in the proportion of mobile behaviour at night (t= 4.724, p<0.001) and a significant decrease in the proportion of mobile behaviour during the day (t= 3.308, p=0.001). The inverse was therefore true for the proportion of time cheetahs spent resting - as moonlight increased, cheetahs were less likely to be resting during the night (t= -4.988, p<0.001) and more likely to be resting during the day (t= 2.781, p=0.006) (Figure 4.3c).

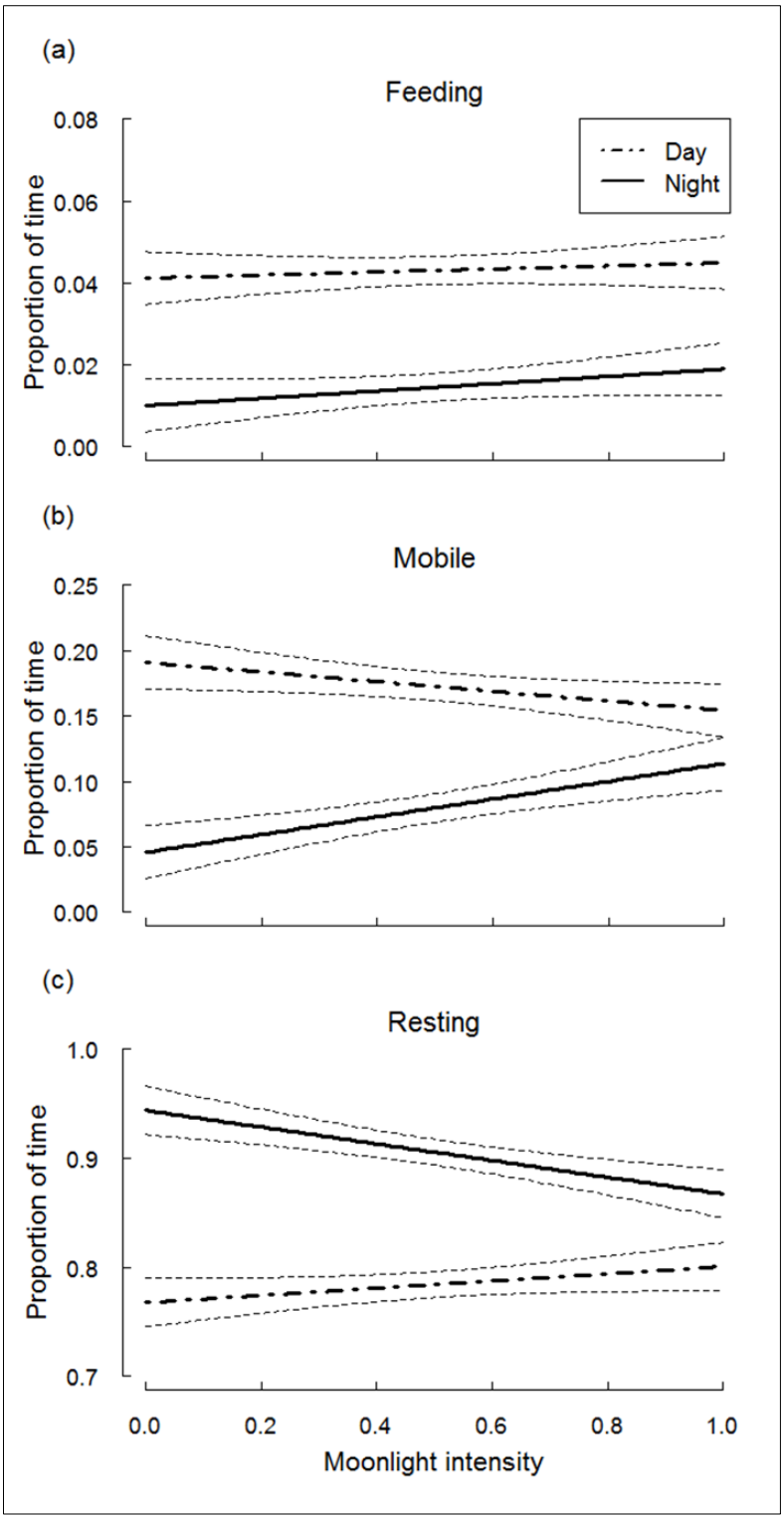


Figure 4.3: Relationship between the amount of moonlight available (0=no moon, 1=full moon) and the proportion of time cheetahs spent a) feeding b) mobile and c) resting.

Feeding frequency and length

The proportion of time cheetahs spent feeding was a function of both the frequency and length of feeding events - these factors were therefore analysed separately. Of the 910 feeding events extracted from the predictive dataset, 12% took place at night, 14% in the crepuscular transitions (i.e. dawn and dusk) and 73% took place during the day. Feeding events at night lasted on average 62.29 ± 3.54 minutes which was significantly shorter than those during the day (97.15 ± 3.55 minutes; Z=6.048, p<0.001; Figure 4.4). Season had a significant effect on both the frequency and the length of feeding events (feeding frequency: Z=11.349, p<0.001; feeding length: Z=1.972, p=0.048). In the wet season cheetahs fed more frequently but feeding events where shorter (97.35 ± 2.52 minutes) compared to the dry season when cheetah fed less often but for longer (104.66 ± 4.34 minutes, Figure 4.4).

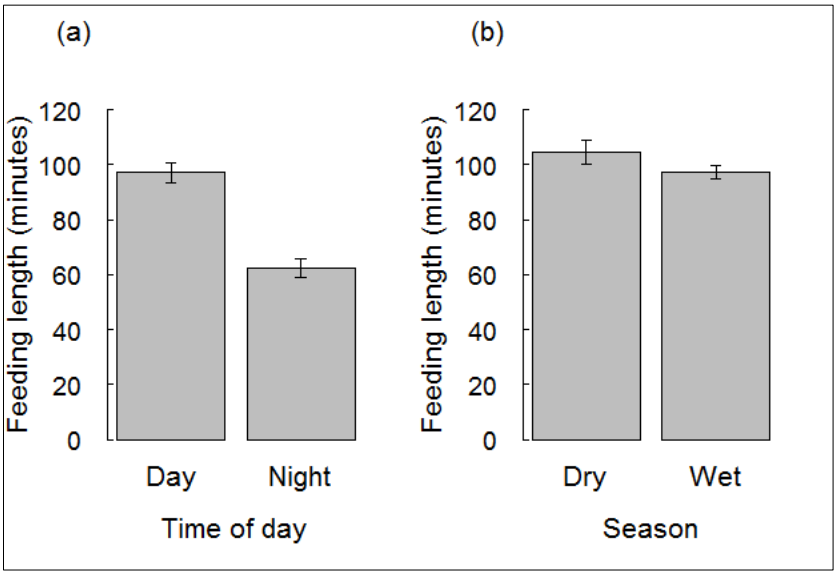


Figure 4.4: The length of cheetah feeding events at a) different times of day and in b) different seasons.

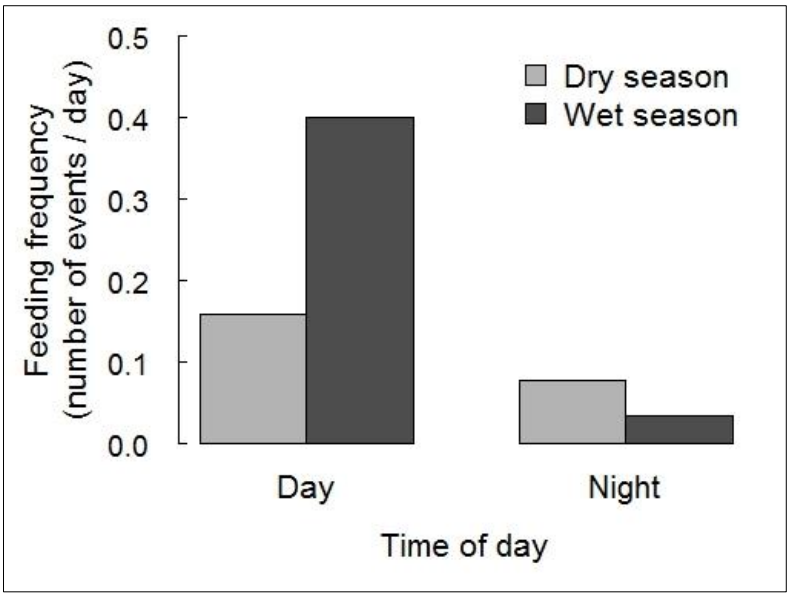


Figure 4.5: Frequency of cheetah feeding events (adjusted for time) in relation to the time of day and season.

Nocturnal feeding events were more frequent in the dry season than in the wet season (Z=-3.235, p=0.001) (Figure 4.5) but it was only in the dry season that feeding frequency at night increased significantly with increasing moonlight (three-way interaction: Z=-2.275, p=0.023) (Figure 4.6). Moonlight intensity had no significant effect on feeding length (Z=1.277, p=0.202).

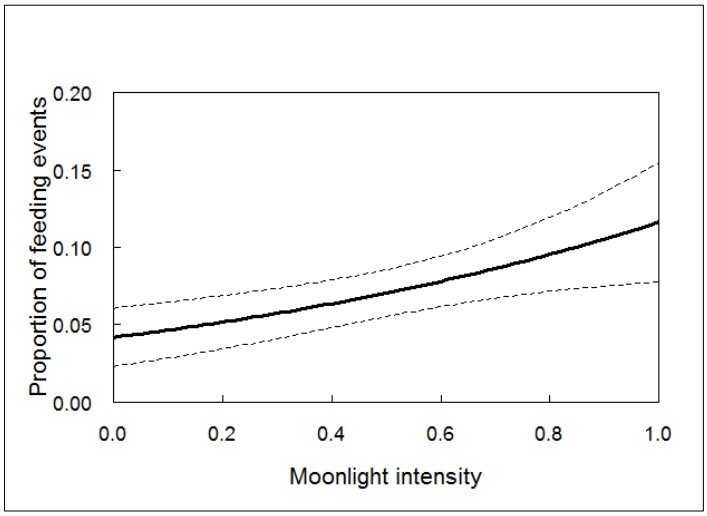


Figure 4.6: The proportion of cheetah nocturnal feeding events in the dry season in relation to moonlight availability (0 = no moon, 1 = full moon).

Discussion

Our results show that a significant proportion of cheetah foraging behaviour took place at night. In addition, the frequency of foraging behaviour increased with increased moonlight availability which in turn was offset by a decreased activity during the day. This suggests that cheetahs actively shifted their behaviour to the night when there was sufficient moonlight available. Nocturnal activity of cheetahs and a similarly competitively subordinate diurnal species, the African wild dog (*Lycaon pictus*), have been observed before, but it has been hypothesised that diurnal pressures such as human activity, were forcing these species to be more active at night (Marnewick et al. 2006, Rasmussen and Macdonald 2012). However, the present study area has no such diurnal pressures, indicating that cheetahs naturally *choose* to be active at night rather than being forced to do so.

These results corroborate recent findings showing a conspicuous nocturnal activity in cheetahs (Chapter 2) and challenge the hypothesis that cheetahs are rarely active at night in order to avoid negative encounters with nocturnal lions and spotted hyaenas (Hayward and Slotow 2009). Cheetahs, like other animals, are most at risk of costly encounters when feeding, not only because less time can be allocated to vigilance behaviour (Lima 1987), but also because their kills attract scavenging lions and spotted hyaenas (Hunter et al. 2007a). The observed nocturnal foraging behaviour, and in particular the increase with nocturnal moonlight intensity, therefore contradicts studies that have shown that non-predator species at risk often reduce their (foraging) activity during full moon nights when the risk of predation is highest (Clarke 1983, Kotler et al. 1991, Daly et al. 1992, Hughes and Ward 1993). However, predators, especially those more suited to diurnal activities, could benefit from increased moonlight. A study on short-eared owls (*Asio flammeus*) showed that hunting efficiency increased with increased moonlight (Clarke 1983). Similarly, cheetahs were more active at night in the dry season when clouds did not obscure the moonlight. We therefore speculate that with enough moonlight at night cheetahs benefit from increased visibility and that the darkness allows them to approach more closely to their prey, increasing the rate of successful hunts and/or decreasing the chase distance and therefore decreasing their energy

expenditure. In addition, impala (*Aepyceros melampus*), cheetahs main prey item (Purchase and du Toit 2000, Hayward et al. 2006), tend to move into open areas on moonlit nights (Jarman and Jarman 1973), a possible advantage to a high-speed, open habitat hunter like the cheetah. The results therefore suggest that the timing of cheetah foraging behaviour is influenced by resource acquisition rather than the avoidance of competitively dominant lions and spotted hyaenas. It is also possible that this temporal distribution of foraging behaviour is state-dependent and that hungry cheetahs are more willing to take the risk of encountering predators as the risk of starvation might be higher than the risk of a negative encounter (Kotler *et al.* 2010).

Complete avoidance of competitors in time is rare as it is often limited by behavioural and environmental factors, normally resulting in partial, rather than complete, temporal segregation (Carothers & Jaksić, 1984; Kronfield-Schor & Dayan, 2003). The fact that cheetah foraging was not strictly determined by the temporal variation of risk suggests that other factors might contribute to the behavioural mechanisms by which cheetahs manage risk. Firstly, it is possible that direct cues, rather than indirect ones such as day-night cycles influence behavioural decisions (Kotler et al. 1991). For example, the great Egyptian sand gerbil (*Gerbillus pyramidum*) showed a stronger response to the direct risk of predation by owls rather than the indirect risk associated with increased moonlight at night (Kotler et al. 1991). Similarly, cheetahs have been shown to adapt their behaviour according to direct perception of risk; for example by reducing hunting effort when lions were thought to be in the vicinity (Durant 2000a). Secondly, habitat heterogeneity can reduce the level of perceived risk by adjusting the probability of encounters (Kotler et al. 1991, Hughes et al. 1994). Dense vegetation can act as a 'competitive refuge', as species at risk are more concealed thereby minimising costly interactions with competitors or predators (Durant 1998, Pettorelli et al. 2009). For example, a study on gerbils showed that there was a shift from open habitat to denser bush during times when predation risk was highest (Kotler et al. 1991). Habitat structure could drive the nocturnal foraging behaviour of cheetahs as kleptoparasitism decreases with increased cover (Paulson 1985) and studies that have observed cheetahs to be active at night were situated in areas

with dense vegetation (Marnewick et al. 2006, Bissett and Bernard 2007). Whether habitat is an important component in risk management will be further investigated in Chapters 5 and 6.

Despite the fact that cheetahs did not seem to adjust the timing of behaviour according to the temporal variation of risk, it is possible that the feeding behaviour itself was influenced by the increased likelihood of encountering competitors at night. This is supported by the fact that feeding events at night were significantly shorter than those during the day. This could be due to an increased rate of kleptoparasitism, however, because kleptoparasitism is energetically costly (Gorman *et al.* 1998) this would counterbalance the possible energy gained by more efficient hunts at night. It is therefore possible that cheetahs either selected for smaller prey at night or that they tried to spend less time on a kill when they were in a risky situation. For example, cheetahs tended to leave kills earlier when in tall grass (where vigilance was hampered) compared to kills in short grass (Hunter et al. 2007b). Feeding length and feeding frequency were also different per season, with cheetahs feeding more frequently and for shorter periods of time in the wet season compared to the dry season. This is likely to be the result of resource acquisition rather than being associated with anti-predator strategies. Impala calving coincides with the onset of the seasonal rains, meaning that in the wet season there is a sudden abundance in small prey which is quicker to consume, but more might be needed to fulfil the cheetahs' energy requirements.

Previous studies have shown that cheetah foraging behaviour is influenced by the abundance of prey and the presence of competitors but that the time of day had no influence (Cooper et al. 2007). This, however, only refers to diurnal foraging as observations on cheetahs are predominantly carried out during the day (Cooper et al. 2007, Hilborn et al. 2012). It is therefore possible that this, comparatively less frequent, nocturnal foraging behaviour has not been detected before because of sampling techniques. Traditional methods of behavioural data collection, such as direct observations, make it difficult to constantly monitor animals thus introducing biases. Detailed studies on the timing of behaviour of elusive, far ranging species such as cheetahs that live at low

densities or in remote areas that are difficult to access have therefore been limited. Previous studies on activity patterns and timing of hunting and feeding have used data collected over short time intervals of 14 days (Mills and Biggs 1993, Hayward and Slotow 2009) and are therefore unable to show trends associated with long-term cycles such as the moon and season. However, with the development of data-loggers that automatically record and store animal activity in the absence of human observers, it is possible to investigate behaviours that have previously not been observed. In this case we show that light availability provides an additional dimension to the optimal foraging of cheetahs.

The influence of the moon on the foraging behaviour and the management of risk has been studied in predator-prey systems, especially in small mammals; however this is the first time that this has been investigated in large carnivores. These results show that competitively subordinate species, such as cheetahs, are more plastic in their behaviour than previously thought. The results clearly illustrate that longer term cycles such as lunar and seasonal variations should be taken into consideration to understand how animals manage risk through time allocation.

Appendix

Appendix 4.1: Summary of model selection statistics for the Generalised Linear Models (GLMs) analysing the proportion of three different cheetah behaviours in relation to time of day (TOD either day or night), season (ssn = wet or dry) and moon phases (continuous where 0 = no moon and 1 = full moon). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a blocking factor (ID).

Response variable	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Feeding behaviour	1	ID + TOD * ssn + moon	11	679.3	-1336	0.00	0.44	0.43
	2	ID + TOD * ssn	10	677.8	-1335	0.76	0.30	0.43
	3	ID + TOD * moon + TOD * ssn	12	679.6	-1334	1.54	0.20	0.43
	4	ID + moon * TOD * ssn	14	680.3	-1331	4.60	0.04	0.43
	5	ID + TOD + moon	9	672.5	-1326	9.25	0.00	0.41
	6	ID + TOD	8	671.1	-1326	9.89	0.00	0.40
	7	ID + TOD * moon	10	672.8	-1325	10.78	0.00	0.40
	8	ID + moon + TOD + ssn	10	672.5	-1324	11.40	0.00	0.40
	9	ID + TOD + ssn	9	671.1	-1323	12.03	0.00	0.40
	10	ID + moon * ssn + TOD	11	673.1	-1323	12.33	0.00	0.40
	11	ID + TOD *moon + ssn	11	672.8	-1323	12.96	0.00	0.40
	12	ID + moon	8	611.3	-1206	129.40	0.00	0.06
	13	ID + ssn	8	610.4	-1204	131.20	0.00	0.05
	14	ID + moon + ssn	9	611.3	-1204	131.60	0.00	0.06
Mobile behaviour	1	ID + TOD * moon + TOD * ssn	12	433.2	-841	0.00	0.65	0.64
	2	ID + TOD *moon + ssn	11	430.6	-838	2.85	0.16	0.64
	3	ID + moon * TOD * ssn	14	433.8	-838	3.19	0.16	0.64
	4	ID + TOD * moon	10	428.5	-836	4.86	0.06	0.63
	5	ID + TOD * ssn + moon	11	417.6	-812	28.92	0.00	0.60
	6	ID + TOD * ssn	10	416.3	-812	29.37	0.00	0.60
	7	ID + moon + TOD + ssn	10	415.3	-810	31.24	0.00	0.60
	8	ID + TOD + ssn	9	414.1	-809	31.65	0.00	0.59
	9	ID + TOD + moon	9	413.5	-808	32.80	0.00	0.59
	10	ID + TOD	8	412.2	-808	33.20	0.00	0.60
	11	ID + moon * ssn + TOD	11	415.4	-808	33.33	0.00	0.59
	12	ID + ssn	8	334.0	-651	189.70	0.00	0.23
	13	ID + moon	8	333.6	-651	190.30	0.00	0.25
	14	ID + moon + ssn	9	334.7	-651	190.40	0.00	0.26
Resting behaviour	1	ID + TOD * moon + TOD * ssn	12	414.7	-804	0.00	0.83	0.70
	2	ID + moon * TOD * ssn	14	415.2	-801	3.31	0.16	0.70
	3	ID + TOD *moon + ssn	11	409.0	-795	9.13	0.01	0.69
	4	ID + TOD * moon	10	407.4	-794	10.24	0.01	0.69
	5	ID + TOD * ssn + moon	11	400.0	-777	27.19	0.00	0.67
	6	ID + TOD * ssn	10	398.0	-775	29.04	0.00	0.66
	7	ID + moon + TOD + ssn	10	394.9	-769	35.16	0.00	0.66
	8	ID + TOD + moon	9	393.4	-768	35.96	0.00	0.65
	9	ID + TOD + ssn	9	393.0	-767	36.88	0.00	0.65
	10	ID + moon * ssn + TOD	11	395.0	-767	37.09	0.00	0.65
	11	ID + TOD	8	391.5	-766	37.66	0.00	0.64
	12	ID + moon	8	287.2	-558	246.20	0.00	0.23
	13	ID + ssn	8	287.0	-558	246.60	0.00	0.23
	14	ID + moon + ssn	9	287.9	-557	247.00	0.00	0.23

Appendix 4.2: Summary of model selection statistics for the Generalised Linear Models (GLMs) analysing the frequency of cheetah feeding events in relation to time of day (TOD either day or night), season (ssn = wet or dry) and moon phases (continuous where 0 = no moon and 1 = full moon). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a blocking factor (ID).

