Site occupancy and habitat selection of cheetahs *Acinonyx jubatus* (Shreber, 1775) in a human-influenced landscape in Mozambique

By

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Supervisor: Prof. M.J. Somers

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I, Leah Andresen, declare that the dissertation, which I hereby submit for the degree Magister Scientiae (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

2014-04-16

Signature **Date**

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SUMMARY

In this study, I estimate cheetah site occupancy and habitat correlates in a human-impacted landscape in south western Mozambique, providing the first empirical data on cheetah ecology in the country. The cheetah (*Acinonyx jubatus*) has suffered dramatic range contractions and population declines as a result of habitat degradation, prey depletion and conflict with humans. Of further concern is that many of Africa's remaining cheetah populations persist in human-dominated and highly fragmented landscapes, where their ecology is poorly understood and population data are lacking. Presence-absence surveys may be a practical means to collect these data, however, failing to account for detection error can lead to biased estimates and misleading inferences; potentially having deleterious consequences for species conservation. In this study, I identify how an occupancy modelling technique that explicitly accounts for detectability can be used for targeted monitoring of less-known cheetah populations. I use replicated camera-trap and track surveys of 100 km^2 sample units to estimate the proportion of area occupied by cheetah and to determine the survey effort required to inform conservation planning. Following this, I explore the influence of prey availability, prey catch-ability and interspecific competition on cheetah habitat selection at two spatial scales in a landscape impacted by agro-pastoralist hunters. Cheetahs avoided human settlement areas across both spatial scales; however, these features contributed considerably more to home range level use. More determining, however, was a strong spatial avoidance of sites with greater bushmeat poaching across spatial scales. Moreover, cheetah exhibited a greater spatio-temporal avoidance of bushmeat poachers and their dogs then they did of lions, suggesting that humans were the greater competitor in the study system. Open habitat patches with dense edges, a landscape feature facilitating prey capture, were strongly determining at the temporary use scale, and contributed considerably more to cheetah site selection than prey occurrence. Cheetahs were negatively correlated with their prey at temporary use patches, but I failed to find support for the hypothesis that this was due to interspecific competition with lions. Two-species occupancy models revealed that cheetah may elicit a strong behavioural response in their prey manifesting as spatial avoidance. This study provides the first unbiased estimate of occurrence for cheetah in LNP that can be used to compare status across different sites and as a basis for long-term monitoring. It also provides some of the few data on cheetah ecology in systems impacted by human hunting and agro-pastoralism; conditions that may characterize many cheetah populations in Africa.

TABLE OF CONTENTS

PAGE

CHAPTER 1: GENERAL INTRODUCTION

CHAPTER 2: USE OF SITE OCCUPANY MODELS FOR TARGETED MONITORING OF CHEETAH

CHAPTER 3: INVESTIGATING CHEETAH HABITAT SELECTION AND CO-OCCURRENCE PATTERNS IN A HUMAN-IMPACTED WOODLAND SAVANNAH

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CHAPTER 1

General Introduction

Context

Large terrestrial carnivores are among the most threatened of mammalian fauna due to their large space requirements and conflicts with humans (*see* Ray *et al*., 2005a *for an overview*). Habitat fragmentation has forced many species populations to persist as a meta-population (Hanski, 1997), with sub-populations persisting in human-dominated landscapes (e.g., Athreya *et al*., 2013; Schuette *et al*., 2013). Although critical for conservation, protected areas may not be large enough to support viable large carnivore populations indefinitely (Woodroffe & Ginsberg, 1998). Therefore, understanding the ecological requirements of carnivores in disturbed systems is essential for effective conservation management.

Prey depletion, habitat degradation and conflict with humans have resulted in considerable population declines and range contractions of the cheetah (*Acinonyx jubatus*) (Ray, Hunter & Zigouris, 2005). Consequently, the species is listed as Vulnerable to extinction by the International Union for the Conservation of Nature. The global population of free-living cheetah is estimated at 10,000 individuals and is thought to be in decline. Of further concern is that many of Africa’s remaining cheetah populations persist in highly fragmented, human dominated landscapes where they are at risk of persecution (Durant *et al*., 2008).

Although often associated with grassland plains (e.g., Caro, 1994; Durant *et al*., 2004), cheetahs are able to persist in a broad array of more densely vegetated habitats (Purchase & du Toit, 2000; Mills, Broomhall & du Toit, 2004; Bisset & Bernard, 2005) and were once widely distributed across Africa and Asia (Turner, 1997). As obligate flesh-eaters, their habitat requirements include the availability of prey and landscape features facilitating prey capture (Mitchell & Hebblewhite, 2012). Cheetahs have evolved a highly specialized rapid-pursuit hunting strategy (Turner, 1997; Wilson *et al*., 2013) and tend to exploit the most common antelopes within their preferred weight range (23-56 kg) (Hayward *et al*., 2006). Due to their lighter build, cheetahs are competitively inferior to sympatric carnivores including lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), suffering from kleptoparasitism (Caro, 1994) and intraguild predation (Laurenson, 1994). In the high prey/predator density system of the Serengeti plains, cheetahs have been shown to experience greater reproductive success when lion densities are lower (Kelly *et al*., 1998), and when individuals express greater vigilance behaviour against potential predators (Durant, 2000a). Mechanisms for co-existence are thought to include comparatively high reproductive potential for cheetah (Caro, 1994), spatial and temporal avoidance (Durant, 1998; 2000b), and differences in prey preferences (Hayward *et al*., 2006). In addition, competition is thought to be reduced with increased cover for concealment (Mills *et al*., 2004; Bisset & Bernard, 2007).

Cheetahs exist at markedly lower population densities compared to sympatric large carnivores such as lions or leopards (*Panthera pardus*) (Durant, 2007), and exhibit a complex social organisation that is unique to felids (*see* Caro, 1994 *for an overview*). Female cheetah home ranges are larger where prey is migratory (mean = 833 km^2) than when prey is sedentary (mean = 105 km^2). Territorial males defend comparatively smaller home ranges, which conversely are greater when prey is sedentary (mean = 37 km^2) than when prey is migratory (108 km^2) (Broomhall, 2006). Low population densities on the Serengeti plains (0.8-1/100 km^2) have been attributed to interspecific competition (Caro, 1994). However, low population densities are also reported in Namibian farmlands (0.2/100km^2) where lion and spotted hyaena have been eradicated (Marker, 2002). In these systems, prey is non-migratory yet both sexes have exceptionally large home ranges (mean = 1651 km^2). That cheetah exhibit low population densities in Namibian farmlands may be due to human persecution (Marker *et al*., 2008). Many of Africa's remaining cheetah populations persist outside of protected areas (Durant *et al*., 2008), in non-equilibrium communities exposed to continued disturbance and competition with humans (*e.g.,* Marker, 2002).

Although cheetah are among the most intensively studied felids (e.g., Caro, 1994; Laurenson, 1994; Durant *et al*., 2004; 2007; Kelly *et al*., 2008; Marker *et al*., 2003; 2008), their conservation management is hindered because there are few data on their status across large portions of their remaining range (Durant *et al*., 2008). Furthermore, because few studies have investigated cheetah habitat selection outside of protected areas (*but see* Marker, 2002; Muntifering *et al*., 2005; Marker *et al*., 2008), little is known about their ecological requirements in human-disturbed landscapes. The goal of this study is to quantify cheetah site occupancy and habitat selection in a human-impacted landscape in south-western Mozambique.

General approach

The use of site occupancy models

Evidence-based management requires reliable population data as well as sound knowledge of the factors driving system change (Conroy & Carroll, 2009). Carnivores are notoriously difficult to study due to their characteristic elusive behaviours and low population densities (Long *et al*., 2008). Most studies on cheetah have relied on unique photographic recognition or the physical capture and collaring of individuals to derive estimates of abundance and density (see Bashir *et al*., 2004 for an overview). However, obtaining reliable estimates of abundance (Williams, Nichols & Conroy, 2002) for cheetah is often time and resource consuming, since the species exists at naturally low population densities and tends to have low re-capture rates (Bashir *et al*., 2004).

Presence-absence data can be an efficient and cost effective means of obtaining sufficient data on low-density, difficult to detect carnivores (Long *et al*., 2008); however, if these (presence-absence) data are to be used as a count index to infer abundance, the proportional relationship between the indices and the true population must first be determined (Anderson, 2001). Recent efforts have been made to determine the linear relationship between track frequency and known cheetah density, and therefore the survey effort required to obtain reliable indices for cheetah (Houser *et al.,* 2009; Funston *et al*., 2010). However, any calibration of indices to known populations is time and site-specific (Anderson, 2003, MacKenzie *et al*., 2006). As such, the use of indices of abundance is considered unreliable because estimates are based on implicit assumptions about the proportion of the population that is counted during each survey (Anderson, 2001, 2003; MacKenzie *et al*., 2006). The underlying weakness of using indices of abundance is that these methods fail to account for false absences (e.g., species being present but going undetected), which can lead to biased estimates and misleading inferences (MacKenzie *et al*., 2006). For example, detection error can lead to inaccurate species distribution models (Lobo, Jiménez-Valverde & Hortal, 2010), underestimates of areas where conservation interventions are required (Rondinini *et al.*, 2006) and distorted species-habitat relationships (Gu & Swihart, 2004). Failing to account for detection error is obviously of particular concern for rare or elusive species, in which case the use of indices of abundance is severely limited (MacKenzie *et al*., 2004a). Efforts to standardize methods for collecting indices (i.e., observer effort, time of day, training etc.,) are an attempt to ensure similar detection probabilities, however there will always be factors that are either unidentified or uncontrollable that lead to variation in detection rates, thereby creating bias in results (Yoccoz *et al.,* 2001; Anderson, 2001, 2003, MacKenzie *et al*., 2006).

More recent statistical and methodological advances in the use of detection/non-detection data allow for detection error to be explicitly accounted for within an occupancy model (MacKenzie *et al*., 2002). Replicated detection/non-detection surveys are used to estimate a detection probability and derive unbiased estimates of occurrence. Hierarchical ranking of covariates are used to explain heterogeneity in occupancy and detectability simultaneously; thereby permitting the testing of ecological hypothesis and providing inferences about variables that affect distribution and resource selection (MacKenzie *et al*., 2006).