Response variable	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Feeding frequency	1	ID + TOD * moon * ssn	13	-400.5	829	0.00	0.53	0.92
	2	ID + TOD * moon + TOD * ssn	11	-403.3	830	1.27	0.28	0.92
	3	ID + TOD * ssn	9	-406.4	832	3.07	0.11	0.91
	4	ID + TOD * ssn + moon	10	-405.7	832	3.83	0.08	0.90
	5	ID + TOD * moon + ssn	10	-440.0	901	72.41	0.00	0.89
	6	ID + TOD + ssn	8	-444.7	906	77.47	0.00	0.89
	7	ID + TOD + moon + ssn	9	-444.0	907	78.21	0.00	0.89
	8	ID + TOD + moon * ssn	10	-444.0	909	80.38	0.00	0.88
	9	ID + TOD * moon	9	-477.7	974	145.56	0.00	0.85
	10	ID + TOD	7	-481.8	978	149.40	0.00	0.85
	11	ID + TOD + moon	8	-481.6	980	151.25	0.00	0.85
	12	ID + ssn	7	-625.8	1266	437.56	0.00	0.48
	13	ID + moon * ssn	9	-625.2	1269	440.56	0.00	0.47
	14	ID + moon	7	-659.3	1333	504.48	0.00	0.31

Appendix 4.3: Summary of model selection statistics for the linear models analysing the length of cheetah feeding events in relation to time of day (TOD either day or night), season (ssn = wet or dry) and moon phases (continuous where 0 = no moon and 1 = full moon). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a blocking factor (ID).

Response variable	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Feeding length	1	ID + TOD + ssn	9	-79.9	179	0.00	0.42	0.30
	2	ID + TOD * ssn	10	-79.8	181	2.06	0.15	0.30
	3	ID + TOD + moon	10	-79.8	181	2.11	0.15	0.28
	4	ID + TOD	8	-82.7	182	3.29	0.08	0.27
	5	ID + TOD + moon * ssn	11	-79.7	183	4.15	0.05	0.27
	6	ID + TOD * ssn + moon	11	-79.7	183	4.18	0.05	0.27
	7	ID +TOD + moon + ssn	11	-79.8	183	4.40	0.05	0.27
	8	ID + TOD + moon	9	-82.6	184	5.45	0.03	0.27
	9	ID + TOD * moon + ssn	12	-79.7	185	6.49	0.02	0.27
	10	ID + TOD * moon	10	-82.6	187	7.69	0.01	0.27
	11	ID + TOD * moon * ssn	14	-79.6	190	10.95	0.00	0.27
	12	ID + ssn	8	-100.8	219	39.56	0.00	0.11
	13	ID + moon * ssn	9	-100.8	221	41.78	0.00	0.07
	14	ID + moon	8	-107.2	231	52.28	0.00	0.04

CHAPTER 5

Risk avoidance in sympatric large carnivores: reactive or predictive?

A modified version of this chapter has been published in *Journal of Animal Ecology*

Abstract

Risk of predation or competition is a major factor shaping species distributions. The way that animals respond to risk can either be reactive (to a direct risk) or predictive (a pre-emptive response to a perceived risk). Whilst different types of spatial responses to risk have been widely studied in various predator-prey systems, knowledge of risk management among large carnivores is lacking. Here we use contemporaneous spatial data from Global Positioning System (GPS) radio-collars deployed on three resident species of large carnivores in the periphery of the Okavango Delta in northern Botswana: cheetahs (*Acinonyx jubatus*) (n=6), lions (*Panthera leo*) (n=5) from five prides, and spotted hyaenas (*Crocuta crocuta*) (n=8) from five clans to investigate their relative spatial distributions. Spatial avoidance has been described as the primary mechanism by which cheetahs minimise costly encounters with more dominant species; lions and spotted hyaenas. In this study we investigated this assertion by asking whether cheetah distribution can be better explained by predator avoidance than by prey availability and if there is predator avoidance, whether this is a reactive or a predictive response. We analysed cheetah spatial distribution in relation to 1) the likelihood of encountering lions, 2) spotted hyaenas, and 3) habitat as a function of prey distribution. The response to risk of encountering lions and spotted hyaenas was explored on three levels; short-term or immediate risk, calculated as the distance to the nearest (contemporaneous) lion or spotted hyaena, long-term risk, calculated as the likelihood of encountering lions and spotted hyaenas based on their cumulative distributions over a six month period and habitat associated risk, quantified by the habitat used by each of the three species. Cheetahs' response to risk seemed to be reactive, rather than predictive: space and habitat use by cheetahs was similar to that of lions and, to a lesser extent, spotted hyaenas but cheetahs avoided short-term risk by positioning themselves further than random from lions and spotted hyaenas. Our results suggest that cheetah spatial distribution is a hierarchical process, firstly driven by resource acquisition and thereafter fine-tuned by predator avoidance. This study gives a first insight into the behavioural decisions made by a competitively subordinate large carnivore under the risk of predation and competition.

Introduction

The risk of predation or competition can significantly alter animal behaviour and species' spatial distribution (Ripple and Beschta 2004, Fortin et al. 2005). However, the probability of costly encounters can be minimised as risk is not homogenously distributed in space and time, but rather varies with the distribution, densities, habitat use and activity of predators and competitors (Durant 1998, Brown et al. 1999). This heterogeneity allows animals to use 'refuges', such as selecting for areas of low risk (Durant 1998, Chesson 2000), or adapting their behaviour, such as changing habitat use, in response to changing levels of risk (Creel et al. 2005). The way that animals respond to risk can either be reactive or predictive. A reactive response to risk is based on an animals' knowledge of actual, real-time risk. For example, elk (*Cervus elaphus*) used coniferous woodland, rather than grassland, when wolves (*Canis lupus*) were in the immediate vicinity (Creel et al. 2005) and African buffalo (*Syncerus caffer*) visited waterholes during the hot, midday hours, rather than at dawn and dusk, when lions (*Panthera leo*) were in the vicinity (Valeix et al. 2009a). A predictive response, on the other hand, is based on a pre-emptive response to a potential for risk, derived from previous knowledge of the competitors or predators' whereabouts or the habitat types intensively used by them. For instance, tawny owls (*Strix aluco*) displayed habitat-mediated avoidance in areas where there was a high risk of encountering eagle owls (*Bubo bubo*) (Sergio et al. 2007) and Egyptian mongoose (*Herpestes ichneumon*) avoided areas that were used by Iberian lynx (*Lynx pardinus*) (Palomares et al. 1996).

Whilst numerous studies have separately investigated animal response to either the immediate or long-term risk, very few studies have compared these behavioural responses simultaneously (but see Sergio et al. 2007, Valeix et al. 2009a, Valeix et al. 2009b), none of which investigated the relationships within the large carnivore guild. Here we investigate the reactive response to actual risk in conjunction with the predictive response to long-term risk of encountering competing, larger carnivores. We distinguish between a 'landscape of risk' that maps known risks, as opposed to a

'landscape of fear' which has been used to map the perception of risk (Laundré et al. 2001, Willems and Hill 2009).

Aggressive interactions between carnivores are not uncommon and have been documented for a variety of carnivore species (Polis and Myers 1989, Palomares and Caro 1999, Macdonald et al. 2010). The mechanisms by which competitively subordinate carnivores minimise interactions with competitively dominant carnivores are fundamental to their survival (Linnell and Strand 2000). Since large mammalian carnivores often need relatively vast amounts of space (Woodroffe and Ginsberg 1998), it is important to understand their spatial requirements and unravel how these could be influenced by other species of predators (Gittleman and Harvey 1982). Due to their smaller body size and solitary nature, cheetahs (*Acinonyx jubatus*) are competitively subordinate to the larger and more social lions and spotted hyaenas (*Crocuta crocuta*) (Caro 1994, Durant 1998, 2000a). Furthermore, these larger predators present real threats to cheetahs: in the Serengeti National Park, Tanzania, lions and spotted hyaenas were reported to be responsible for 73% of cheetah cub mortality and the kleptoparasitism of 12.9% of cheetah kills (Laurenson 1995, Hunter et al. 2007b). Hence, cheetahs have been described as a 'refugial species'. Spatial avoidance is believed to be one of the main mechanisms by which these competitively subordinate carnivores can minimise interactions with more dominant ones (e.g. Durant 1998). However, whether spatial avoidance is a reactive or a predictive response has, so far, not been investigated simultaneously.

Here, we use contemporary GPS (Global Positioning System) radio-collar data from cheetahs, lions and spotted hyaenas to explore this and test a set of predictions on cheetah spatial avoidance of lions and spotted hyaenas based on previous studies. More specifically we expected that:

1. Cheetahs avoided areas that are intensively used by lions and spotted hyaenas (long-term risk),
2. Cheetahs avoided immediate, short-term encounters with lions and spotted hyaenas (short-term risk),

3. Cheetah habitat use was negatively influenced by the habitat used by lions and spotted hyaenas,
4. The response to short- and long-term risks changed depending on the structural characteristics of the habitat.

We investigated the spatial distribution of cheetah locations in terms of the short- and long-term risk of encountering lions and spotted hyaenas in different habitat types. Short-term risk was calculated as the distance to the nearest lion and spotted hyaena. For long-term risk, we used a 'landscape of risk' derived from the ranging data of lions and spotted hyaenas over 6 months to reflect the probability of their presence. Finally, we investigated whether habitat use by lions and spotted hyaenas influenced habitat use by cheetahs and whether habitat affected the way in which cheetahs responded to both the short- and long-term risk of encountering predators. To determine whether cheetah habitat selection is driven by prey distribution, we calculated the abundance of impala (*Aepyceros melampus*), cheetahs preferred prey (see Appendix 5.1), for the different habitat types.

Methods

Study area

This research took place on the periphery of the Okavango Delta, a permanent inland delta situated in northern Botswana. The core study site (19°31'S, 23°37'E; elevation ca. 950m) encompassed an area of approximately 2 720 km^2 which included Moremi Game Reserve and the adjacent Wildlife Management Areas (for details see McNutt 1996). It is a semi-arid ecosystem characterised by five distinct transitional habitat types; open grassland, mixed woodland dominated by Acacia *spp*. (*Acacia erioloba* and *A. tortilis*), mopane (*Colophospermum mopane*) woodland, riparian woodland and floodplains created by the extremities of the Okavango Delta (McNutt 1996). The climate is characterised by two distinct seasons; a dry season between April and October and a wet season between November and March with an annual rainfall of 450-600 mm/year (Mendelson et al. 2010).

Data collection

Carnivore data - Between October 2008 and July 2011 we fitted GPS radio-collars (VECTRONIC Aerospace GmbH, Germany) on six individual cheetahs, five lions each in different neighbouring social groups and eight spotted hyaenas in five different neighbouring social groups. The radio-collars were deployed on all known social groups within the study area and all species overlapped extensively in space. The radio-collars were programmed to collect GPS fixes four times a day for cheetahs (00h00, 06h00, 12h00 and 18h00) and eight times a day for lions and spotted hyaenas (00h00, 02h00, 04h00, 06h00, 12h00, 18h00, 20h00 and 22h00). For accuracy, GPS fixes with a dilution of precision (DOP) < 10 were removed (Frair et al. 2010). Data were recorded for a mean of 329 days for cheetahs (range: 217–472 days); 416 days for lions (range: 328–486 days) and 432 days for spotted hyaenas (range: 310–587 days).

Habitat types - The term 'habitat' was used to categorise areas with similar vegetation types and structure. Based on a vegetation map provided by the Okavango Research Institute we created a raster map of five habitat types with a resolution of 50 x 50 meters. The habitat types used for the analyses are summarised in Table 5.1.

Table 5.1: Summary of the five main habitat types found in the Okavango Delta, Botswana. Habitat classification was based on vegetation composition (type of vegetation) and structure (open-medium-dense).

Habitat type	Vegetation composition	Vegetation structure	Area (km^2)*	%*
Grassland	Former floodplains characterised by shrubbed grassland dominated by *Cynodon dactylon*, *Chloris virgata* and *Eragrostis spp*.	Open	411	15.1
Mixed woodland	Predominately *Acacia spp.* with a grassy understory consisting of *C. dactylon*, *Panicum spp.* and *Eragrostis spp.*	Medium	638	23.5
Mopane	Characterised by *C. mopane* shrubs and trees	Medium/ dense	1201	44.1
Riparian	Tall mixed woodland located on (historic) riverine areas characterised by *A. nigrescens* and *Combretum imberbe* trees	Dense	143	5.3
Swamp	Moist and seasonally flooded open grasslands usually along a river course characterised by sedges and grass species *Panicum repens* and *C. dactlyon*	Open	326	11.9

*Area and percentage of the core study area. The core study area was defined by the outermost boundary delimiting the total sum of the 90% kernels of all three species (cheetahs, lions and spotted hyaenas).

Prey – Data on prey selection by cheetahs, lions and spotted hyaenas indicated that impala were the primary prey for cheetahs and that there was extensive overlap in prey choice between cheetahs, lions and spotted hyaenas (Appendix 5.1). As a result, the impala density in each of the five habitat types was calculated using the distance sampling method (Buckland et al. 2001). In total, four count surveys were conducted between 2009 and 2010. The transect lengths were corrected for variation in visibility so that the same amount of area was surveyed in each habitat type (4.95 km^2 per habitat type apart from riparian as it was scarce and difficult to survey) and each transect was randomly positioned within the study area. The data were analysed using Distance 6.0 (Thomas et al. 2006). We discarded all data beyond 200m and we used three key-function models (half-normal, uniform, and hazard-rate all with cosine series expansion) to calculate impala density (Buckland et al. 2001).

The most parsimonious model was selected based on the lowest Akaike Information Criterion (AIC) value (Burnham and Anderson 2002).

Data analyses

First, we investigated habitat selection for all three carnivore species. We then investigated whether the probability of cheetah presence was influenced by the long-term risk of encountering either lions or spotted hyaenas. Finally, we investigated whether the probability of cheetah presence was influenced by the immediate proximity of lions and spotted hyaenas. All data extractions and calculations were carried out either in Geospatial Modelling Environment (GME) (Beyer 2012, R Development Core Team 2012) or ArcGIS 10.0 (Environmental Systems Research Institute Inc. 2010).

Due to the timing of when radio-collars were deployed, we used three different datasets. We used data on cheetahs, lions and spotted hyaenas collected between October 2008 and July 2011 to determine species-specific habitat selection. We then used two different datasets, each of six months, to investigate cheetah response to short- and long-term risk; 1) when cheetahs and lions were collared simultaneously (September 2010 - March 2011) and 2) when cheetahs and spotted hyaenas were collared simultaneously (August 2009 - February 2010). The subsequent analyses on short- and long-term risk are the same for both these datasets.

Analyses of habitat selection

To test whether cheetahs (n=6), lions (n=5) and spotted hyaenas (n=8) selected for specific habitat types we carried out a compositional analysis (Aebischer et al. 1993) using the package 'adehabitatHS' in the statistical software R (Calenge 2006, R Development Core Team 2012). To reduce temporal and spatial autocorrelation we randomly selected 1000 GPS points per individual. We then analysed the data on two spatial scales. First, the proportion of habitat types within the home-range of each individual was compared to the proportion of habitat types available within the

study area (2nd order habitat selection). Second, habitat types at each GPS location were compared to habitat types available within the home-range of the respective individual (3rd order habitat selection) (Johnson 1980). Home-ranges were based on the 90% isopleth (Börger et al. 2006) from kernels created using fixed Gaussian Kernel Density Estimate (KDE) function. Kernel bandwidth was estimated using the Least Square Cross Validation (LSCV) method (Powell 2000, Gitzen et al. 2006). The study area was defined by the outermost boundary delimiting the total sum of the 90% kernels of all three species (n=19). The Ivlev's electivity index was used to investigate whether each species used habitat types in accordance to their availability (Krebs 1999). The formula $E=(p-q)/p+q$) standardized the habitat used (p) to the habitat available (q) with values ranging from -1 to 1. Habitat preference occurred when p was greater than q ($E>0$) and avoidance when p was less than q ($E<0$) (Krebs 1999). Ivlev indices were calculated for both the 2nd order (home-ranges vs. study area) and 3rd order (locations vs. home-ranges) habitat selection.

Analyses of predator risk

Long-term risk - To quantify long-term lion and spotted hyaena risk we created species-specific landscapes of risk based on kernel density estimates. Kernels (90%) were created for each individual using a fixed Gaussian function with a kernel bandwidth based on the LSCV method (Powell 2000, Gitzen et al. 2006). To reduce temporal and spatial autocorrelation we used 1000 randomly selected GPS locations for each individual. The cell size was set to 50 x 50 m so the value of each pixel of the raster map was a proxy of the likelihood of encountering a predator. Once all the individual maps were created they were summed per species to create a species-specific landscape of risk.

To test whether the probability of finding a cheetah was influenced by the risk of encountering lions and spotted hyaenas we compared the predator risk at actual GPS locations of each cheetah to the risk at randomly generated points (Manly et al. 2002). To reduce temporal autocorrelation we randomly selected 500 GPS locations per cheetah and generated the same number of random points within each species-specific landscape of risk.

Immediate risk – To test whether cheetahs were closer (or further away) from predators than expected assuming a random distribution, we calculated the distance from each cheetah GPS location to the nearest lion and spotted hyaena and compared this to the distance that these predators were to randomly generated points. To reduce temporal and spatial autocorrelation we randomly selected 500 GPS locations per cheetah and selected the same number of random points within the cheetah's home-range. Each random point was associated with the same time sequence that mimicked that of the cheetah.

Statistical analysis – The effect of both long-term and immediate risk on the probability of cheetah presence was analysed using generalized linear mixed models (GLMM) with a binomial error structure and logit-link function. The binomial response variables were 0/1 – where 1 represented the GPS locations for cheetah and 0 the randomly generated points. For the long-term risk analysis the predictor variables were risk (continuous) and habitat type (categorical) whereas for the immediate risk analysis the predictor variables were distance to nearest lion and spotted hyaena (continuous) and habitat type (categorical). In each model the identity of the cheetah was entered as a random factor. Four *a-priori* candidate models predicting the probability of cheetah presence as a function of risk and habitat type were created. Models were ranked using Akaike Information Criterion corrected for small sample size (AICc). If one model was clearly dominant ($w_i > 0.9$) this was used, otherwise model averaging was performed to estimate the parameters (Burnham and Anderson 2002). Statistical analyses were performed using statistical software R 2.14.2 (R Development Core Team 2012).

Results

Habitat use and prey distribution

Cheetah habitat selection was significantly non-random both within the study area (2nd order selection: $\lambda = 0.068$, $p = 0.003$) and within their home-ranges (3rd order selection: $\lambda = 0.035$, $p <$

0.001). The home-ranges of cheetahs included more grassland and mixed woodland than would be expected from their availability, while the amount of mopane, riparian and swamp was lower. Within their home-ranges cheetahs preferred grassland over mixed woodland (Figure 5.1, Appendix 5.2). Similarly, for lions both 2nd and 3rd order habitat selection were significantly non-random (2nd order selection: $\lambda = 0.053$, $p < 0.001$; 3rd order selection $\lambda = 0.168$, $p = 0.014$). Lion home-ranges included more grassland and mixed woodland and less mopane and swamp than expected. However, within their home-ranges lions preferred mixed woodland over grassland (Figure 5.1, Appendix 5.2). Spotted hyaena non-randomly selected habitat types within the study area, preferring grassland and mixed woodland and avoiding swamp (Figure 5.1, Appendix 5.2). Within their home-ranges, however, habitat selection was random. In other words, spotted hyaenas used habitat types in proportion with their availability (2nd order selection: $\lambda = 0.058$, $p = 0.002$; 3rd order selection: $\lambda = 0.120$, $p = 0.228$).

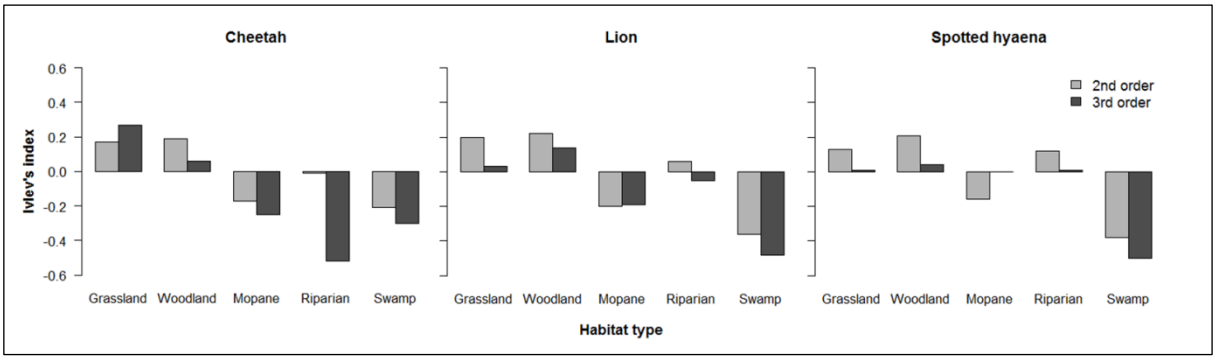


Figure 5.1: Habitat selection for cheetahs (n=6), lions (n=5) and spotted hyaenas (n=8) in northern Botswana using the Ivlev's index for preference/avoidance. Values >0 indicate that a habitat type was used more than available (preference) and values <0 indicate habitat types that were used less than available (avoidance). This was done on two levels; 2nd order (light grey – home-ranges vs. study area) and 3rd order (dark grey – locations vs. home-ranges) habitat selection (Johnson 1980).

Impala density varied between habitat types, with the highest densities in mixed woodland and riparian (but large variance for this habitat type due to small sample size) and the lowest density in the mopane woodland (Figure 5.2).

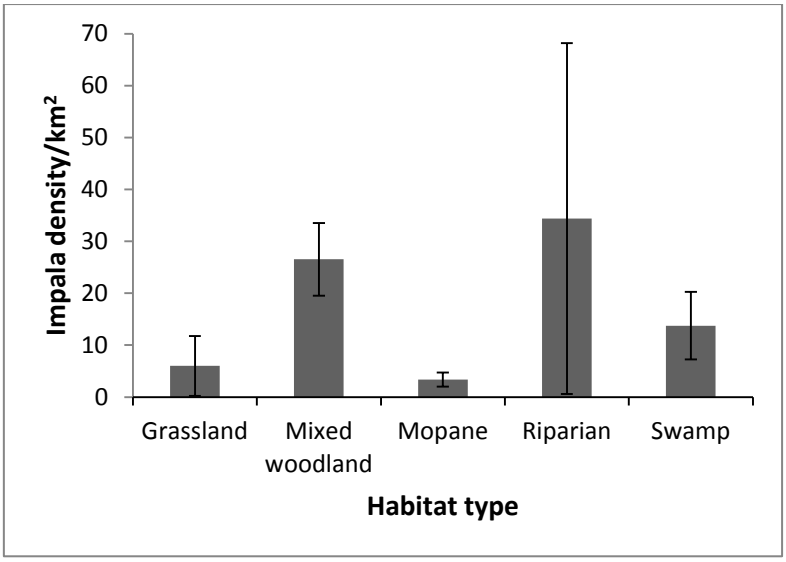


Figure 5.2: Estimated impala densities (± s.e.m.) for five different habitat types found in the Okavango Delta, northern Botswana.

Risk

The best models predicting the spatial distribution of cheetahs included habitat types, risk (both short- or long-term) and an interaction between these two predictor variables, indicating the effect of risk was dependent on habitat type (Tables 5.2 and 5.3).

Table 5.2: Summary of model selection statistics for the Generalised Linear Mixed Models (GLMMs) analysing the probability of cheetah occurrence (presence/absence) in relation to habitat type and long-term predator risk (six months). Models were ranked according to Akaike weights (w_j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values.

Predator	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Lion	1	habitat type x risk	11	-1811.56	3645.20	0	1.00	0.39
	2	habitat type + risk	7	-1829.65	3673.34	28.14	0.00	0.38
	3	habitat type	6	-1903.70	3819.43	174.22	0.00	0.34
	4	risk	3	-2188.44	4382.89	737.69	0.00	0.16
Spotted hyaena	1	habitat type x risk	11	-2530.50	5083.07	0.00	0.99	0.19
	2	habitat type	6	-2540.29	5092.60	9.53	0.01	0.18
	3	habitat type + risk	7	-2540.21	5094.45	11.38	0.00	0.17
	4	risk	3	-2832.18	5670.37	587.30	0.00	0.00

Table 5.3: Summary of model selection statistics for the Generalised Linear Mixed Models (GLMMs) analysing the probability of cheetah occurrence (presence/absence) in relation to habitat type and the immediate predator risk measured as the distance to nearest predator. Models were ranked according to Akaike weights (w_j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values.

Predator	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Lion	1	habitat type x distance	11	-1554.19	3130.48	0	1.00	0.19
	2	habitat type + distance	7	-1586.17	3186.38	55.90	0.00	0.16
	3	habitat type	6	-1603.39	3218.82	88.34	0.00	0.14
	4	distance	3	-1732.89	3471.79	341.31	0.00	0.01
Spotted hyaena	1	habitat type x distance	11	-2736.42	5494.89	0.00	0.63	0.10
	2	habitat type	6	-2742.38	5496.77	1.88	0.25	0.09
	3	habitat type + distance	7	-2742.12	5498.27	3.37	0.12	0.10
	4	distance	3	-2895.27	5796.55	301.66	0.00	0.00

Surprisingly, cheetahs were more likely to be found in areas where there was a high, long-term risk of encountering lions. In other words, cheetahs did not actively avoid areas that were intensively used by lions. This was significant for all habitat types (grassland: Z = 4.46, p ≤ 0.001, mixed woodland: Z = 8.17, p ≤ 0.001, mopane: Z = 8.34, p ≤ 0.001 and riparian: Z = 2.89, p = 0.004) apart from swamp (Z = 0.30, p = 0.762; Figure 5.3 – top row). The probability of finding a cheetah with regards to the long-term risk of encountering spotted hyaena was only predictable in mixed woodland (Z = -3.16, p = 0.002) and mopane (Z = 3.10, p = 0.002). Cheetahs were less likely to be found in areas where there is a higher chance of encountering spotted hyaenas when they were in mixed woodland but were found in high risk areas in mopane (Figure 5.3 – bottom row).

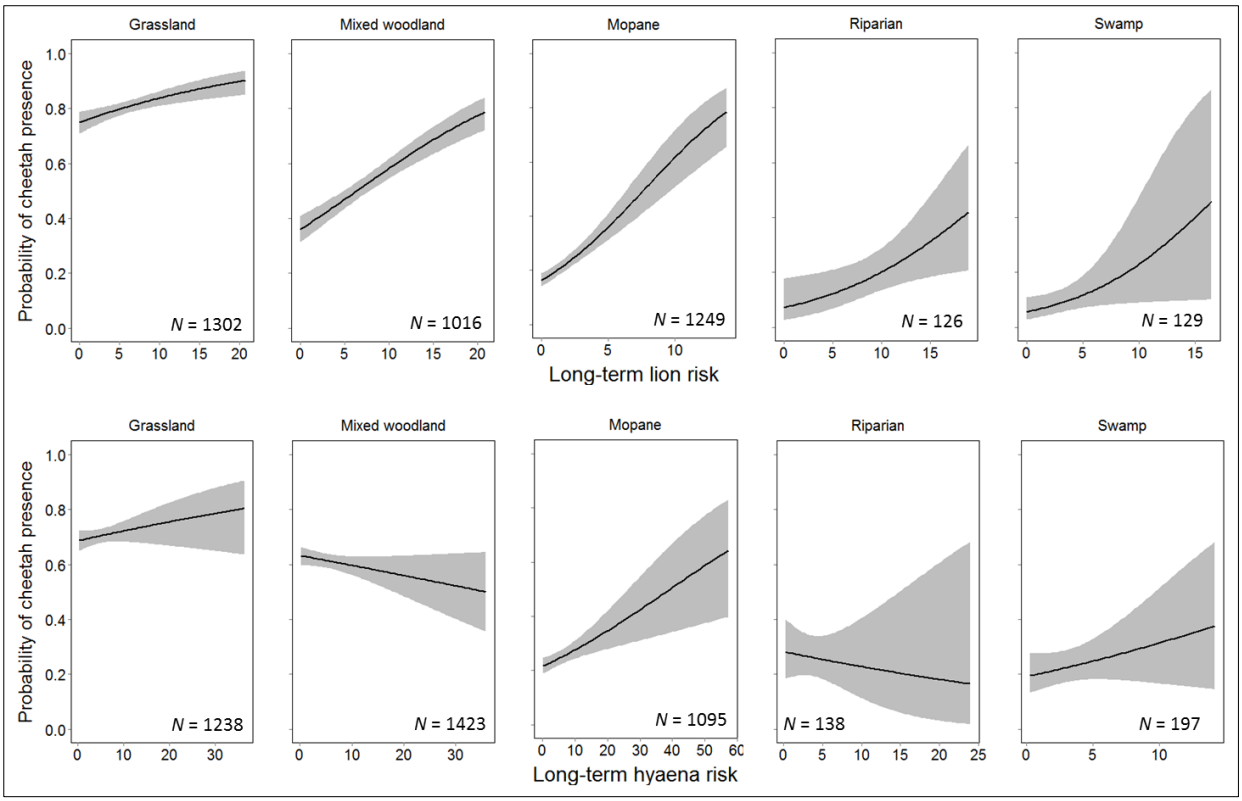


Figure 5.3: Relationship between the long-term risk of encountering lions (top row) and spotted hyaenas (bottom row) and the probability of cheetah presence in different habitat types. Long-term risk is proportional to the likelihood of predator presence calculated using kernel density estimates (KDE) at a 50 x 50m resolution. Fitted lines are displayed ± 95% confidence intervals.

At the immediate scale the probability of cheetah presence in relation to distance to the nearest lion was dependent on habitat type. In grassland and mopane cheetahs were significantly further from lions than expected (grassland: $Z = 6.73$, $p \leq 0.001$; mopane: $Z = 4.05$, $p \leq 0.001$) but in mixed woodland cheetahs were significantly closer to lions than expected ($Z = -3.99$, $p \leq 0.001$; Figure 5.4) indicating that habitat type possibly plays a role in the way that cheetahs perceive and respond to risk. On average, regardless of habitat type, cheetahs were 5.10 ± 0.09 km (mean ± 95% CI) from the nearest lion. Apart from in swamp habitat, the distance to the nearest spotted hyaena did not significantly influence the probability of cheetah presence (figures not shown).

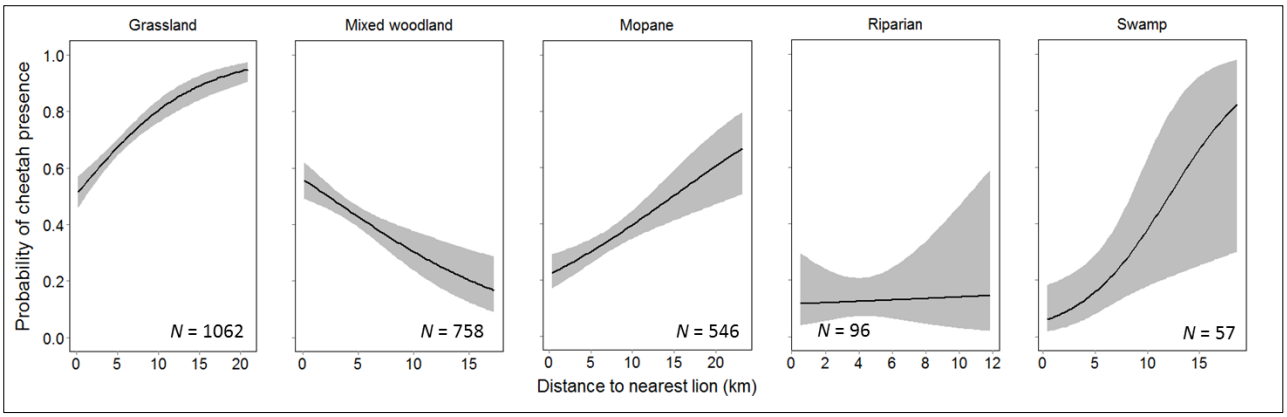


Figure 5.4: Relationship between the immediate risk of encountering lions, determined by the distance to the nearest lion, and the probability of cheetah presence in different habitat types. Fitted lines are displayed ± 95% confidence intervals.

Discussion

Our findings demonstrate that the response of cheetahs to the risks posed by the larger and competitively stronger lions and spotted hyaenas is predator-specific, habitat-specific and dependent on the immediacy of the risk. In fact, we did not detect any spatial segregation between cheetahs and lions or between cheetahs and spotted hyaenas when we analysed the dataset over a relatively prolonged time span of six months. In contrast, we found that cheetahs reacted to an immediate risk posed by their stronger competitors, especially lions, by being farther from them than would be expected following a random distribution when cheetahs were in grassland or mopane. These results show that cheetahs do not consistently avoid areas with a high likelihood of encountering lions or spotted hyenas (risky areas) but instead they adjust their behaviour to short-term alterations of risk.

It has been shown that habitat heterogeneity is a key component in coexistence as competitively subordinate species can seek spatial refuge from negative interactions with competitively dominant species. With carnivores, for example, the species at risk may select for habitat types or regions - such as prey-poor areas - that attract fewer predators and competitors (Chesson 1986, Rosenzweig 1991, Durant 1998). A reduced encounter rate with competitors may thus come with the cost of reduced hunting success and food intake (Sih 1980, Lima and Dill 1990). In this study, however, we

found that cheetahs selected for areas with a high risk of encountering lions. This extensive overlap in space and habitat use is likely driven by the distribution and acquisition of prey. This is supported by the findings that cheetahs and lions avoided prey-poor areas (e.g. mopane) or areas where prey was not easily accessible (e.g. swamp) and preferred prey-rich habitat types such as mixed woodland and grasslands where prey was more accessible. Within individual home-ranges there was a slight differentiation in habitat selection, but this did not give rise to strict spatial segregation. Furthermore, differences in habitat preference on a finer spatial scale suggest that, within the preferred habitat types, species adjust their habitat use depending on behavioural traits, such as hunting strategies. For instance, cheetahs being high speed hunters tend to prefer more open habitat types, while lions, being ambush hunters, are more successful when there is vegetation cover and may thus prefer slightly more vegetated habitat types such as mixed woodland (Mills et al. 2004, Hopcraft et al. 2005). It is possible that the absence of spatial avoidance over the long-term is either due to the inability of cheetahs to detect and assess long-term risk or to the lack of benefits of doing so. Olfactory cues to the presence of sympatric carnivore species, such as scent-marks and scat, could be used to assess the former presence of predators (Kats and Dill 1998), but even relatively fresh scats do not necessarily relate to present risk in terms of spatial proximity for these highly mobile predator species. The lack of differential habitat use and long-term (predictive) avoidance is consistent with the idea that habitat selection is a hierarchical process and that on the broad-scale this is firstly driven by resource acquisition and thereafter fine-tuned by predator avoidance (Orians and Wittenberger 1991, Chapters 4 and 6).

The immediate risk of encountering lions seems to be an important factor in the spatial distribution of cheetahs as they were generally further away from lions than was expected under random distribution. This suggests that lions pose a threat to cheetahs and that cheetahs can detect lion presence, assess the level of risk and adjust their behaviour accordingly, probably responding to more immediately and spatially reliable cues such as visual or auditory detection (Durant 2000a, Webster et al. 2010). However, in mixed woodland, cheetahs were found to be closer to lions than

expected. Since it is unlikely that cheetahs would actively move towards lions, it suggests that when cheetahs are in mixed woodland and lions are in the vicinity, that they do not feel the need to move away. Mixed woodland may be a relatively safe refuge for cheetahs as the relatively dense vegetation reduces visible detection (Janssen et al. 2007), decreasing the likelihood of encounters with lions. This interpretation is supported by studies elsewhere showing that vegetation cover minimised cheetah interactions with lions and spotted hyaenas (Bissett and Bernard 2007, Hunter et al. 2007a). Similarly elk have been shown to move into denser vegetation when wolves were nearby (Creel et al. 2005). Whilst the results suggest that short-term space and habitat use by cheetahs is likely to be driven by predator avoidance rather than resource acquisition, we suggest a more dynamic approach should be taken in the future.

In general, cheetah response to both the long-term and immediate risk was less pronounced for spotted hyaenas than for lions. This is probably because of differences in ecological needs and threats posed by spotted hyaenas. Spotted hyaenas are extremely flexible in their prey preference, foraging strategies and habitat selection (Kruuk 1972, Hayward 2006). Cheetahs therefore are not only less likely to encounter spotted hyaenas but are also less able to predict their behaviour. It is however important to note that quantifying spotted hyaena risk was difficult due to the inherent nature of spotted hyaena social system and structure. Spotted hyaenas live in complex, hierarchical fission-fusion systems (Kruuk 1972). Social groups can be as large as 80 individuals, but unless there is a large carcass, spotted hyaenas generally occur alone or in smaller sub-groups. In addition, because of the hierarchical structure of spotted hyaena clans, not all individuals within a clan use space and habitat in the same way (Boydston et al. 2001, Boydston et al. 2003). Therefore, having a collar on one or two individuals in a clan possibly gives little insight into space and habitat use of all the individuals. Despite this, studies have shown that cheetahs exhibited a less marked reaction to spotted hyaenas compared to lions (Laurenson 1995, Durant 1998, Webster et al. 2010). This could be because encounters with lions are more likely to be fatal compared to those with spotted hyaenas (Laurenson 1995).

Previous studies of sympatric competitive large carnivore species have concluded that competitively subordinate species may avoid areas preferred by dominant species even while incurring the cost of lower prey availability (Creel and Creel 1996, Durant 1998). In contrast, in this study we found that the general spatial distribution of a competitively subordinate carnivore is driven primarily by resource acquisition rather than predator avoidance. However, on an immediate scale their behaviour is driven by predator avoidance, indicating that their primary behavioural risk management with respect to lions (the dominant large predator) is reactive rather than predictive. This is the first time that the processes driving the spatial distribution of competing carnivores have been explored using a multi-scale approach. Coexistence is complex and we show that spatial resolution, temporal context and environmental complexity all need to be taken into consideration to understand the mechanisms by which competing carnivores coexist.

Appendix

Appendix 5.1 – Prey selection among large carnivores in the Okavango Delta

As prey is a renewable, it is often the principle consumable resource used to investigate the potential for exploitation competition (Linnell and Strand 2000, Murdoch et al. 2010). For carnivores that are ecologically and morphologically similar, the degree of dietary overlap is likely to be substantial (Mills and Biggs 1993). If this is the case, species searching for similar prey are likely to occupy similar habitats or hunt at similar times, increasing the encounter rate of competitors. Whilst prey selection has been quantified for cheetahs, lions and spotted hyaenas independently the overlap in prey selection has not yet been reported for areas where these three species occur sympatrically.

Here I present the data and results of both the range of species consumed by each carnivore species, thereby indicating where feeding behaviour lies on the continuum from generalist to specialist, and the degree of overlap between species to determine the likelihood of competition (Pianka 1974, Schoener 1983).

Methods

Between November 2008 and December 2009 data on prey selection by cheetah, lion and spotted hyaena were obtained through incidental sightings of kills, scavenging events and kills made during continuous follows of radio-tracked individuals. These individuals were regularly followed for a minimum of 1 hour, reducing the bias towards larger prey species which might occur if all data were based purely on incidental sightings. When a feeding event was observed, the date, time, species, sex and age of prey species were recorded. In addition, it was noted whether the feeding event involved a kill by the study species or if it was a scavenging event. Individuals seen feeding on the same carcass for consecutive days were considered as one data point. Prey selection was quantified

as the number of different prey species consumed. The range of prey (B_d) that cheetahs, lions and spotted hyaenas select for was calculated using the Levin's index (Krebs 1999):

$$B_d = \frac{\left(\frac{1}{\sum p\, i^2}\right) - 1}{n - 1}$$

Where p_i is the proportion of prey species *i* selected for by predator *p* and *n* are the number of prey species that are available. In this case *n* is taken as the sum of all the prey species consumed by cheetahs, lions and spotted hyaenas. Values close to 1 indicate that resource selection is evenly distributed amongst the available prey species (generalist) whereas values close to 0 indicate that resource selection is focused on a limited number of prey species (specialist).

The overlap in prey selection (O_d) was calculated to determine whether cheetahs, lions and spotted hyaenas utilise a common prey base. The percentage overlap of prey selected for by each pair of predators was calculated following (Krebs 1999):

$$O_d = \left[\sum_{i=1}^{n} \left(minimum\, p_{ij}\, , p_{ik}\right)\right] 100$$

Where p_{ij} is the proportion of prey species *i* selected for by predator *j* and p_{ik} is the proportion of the same prey species *i* selected for by predator *k*.

Results

Of the 42 cheetah kills recorded, impala (*Aepyceros melampus*) was the predominant prey species, accounting for 79% (n=33) of the total prey consumed (Figure 5.5). The remaining prey species consisted of other small- and medium-sized mammals such as warthog (*Phacochoerus africanus*), scrub hare (*Lepus saxatilis*) and the occasional young of larger ungulates such as kudu (*Tragelaphus strepsiceros*) and reedbuck (*Redunca arundinum*). Of the 42 kills there were 3 occasions where spotted hyaena attempted to steal the kill of a cheetah. On 2 (5.76%) of these occasions the spotted hyaena were successful.

In total, 80 independent feeding events were recorded for lion of which 75 (94%) were kills and 5 (6%) were scavenging events. Zebra (*Equus burchelli*) was the most common prey species, comprising 37.5% (n=30) of the total prey items consumed. This was followed by 17.5 % impala (n=14), 16.3% giraffe (*Giraffa camelopardalis*) (n=13) and 11.3% kudu (n=9). The 5 scavenging events included 3 elephants (*Loxodonta Africana*) that were shot by trophy hunters and 2 impala, one of which was kleptoparasitised and the other the cause of death was unknown.