Where absolute abundance estimates cannot be practically obtained, occupancy (i.e., the proportion of area occupied or probability of site use) is considered a robust alternative state variable (Karanth, Nichols & Kumar, 2004; MacKenzie *et al*., 2004a). Occupancy is a useful metric for assessing species status (Conroy & Carroll, 2009) and is a natural state variable for investigating species distribution, habitat relationships and meta-population dynamics. Since detection/non-detection data are relatively easy to obtain, occurrence models are useful for long-term monitoring programs and can be used to estimate the dynamic processes of local extinction and colonization (MacKenzie *et al*., 2006). Two-species occupancy models can be used to investigate co-occurrence patterns while accounting for individual species detection probabilities and habitat correlates, thereby providing robust inferences on species interactions (MacKenzie, Bailey & Nichols, 2004b). Site occupancy models have become widely adopted for landscape-scale status assessments and habitat use of tigers (*Panthera tigris*) in Asia (Karanth *et al*., 2011; Wibisono *et al*., 2011; Sunarto *et al*., 2012; Barber-Meyer *et al*., 2013) and have gained some use with carnivore studies in Africa (Thorn *et al*., 2011; Schuette *et al*., 2013). In this study, I use detection/non-detection data obtained from camera-traps and track surveys to estimate cheetah site occupancy and habitat correlates in a human-impacted landscape in south western Mozambique.

Thesis objectives and structure

My thesis is comprised of four chapters including a general introduction and discussion. In the second chapter, my goal was to identify how an occupancy modelling approach could be used to quantify cheetah population status and to simultaneously obtain inferences on factors limiting their occurrence (i.e., 'targeted monitoring') in a human-impacted landscape. I provide initial occupancy and detectability estimates for the species that can be used to explore sampling design trade-offs and illustrate how detection data can be used to design robust ecological studies and occupancy monitoring programs. In the third chapter, I explore the influence of prey availability, prey catch-ability and competition on cheetah's use of habitat at multiple spatial scales. My goal was to determine what fitness related factors best describe cheetah habitat selection in a human-impacted woodland savannah. Although in both chapters I use site occupancy models, my parameter of interest differs; in the first my goal was to estimate the *proportion of area occupied*, whereas in the second I explore *site use*. The thesis was written with the intention that chapters two and three be published in scientific journals and co-authored with K.T. Everatt and M.J. Somers. I therefore use "we/our" throughout chapters 2-3.

Study area and population

This study was conducted in the Limpopo National Park (LNP), which forms a key component of the Greater Limpopo Transfrontier Park (GLTFP) together with the Kruger National Park

(KNP) in South Africa and the Gonarezhou National Park in Zimbabwe (Fig. 1.1). The research was conducted under authorization of the Director Nacional das Conservation Areas (permit #'s 005-2011; 003-2012). Large mammal populations were over-exploited during armed conflict (1974-1990) in Mozambique (Hatton, Couto & Oglethorpe, 2001); however, the formation of LNP in 2002 and formation of the GLTFP has provided the opportunity for wildlife recovery. Cheetahs were thought to have been extirpated from the Limpopo Valley in Mozambique (Purchase, 2007); however, LNP was listed as possible cheetah range due to a lack of empirical data from the area and its contiguousness with KNP (IUCN/SSC, 2007).

LNP presently supports considerable mammalian biodiversity (Appendix I); however, wildlife species populations are nevertheless inhibited by anthropogenic pressures (Everatt, 2013; *this study*). There is limited enforced wildlife protection, road network and tourism infrastructure. The Limpopo River forms the eastern boundary, which is characterized by human settlements, with an estimated population of 20,000. There are eight additional communities situated within the park boundary, inhabited by approximately 6,500 humans, located primarily along the seasonal Shingwedzi River that stretches through the centre of the park (Huggins *et al.*, 2003). Residents practice land-clearing for subsistence farming, free-grazing of livestock, fishing and (illegal) hunting of wildlife for meat (i.e., 'bushmeat') with snares, bows and arrows, spears, traps and hunting dogs (*Canis lupus familiaris*) (*this study.*) (Fig.1.2).

The region is comprised of woodland savannah plains. The predominant landscape is sandveld, which is comprised of woodlands and thickets on sandy substrates, characterized by the absence of well-defined drainage lines and the presence of pans (depressions flooded for long periods). Distinguishing sandveld vegetation includes low woodlands of *Terminalia sericea*, *Combretum apiculatum* and *Pogonarthria squarrosa* and dense thickets dominated by *Baphia* *massaiensis*. The Lebombo hills (500 m.a.s.l.) run the boundary with KNP and are characterized by short woodlands and tall shrublands on undulating hills of stony, rhyolite soils with well-defined ridge lines and rocky outcrops. Distinguishing Lebombo hill vegetation includes *Combretum apiculatum, Andropogon gayanus* and *Colophospermum mopane*. This region is bordered by the combretum/mopane ruggedveld, which follows much of the Shingwedzi river valley running through the centre of the park and is characterized by woodlands and shrublands typified by the species *Combretum apiculatum*, *Combretum imberbe*, *Colophospermum mopane* and *Acacia nigrescens* on shallow clay soils. The rest of the park is largely comprised of mopane shrubveld, which is characterized by shrublands and thickets on calcareous soils, dominated by the species *Colophospermum mopane*. According to the Köppen Classification System, the region has a warm arid climate with a mean annual temperature exceeding 18°C and annual precipitation of <450 mm, falling almost exclusively in summer months (November – April) (Stalmans *et al*., 2004).

I initiated research on cheetah in LNP in September, 2011 in collaboration with Kristoffer Everatt who simultaneously began a study on lions. Together our projects represent the first empirical investigation into ecology of mammalian carnivores in LNP. In addition, my study represents the first investigation into cheetah ecology in the country. During 2011-2012 we documented 18 mammalian carnivore species and 21 ungulate species with the use of camera-traps (Appendix I). Preliminary assessment of photographic data provided evidence of a resident population of cheetah that included multiple females with young (Andresen *et al*., 2013). The lion population was estimated at 66 individuals or 0.99/100 km^2 (Everatt, 2013). Other large carnivores in the area include leopard, spotted hyaena and wild dog (*Lycaon pictus*), although we only documented a single pack of six animals of the latter. The principal prey species of cheetah in this part of Africa are impala (*Aepyceros melampus*). Other important prey species include common duiker (*Sylvicapra grimmia*) steenbok (*Raphicerus campestris*) and kudu (*Tragelaphus strepsiceros*) (Hayward *et al*., 2006).