For spotted hyaena 42 feeding events were recorded of which 19 % (n= 8) were own kills, 33% (n=15) were scavenging events and 42% (n= 19) were events of unknown cause. Of the 8 kills made, 50% (n=4) were of impala, 37.5% (n=3) of giraffe and 12.5% (n=1) of tsessebe (*Damaliscus lunatus*). Of the scavenging events there were two occasions where spotted hyaena stole an impala kill from cheetah. The remaining events all involved kleptoparasitism from lion (n=5), leopard (*Panthera pardus*) (n=2) and wild dog (*Lycaon pictus*) (n=2). The 4 elephants were a result of trophy hunting.

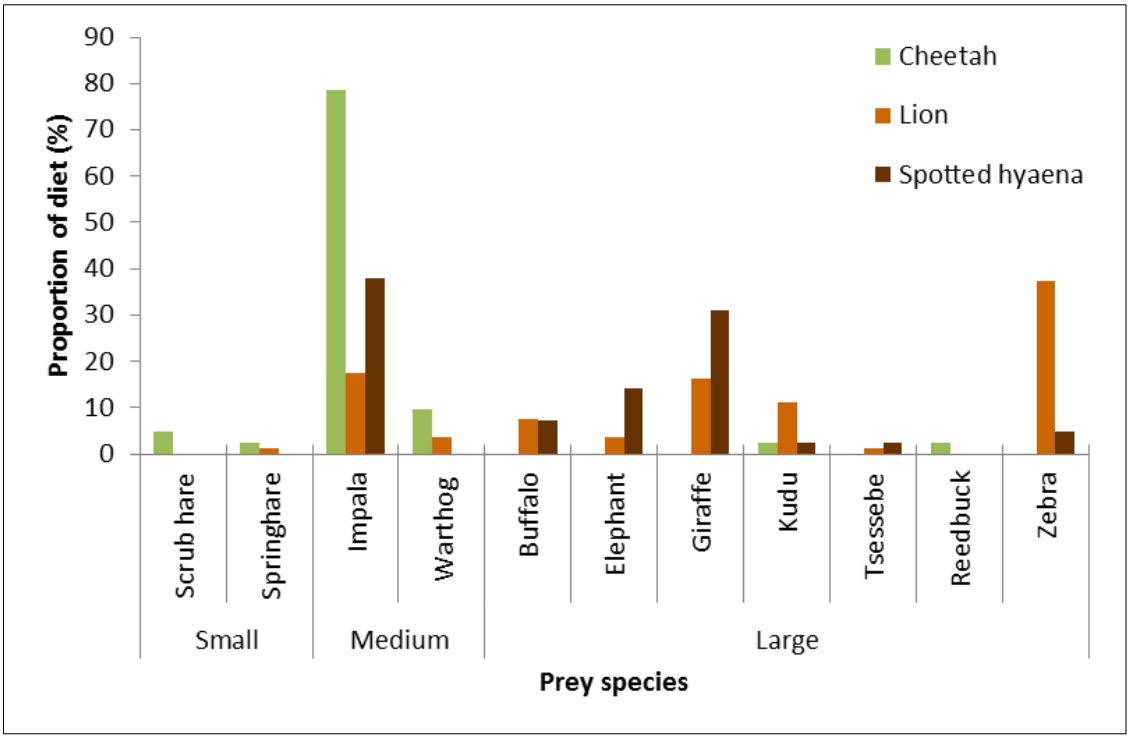


Figure 5.5: Prey selection by cheetahs (n=42), lions (n=80) and spotted hyaenas (n=42) in the Okavango Delta, northern Botswana. The prey species have been divided according to three size categories; small (<25 kg), medium (25-100 kg) and large (>100 kg). All values have been expressed as a percentage of the total number of kills observed.

The range of prey species selected for by cheetahs (B_d= 0.098) was low compared to lions (B_d= 0.446) and spotted hyaenas (B_d= 0.451) (Table 5.4). This is because prey selection by cheetahs was unevenly distributed amongst prey species, focusing on impala (Figure 5.5). The range of prey species selected for by lions and spotted hyaenas were similar, indicating that consumption was evenly distributed amongst the prey species. Prey selection by cheetahs overlapped 32.5% with lions and 38.1% with the spotted hyaenas.

Table 5.2: Prey selection range and overlap for cheetahs, lions and spotted hyaenas in the Okavango Delta, northern Botswana. The prey selection range was calculated using the Levin's index. Values close to 0 indicate a narrow selection range whereas values close to 1 indicate a broad selection range. The degree of overlap between cheetahs, lions and spotted hyaenas were calculated as the percentage for both cheetahs and lions and cheetahs and spotted hyaenas.

	Selection range	Overlap (%)
Cheetah	0.098	-
Lion	0.446	32.50
Spotted hyaena	0.451	38.10

The results clearly indicate overlap in the prey that is selected for by cheetahs, lions and spotted hyaenas, with impala being the main prey species that is simultaneously consumed by all three carnivore species. Despite the high degree of overlap, the potential for competition is likely to be low as impala, being the most abundant prey species, is not likely to be a limiting resource.

Appendix 5.2

Table 5.5: Compositional analysis (Aebischer et al. 1993) for both the 2nd and 3rd order habitat selection for cheetahs, lions and spotted hyaenas in the Okavango Delta, Botswana. A '+' indicates that habitat type in the row was more used than in the column and a '-' that the habitat type in the row was less used than in the column. When the difference was significant the signs were tripled and '0'meant that there was no difference.

		Grassland	Mixed woodland	Mopane	Riparian	Swamp
	Cheetah					
2nd order	Grassland	0	-	+++	+++	+++
	Mixed woodland	+	0	+++	+++	+++
	Mopane	---	---	0	---	+
	Riparian	---	---	+++	0	+++
	Swamp	---	---	-	---	0
3rd order	Grassland	0	+++	+++	+++	+++
	Mixed woodland	---	0	+++	+++	+++
	Mopane	---	---	0	+++	+++
	Riparian	---	---	---	0	+
	Swamp	---	---	---	-	0
	Lion					
2nd order	Grassland	0	+	+++	+++	+++
	Mixed woodland	-	0	+++	+++	+++
	Mopane	---	---	0	-	+
	Riparian	---	---	+	0	+++
	Swamp	---	---	-	---	0
3rd order	Grassland	0	-	+++	+	+++
	Mixed woodland	+	0	+++	+++	+++
	Mopane	---	---	0	-	+++
	Riparian	-	---	+	0	+++
	Swamp	---	---	---	---	0
	Spotted hyaena					
2nd order	Grassland	0	-	+	+	+++
	Mixed woodland	+	0	+	+	+++
	Mopane	-	-	0	-	+
	Riparian	-	-	+	0	+++
	Swamp	---	---	-	---	0
3rd order	Grassland	0	+	+	+	+++
	Mixed woodland	-	0	+	-	+++
	Mopane	-	-	0	-	+++
	Riparian	-	+	+	0	+++
	Swamp	---	---	---	---	0

CHAPTER 6

The ecological small print: fine-scale adaptations in relation to risk and habitat use

Abstract

Environmental heterogeneity, both in space and time, can facilitate coexistence between competing species by providing refuges. Whilst most large carnivore studies are constrained to looking at the presence and use of these refuges on a broad-scale, their relevance could vary depending on subtle differences in behaviour. We use data on resting, moving and feeding behaviour of cheetahs (*Acinonyx jubatus*) to investigate whether the likelihood of lion (*Panthera leo*) encounters, the habitat that cheetahs were in or a combination of the two differed depending on their behavioural state. In addition, we explored temporal variations in the behavioural responses in terms of time of day and moonlight intensity during the night, with light availability inversely related to the risk of encountering comparatively more nocturnal lions. Cheetah behaviour was not influenced by the presence of lions. However, the presence of lions did influence habitat use, with cheetahs selecting a high percentage of grassland when in high risk areas, possibly to increase the likelihood of detecting approaching lions. Cheetahs' habitat choice was related to their behaviour, time of day and moonlight intensity at night. Cheetahs used areas characterised by grassland when resting and mixed woodland when feeding or moving. The advantages of using mixed woodland when feeding or moving are twofold; relatively high prey abundance and concealment from predators. For all three behaviours, cheetahs used areas with more mixed woodland habitat and less grassland at midday compared to midnight. However, the habitat at midnight was dependent on the moonlight, selecting more mixed woodland as moonlight intensity increased. These results suggest that, in addition to maximising resource acquisition, differential habitat use could be key in anti-predator behaviour, effectively minimising direct interactions with competitively more dominant species. We show that by taking a fine-scale behavioural and temporal approach we gain insights into the functional role of habitat selectivity in carnivore coexistence.

Introduction

Differential patterns of habitat use and diel activity are believed to be important factors in species coexistence, giving competitively subordinate species the opportunity to seek spatial and temporal refuge from more dominant species (Chesson and Rosenzweig 1991, Durant 1998). Through differential habitat use and timing of activity, some direct effects of competition and predation can be minimised by reducing the probability of encounters (Schoener 1974a, Rosenzweig 1981). For example, risky areas – i.e. areas with a relatively high likelihood of encountering competitors and predators – may be consistently avoided, or avoided at particular times (Schoener 1974b, Kronfeld-Schor and Dayan 2003).

Whilst in some species minimising competition or predation through spatial and temporal avoidance is clear cut (e.g. Hersteinsson and Macdonald 1992), there have been several studies demonstrating that competing species can coexist despite broad-scale overlap (Paquet 1991, Karanth and Sunquist 2000, Harmsen et al. 2009). In these cases it is likely that avoidance occurs on a much finer behavioural scale. Different behaviours come with different levels of vulnerability to predation and competition and individuals might therefore alter their responses accordingly (Sweitzer and Berger 1992). Take three common, fundamental animal behaviours; resting, moving and feeding, as an example. When resting, animals may have a high chance of going undetected in addition to having time to allocate to anti-predator behaviours such as vigilance (Caro 2005). However, when animals are on the move they are more conspicuous and therefore have a higher risk of being detected, increasing chances of predation (Ebenhard 1987, Norrdahl and Korpimäki 1998). Similarly, when feeding, animals are vulnerable to predation and competition as other animals might be attracted to the food sources being exploited and because there is less time available for anti-predator behaviours (Lima and Dill 1990, Fuller and Berglund 1996, Caro 2005). Depending on these inherent differences, animals could exhibit differential space and habitat use i.e. carry out risky behaviours, such as feeding, in concealed habitat types. Thus spatio-temporal distribution and habitat use are, if considered alone, unlikely to be sufficient for a complete understanding of how animals perceive and

respond to risk and it may therefore be necessary to analyse, and discriminate between behaviours at a finer scale.

In carnivore ecology taking a fine-scale approach in understanding coexistence is still relatively rare. This is mostly due to the fact that collecting large amounts of detailed behavioural data is difficult as carnivores tend to be wide-ranging, nocturnal and elusive and generally exist in low densities. However, recent technological advances such as camera-traps and Global Positioning System (GPS) radio-collars have facilitated fine-scale studies of coexistence (e.g. Moorcroft et al. 2006, Harmsen et al. 2009). Despite this, these data are often pooled together and analysed irrespective of the time of day at which the data were collected or what the individuals in question were doing at the time (Hebblewhite and Haydon 2010). For example, camera-traps were used to investigate spatial avoidance between jaguars (*Panthera onca*) and pumas (*Puma concolor*) in Belize (Harmsen et al. 2009) and between common genets (*Genetta genetta*), red foxes (*Vulpes vulpes*) and stone martens (*Martes foina*) in Portugal (Pereira et al. 2012). Whilst these types of camera-trap studies give a unique insight into habitat use, they are generally biased towards habitats used when animals are active. Similarly, spatial data collected through GPS radio-collars provide insight into broad-scale habitat and space use but are limited by our knowledge of the animal's behaviour at the time (Hebblewhite and Haydon 2010). Studies using data from camera-traps and radio-collars often have the underlying assumption that risk avoidance strategies are identical across behaviours, despite the fact that there is evidence that this might not be the case (Sweitzer and Berger 1992, Cowlishaw 1997). This simplification of ecological process could therefore limit the insights achievable (Mysterud and Ims 1998, Beyer et al. 2010). In order to fill this gap we use data on resting, moving and feeding behaviour of cheetahs (*Acinonyx jubatus*) to investigate potential differences in response to encountering lions (*Panthera leo*), a larger and competitively dominant carnivore.

Cheetahs are negatively influenced by lions both directly through predation and indirectly through kleptoparasitism (Laurenson et al. 1995, Hunter et al. 2007a). This is mostly due to their smaller body

size and predominately solitary nature (Caro 1994). As a result their distribution, habitat use and activity patterns are believed to be mainly driven by the avoidance of larger carnivores, such as lions (Caro 1994, Hayward and Slotow 2009). Nevertheless, several studies have shown similarities in the choice of habitat types by both species (Mills and Biggs 1993, Chapter 5), and extensive spatial overlap (Bissett and Bernard 2007, Chapter 5). More recently it has also been shown that there is considerable temporal overlap between the two, mainly due to cheetahs' nocturnal activity which makes up 44% of their total diel activity budget (Chapter 2). The aim of this study is therefore to test whether fine-scale spatial and temporal behavioural adaptations are important in minimising encounters, thus facilitating coexistence between competing large carnivores. We do this by investigating the habitat composition and the likelihood of encountering lions at cheetah locations in relation to cheetah behaviour, the time of the day and the light availability at night (moonlight). We differentiated between three fundamental behavioural categories: feeding, moving and resting. The likelihood of encountering lions was quantified using GPS data for lions that were recorded parallel to the cheetah data. The time of day was used as a proxy for lion activity, with night time being risky as lions are predominantly nocturnal (Hayward and Slotow 2009, Chapter 2), whereas moonlight was used as a proxy for detectability at night. This can either be improved detectability of prey and predators by cheetahs or improved detectability of cheetahs by predators and prey. In general, we expect that cheetahs will adapt their behaviour according to their perceived risk of encountering lions, for example by carrying out risky behaviours such as feeding, in low risk areas, habitats or times. We also anticipate that cheetah behaviour will differ per habitat type depending on temporal risk and anti-predator tactics such as detectability, concealment and escape.

Methods

Study area

The study took place on the periphery of the Okavango Delta, a permanent inland delta situated in northern Botswana. The core study site (19°31'S, 23°37'E; elevation ca. 950m) encompassed an area of approximately 2 720 km^2 which included the southern part of Moremi Game Reserve and the adjacent Wildlife Management Areas (for details see McNutt 1996, McNutt and Silk 2008). The study area is part of a semi-arid ecosystem characterised by five distinct transitional habitat types; open grassland, mixed woodland dominated by Acacia *spp*. (*Acacia erioloba* and *A. tortilis*), mopane (*Colophospermum mopane*) woodland, riparian woodland and floodplains created by the extremities of the Okavango Delta (McNutt 1996). The annual rainfall is 450-600mm, falling predominantly between November and March, with a dry season between April and October (Mendelson et al. 2010).

Cheetah data

Between September 2010 and March 2011 we attached Global Positioning System (GPS) radio-collars (VECTRONIC Aerospace GmbH, Germany) to four individual cheetahs (one male and three females). The radio-collars were programmed to collect GPS fixes four times a day (00h00, 06h00, 12h00 and 18h00 local time) and recorded activity bursts at 5 minute intervals. The activity was measured by bi-axial accelerometers measuring both the lateral (y-axis) and the anterior-posterior (x-axis) movement of the collared individual. These 5 minute activity measures were translated into one of the following behavioural states: feeding, moving or resting using behavioural observations collected in the field and an algorithm based on a combined Support Vector Machine (SVM) and hidden Markov model (HMM) (see Chapter 3 for methodologies and data validation). The behaviours at the time that GPS fixes were recorded were filtered out, resulting in a geo-referenced behavioural dataset. Environmental variables were extracted for each geo-referenced behaviour.

Environmental variables

Lion risk – Both the short-term and long-term lion risks were quantified using GPS locations recorded by GPS radio-collars (VECTRONIC Aerospace GmbH, Germany) fitted on five female lions, each in five different neighbouring social groups. The radio-collars were deployed for the same six month period as the cheetah radio-collars and recorded GPS fixes eight times a day (00h00, 02h00, 04h00, 06h00, 12h00, 18h00, 20h00 and 22h00 local time). Short-term risk to cheetahs from lions was quantified by calculating the distance from each cheetah location to the nearest lion at the time that the GPS locations were recorded. The long-term lion risk was quantified by using 1000 randomly selected lion GPS locations to create a continuous raster map of the intensity of space-use which translated into the risk of encountering a lion. The risk of encountering each individual lion was calculated using 90% kernels (Börger et al. 2006) created using fixed Gaussian Kernel Density Estimate (KDE) function in the Geospatial Modelling Environment (GME) (Beyer 2012, R Development Core Team 2012). Kernel bandwidth was estimated using the Least Square Cross Validation (LSCV) method (Powell 2000, Gitzen et al. 2006). The individual maps were then summed to create a landscape of lion encounter risk. Whilst the presence of uncollared lions would weaken our hypothesis testing, we believe this influence to be minimal mainly because lions defend their territories and non-pride members are not tolerated (Schaller 1972). We had radio-collars on all known prides within the study area and pride females were seen together 78.6 ± 6.6 % (mean ± 95% CI) of the time. In addition, we only used cheetah data that fell within the 90% lion kernels, thereby minimising the edge effects where unknown lions could overlap with the collared individuals.

Habitat data – A habitat map was created based on two SPOT5 multispectral satellite images, acquired in October 2009, with a 10m spatial resolution. The images were pre-processed in ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado) using calibration factors, the atmospheric correction tool FLAASH and mosaicking. Corrected images were classified based on a Support Vector Machine model trained with nine classes using reference coordinates acquired in the

field. The overall accuracy of the final vegetation map was 72.4%. The resulting classes were merged into five final classes representing the five dominant habitat types: grassland, mixed woodland, mopane, riparian and swamp. Of these, only grassland and mixed woodland were used for further analysis as these were the two habitat types that cheetahs and lions both actively selected (Chapter 5). Using ArcGRID the percentage of each habitat type within a 200 x 200m pixel was calculated and used for further analysis creating a separate raster map for each habitat type. Grassland, which included the seasonal and ephemeral floodplains, was predominantly characterised by short grass and an absence of trees and shrubs. Mixed woodland was dominated by *Acacia spp.* with a grassy understory. The visibility, or line of sight, influences the probability of detection (Cowlishaw 1997) and was therefore measured for both habitat types using the methods laid out by Muntifering et al. (2006) (see Appendix for more details on methods). The visibility in grassland in the dry season was 156.16 ± 6.32m (mean ± 95% CI) and in the wet season 118.23 ± 10.00m (mean ± 95% CI), in mixed woodland the visibility in the dry season was 55.92 ± 3.01m (mean ± 95% CI) and 50.95 ± 2.19m (mean ± 95% CI) in the wet season.

Moonlight intensity and day vs. night - Data on moonlight intensity and day/night cycles were obtained from the United States Naval Observatory (USNO) website (http://aa.usno.navy.mil/data/). Moonlight intensity was taken as a measure of light availability at night and was defined as the proportion of the lunar disc that was illuminated. This was a continuous variable from 0 = new moon to 1 = full moon. During the year there is little variation in the day/night cycle with daylight spanning from 05h40-19h15 during the winter solstice (21st June) and from 04h30-20h20 during the summer solstice (21st December).

Statistical analysis

We tested whether habitat composition at sites selected by cheetahs was a function of their behaviour (category with three levels; feeding, mobile and resting), time of day when the GPS fixes

were taken (categorical with four levels; 00h00, 06h00, 12h00 and 18h00) and the moonlight intensity (continuous variable from 0 (new moon) to 1 (full moon)). The percentage of grassland and the percentage of mixed woodland at cheetah locations were each used as a dependent variable in a Generalized Linear Mixed Model (GLMM) with a Poisson error structure. For each of the habitat models (i.e. those models with % habitat as responses), six *a-priori* candidate models were created including each of the main effects (behaviour, time of day and moonlight intensity) and their interaction terms. Using a linear mixed model we then separately investigated whether the long-term risk and distance to the nearest lion (short-term risk) from cheetah locations differed depending on cheetah behaviour, the time of day and habitat composition (continuous variable for both the percentage of grassland and the percentage of mixed woodland). Both the long-term and short-term risk was used as response variables and log transformed to meet the assumption of normality. For both the long-term and short-term risk 10 *a-priori* candidate models were created including each of the main effects (behaviour, time of day, percentage of grassland and the percentage of mixed woodland) and their interaction terms. All models included the identity of the individual cheetahs as a random term.

Statistical analyses were performed using the statistical software R 2.14.2 (R Development Core Team 2012). The *a-priori* candidate models were ranked using Akaike Information Criterion corrected for small sample size (AICc). If one model was clearly dominant ($w_i > 0.9$) this was used, otherwise model averaging was performed to estimate the parameters (Burnham and Anderson 2002). In addition, the adjusted R^2 values were reported to indicate the proportion of the variance that was explained by each of the models. Models and model comparison statistics are presented in the Appendix. A Tukey post-hoc test was carried out if any of the categorical variables were in the top ranked models. Central tendencies are reported as mean ± 95% confidence interval (CI).

Results

In total, we had 1555 geo-referenced records of behaviour, of which 84% were resting, 12% were mobile and 4% were feeding. Cheetah behaviour differed between different habitat types (Figure 6.1). Sites where cheetahs rested contained significantly more grassland (45.96 ± 0.93 %) than did sites where cheetahs were either feeding (33.16 ± 4.88 %) or mobile (30.45 ± 2.30 %; Z=-14.36, p<0.001). However, sites where cheetahs were mobile were characterised by a significantly greater percentage of mixed woodland (41.05 ± 2.24) compared to feeding sites (36.73 ± 3.91 %; Z=-2.51, p=0.011). Mobile and feeding sites both had more mixed woodland present compared to resting sites (32.22 ± 0.73 %; Z=9.06, p<0.001; Figure 6.1).

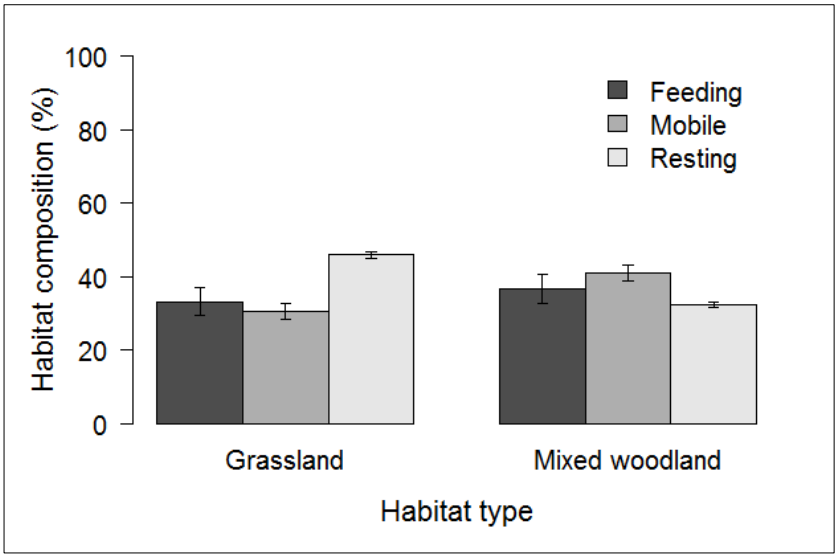


Figure 6.1: Habitat composition at feeding sites (dark grey, n=68), mobile sites (grey, =187) and resting sites (light grey, n=1300) for cheetahs in northern Botswana. Mean ± 95% CI.

For all three behaviours the habitat composition at cheetah locations differed depending on the time of day (Figure 6.2). At midnight cheetahs used areas with a higher percentage of grassland (52.4 ± 3.3 %) than those used at midday (32.4 ± 3.1 %; midday-midnight: Z=2.15, p=0.030). However, at midday they used more mixed woodland (39.2 ± 3.9 %) than at midnight (27.2 ± 2.8 %; midday-midnight: Z=-10.63, p<0.001). The habitats used at dawn and dusk were similar.

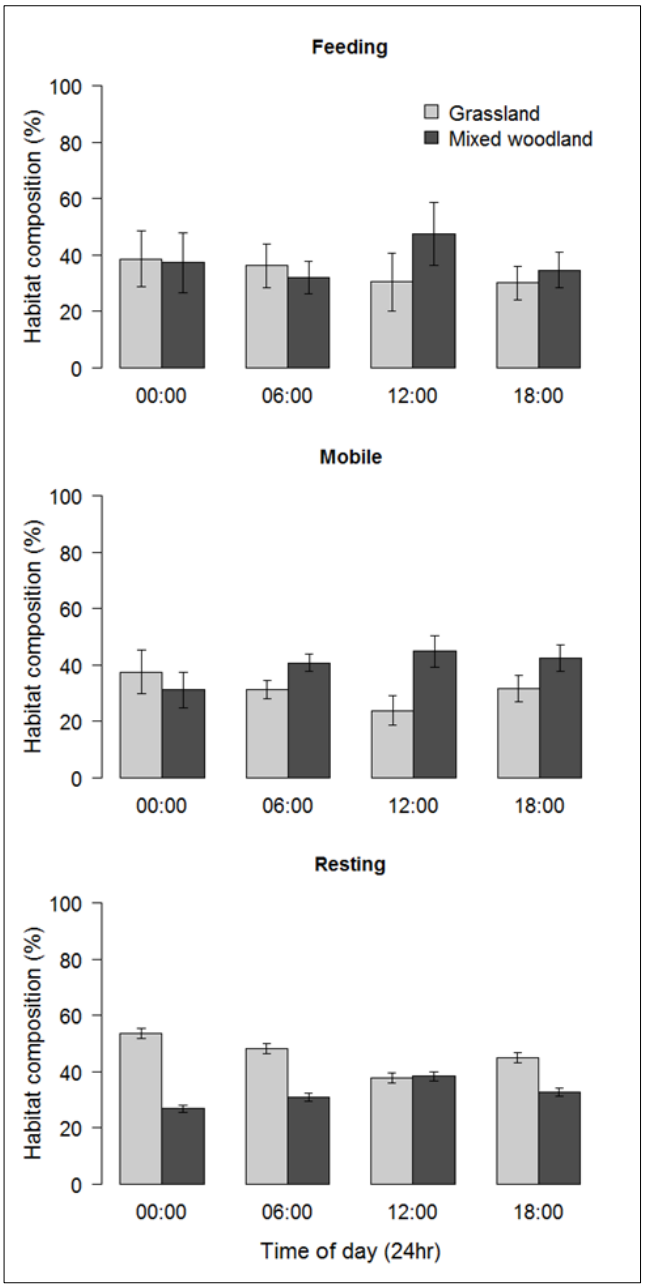


Figure 6.2: Habitat composition at cheetah locations at different times of day for three different behaviours, feeding, mobile and resting. Mean ± 95% CI.

The top ranked models (w_i > 0.9) investigating the habitat composition at cheetah locations included a three way interaction between behaviour, time of day and moon. These models explained 65% of the variation in the percentage of mixed woodland and 80% of the variation in the percentage of grassland at cheetah locations (Appendix 6.1). As expected, moonlight influenced habitat composition only at the midnight points and only when cheetahs were feeding or moving (Figure

6.3). At sites where feeding occurred and those where cheetahs were mobile, the amount of mixed woodland increased with increased moonlight intensity (feeding$_{midnight}$: Z=12.44, p<0.001; mobile$_{midnight}$: Z=5.54, p<0.001) whereas the amount of grassland available at feeding sites decreased with increased moonlight intensity (Z=-9.21, p<0.001). At feeding sites, there was about 10% mixed woodland present but this increased to almost 70% during full moon. Whilst not as dramatic a change, the amount of mixed woodland similarly increased from new moon to full moon at mobile sites (Figure 6.3). Whilst the amount of grassland decreased from about 68% at new moon to 25% at full moon for feeding sites, this did not differ significantly when cheetahs were moving. Neither the percentage of mixed woodland nor that of grassland varied with increased moonlight intensity for resting sites.

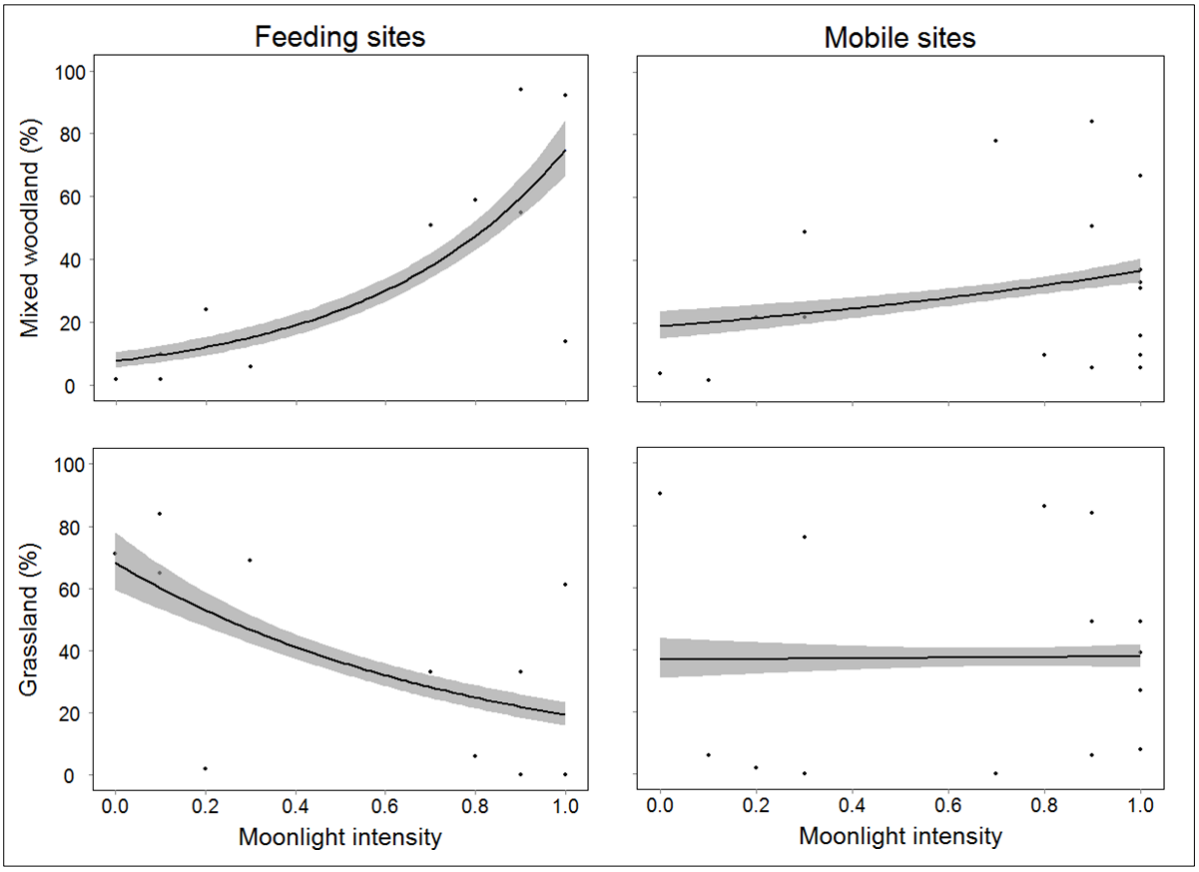


Figure 6.3: Relationship between moonlight intensity and percentage of mixed woodland (top row) and grassland (bottom row) that was available at midnight locations where cheetahs were feeding (left column) and mobile (right column). The moonlight intensity ranges from 0 (new moon) to 1 (full moon). Results are from a generalised linear model with a Poisson error structure. The grey areas represent the 95% CI for the fitted line. As moonlight intensity did not influence the habitat composition at resting sites, these figures are not shown.

If cheetahs were to actively avoid encounters with lions we would expect that they would select for low risk areas at night, when lions are active and that risky behaviours, such as feeding, would be less likely to occur in areas regularly used by lions or when lions were in close proximity. The results, however, show that neither the time of day, nor the cheetahs' behaviour influenced whether they were more likely to be found in low or high risk areas (Appendix 6.2). The long-term likelihood of encountering lions was, however, positively related to the percentage of grassland that was available at cheetah locations (t=18.06, p<0.001; Figure 6.4). In other words, when cheetahs were in high risk areas they tended to be in places at which a higher percentage of grassland was available than when they were in low risk areas. The amount of mixed woodland in the vicinity of the cheetahs was not influenced by long-term likelihood of encountering lions there (Z=1.544, p=0.122).

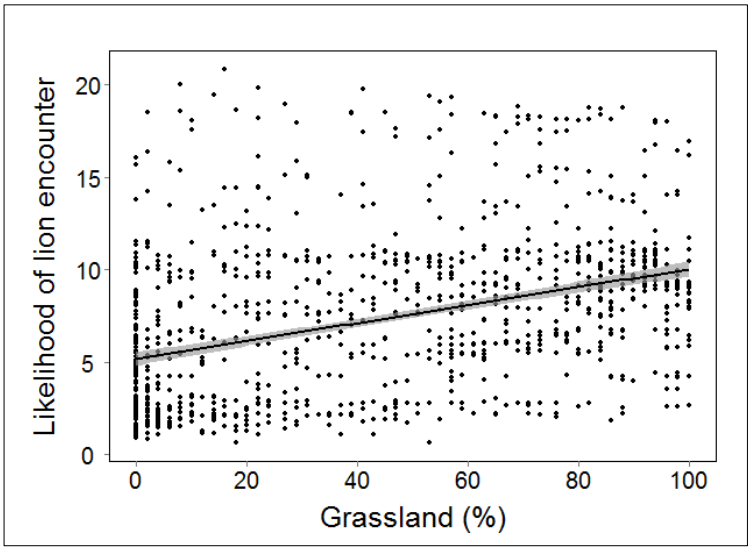


Figure 6.4: Relationship between the level of long-term lion risk and the amount of grassland present within a 200 x 200m pixel at cheetah locations. The fitted line (solid line) is drawn with its 95% confidence interval (shaded area).

Discussion

In short, our results show that cheetah behaviour was associated with habitat type but not with the risk (either short- or long-term) of encountering lions. However, the type of habitat that cheetahs

used did vary depending on the time of day and at night this was influenced by the amount of moonlight available.

Lion risk

Contrary to our expectations, cheetah behaviour could not be predicted by either the short- or long-term risk of encountering lions nor did cheetahs select for less risky areas at night, when lions were active. This is at odds with the findings of studies of some other species that reported a decrease or change in activity in response to predator cues. For example, Norway rats (*Rattus norvegicus*) altered the timing of foraging in response to olfactory cues from foxes (*Vulpes vulpes*) (Fenn and Macdonald 1995). Similarly, cheetahs in the Serengeti National Park, Tanzania, ceased hunting in response to lion roars during playback experiments (Durant 2000a). Based on this we expected, all else being equal, that risky behaviours such as feeding would be more likely to occur in areas that are rarely used by lions or further away from lions. Similarly, we expected that cheetahs would use low risk areas at night, and high risk areas (which may coincide with those of high prey abundance) during the day when lions are inactive. The fact that this was not the case suggests that, in this study area, cheetahs do not adjust their broad-scale behaviour according to the potential risk of encountering lions. However, it is possible that the proximity to lions affected cheetah behaviour on a much finer behavioural scale by, for example, becoming more restless or increasing their vigilance when they perceived that there was a risk of encountering lions. In addition, the cheetahs' behaviour at the time of the GPS location (t1) could be a response to lion behaviour at the time before (t-1). However, with a spatial resolution of every six hours these behavioural changes would not be detected. With the development of technology allowing for the collection of higher resolution data a dynamic, rather than a static, approach will give a better insight into the action and reaction of interacting species (Moorcroft et al. 2006). Whilst it is possible that the presence of other large carnivores, such as the spotted hyaena (*Crocuta crocuta*), influenced cheetah behaviour (Caro 1994, Hunter et al. 2007a), we believe that this would not greatly affect our results, mainly because cheetahs have a

more pronounced response to lions than to spotted hyaenas (Durant 2000a, Chapter 5). The results also suggest that the potential threat of lions can be minimised through the use of habitats, such as mixed woodland, that provide concealment.

Habitat-use

The habitat type that cheetahs used was dependent on their behavioural state: using more mixed woodland when feeding and moving compared to when they were resting. Habitat use is seen as a trade-off between maximising resources whilst minimising risky encounters (Schoener 1974a). In addition the choice of habitat, both for hunting and anti-predator behaviour, is a balance between visibility and concealment (Camp et al. 2012). Based on this we believe that the advantages of using mixed woodland while moving and feeding are two-fold. Firstly, cheetahs' preferred prey, impala (*Aepyceros melampus*) (Purchase and du Toit 2000, Hayward et al. 2006), predominantly select for mixed woodland (Chapter 5). Secondly, despite the fact that mixed woodland is the preferred habitat type for lions (Chapter 5), the availability of cover gives the added advantage of going undetected by lions and other scavengers such as spotted hyaenas (*Crocuta crocuta*) and vultures, who are attracted to cheetah kills (Hunter et al. 2007a). In other words, the cover provided by mixed woodland could reduce the risk posed by lions to a level that enables cheetahs to use this habitat profitably. Indeed, habitat structures can alter the detection probability which in turn influences anti-predator behaviours (Caro 2005) such as grouping (Fortin et al. 2009), decreased activity (Sweitzer and Berger 1992), escape tactics (Wirsing et al. 2007) and vigilance (Repasky 1996, Altendorf et al. 2001). For example, a study on bison (*Bison bison*) demonstrated that bison in small groups, which are more at risk of predation, were more likely to select for dense vegetation cover than those in large groups (Fortin et al. 2009). Similarly, with carnivores it has been documented that vegetation cover aids concealment and thus reduces kleptoparasitism (Paulson 1985).

When resting, cheetahs selected for a high percentage of grassland, the habitat type with the highest visibility (Appendix), at times when lions were most active (06h00, 18h00 and 00h00) (Hayward and

Slotow 2009). Several studies have observed that prey species select for open habitat types suggesting that there are greater benefits associated with increased detection of approaching predators rather than increased concealment (Jarman and Jarman 1973, Creel et al. 2005, Valeix et al. 2009b). When cheetahs are resting they can spend more time being vigilant. Therefore, by using grassland, cheetahs can detect both prey and approaching dangers. The use of open grassland habitat types when resting has likewise been observed in the African wild dog (*Lycaon pictus*), a competitively subordinate predator under similar predation and competition pressure from lions (Fuller and Kat 1990).

Time of day and moonlight intensity

Habitat use by cheetahs was also influenced by the time of day and the moonlight intensity at night. For all three behavioural categories, cheetahs selected for a higher percentage of mixed woodland at midday compared to midnight. The use of more mixed woodland at midday is likely to be related to the need for shade as this is the hottest period of the day. At midnight however, cheetahs selected for more grassland but this was dependent on the intensity of the moonlight. When cheetahs were feeding and mobile at night, the amount of mixed woodland increased with increasing moonlight intensity. During new moon cheetahs are less active, and in addition to the cover of darkness, are less conspicuous to lions. However, as the amount of moonlight at night increases, cheetahs become more active (Chapters 2 and 4) and might therefore select for increased cover to minimise detection, not just from lions, but other predators such as spotted hyaenas. These findings are in line with several studies on rodents demonstrating shifts in habitat-use with changes in moonlight intensity with individuals moving away from open areas during periods of full moon to avoid predation (Daly et al. 1992, Dickman 1992, Kotler et al. 2010). The increased use of mixed woodland during periods of full moon could also be related to the distribution of prey. Whilst impala generally shift to more open habitat types with increased moonlight intensity (Jarman and Jarman 1973), possibly to

increase detection of approaching predators, cheetahs would have a higher probability of catching those that remain in mixed woodland.

Conclusion

In summary, cheetah behaviour on a broad-scale did not differ depending on the risk of encountering lions. Whilst we cannot exclude the fact that other factors might influence cheetahs' decisions, and that these are likely to vary between individuals, our results suggest that differential habitat use by cheetahs is driven by a combination of resource acquisition and anti-predator behaviour.

With the help of technology we have given a detailed insight into the behaviour and ecology of a large carnivore which hitherto has been difficult to come by. Whilst even this study might not be fine-scale enough to understand fully the mechanisms by which carnivores coexist with each other, it does highlight the importance of choosing the appropriate behavioural resolution. With the rapid advances in technology we expect that even finer-scale adaptations will be uncovered, allowing us to burrow yet more deeply into the detail of animal behaviour of elusive mammals in the wild.

Appendix

Visibility survey

Data collection was based on the method outlined by Muntifering et al. (2006). We defined visibility as the distance at which a marker (60 x 60 cm piece of brown cardboard attached to a pole) was no longer visible to an observer crouched at 1 m above ground. For each habitat type we calculated the visibility at 20 locations that were randomly allocated using Home Range Tools (HRT) in ArcGIS 9.2 (Rodgers et al. 2007). At each location we placed the marker in the ground. The observer then walked away from the marker until it was no longer visible. The distance from the marker was measured using a handheld GPS device (Garmin eTrex HC; Garmin, Olathe, Kansas, USA) with an accuracy of ± 4 m. This procedure was repeated in the four cardinal directions and the four values were then averaged. For safety reasons, visibilities beyond 200 meters were not measured. Due to seasonal variation in the vegetation, the visibility was sampled at the end of each season.