Figure 1.1. Location of the Limpopo National Park (dark green) in Mozambique and southern Africa, and in relation to the Greater Limpopo Transfrontier Park (light green). The area to the south of LNP in Mozambique (light green) has been recently separated by a wildlife barrier fence.

Figure 1.2. Scenes from the Limpopo National Park in Mozambique. From left to right: view of the Shingwedzi River drainage line; painted houses in the village of Chimangue; a herd of impala; a bushmeat hunter and his dogs.

Why study cheetah in Limpopo National Park?

There are several characteristics of LNP that contributed to my decision to conduct scientific research there. First, in order to identify how an occupancy modelling approach could be feasibly used to quantify the population status of less known cheetah populations, I needed to select a place that could be considered characteristic of cheetahs remaining range where data are deficient. I selected LNP because the infrastructure (i.e., road networks) is limited, predator/prey populations are low and cheetahs had rarely been seen. Second, I saw LNP as an ideal place to investigate the ecological requirements of cheetah in the context of human pressures including agro-pastoralism and bushmeat hunting. While cheetah habitat use has been investigated in commercial game and cattle ranches (Marker, 2002; Muntifering *et al*., 2005; Marker *et al*., 2008), I wanted to explore the impact of rural subsistence living on cheetah ecology. Finally, LNP forms part of a transboundary conservation area that cheetah have the potential to benefit from (Andresen *et al*., 2012). LNP offers considerable habitat for range recovery, and can also potentially serve as a 'gateway' for cheetah to recolonize other nearby reserves in Mozambique (i.e., Banhine and Zinave National Parks). By collecting baseline data on cheetah occurrence and limiting factors in LNP, this study can serve as an important benchmark that future change can be measured against.

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CHAPTER 2

Use of site occupancy models for targeted monitoring of cheetah

Abstract

The cheetah (*Acinonyx jubatus*) has suffered dramatic range contractions and population declines as a result of habitat degradation, prey depletion and conflict with humans. Of further concern is that many of Africa's remaining cheetah populations persist in human-dominated and highly fragmented landscapes, where their ecology is poorly understood and population data are lacking. Presence-absence surveys may be a practical means to collect these data, however, failing to account for detection error can lead to biased estimates and misleading inferences; potentially having deleterious consequences for species conservation. The goal of this study was to identify how an occupancy modelling technique that explicitly accounts for detectability could be used for quantifying cheetah status in human-impacted landscapes. Replicated camera-trap and track surveys of 100 km^2 sample units were used to estimate the proportion of area occupied by cheetah and to determine the survey effort required to inform conservation planning. Based on our results, 16 km (±SE = 12-22) of walking or 193 camera-trap nights (±SE = 141-292) are required to confirm cheetah absence at a given 100 km^2 grid cell (with 95% certainty). Accounting for detection resulted in an overall cheetah occurrence estimate of 0.40 (±SE = 0.13), which is 16% higher than the traditional presence-absence estimate that ignores detection error. We test *a priori* hypotheses to investigate factors limiting cheetah using an occurrence probability model of their preferred prey. The results show that both cheetah and their prey were strongly negatively influenced by human settlements. Our study provides an unbiased estimate

of occurrence that can be used to compare status across different sites and as a basis for long-term monitoring. Based on our results, we suggest that track and/or camera-trap surveys coupled with site occupancy models may be useful for targeted monitoring of cheetah across their distribution.

Introduction

Prey depletion, habitat degradation and conflict with humans have resulted in considerable population declines and range contractions of the cheetah *Acinonyx jubatus* (Ray, Hunter & Zigouris, 2005). Of further concern is that many of Africa's remaining cheetah populations persist in human-dominated, highly fragmented landscapes where they are at risk of persecution (IUCN/SSC, 2007). Cheetah conservation management is hindered because few studies have investigated their ecology in human-impacted landscapes (but see Marker *et al*., 2003). Evidence-based management requires reliable population data as well as sound knowledge of the factors driving system change (Conroy & Carroll, 2009). A targeted monitoring approach that uses hypothesis testing to gain knowledge of the underlying mechanisms behind system change can be an efficient means to meet these goals (Yoccoz, Nichols & Boulinier*,* 2001).

Acquiring absolute abundance or density estimates for cheetah is both time and resource consuming and many of the required methodologies cannot be practically implemented across their distribution (Bashir *et al*., 2004). The collection of presence-absence data by contrast is cost-effective and surveys can be implemented rapidly across large areas. However, neglecting to account for detection error can provide biased estimates and misleading inferences (Anderson, 2001; MacKenzie *et al*., 2002). For example, detection error can lead to inaccurate species distribution models (Lobo, Jiménez-Valverde & Hortal, 2010), underestimates of areas where conservation interventions are required (Rondinini *et al.*, 2006) and distorted species-habitat relationships (Gu & Swihart, 2004). Efforts to standardize data collection methodologies cannot account for all heterogeneity in detection over space and time (Anderson, 2001; Yoccoz *et al.,* 2001; MacKenzie *et al.*, 2006).