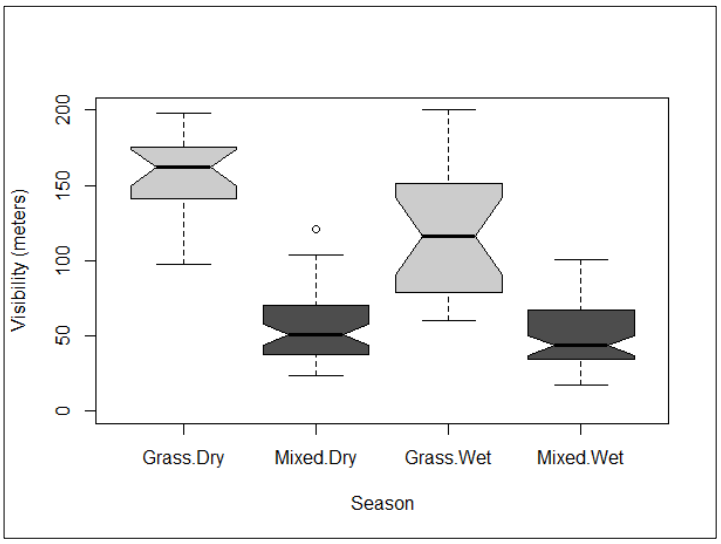


Figure 6.5: Boxplot with the mean visibility in grassland and mixed woodland habitat types in both the dry and the wet season.

Figure 6.6: A photograph of an area in the Okavango delta, Botswana dominated by grassland.

Figure 6.7: A photograph of an area in the Okavango delta, Botswana dominated by mixed woodland with a grassy understorey.

Appendix 6.1: Summary of model selection statistics for the Generalised Linear Mixed Models (GLMMs) analysing the percentage of different habitat types (mixed woodland and grassland|) at cheetah locations in relation to behaviour (behav = feeding, mobile or resting), time of day (TOD = day or night) and moonlight intensity (continuous where 0 = no moon and 1 = full moon). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a random effect.

Response variable	Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
Mixed woodland (%)	1	behav * TOD * moon	25	-17004.1	34059	0.00	1.00	0.65
	2	behav + TOD * moon	11	-17203.1	34428	369.4	0.00	0.56
	3	behav + TOD	7	-17228.6	34471	412.2	0.00	0.54
	4	TOD	5	-17501.4	35013	953.8	0.00	0.35
	5	behav	4	-17545.7	35099	1040.4	0.00	0.31
	6	moon	3	-17833.9	35674	1614.7	0.00	0.01
Grassland (%)	1	behav * TOD * moon	25	-22742.5	45536	0.00	1.00	0.80
	2	behav + TOD * moon	11	-22889.5	45801	265.5	0.00	0.77
	3	behav + TOD	7	-22910.9	45836	300.0	0.00	0.76
	4	behav	4	-23326.3	46661	1124.9	0.00	0.59
	5	TOD	5	-23609.9	47230	1694.0	0.00	0.42
	6	moon	3	-24019.9	48046	2510.0	0.00	0.01

Appendix 6.2: Summary of model selection statistics for the linear mixed models analysing the likelihood of encountering lions (long-term lion risk) at cheetah locations in relation to behaviour (behav = feeding, mobile or resting), time of day (TOD = day or night), the percentage of grassland (% grass) and the percentage of mixed woodland (% mw). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a random effect.

Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
1	% grass + % mw	5	-848.3	1707	0.0	0.99	0.27
2	behav + % grass + % mw	7	-851.5	1717	10.6	0.01	0.26
3	behav + TOD + % grass + % mw	10	-856.8	1734	27.2	0.00	0.25
4	behav* TOD + % grass + % mw	16	-856.3	1745	38.5	0.00	0.25
5	behav * % grass + behav * % mw + TOD	14	-876.7	1782	75.3	0.00	0.21
6	behav + TOD * % grass + TOD * % mw	16	-883.8	1800	93.5	0.00	0.20
7	behav	5	-979.1	1968	261.6	0.00	0.00
8	TOD	6	-983.3	1979	272.1	0.00	0.00
9	behav + TOD	8	-984.8	1986	279.1	0.00	0.00
10	behav * TOD	14	-984.2	1997	290.3	0.00	0.00

Appendix 6.3: Summary of model selection statistics for the linear mixed models analysing the distance to the nearest lions (a proxy for immediate lion risk) from cheetah locations in relation to behaviour (behav = feeding, mobile or resting), time of day (TOD = day or night), the percentage of grassland (% grass) and the percentage of mixed woodland (% mw). Models were ranked according to Akaike weights (*w*j) based on the Akaike Information Criterion for small samples (AICc). Included are the number of parameters (K), the log likelihood, the AICc differences (Δ_i) and the adjusted R^2 values. The identity of the individual cheetahs was entered as a random effect.

Rank	Model	K	log likelihood	AICc	Δ_i	w_i	Adj. R^2
1	% grass + % mw	5	-1061.3	2133	0.00	0.99	0.08
2	behav + % grass + % mw	7	-1064.1	2142	9.7	0.01	0.07
3	behav + TOD + % grass + % mw	10	-1069.2	2159	26.0	0.00	0.06
4	behav* TOD + % grass + % mw	16	-1069.9	2172	39.7	0.00	0.06
5	behav * % grass + behav * % mw + TOD	14	-1087.3	2203	70.3	0.00	0.02
6	behav	5	-1100.2	2211	77.9	0.00	0.00
7	TOD	6	-1103.1	2218	85.7	0.00	0.00
8	behav + TOD	8	-1105.5	2227	94.5	0.00	0.00
9	behav + TOD * % grass + TOD * % mw	16	-1097.9	2228	95.8	0.00	0.00
10	behav * TOD	14	-1106.3	2241	108.4	0.00	0.00

CHAPTER 7

General discussion

Synthesis

Interactions between species, both in terms of predation and competition, are topics of increasing interest as they not only affect the behaviour and ecology of the species in question, but could have effects further down the trophic cascade (Fortin et al. 2005). Whilst a large number of studies have investigated the behavioural and ecological effects of interactions between intraguild species of small mammals or in predator-prey systems (Kotler et al. 1993, Caro 2005, Creel et al. 2005, Valeix et al. 2009b), comparatively little research has focussed on intraguild large carnivore systems where members of the guild can be affected by both predation and competition simultaneously. This paucity of knowledge is partially due to the difficulties associated with simultaneous data collection on multiple species of often elusive and nocturnal carnivores that generally occur at low densities.

In this study I used a combination of advanced technologies and direct field observations to provide deeper insights into large carnivore coexistence through detailed analysis of activity, behaviour and habitat use in space and time. More specifically I investigated the ecological and behavioural mechanisms that cheetahs (*Acinonyx jubatus*), a competitively subordinate species, adopt to minimise negative interactions with more dominant lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). The results presented in this thesis are consistent with experiments conducted on species of small mammals (e.g. Kotler et al. 2010), providing an important insight into the mechanisms of coexistence and a solid foundation for future research in this area. Chapters 2, 4 and 5 focused on broad-scale resource partitioning and overlap to identify dimensions within the cheetahs' niche where avoidance and interference competition could potentially occur. Chapter 6 explored the fine-scale ecological and behavioural mechanisms by which cheetahs could minimise direct interactions with lions and spotted hyaenas. In this chapter I differentiated between three fundamental behaviours: feeding, moving and resting, for a spatially explicit understanding of the patterns of space and habitat use. Overall, the results of this study demonstrate that cheetahs were more plastic in their behaviour than was previously thought. Within this study area, there was no

well-defined resource partitioning, both in space and time, with lions and spotted hyaenas. Rather, on a broad-scale, cheetah behaviour seemed to be predominantly influenced by the distribution of their primary prey. However, on a finer scale their spatial distribution was influenced by the immediacy of encounter risk and on the potential vulnerability of the cheetah. For example, cheetahs were found to use dense, rather than open, habitat types when temporal risk increased (i.e. when moonlight intensity at night increased, increasing the likelihood of detection) and for riskier behaviours such as feeding and moving when cheetahs are more conspicuous to lions and spotted hyaenas. The fact that cheetah behaviour on a broad-scale is driven by prey distribution rather than predator avoidance suggests that, generally, cheetahs are not forced to use sub-optimal habitat types or hunt at sub-optimal times.

These results are in contrast to those found in the Serengeti National Park, Tanzania. There cheetahs avoided prey-rich areas that were intensively used by lions and spotted hyaenas (Durant 1998) and in addition to moving away from potential threats, they changed their behaviour when they perceived lions and spotted hyaenas to be in close proximity (Durant 2000a). There are several differences between the Serengeti and the Okavango Delta including habitat structure and relative carnivore densities. The Serengeti is a homogenous ecosystem dominated by large open plains, while the Okavango Delta is comparatively heterogeneous and the range of available habitat types differ in their structural complexity. Our results therefore suggest that habitat heterogeneity is an important component in coexistence as cheetahs can overcome the potential costs of competitive interactions with lions and spotted hyaenas through differential habitat-use. The importance of patterns of habitat use in reducing interactions between species, and thus promoting coexistence, has been well established in both marine and terrestrial ecosystems (Schoener 1974a, Hanski 1995, Heithaus and Dill 2006). For cheetahs, the importance of habitat in avoiding lions and spotted hyaenas has been implied, but this study represents the first focal analysis of space and habitat use by cheetahs with comparable contemporaneous data on the other predators. The fact that cheetahs

seem to have different avoidance strategies depending on the structural complexity of the ecosystem could have important conservation implications, as discussed below.

Other factors influencing coexistence

In addition to relatively proximate adaptive behaviours, there are more ultimate adaptive variables and life history characteristics, such as reproductive rates and comparatively high hunting success, that could further contribute to coexistence (Krebs and Davies 1997). High juvenile mortality, characteristic of cheetahs, could be compensated by relatively high reproductive rates. On average, female cheetahs give birth to their first litter at 2.4 years of age, have an inter-birth interval of 20.1 months (Kelly et al. 1998) with litter sizes range between 1-6 cubs (Caro 1994, Macdonald 2001). However, only about 5% of cheetah cubs survive (Laurenson 1995) and therefore their reproduction success is unlikely to put them at an advantage over lions and spotted hyaenas. Lionesses have their first litter at 3-4 years of age and litter sizes range between 1-4 cubs, of which approximately 27% die as a result of infanticide (Pusey and Packer 1994, Macdonald 2001) while spotted hyaenas have their first litter at 2-3 years and give birth to 1-2 cubs, of which only one will usually survive (Kruuk 1972, Macdonald 2001).

Furthermore, theoretical models indicate species can only coexist when the less dominant species is more efficient at securing resources than a more dominant species (Polis and Holt 1992, Revilla 2002). Whilst this has been suggested to be the case for cheetahs (Purchase 2004), evidence from several field studies do not support this suggestion. Hunting success for cheetahs was found to range from 30-40% (Caro 1994, Mills et al. 2004, Hilborn et al. 2012), consistent with the 30% hunting success by lions in Kruger National Park, South Africa (Funston et al. 2001b). Spotted hyaenas have also been observed to have similar rates of hunting success (30.5%) in the Masai Mara, Kenya (Holekamp et al. 1997), with comparable findings reported in other study areas (Kruuk 1972, Mills 1990).

This suggests that coexistence might be facilitated more through behavioural adaptations rather than through higher reproductive rates or hunting success. However, whilst the general results show that fine-scale behavioural mechanisms may be more important than broad-scale resource partitioning, I do not exclude the possibility that there may be other behavioural adaptations, beyond the scope of this thesis, that could facilitate coexistence. As mentioned in the discussion of Chapter 6, variance in anti-predator behaviours, such as vigilance, could influence the likelihood and frequency of interspecies encounters. For example, Hunter et al. (2007b) showed that cheetahs adapted their vigilance behaviour in accordance to what was perceived as 'risky' situations.

Interference competition

The rates of kleptoparasitism and cub predation during the study period were lower than those found in the Serengeti. During this study 5.35% of the 56 observed cheetah kills were kleptoparasitised by spotted hyaenas but none by lions (see Appendix 5.1). This is lower than the total of 12.9% of the kills that were stolen in Serengeti National Park, Tanzania (Hunter et al. 2007b). In addition, 4 of the 21 cubs born survived to independence, a higher survival statistic than in the Serengeti where only about 5% of cheetah cubs survived (Laurenson 1995). In the Serengeti, predation was reported to account for 73% of cub deaths with 78% of these predation events attributed to lions (Laurenson 1994). However, based on field observations of mothers with dependent cubs none of the cub mortalities in the current study could be directly linked to predation by either lions or spotted hyaenas.

The frequency of direct interactions is partially correlated to the relative density of predators. The low occurrences of kleptoparasitism and predation in this study could therefore be confounded by the fact that the densities of lions and spotted hyaenas in the Okavango Delta are lower than those in the Serengeti. We however found that this was not the case. Using playback experiments it was estimated that lions occurred at an average density of 16.43 adults per 100 km^2 but this varied with

habitat type, reaching 34.6 adults per 100 km^2 in the more open habitat types (G. Cozzi, unpublished data. This was higher than a lion density of 11 adults per 100 km^2 estimated in the Serengeti (Creel and Creel 1996). However, for spotted hyaenas, the average density in Okavango Delta was 15.4 adults per 100 km^2 (G. Cozzi, unpublished data), considerably lower than the average density of 32 adults per 100 km^2 found in the Serengeti (Creel and Creel 1996). A full count of the cheetah population using camera traps and photographs provided by tourists estimated the cheetah density to be 0.6 adults per 100 km^2 (F. Broekhuis, unpublished data), whilst the cheetah in the Serengeti has been estimated to be around 0.8-1.0 adults per 100 km^2 (Caro 1994).

The comparatively high lion density in the Okavango Delta suggests that interactions with lions in the present study are low not because of reduced densities but because the behavioural strategies that cheetahs have adopted are effective in minimising interactions. For example, by feeding in dense, rather than open habitat types, the chance of falling victim to kleptoparasitism is reduced (Paulson 1985, Hunter et al. 2007a). The importance of the availability and accessibility of competition refuges in minimising negative encounters was similarly observed in a comparative study of foxes (*Vulpes* spp.) and coyotes (*Canis latrans*). In Canada, swift foxes (*V. velox*) had fewer refuges to avoid coyotes and thus their survival rate was lower than in Mexico where there was a higher availability of refuges (Moehrenschlager et al. 2007).

Exploitation competition

Indirect competition over resources tends to be strongest when there is a large degree of overlap and when the common resource is limited (Pianka 1974, Wootton 1994, Keddy 2001). Indirect competition over resources is however difficult to quantify, especially without experimental manipulations (Schoener 1983). However, I believe that competition over food resources in this ecosystem is minimal, as cheetahs, lions and spotted hyaenas differed in the range of prey species that they selected for (see Appendix 5.1, page 95) and because the Okavango Delta has a relatively

high ungulate biomass (Fynn and Bonyongo 2011). Even though, cheetahs, lions and spotted hyaenas did all, to some degree, select for impala, this is also the most abundant prey (Chapter 5), and therefore unlikely to be a limiting factor. There are some seasonal fluctuations in prey availability, with impala abundance increasing dramatically in the wet season when females give birth and zebra and wildebeest (*Connochaetes taurinus*) abundances increasing in the dry season when they migrate to the Okavango Delta (Bartlam-Brooks et al. 2011). However, these events occur asynchronously and therefore the overall seasonal biomass is fairly constant and it is unlikely to influence exploitation competition.

Not all predators are equal risk

The impact of encountering predators can vary across predator species (Morosinotto et al. 2010, Thaker et al. 2011), and cheetahs showed a greater response to the risk of encountering lions than they did to spotted hyaenas. This differential response could be because lions and spotted hyaenas differ in both their ecology and the threats they pose. Whereas lions and cheetahs selected for similar resources, spotted hyaena habitat selection was less distinct. The greater ecological overlap that cheetahs have with lions implies a greater chance of negative interactions between these two species. In addition, encounters with lions are more likely to include the possibility of fatal consequences and therefore (by definition) represents greater risk than encounters with spotted hyaenas. In other studies, lions were responsible for the majority of fatalities from predation, whereas the costs of interactions with spotted hyaenas were typically characterised by kleptoparasitism (Laurenson 1995, Hunter et al. 2007a).

Whilst the results suggest that cheetahs were more affected by lions than by spotted hyaenas, the risks posed by spotted hyaenas were more difficult to quantify. Unlike lions, spotted hyaenas live in complex, hierarchical fission-fusion systems (Kruuk 1972). Social groups can be as large as 80 individuals, but unless there is a large carcass, spotted hyaenas generally occur alone or in smaller

sub-groups. This means that by deploying collars on one or two individuals, there is no data on the whereabouts of the other clan members. This is in contrast to lions where radio-collars were fitted on all known prides within the study area and pride females were seen together 78.6 ± 6.6 % (mean ± 95% CI) of the time. In addition, spotted hyaena social groups have a strict hierarchical structure and an individual's position within that hierarchy determines its accessibility to resources (Kruuk 1972, Mills 1990). This means that space use and activity patterns may vary significantly between individuals depending on their sex and/or status (Boydston et al. 2003, Kolowski et al. 2007). Because of this, spotted hyaenas might be less predictable in their behaviour compared to lions. Despite this, the results correspond with those of Durant (2000a) who found that cheetahs were more affected by playbacks of lion calls than they were by those of spotted hyaenas. Overall, the results demonstrate that cheetah behaviour is not influenced by long-term risk and that behavioural adaptations, like feeding in denser habitat types, could benefit cheetahs regardless of the predator species.

Individual differences

It has been observed that within species, choices of space and habitat use can differ depending on the age, sex and reproductive status of an individual (Thomas and Taylor 1990, Spong 2002, Yamaguchi et al. 2003, Pettorelli et al. 2009). In cheetahs, for example, habitat use can vary depending on the social grouping and the sex of an individual (Marker 2002, Broomhall et al. 2003, Bissett and Bernard 2007). In the Eastern Cape, South Africa, male cheetahs used open habitats compared to female cheetahs, which had a greater affinity for thicket vegetation. As there were no differences in hunting success between the two habitat types it was hypothesised that thicket vegetation was used to minimise encounters with other predators (Bissett and Bernard 2007). However, a study of cheetahs in the Serengeti found that habitat use did not differ with sex but rather depended on the age and reproductive status of females (Pettorelli et al. 2009).

In general, male cheetahs might be less sensitive than females to encounters with lions as one study observed overlap both in space and time between a coalition of males and a pride of lions (Bissett and Bernard 2007). Female cheetahs, on the other hand, tend to avoid lions, but once again the response to risk varied depending on the age and reproductive status of the females (Durant 2000b, Bissett and Bernard 2007). These sex differences could stem from the slight sexual dimorphism (males are slightly larger than females – see Chapter 1, Table 1.1) and that males sometimes form coalitions whereas females are usually solitary, unless accompanied by dependent cubs (Caro 1994). Sex differences in response to risk have been observed in other species such as the Eurasian lynx (*Lynx lynx*) where females, especially those with cubs, were more likely to avoid human activity compared to males (Bunnefeld et al. 2006). Unfortunately, the differences between male and female cheetah responses to encounters with lions and spotted hyaenas could not be tested due to the small sample size. However, this does not detract from the overall observation as there is no evidence that the inherent behavioural mechanisms adopted by cheetahs to minimise risky encounters vary between the sexes, although they may be more pronounced for females.

Conservation implications

Although the focus of this thesis was the coexistence between large carnivores, it is undeniable that humans are as much a component in coexistence and community structure as any other species (Woodroffe et al. 2005). Whilst in this study the human impact was minimal, humans can exert similar pressures on carnivores, forcing species to adjust their behaviour both in space and time. For example, African wild dogs (*Lycaon pictus*) have been shown to shift their activity patterns (Rasmussen and Macdonald 2012) while lynx and lions have been shown to adapt their use of space and habitat (Bunnefeld et al. 2006, Valeix et al. 2012) in the presence of humans. These behavioural responses, in combination with natural ones, could shift the dynamics of a community even more.

Adding humans to the equation is therefore essential in gaining a fuller understanding of ecosystem functions.

In addition, taking a multi-species approach in understanding the mechanisms by which sympatric carnivore species can coexist is important when actively managing populations. For example, protected areas and reserves are often selected on the merit of diversity and density, however, when species interactions are considered it is possible that, above a certain threshold, these two criteria cannot persist simultaneously (Travaini et al. 1997). Furthermore, conservation planning is often based on species distribution and habitat suitability inferred from studies that have investigated broad-scale habitat selection (Araújo and Williams 2000). However, as shown in this study, it is necessary to consider behaviours on a finer scale as not all behaviours have the same habitat requirements or occur at the same frequency. In Chapter 5 the results showed that, within their respective home-ranges, cheetahs predominantly selected for grassland habitat types. However in Chapter 6 it becomes apparent that this result could be biased by the fact that grassland is predominantly used during resting behaviour, which makes up more than 80% of the cheetahs daily behavioural budget (Chapter 4). There is therefore a possibility that habitat types that are less frequently used, but are nonetheless just as important, might not be valued appropriately.

Whilst a specific set of behavioural adaptations can facilitate the coexistence between species in one scenario, this could change with changes in the environment through processes such as human-induced habitat loss (Kareiva 1987, Cantrell et al. 1998, Fagan et al. 1999). Changes in habitat composition through fragmentation or bush encroachment could negatively influence the impact of interactions as it can change the intensity of interactions between species and can alter the efficiency of habitat-based avoidance behaviours (Dickman 1996). Enhanced predation as a result of habitat fragmentation has been observed amongst a variety of species (Andren 1995, Evans 2004) as animals are forced into ever-smaller areas, increasing their absolute densities (number of individuals per unit area) and their exposure to edge effects (Woodroffe and Ginsberg 1998, Fagan et al. 1999).