Where absolute abundance estimates cannot be practically obtained, occupancy (i.e., the proportion of area occupied or probability of site use) is considered a robust alternative state variable (Karanth, Nichols & Kumar, 2004; MacKenzie *et al.*, 2004). Occupancy is a useful metric for assessing species status (Conroy & Carroll, 2009) and is a natural state variable for investigating species distribution, habitat relationships and meta-population dynamics. Since detection/non-detection data are relatively easy to obtain, occurrence models are useful for long-term monitoring programs and can be used to estimate the dynamic processes of local extinction and colonization (MacKenzie *et al.*, 2006). The occupancy models of MacKenzie *et al.*, (2002) use replicated detection/non-detection surveys to estimate a detection probability and derive unbiased estimates of occurrence. Hierarchical ranking of covariates are used to explain heterogeneity in occupancy and detectability simultaneously; thereby permitting the testing of ecological hypothesis and providing inferences about variables that affect distribution and resource selection (MacKenzie *et al.*, 2006).

The goal of this study was to identify how an occupancy modelling approach could be used to quantify cheetah status and to obtain inferences on the factors limiting their occurrence in a human-impacted landscape. We provide initial occupancy and detectability estimates for the species that can be used to explore sampling design trade-offs and illustrate how detection data can be used to design robust ecological studies and occupancy monitoring programs. Our study was conducted in the Limpopo National Park (LNP) in Mozambique, a legally protected area that is inhabited by both humans and livestock. LNP is potentially important habitat for cheetah because it borders on a protected population in the Kruger National Park (KNP) in South Africa, and could facilitate dispersal to other areas in Mozambique. However, prior to this study there had been no empirical investigation into cheetah status in the region. We applied replicated track and camera-trap surveys across a 2400 km^2 study area to provide baseline data on the status of cheetah in LNP and test *a priori* hypotheses to investigate factors that may be limiting cheetah using an occurrence probability model of their preferred prey.

Materials and Methods

Study area

The 8, 238 km^2 LNP is located in south-western Mozambique and forms a component of the Greater Limpopo Transfrontier Park. South Africa's KNP forms the western boundary, characterized by high wildlife densities, and the Limpopo River forms the northern and eastern boundaries, characterized by human settlements and habitat degradation. LNP is inhabited by approximately 6,500 humans residing in eight villages located in the core area of the park (Huggins *et al*., 2003) (Fig. 2.1). There is a limited road network and limited infrastructure. Settlements are characterized by free-grazing of livestock, packs of free-roaming domestic dogs (*Canis lupus familiaris*), land clearing for subsistence farming and 'bushmeat poaching' (illegal hunting of wildlife for local consumption). Large mammal populations were significantly depleted during armed conflict (1980-1992) in Mozambique (Hatton, Couto & Oglethorpe, 2001); however, the formation of LNP (2000) and removal of sections of fence along the KNP boundary provided the potential for movement of wildlife into the area.

As habitat generalists, cheetahs are able to persist in a broad array of woodland savannahs and were once widely distributed across southern Africa (IUNC/SSC, 2007). LNP is comprised of woodland savannah plains with short to tall woodlands, shrublands and thickets. The predominant landscape is sandveld, which is comprised of short woodlands and thickets on sandy substrates, characterized by the absence of well-defined drainage lines and the presence of pans (depressions flooded for long periods) (Stalmans *et al.,* 2004).

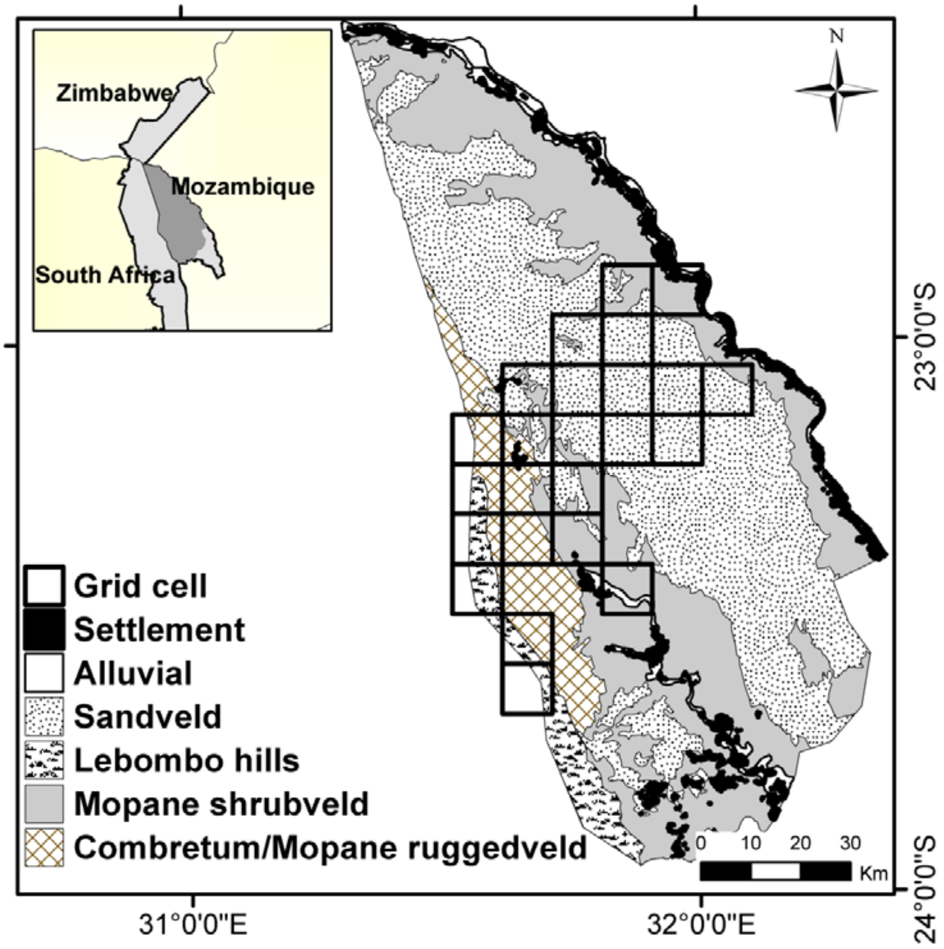

Figure 2.1. The Limpopo National Park (LNP) in Mozambique, bounded to the west by the Kruger National Park in South Africa, characterized by high wildlife densities, and to the east by the Limpopo River, characterized by human agro-pastoralist settlements; Surveyed grid cells overlaid across a gradient of distinguishing landscapes and settlement areas. Inset map: Location of LNP (dark grey) in relation to the Greater Limpopo Transfrontier Park (light grey) and to Zimbabwe and South Africa (Shape file: gltp_lnpLandscapes, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch).

Survey design

Model assumptions and identification of covariates

In this study, the parameter of interest is the proportion of area occupied by cheetah, and the following assumptions of an occupancy (Ψ) model are made: (1) Sites are closed to changes in occupancy (i.e., are either occupied or unoccupied *by the species* during the sampling period); (2) Detection histories at each site and survey are independent ; (3) Species are never falsely identified (4); Heterogeneity in occupancy and detection probability is modelled with covariates (MacKenzie *et al*., 2006). Cheetah home ranges have been estimated at 126-185 km^2 in the adjoining KNP (Broomhall, Mills & du Toit, 2003). To interpret our estimator (Ψ) as the proportion of area occupied, we defined sample units (sites) as 10 x 10 km grid cells, considering this a conservative size to assume that if cheetah were detected within a grid cell the entire unit was occupied, but large enough to minimize the risk of spatial autocorrelation among neighbouring grid cells. Our survey design was limited by lack of accessibility to large portions of LNP. Given these constraints, we selected 24 grid cells to be surveyed such that the resulting area represented approximately one third of LNP and followed a gradient of distinguishing bio-physical features and thus incorporated important environmental strata (Fig. 2.1).

Cheetahs become independent of their mother at approximately 18 months, but will often remain in their natal range for several additional months. Males are known to centre their territories on areas where females cluster around prey resources (Caro, 1994). To minimize the chance that an unoccupied cell would become colonized by dispersers or that an occupied cell would become permanently vacated by the species during our survey, we sampled over a 5 month period (May 7 to October 13, 2012) in the dry season.

The utilization of multiple detection methods may increase survey efficiency and the probability of detecting low density carnivores (O'Connell & Bailey, 2011). We chose to use two sampling methodologies; camera-traps and track transects. Sample occasions were represented by 14 day camera-trap surveys and temporally replicated 3 km track transects (replicates separated by $\geq$14 days). Twenty grid cells were sampled with cameras ($\bar{x} = 90$ camera-trap nights/grid cell) and 23 were sampled with track surveys ($\bar{x}$ = 13 km/grid cell). We note that the occupancy model accounts for unequal sampling across sites (MacKenzie *et al*., 2002). Due to the limited road network, track transects were conducted along game trails on foot. Within each grid cell, camera stations ($\bar{x} = 2$) and/or fixed length track transects ($\bar{x} = 2$) were established to optimize spatial representation. Grid cells were sub-divided into quadrants and one from each cell was randomly selected for obligate sampling. Because of logistical constraints three cells were sampled in only one quadrant while the rest were sampled in 2-4. Multiple surveys were not conducted within the same quadrant over the same 14 day interval. Detections were represented by unambiguously identified cheetah tracks or photographs.

We identified three predictor variables (covariates) to explain heterogeneity in cheetah occurrence in LNP. These were prey resource, anthropogenic pressure and landscape structure for prey capture (Table 2.1). We investigated the influence of prey availability on cheetah occurrence using a probability of occurrence model of their main prey species. The preferred prey of cheetah in the region are impala (*Aepyceros melampus*) (Hayward *et al*., 2007), which are a non-migratory, comparatively abundant antelope (Estes, 1992). We assume that our occurrence probability model is biologically representative of the encounter probability of preferred prey for cheetah.

A prey occupancy model for the probability of impala site use (Ψ) was developed for each grid cell based on detection/non-detection surveys of 260 sites ($\bar{x}$ = 11/ grid cell) conducted during September 9, 2011-October 13, 2012. Sampling occasions ($\bar{x}$ = 5 /site) were represented by temporally replicated 1 km transects (n = 602) or by 7 day camera-trap intervals (n = 666). Detections were represented by sightings of impala along transects or photographs recorded by camera-traps. Of the 260 sites, 184 were sampled only by transects, 48 were sampled by both a transect and a camera station and 28 were sampled only by camera-traps. Where sites were surveyed by both methods during the same 7 day interval, occasions/detections were pooled. We note that the closure assumption could be relaxed because our parameter of interest was site use (MacKenzie *et al*., 2006). An impala occupancy model was developed from 360 camera-trap detections and 154 sightings along transects (maximum value = 1). To explain heterogeneity in impala site use, we included covariates to account for variation in nutritional quality of vegetation, availability of surface water and human disturbance. We used four landscape covariates to account for variation in nutritional quality of vegetation, based on distinct landscape types that describe differences in vegetation communities and underlying geology, as classified by Stalmans *et al.,* (2004). The corresponding landscape type for each site was evaluated using a shape file of distinguishing landscapes (gltp_lnpLandscapes, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch). In addition, we considered the proximity to water and to agro-pastoralist settlements (Table 2.2). Mean impala occurrence for each grid cell was extracted using Spatial Analyst ArcGIS 9.3.1 from the inverse weighted distance of impala $\widehat{\overline{\Psi}}$.