The consequences are that either negative interactions between species increase, or that the subordinate competitors seek competitive refuges outside protected areas (van der Meer et al. 2011, Cozzi et al. 2013) where they could come into conflict with humans (Woodroffe and Ginsberg 1998). Carnivores are thought to be particularly sensitive to these changes mainly due to their extensive ranging behaviour, low numbers and direct persecution by humans (Woodroffe and Ginsberg 1998). In addition, changes in the dynamics between species could have effects further down the trophic cascade (Crooks and Soule 1999, Fortin et al. 2005).

If complex habitat structures minimise direct interactions, the consequences of fragmentation could be more severe in open areas. In the case of cheetahs their avoidance tactics in heterogeneous environments seems to be through differential habitat-use whereas in open ecosystems it is by avoiding areas that are intensively used by lions and spotted hyaenas (Durant 1998). These differences in space use and predator avoidance should be taken into consideration when developing conservation strategies.

Future research

During the study there were several problems associated with the malfunctioning of radio-collars. Because of this I could not obtain continuous data for all individuals at the same time for the entire duration of the study. I therefore had to use different subsets of data for the different chapters. For example, I did not use any data on spotted hyaenas in Chapter 6 as the dataset was not complete for the period for which I had the behavioural data for cheetahs. In addition, data collection was limited by the battery life of the radio-collars which meant that if I wanted a year's worth of data on cheetahs, GPS locations could only be recorded four times a day. Unfortunately, the average lifetime of the collars deployed during this study were lower than the worst case scenario specified by the manufacturer (Table 7.1).

Table 7.1: A summary of the GPS Plus radio-collars (VECTRONIC Aerospace GmbH, Germany) that were used in this study, including the expected lifetime.

Species	Battery type and number	Weight (grams)	Fixes per day	Main battery lifetime (days)			
				Worst case	Average case	Best case	This study (average)
Cheetah	C (x1)	300	4	479	549	575	295
Lion/ spotted hyaena	D (x2)	650	8	877	1370	1914	320

Despite these limitations I managed to collate a unique dataset of three sympatric large carnivore species simultaneously. The data collected from the collars give a unique insight into the ecology and behaviour of large carnivores, in particular the unexpected nocturnal activity of cheetahs, which has not been investigated and quantified before. As technology develops, similar questions will be able to be answered on a much finer scale.

By taking a multi-scale and multi-species approach this research provides a solid platform for future research into carnivore coexistence. There are many aspects that can build on this research to give a better insight into the way that co-occurring species interact and avoid each other. This research, in a sense, was relatively static (Minta 1992). However to get a deeper understanding of how cheetahs react to lions and spotted hyaenas it would be worthwhile taking a more dynamic approach by looking at behaviour with different time lags. In addition it would be worthwhile investigating what cues cheetahs detect and respond to. The results in this thesis and personal observations from the field suggest that cheetahs do not respond to olfactory cues – as they did not respond to long-term risk – but that they are more likely to respond to acoustic and visual cues. Durant (2000a) showed that cheetahs responded to acoustic cues, but whether this was influenced by distance from predators or habitat type has not yet been investigated.

Whilst this research covers the behavioural and ecological mechanisms by which cheetah respond to lions and spotted hyaenas, it would be interesting to see if these observations extend to other competitively subordinate species, such as the African wild dogs. Cheetahs and wild dogs co-occur and face similar pressures from lions and spotted hyaenas. However, these two species differ greatly in their life history, ecology and behaviour (Caro 1994, Creel and Creel 2002). Whereas cheetahs are a predominantly solitary felid with less restricted ranging behaviour, wild dogs are a canid that, like other canids, live in large social groups and are strictly territorial (Kleiman and Eisenberg 1973, Courchamp and Macdonald 2001). This study on cheetahs was carried out in parallel to a study on wild dogs and thus the data could be combined to investigate these differences (e.g. Cozzi et al. 2012). By using data of these two species simultaneously, broad-scale ecological and environmental variations would be excluded, thereby providing a robust comparison.

Conclusion

In conclusion, the response of cheetahs to the risks posed by the larger and competitively stronger lions and spotted hyaenas is predator-specific, habitat-specific and dependent on the immediacy of the risk. Resource partitioning was not the main mechanism for coexistence as cheetahs overlapped extensively with lions and spotted hyaenas in time, space and habitat use. Instead, cheetahs adjusted their spatial distribution in response to immediate risks or adapted their habitat use depending on their vulnerability (e.g. behaviour or the amount of moonlight at night). A comparison with other studies suggests that the structural complexity of the environment is a key component in large carnivore coexistence.

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APPENDIX I

Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores

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Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores

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Abstract. Africa is home to the last intact guild of large carnivores and thus provides the only opportunity to investigate mechanisms of coexistence among large predator species. Strong asymmetric dominance hierarchies typically characterize guilds of large carnivores; but despite this asymmetry, subdominant species may persist alongside their stronger counterparts through temporal partitioning of habitat and resources. In the African guild, the subdominant African wild dogs and cheetahs are routinely described as diurnal and crepuscular. These activity patterns have been interpreted to result from the need to avoid encounters with the stronger, nocturnal spotted hyenas and lions. However, the idea that diel activity patterns of carnivore species are strongly shaped by competition and predation has recently been challenged by new observations. In a three-year study in the Okavango Delta, we investigated daily activity patterns and temporal partitioning for wild dogs, cheetahs, spotted hyenas and lions by fitting radio collars that continuously recorded activity bursts, to a total of 25 individuals. Analysis of activity patterns throughout the 24-h cycle revealed an unexpectedly high degree of temporal overlap among the four species. This was mainly due to the extensive and previously undescribed nocturnal activity of wild dogs and cheetahs. Their nocturnal activity fluctuated with the lunar cycle, represented up to 40% of the diel activity budget and was primarily constrained by moonlight availability. In contrast, the nocturnal activity patterns of lions and hyenas were unaffected by moonlight and remained constant over the lunar cycle. Our results suggest that other ecological factors such as optimal hunting conditions have shaped the diel activity patterns of subdominant, large predators. We suggest that they are "starvation driven" and must exploit every opportunity to obtain a meal. The benefits of activity on moonlit nights therefore offset the risks of encountering night-active predators and competitors.

Key words: activity data-loggers; African carnivore guild; coexistence; costs-benefits; moonlight; nocturnal activity; predator–predator relationships; temporal niche.

Introduction

Intraguild competition and predation have been recognized as important ecological factors influencing the population dynamics of carnivores (Palomares and Caro 1999, Linnell and Strand 2000, Caro and Stoner 2003). For example, interactions with dominant species could be responsible for the general rarity of competitively inferior carnivore species (Palomares and Caro 1999, Caro and Stoner 2003) and may push some species, such as the African wild dog (*Lycaon pictus*), to the edge of extinction (Vucetich and Creel 1999). Understanding the relationships among the members of a guild is particularly important for large carnivores as they tend to be extinction prone, due to low population densities and low reproductive rates (Purvis et al. 2000). Furthermore, human-induced habitat loss and fragmentation are forcing carnivores to inhabit ever-smaller areas, increasing the frequency of antagonistic interactions and hence potentially accelerating extinction rates (Creel 2001, Caro and Stoner 2003).

Prior to a wave of extinctions during the Late Pleistocene and the modern era, guilds of large predators were widespread on all five continents (Barnosky et al. 2004, Koch and Barnosky 2006, Turvey and Fritz 2011). Today, however, an intact guild of large predator species can be found only in Africa (Valkenburgh 1988, Dalerum et al. 2009). The African guild, which consists of the African wild dog, the cheetah (*Acinonyx jubatus*), the leopard (*Panthera pardus*), the spotted hyena (*Crocuta crocuta*), and the lion (*P. leo*), thus offers the last opportunity to investigate a complete range of interactions among large predators. Large predators in extant and extinct guilds are known to compete for

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similar prey species, despite the variation in body size among guild members (Sinclair et al. 2003, Radloff and Du Toit 2004). This body-size variation has led to strong interspecific dominance hierarchies, resulting in larger members of the guild dominating the smaller ones (Rosenzweig 1966, Maynard-Smith and Parker 1976, Polis and Holt 1992, Carbone et al. 1997, Palomares and Caro 1999, Woodward and Hildrew 2002). Lions and hyenas are, for example, known to kill wild dogs and cheetahs, steal their food, and exclude them from prey-rich areas, whereas wild dogs and cheetahs have little or no influence on the dominant members of the guild (Laurenson et al. 1995, Mills and Gorman 1997, Durant 1998, Gorman et al. 1998, Creel and Creel 2002).

It has been suggested that smaller, subdominant species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources (Pianka 1974, Schoener 1974*a*, Durant 1998, Linnell and Strand 2000, Harrington et al. 2009). Temporal partitioning as a mechanism to reduce competition or predation has been suggested, for example, between predators and prey (Sih 1980, Kotler et al. 1993, Ziv et al. 1993) and between the early mammals and the dominant dinosaurs (Crompton et al. 1978, but see Schmitz and Motani 2011). Accordingly, it is widely accepted that lions and hyenas have strongly shaped the temporal niches of wild dogs and cheetahs. In particular, the previously described diurnal and crepuscular activity pattern of wild dogs and cheetahs has commonly been interpreted as a behavioral adaptation to avoid encounters with the predominantly night-active lions and hyenas (Hayward and Slotow 2009).

Direct field evidence for temporal partitioning in African large predators is, however, lacking, and there has been no detailed study of activity patterns conducted on all species of the guild at the same time and in the same place. In the only published paper dealing with the topic, Hayward and Slotow (2009) conclude that "top-down effects appear to drive temporal partitioning within the [African] large-predator guild" and that "the remaining members of the guild probably evolved to become active in periods that limit their potential for interaction with lions." In fact, anecdotal observations (Schaller 1972, Creel and Creel 2002) and a more recent study (Rasmussen and Macdonald 2011) suggest that light availability at night may influence activity patterns of wild dogs and cheetahs, and that nocturnal activity may be more pronounced than previously thought, thus questioning the real role of lions and hyenas in influencing the activity patterns of the two subdominant species.

While a critical test of the temporal partitioning hypothesis would involve removing the dominant predators and looking for a change in the behavior of the subdominant species, such a study is clearly impractical. Instead, by carrying out a detailed study of activity patterns of a population of sympatric large predators, we aimed to test whether the activity patterns of wild dogs and cheetahs appear to have been primarily shaped by light availability, rather than by avoidance of lions and spotted hyenas. For this purpose, we attached radio collars equipped with activity sensors to a total of 25 individuals of the four species, in a region of the Okavango Delta in northern Botswana. We first investigated how activity was distributed throughout the 24-h cycle for all species. Second, we tested if the nocturnal activity patterns were correlated with moonlight availability. A strong positive relationship would suggest that light availability plays an important role in determining activity at night. Third, for wild dogs and cheetahs, we investigated whether there were trade-offs in activity during different periods of the 24-h cycle. Specifically, we investigated whether increased nocturnal activity resulted in reduced activity on the following day. Trade-offs in activity within the 24-h cycle would suggest that, when moonlight is sufficient, subdominant predators shift their diurnal activities to the night hours, despite the risk associated with a higher likelihood of encountering more dominant members of the guild.

Methods

The African large predator guild

The African large predator guild consists of five species: the African wild dog, the cheetah, the leopard, the spotted hyena, and the lion (Hayward and Slotow 2009), which are characterized by a pronounced predatory behavior. The members of the guild vary in body mass ranging from 200 kg (lion) to 25 kg (wild dog), giving rise to a dominance hierarchy where the larger lions and hyenas clearly dominate the smaller wild dogs and cheetahs. In contrast to lions and hyenas, the outcome of interactions between leopards vs. wild dogs and cheetahs is less unidirectional. Leopards have furthermore been shown to be almost equally active during day- and nighttime and therefore not unequivocally categorized as nocturnal/crepuscular or as diurnal/crepuscular (Hayward and Slotow 2009, McManus 2009). Because leopards are active throughout the 24-h cycle, they are not likely to bias the behavior of the other species toward or away from any particular time of the day. For this reason, they were not included in the study.

Field work

Radio collars equipped with sensors (Vectronic Aerospace GmbH, Berlin, Germany) specifically designed to record activity data (more detail follows) were fitted to the study animals (following Osofsky et al. 1995, Kock et al. 2006) by a registered veterinarian in compliance with Botswana law. After immobilization, the collared individuals safely rejoined their group showing no signs of distress. Between 2008 and 2010, we monitored the activity of a total of seven wild dogs in five packs, six cheetahs, six hyenas in five clans, and six lions in five prides. All four species were found throughout the entire study area. The collared animals ranged over an area of approximately 4000 km^2 and

their territories largely overlapped (Appendix A). Throughout the duration of this study, at least two individuals of each species were collared at any time. However, no more than one individual per social group was collared at any given time to avoid data duplication owing to the collective movement of group members. Data were recorded for a mean of 329 d for cheetahs (range, 217–472 d); 368 d for wild dogs (range, 217–448 d); 416 d for lions (range, 328–486 d); and 432 d for hyenas (range, 310–587 d).

Subdivision of a 24-h cycle

To investigate activity patterns, we divided each 24-h cycle into five periods: night, morning twilight, morning, afternoon, and evening twilight. These periods reflect the main activity periods for wild dogs and cheetahs (day and twilight) and for lions and hyenas (night and twilight) as currently described in the literature (Hayward and Slotow 2009). Night stretched between the astronomical dusk and dawn, when the sun is 18° below the horizon and sunlight contribution to overall luminosity is nil. The morning twilight started at dawn and ended at sunrise; the evening twilight started at sunset and ended at dusk. The day lasted from sunrise to sunset and the division between morning and afternoon occurred around noon each day (Appendix C).

Nighttime was further divided into seven periods; three periods before midnight, one period across the midnight hour, and three periods after midnight. Each period (apart from the midnight period) had an exact duration of 1.2 h and was therefore directly comparable to the duration of the morning and afternoon twilight periods. Because the overall night length slightly changes over time, we had to adjust the length of the period spanning midnight, which therefore varied slightly in length (±30 minutes).

Light availability and environmental factors

Moonlight intensity, our main predictor variable, was taken as a measure of light availability at night and was defined as the percentage of the lunar disc illuminated (United States Naval Observatory 2011). Full-moon nights and new-moon nights were defined when respectively $\geq$95% and $\leq$5% of the lunar disc was illuminated, giving four or five full-moon and four or five new-moon nights per lunar cycle. First-quarter and third-quarter moon (i.e., half of the moon visible from the Earth's surface) were defined when the percentage of the lunar disc illuminated was between 45% and 55%. We refer to these phases of the lunar cycle as half-moon waning and half-moon waxing. Since cloud cover reduces available moonlight during the wet season, we only considered data collected during the dry season (April–October) when cloud cover was negligible. Because temperature has been shown to influence activity patterns of carnivore species (Theuerkauf 2009), we obtained records for the study area and used temperature as a covariate in our statistical models. For each day, average temperatures for the five periods of the 24-h cycle were calculated using the data recorded at 15-minute intervals by a fixed weather station situated in Maun, the town closest to the study area (Jacana raw weather data for 2006–2011 are *available online*).[5] Maun lies at the southern edge of the Okavango Delta and is part of the same geo-ecological system as the study site.

Data analysis

The activity data used in our analyses were systematically collected by radio collars equipped with two motion sensors mounted on the study animals. The two motion sensors continuously recorded activity bursts and summed them over 5-minute intervals; a raw data point consisted of the number of activity bursts per 5 minutes (thus the data are continuous, not categorical). To control for the highly pseudo-replicated nature of the raw data, we averaged, for each day, the activity data recorded by each collar over the five periods of the 24-h cycle. Thus, the data set consisted of one activity value for night, morning twilight, morning, afternoon, and evening twilight, for each day and for each individual. Study animals were followed during daytime and the observed behavior matched with the data collected by the collars at the time of observation. Resting animals usually showed activity levels of about 5–15 counts per 5 minutes depending on the species, and we include this threshold line in some of our graphs to help visual interpretation of the results.

For the four species, we calculated mean activity values during each period of the 24-h cycle during full-moon and new-moon days, as well as mean activity values for the seven periods of the night during full-moon, half-moon (waning and waxing), and new-moon days. Periodicity in the nocturnal activity of the four species was analyzed using Fourier spectral analysis, performed using the statistical software R (R Development Core Team 2011). The Fourier algorithm isolates the period of a sinusoidal waveform (e.g., Polansky et al. 2010), and was applied to nocturnal activity values of each individual separately. Because Fourier analysis does not reveal the directionality and strength of the relationship between variables, we analyzed nocturnal activity using linear mixed-effects models (performed using the statistical software GenStat [VSN International, Hemel Hempstead, UK]) with moonlight intensity as an explanatory variable. Nocturnal activity, the response variable, was log-transformed to meet the assumptions of normality and homoscedasticity. Animal identity was treated as a fixed effect; night temperature and activity during the previous day time were entered as covariates; moon cycles and days nested within moon cycles were treated as random effects. We included a first-order auto-regressive error structure when necessary, based on diagnostic plots of residuals.

[5] http://www.jacananet.com/Weather.htm

To further investigate the effects of nocturnal activity on the activity levels during the following day and to understand how activity was partitioned across the 24-h cycle, we constructed four additional mixed-effects models with, respectively, morning twilight activity, morning activity, afternoon activity, and evening twilight activity as response variables. The activity variables were log-transformed to meet the assumptions of normality and homoscedasticity. For each model, animal identity, moonlight intensity, activity during the previous periods of the 24-h cycle (e.g., morning twilight activity when analyzing morning activity), and temperature of the respective period were treated as fixed effects. For both models, moon cycles and days nested within moon cycles were treated as random effects. Model simplification started from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2009). Denominator degrees of freedom reported in the text were rounded to the nearest integer. Significance was assessed at $P = 0.01$. Throughout the *Results*, central tendency values are expressed as mean ± SE.

Results

Nocturnal activity of wild dogs and cheetahs comprised, respectively, 25.9% ± 2.1% (mean ± SE) and 25.6% ± 3.5% of the overall diel activity budget, a high value for two species currently described as day active. In contrast, for lions and hyenas, nocturnal activity made up 60% ± 2.7% and 67.9% ± 2.6% of their respective activity budgets (Table 1). In addition, wild dogs and cheetahs conducted roughly half of their total activity (wild dogs, 51.3% ± 1.3% and cheetahs, 43.8% ± 1.9%; Table 1) during the main activity periods of lions and hyenas (night and twilight). This rather extensive and unexpected overlap between the activity patterns of the subordinate and the dominant predators is inconsistent with the idea of strict temporal partitioning.

Mean activity values over the five periods of the 24-h cycle (night, morning twilight, morning, afternoon, and evening twilight) showed significant differences between full-moon days and new-moon days for wild dogs and cheetahs but not for lions and hyenas (Fig. 1 and Table 1). This suggests that the activity pattern of wild dogs and cheetahs changes over a lunar cycle, while the activity pattern of lions and hyenas remains constant and is thus uncoupled from the phases of the moon (Fig. 1 and Table 1). On full-moon days, about 40% (wild dogs, 40.4% ± 3.8%; cheetahs, 39.7% ± 4.4%) of the total diel activity of wild dogs and cheetahs occurred at night while this figure dropped to approximately 15% (wild dogs, 15.9% ± 2.2%; cheetahs, 13.8% ± 2.4%) during new-moon days (Table 1). In contrast, the nighttime activity of lions and hyenas did not change between the different phases of the lunar cycle (Table 1).

The Fourier spectral analysis showed that the nocturnal activity of six of the seven wild dogs had a main period of 29.17 ± 0.75 d (mean ± SE) corresponding very closely with the lunar cycle of 29.53 d (Figs. 2 and 3); one wild dog (#4) did not show any periodicity (Fig. 3b). Five of the cheetahs exhibited a main period of 30.45 ± 0.49 d (Figs. 2 and 3), while one individual (#3) showed little signature at this wavelength (Fig. 3c). In contrast to wild dogs and cheetahs, the nocturnal activity of lions and hyenas showed no relationship with the lunar cycle, although they exhibited shorter activity cycles of a few days (Fig. 2). A fine-scale investigation of the nighttime activity between different phases of the lunar cycle showed that wild dogs and cheetahs adjusted their nocturnal behavior according to the presence of the moon in the sky. For example, during a waning moon, when the moon is in the sky during the first half of the night, both species were highly active during the hours preceding midnight (Appendices D and E). With sufficient moonlight, the night activity levels of wild dogs and cheetahs was comparable with activity levels exhibited during the morning twilight on full-moon days (compare Fig. 1 with Appendices D and E). In contrast, the activity of lions and hyenas was not related to the presence of the moon in the sky and remained generally constant during the night (Appendices F and G). This further supports our prediction that moonlight intensity, rather than the activity of lions and hyenas, is a major driver influencing the nocturnal activity of wild dogs and cheetahs.