Other than prey resources, cheetah may also be influenced by anthropogenic factors including persecution by livestock herders, accidental snaring (IUCN/SSC, 2007) and harassment from domestic dogs. We considered the proximity to human-settlements as a proxy for these factors, calculated as the mean Euclidean distance of each 30 m x 30 m pixel in a grid cell to the nearest human settlement using a raster layer of landscape cover classified as 'villages' (GLTF Landcov_Banhine, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch) and Spatial Analyst ArcGIS 9.3.1.

Cheetahs are specialized predators, requiring concealment for stalking and suitable terrain for short high-speed chases (Estes, 1992). In woodland savannahs where there is adequate cover for concealment, cheetahs have been shown to center their territories on more open habitats (Broomhall *et al*., 2003). LNP is characterized by continuous woodland, shrubland or bushland with small, discrete open patches of land (i.e., pans) (Stalmans *et al*., 2004). Considering that these features may be limiting for cheetah, we included a covariate 'open habitat patches' as proxy for the landscape structure offering suitable prey capture. The proportion of a grid cell represented by open habitat patches was evaluated using a raster layer of landscape cover classified as 'bare' or 'grassland' (GLTF Landcov_Banhine, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch).

Table 2.1. Predictor variables (covariates) expected to influence cheetah occupancy, their unit, relationship to cheetah fitness, range of values and *a priori* prediction of the direction of impact.

Covariates (unit)	**Relationship to cheetah fitness**	**Range of values (mean)**	***A priori* prediction**
Preferred prey (occurrence probability)	Encounter probability of food resources	0.11-0.79 (0.44)	+
Agro-pastoralist settlement (km)	Persecution from livestock herders, harassment from domestic dogs, loss of cover	2.01-20.41 (11.17)	-
Open habitat patches (%)	Landscape structure for prey capture (large edge for concealment and suitable terrain for high speed chase)	0.09-5.85 (2.63)	+

Table 2.2. Predictor variables (covariates) expected to influence impala site use in the Limpopo National Park, Mozambique, their description and value.

Covariate	Description	Value
Mopane shrubveld	Shrublands and thickets on calcerous soils	1 or 0†
Sandveld	Short woodlands and thickets on sandy substrates	1 or 0†
Lebombo Hills	Short woodland to tall shrubland on stony, rhylolite soils, undulating hills	1 or 0†
Combretum/Mopane Ruggedveld	Short to tall woodlands and tall shrublands on shallow clay soils	1 or 0†
Water	Drainage lines/seepage points	Proximity (km)*
Anthropogenic	Cultivation and livestock grazing (agro-pastoralist settlements)	Proximity (km)*

†gltp_lnpLandscapes, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch
*GLTF Landcov_Banhine, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch

Data collection

Fixed length, 3 km track transects were walked on suitable substrate by LA and KE during morning and afternoon hours. One digital remote camera (Reconyx HC500, Bushnell Trophy Cam, or SpyCam) was placed at each camera station approximately 0.15 m from the ground, towards the trail. Sampling (hereafter surveys) were conducted where one would expect to find cheetah if they were present (i.e., trails, waterholes, open habitat patches). Male cheetah exhibit scent-marking behaviour and will deposit their faeces and urine on conspicuous objects (e.g., termite mounds, fallen trees or exposed rocks) (Caro, 1994). We actively searched for locations that cheetahs may have scent-marked in an effort to increase the probability that they would be detected (Fig. 2.2).

Figure 2.2. Data collection methodologies. From left to right: Cheetah tracks recorded on a track survey; the location of four cheetah scent marking sites (termite mound, fallen tree, clump of trees and exposed rock); a cheetah photographed by a camera-trap.

Data analysis

The maximum likelihood estimates for cheetah and impala occupancy (*Ψ*) and detection probability (*p*) were estimated in program PRESENCE ver 4.4 using single season occupancy models.