In the linear mixed-effects models, the nocturnal activity of lions and hyenas showed no relationship with moonlight intensity, despite reports that the hunting success of lions increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). In contrast, there was a strong positive relationship between wild dogs' nocturnal activity and moonlight intensity ($F_{1, 571} = 231.06$, $P < 0.001$), although one individual (#4) showed no nocturnal activity (interaction term individual by moonlight, $F_{6,1020} = 4.33$, $P < 0.001$; Fig. 3). For cheetahs, there was a similar positive relationship between nocturnal activity and moonlight intensity ($F_{1, 981} = 164.02$, $P < 0.001$) although one male (#3) showed consistently high levels of activity at night (interaction term individual by moonlight, $F_{5, 981} = 6.38$, $P < 0.001$; Fig. 3). For both wild dogs and cheetahs, the total diel activity remained roughly constant over a lunar cycle and hence showed no relationship with moonlight intensity (wild dog, $F_{1, 512} = 0.69$, $P = 0.41$; cheetah, $F_{1, 980} = 1.37$, $P = 0.24$). This suggests that wild dogs and cheetahs trade off and partition nocturnal and diurnal activity according to available moonlight.

To further investigate this suggestion and understand how diel activity was partitioned, we carried out additional analyses for each period of the 24-h cycle. For both wild dogs and cheetahs, high levels of moonlight intensity negatively influenced the activity during each period of the following day, with the exclusion of the evening twilight activity of cheetahs (all

TABLE 1. Portion of activity during the five periods of the 24-h cycle over an entire lunar cycle and for two different phases of the lunar cycle.

Time period	Portion of activity (%)			
	Wild dog	Cheetah	Spotted hyena	Lion
Overall				
Night	25.9 ± 2.1	25.6 ± 3.5	67.9 ± 2.6	60.0 ± 2.7
Morning twilight	11.0 ± 0.9	9.9 ± 1.4	8.1 ± 0.8	7.4 ± 0.7
Morning	28.7 ± 1.6	34.3 ± 2.1	10.4 ± 1.7	16.3 ± 1.4
Afternoon	19.9 ± 1.5	21.9 ± 1.5	5.0 ± 1.1	9.3 ± 1.8
Evening twilight	14.4 ± 0.8	8.3 ± 0.7	8.6 ± 0.5	7.9 ± 0.8
Partial overlap	51.3	43.8	84.6	75.3
Full moon				
Night	40.4 ± 3.8	39.7 ± 4.4	66.7 ± 2.3	57.7 ± 4.0
Morning twilight	8.5 ± 0.5	7.1 ± 1.6	9.3 ± 0.4	7.7 ± 0.5
Morning	21.2 ± 2.4	28.1 ± 2.1	10.5 ± 1.7	16.9 ± 2.1
Afternoon	16.9 ± 1.8	17.2 ± 1.0	4.9 ± 1.2	9.8 ± 2.0
Evening twilight	13.1 ± 1.3	7.8 ± 0.7	8.6 ± 0.6	8.0 ± 0.9
Partial overlap	62.0	54.6	84.6	73.4
New moon				
Night	15.9 ± 2.2	13.8 ± 2.4	67.7 ± 2.9	60.9 ± 2.4
Morning twilight	13.6 ± 1.0	12.3 ± 1.2	7.6 ± 1.3	7.4 ± 0.8
Morning	32.2 ± 1.9	40.1 ± 2.0	10.8 ± 1.6	14.5 ± 1.4
Afternoon	21.9 ± 1.9	24.7 ± 1.8	5.0 ± 1.1	9.2 ± 1.4
Evening twilight	16.3 ± 1.3	9.1 ± 0.7	8.9 ± 0.5	8.0 ± 0.8
Partial overlap	45.8	35.2	84.2	76.3

Notes: Values are means ± SE. Partial overlap is the sum of the activities recorded during the three periods of major lion and hyena activity (night, morning twilight, and evening twilight) and shows how much of the diel activity of wild dogs and cheetahs takes place during times of overlapping activity with their two stronger competitors.

P values <0.001; Appendix B). For wild dogs, high activity levels during moonlit nights led to decreased activity the following day (except for the evening twilight activity, which was independent of the activity during the previous night; Fig. 1 and Appendix B). Morning twilight and morning activity showed a positive relationship as did afternoon and evening twilight activity (Appendix B). Wild dogs thus show three distinct activity periods (night; morning twilight and morning; afternoon and evening twilight) clearly separated by phases of inactivity. The patterns for cheetahs were different: after correcting for differences in activity due to differences in moonlight intensity (Fig. 1 and Appendix B), we found that levels of activity in adjacent periods showed a positive relationship; hence it seems that, once active, cheetahs remain active over long periods (Appendix B). For both species, temperature negatively influenced activity only during the hottest part of the day (i.e., morning and afternoon periods; Appendix B).

DISCUSSION

In contrast to previous studies suggesting a high degree of temporal partitioning among African large predators (Hayward and Slotow 2009), our study in the Okavango Delta revealed extensive temporal overlap. This was mainly due to the unexpected nocturnal activity of wild dogs and cheetahs, the two species previously regarded as diurnal, and the partly diurnal habits of lions and hyenas. Only for wild dogs and cheetahs was nocturnal activity correlated with the lunar cycle: with sufficient moonlight, both species were considerably active at night and nocturnal activity constituted almost half of the total diel activity on full-moon days. It therefore seems that activity patterns of these subdominant species are primarily constrained by light availability, rather than by the activities of the larger, dominant species. Our findings support the idea that, at the diel level, temporal niche partitioning may be a relatively rare event (Schoener 1974*b*).

Our results conflict with those from the meta-analysis carried out by Hayward and Slotow (2009) who concluded that available studies did not support nocturnal behavior for wild dogs and cheetahs. However, the authors used data from different sites that had been collected opportunistically using a range of different methodologies for different species. In addition, they often assumed that the timing of sunrise and sunset were constant through the year and along a latitudinal gradient. These assumptions can lead to incorrect conclusions, as pointed out by Nouvellet et al. (2011). Although our results are not consistent with the hypothesis that activity patterns of dominant competitors have been the main force shaping the temporal niches of wild dogs and cheetahs, we nonetheless acknowledge that lions and hyenas pose a real threat

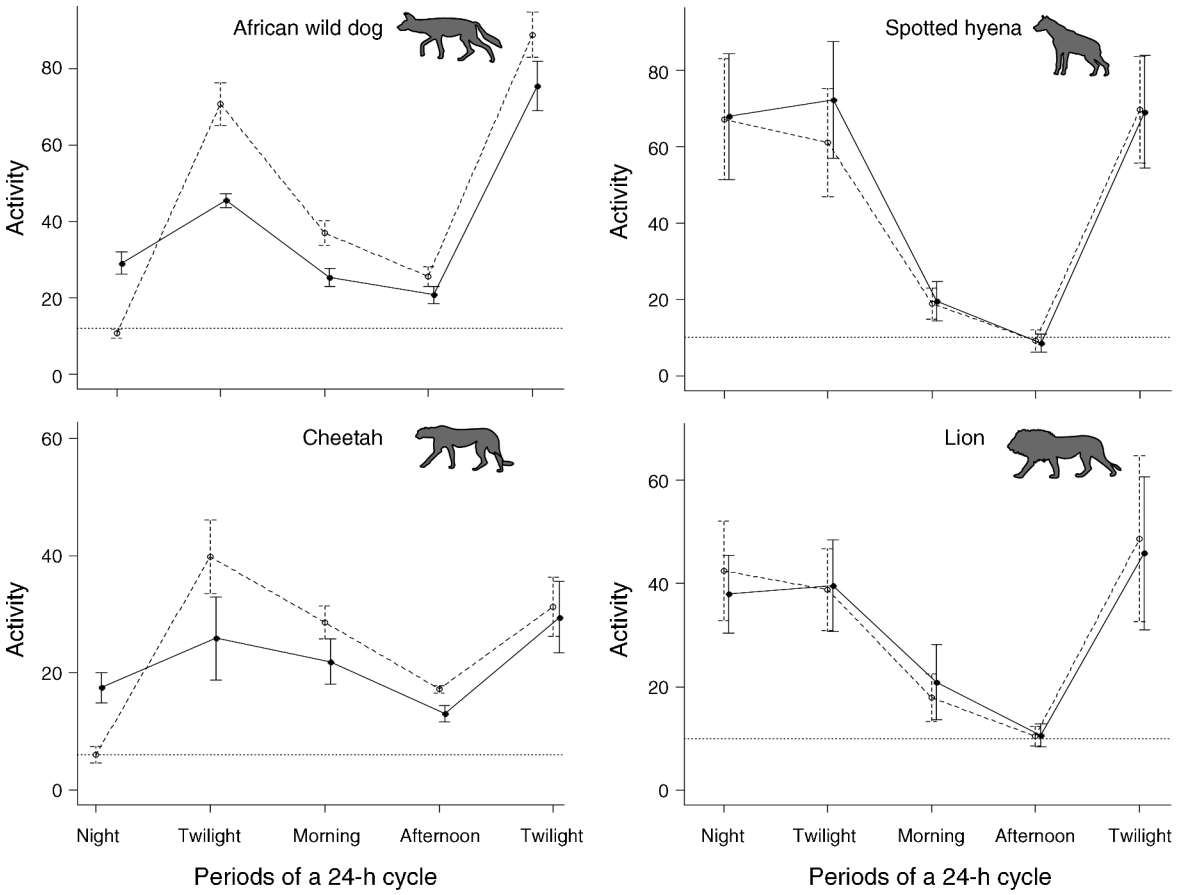

FIG. 1. Mean activity values (defined in *Methods: Data analysis*) during five periods of the 24-h cycle for full-moon days (solid lines) and new-moon days (dashed lines). Error bars represent standard errors of the mean. Connecting lines between mean values have been added for visualization purposes. The horizontal dotted line shows the inactivity threshold.

(Laurenson et al. 1995, Mills and Gorman 1997, Gorman et al. 1998). Playback experiments have for example revealed short-term behavioral modifications in response to the presence of lions and hyenas such as reduced hunting activity and fleeing behavior (Durant 2000, Webster et al. 2011), and simulation models revealed the sensitivity of wild dog populations to lion predation (Vucetich and Creel 1999).

Only wild dogs and cheetahs showed nocturnal activity patterns that were correlated with the availability of moonlight while the nocturnal activity of hyenas and lions did not vary over the lunar cycle. This raises the question of why good light is a key requirement for activity in wild dogs and cheetahs but not in lions and hyenas. Both wild dogs and cheetahs hunt small and medium-sized antelopes, e.g., impala (*Aepyceros melampus*), and conduct high-speed chases over relatively long distances. During such chases, wild dogs can pursue their prey at 40–60 km/h for more than 1 km and cheetahs reach speeds of over 100 km/h for several hundred meters. Such long, high-speed chases are inherently risky and good light conditions (i.e., during the day and on moonlit nights) and sufficient visibility are likely to be essential to maintain contact with the prey, avoid fatal injuries, and increase hunting success (Schaller 1972, Bertram 1979, Creel and Creel 2002, Rasmussen and Macdonald 2011). This cursorial hunting technique is in clear opposition to the ambush hunting technique of lions, whose success increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). Different foraging techniques may thus explain the different activity patterns among the species of the guild, and stress the evolutionary importance of bottom-up forces (e.g., prey acquisition) in shaping the behavior of large predators.

If lions and hyenas pose a threat to wild dogs and cheetahs, why do they not completely avoid nocturnal activity? One possibility is that they must take every opportunity to catch prey and that they cannot afford to miss exploiting nights with sufficient moonlight. Thus, wild dogs and cheetahs may have evolved short-term visual, auditory, and olfactory cues, e.g., fleeing on hearing lion calls, to avoid potentially dangerous situations, rather than completely avoiding being night

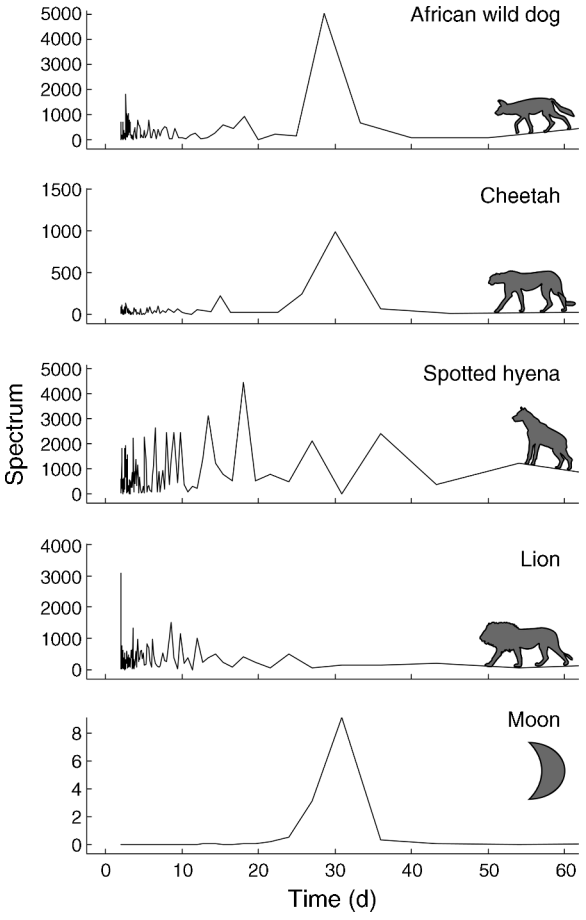

FIG. 2. Spectrogram showing periodicity in the nocturnal activity pattern of a typical African wild dog, cheetah, spotted hyena, and lion. Activity data recorded by the collars were averaged per night and investigated using Fourier spectral analysis. For comparison, the spectrogram of the moon is shown. While the activity of wild dogs and cheetahs shows a main period of 30 days (similarly to the period of the lunar cycle), the activity of spotted hyenas and lions show cyclicity every few days. The width of each peak is a measure of accuracy.

active. Neither wild dogs nor cheetahs showed any cyclical pattern in their total diel activity over the course of a lunar cycle, suggesting that nocturnal activity was not a strategy to increase the overall activity budget. Instead, wild dogs showed clear trade-offs in activity between adjacent periods within a 24-h cycle. For example, a night with high activity was followed by a morning with reduced activity, implying that nocturnal activity allowed or forced subdominant species to rest the next day. We therefore assume that the benefits of nocturnal activity offset the risks of encountering night-active predators and competitors. Indeed, we might expect hunting success to be higher at night because prey animals have a reduced chance of spotting predators under dim light conditions. For example, it is known that hunting success in cheetahs is higher when they can stalk undetected very close to intended prey (FitzGibbon and Fanshawe 1988) and that wolves (*Canis lupus*) are almost twice as successful when hunting on moonlit nights (Theuerkauf et al. 2003). To the contrary, the high levels of activity during early mornings that followed moonless nights, when activity was limited, suggest a behavioral response to an increasing hunger risk.

The influence of moonlight on the hunting behavior of predator species has been widely described for nocturnal species (Horning and Trillmich 1999, Lang et al. 2006), and our results suggest that moonlight can equally influence (allegedly) diurnal species. Understanding and quantifying the energetic budget of single species based on patterns of activity is beyond the scope of this study; nevertheless, on the basis of our findings, it is evident that wild dogs and cheetahs have more time to fulfill their energetic requirements than just a few hours in the morning and in the late afternoon as currently assumed. Further research is thus required to understand the role of each period of the 24-h cycle for the diel energetic budget as compared to the diel activity budget.

Our findings suggest that the temporal niches of subdominant large predator species are only moderately shaped by the need to avoid predation and competition (Schoener 1974*b*, Lima and Dill 1990, Theuerkauf 2009). This is in contrast to findings at other trophic levels, for example, in guilds of herbivore species (Sinclair et al. 2003, Chesson and Kuang 2008). Subdominant large predators must trade off the risk of encountering dominant species against the risk of starvation (e.g., Lima 1988, Roth and Lima 2007) and subdominant large predators appear to be mainly "starvation driven." The well-documented positive relationship between the distribution and density of prey species and their predators (e.g., Carbone and Gittleman 2002) further suggests a tight casual association between bottom-up forces and communities of large predators. Additional research in ecosystems characterized by different densities of competitors and prey species will be necessary to better understand the role of top-down and bottom-up forces in shaping animal communities and facilitating coexistence. In contrast to herbivores, large carnivores must invest a lot of energy finding and catching food, as prey are widely scattered, often rare, and difficult to catch, and hunting is energy-intensive, time-consuming, and often unsuccessful (e.g., Carbone et al. 1999). Given the relative difficulty of catching a meal vs. the relatively low likelihood of encountering a dominant species (large predators live at relatively low densities [Carbone and Gittleman 2002]), we conclude that, on moonlit nights, wild dogs and cheetahs prioritize hunting opportunities and success over the need to avoid been hunted and over the possibility of losing their kill. In conclusion, it appears that under favorable light conditions, the benefits of nocturnal activity outweigh the costs of encountering stronger competitors and predators.

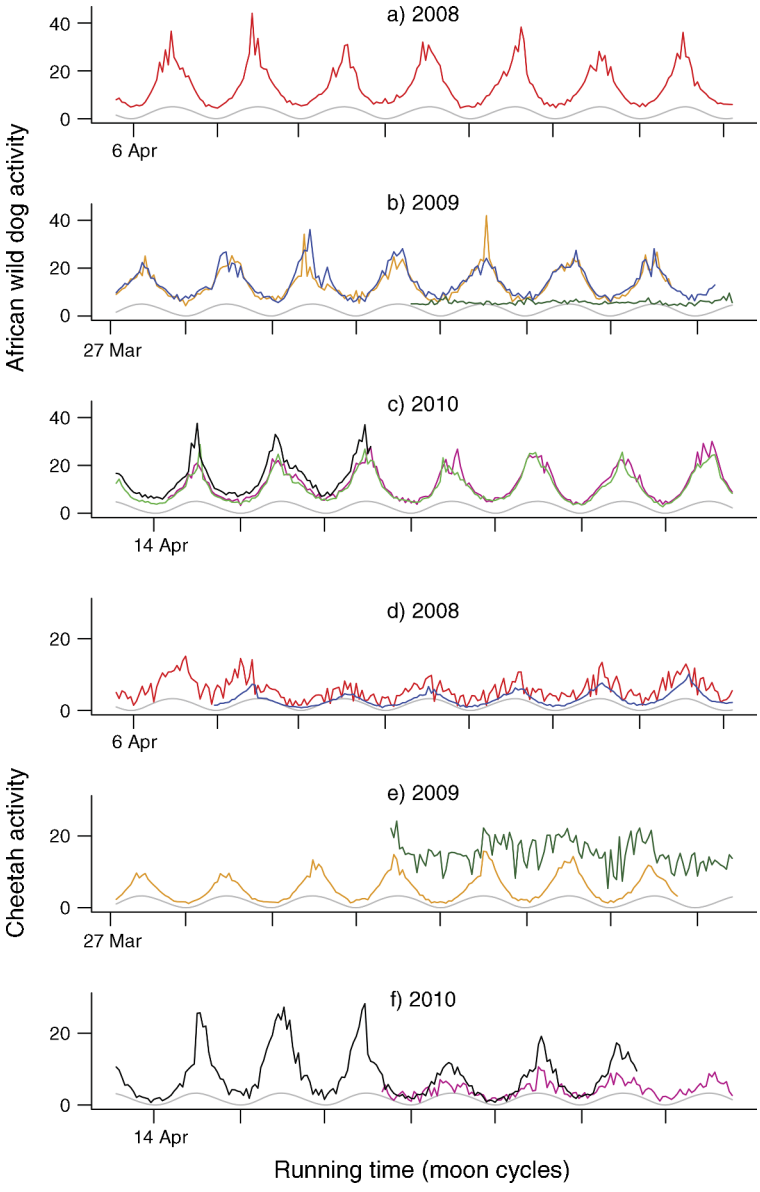

FIG. 3. Fitted values from mixed-effects models showing the nocturnal activity patterns of (a–c) African wild dogs ($n = 7$ individuals) and (d–f) cheetahs ($n = 6$ individuals) during the dry season in three consecutive years. Each color represents a different individual. Tick marks on the x-axis represent the beginning of a moon cycle (new moon). The beginning dates of moon cycles change from year to year; thus the x-axes are not aligned between years. The date of the first new moon for each year's data is shown under the first tick. Only data collected beginning 1 April of each year (the beginning of the dry season) have been considered for analysis, and the fitted (colored) lines all start on 1 April. Variation in moonlight intensity is depicted for comparison in each panel (gray line; not to scale) and highlights the strong positive relationship between animals' activity and moonlight availability. One wild dog [panel (b), green line] shows no nocturnal activity, while one male cheetah [panel (e), green line] shows consistently high nocturnal activity.

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Supplemental Material

Appendix A

A table showing the spatial range and overlap of the studied animals (*Ecological Archives* E093-242-A1).

Appendix B

A table including the detailed mixed-effect models used to investigate partitioning of activity within the 24-h cycle (*Ecological Archives* E093-242-A2).

Appendix C

A figure depicting the division of the 24-h cycle into five periods: morning twilight, morning, afternoon, evening twilight, and night (*Ecological Archives* E093-242-A3).

Appendix D

Mean activity values for African wild dogs during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A4).

Appendix E

Mean activity values for cheetahs during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A5).

Appendix F

Mean activity values for spotted hyenas during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A6).

Appendix G

Mean activity values for lions during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A7).