Prey occupancy model

Impala detection histories from camera and track surveys were compiled into a single detection matrix for each site (n = 260), assigning a '1' for surveys where impala were detected and '0' where impala were not detected. Following this, a survey-specific matrix was constructed to account for differences in sampling methods, recording a '1' for camera-trap surveys and a '0' for transect surveys (excluding pooled samples). An additional survey-specific matrix was constructed, recording a '1' for occasions represented by both a camera-trap and a transect survey (pooled samples) and a '0' for occasions represented by only one method. Finally, a survey-specific matrix was constructed, recording a '1' or '0' for surveys conducted during wet (November 1-April 30) and dry (May 1-October 31) seasons, respectively. Continuous variables were assessed for collinearity (none found) using a Pearson's r test (with cut off value of r = 0.5) (Green, 1979), and were standardized using z-transformation prior to inclusion into models. Variables found to be correlated were not included in the same models. Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2002) was used in the model selection procedure to rank the relative support for different models in order of parsimony, with the effective sample size defined conservatively as the number of sites. First, we considered covariates for impala detectability (*p*). We include survey method (Mm), pooled samples (Mp) and season (SN) as covariates for impala *p* in subsequent analysis of impala site use (*Ψ*); models containing these covariates were strongly supported ($\sum w > 0.99$; $\Delta AICc < 2$) and ranked higher than the constant model ($\Delta AICc = 12.77$). To determine the factors that best explained impala occurrence, we compared all possible combinations of Ψ covariates ($n = 63$ models). AICc weights were used to evaluate the weight of evidence for each model, and were summed for all models containing each predictor variable. Variables resulting in high summed model weights were considered more important in explaining heterogeneity in occupancy. We considered all models showing good support (AICc $\Delta < 7$), and obtained final parameter estimates from a 95% confidence set ($\sum w > 0.95$), using a model-averaging technique (Burnham & Anderson, 2002). The strength and direction of impact of covariates was determined by examining the beta-coefficient (β) values. Covariates were considered to have strong or robust impact if their β-coefficients were significant ($\beta \pm 1.96 \times SE$ not overlapping 0) (MacKenzie *et al*., 2006). Goodness of fit for the general model was tested using chi-square tests and 10,000 boot strap samples (Burnham & Anderson, 2002).

Cheetah occupancy model

Cheetah detection histories from camera and track surveys were compiled into a single detection matrix for each sample unit (100 km^2 grid cell, $n = 24$), assigning a ‘1’ for surveys where cheetah were detected, and a ‘0’ where cheetah were not detected. Following this, a survey-specific matrix was constructed to account for differences in sampling methods (as above). Five scent-marking sites were located in three grid cells over the survey period. Considering that multiple detections at these sites were likely due to a dependent behavioural response, we applied a ‘removal design’ as recommended by MacKenzie *et al.* (2006); removing surveys conducted at scent-marking sites after cheetah were first detected.

To investigate factors that may be limiting cheetah occurrence in LNP, we used AICc to compare a simple set of three univariate models representing our *a priori* hypothesis (Table 2.1) to the model that accounts for variation in detectability with survey method, $\Psi(.)p(\mathrm{M})$ (the inclusion of method outranked the constant model (ΔAICc = 6.45)). Models with ΔAICc<2 were considered more strongly supported (Burnham & Anderson, 2002). The above mentioned procedures for parameter estimation and goodness of fit were applied.

To provide data that can be used to design occupancy surveys for cheetah, we generated detectability curves and calculated the minimum number of surveys required to infer absence with a given certainty. The probability P_k of detecting cheetah at least once at an occupied site after k repeat surveys was calculated as $P_k = 1-(1-p)^k$ where p is the per-survey detection probability of the species MacKenzie & Royle, (2005). Following this, the minimum number of surveys required (Nmin) to infer cheetah absence with a 95% certainty was calculated as (Kéry, 2002): $Nmin = log(0.05)/log(1-p)$. We estimated the optimal number of sites (S) to survey to achieve a given model precision in the occupancy estimate for Ψ = 0.2-0.9 using MacKenzie & Royle (2005):

$$S = \frac{\psi}{Var(\hat{\psi})}\left[(1-\psi)+\frac{(1-p^*)}{p^*-Np(1-p)^{Nmin-1}}\right]$$

Where p^* is the expected probability of detecting cheetah at least once (i.e., $p^* = 1-(1-p)^{Nmin}$ where p is the averaged parameter estimate of cheetah detectability).

Results

A total survey effort of 1903 camera trap nights across 47 camera stations and 303 km of transects resulted in 60 cheetah photographic events and 22 sets of cheetah tracks. The final data set consisted of 197 surveys, with each cell sampled on $\bar{x} = 8$ occasions ($\bar{x} = 5$ camera, $\bar{x} = 4$ track).

Prey occupancy model

The factor contributing the most to impala site use was proximity to agro-pastoralist settlements ($\sum$w = 0.96; Table 2.3), which strongly decreased with increasing proximity ($\hat{\beta} = -1.569$, SE 0.385; Table 2.4; Fig. 2.3). The model averaged estimate of impala detectability was <1 ($\hat{\bar{p}} =$ 0.285, SE = 0.038) and the overall estimate of occurrence was $\hat{\bar{\Psi}} = 0.482$ (SE = 0.090), or impala used approximately 48% of the sites we surveyed. Impala occurrence was significantly higher in the Lebombo hills ($\hat{\beta} = 1.511$, SE = 0.558) than in the other landscapes (Table 2.4). There was no evidence of lack of fit (p = 0.22) or overdispersion ($\hat{c} = 1.09$).

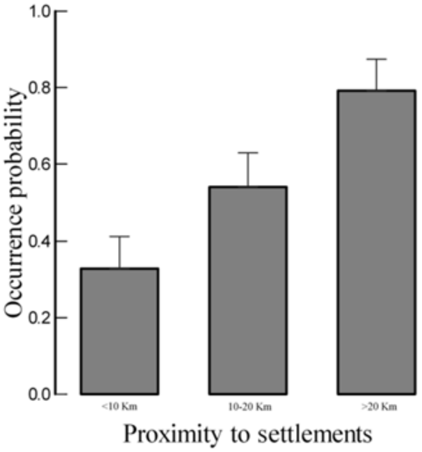

Figure 2.3. Influence of agro-pastoralist settlements use on the occurrence probability of cheetahs preferred prey. Site occupancy estimates are based on the averaged model ($\sum$w >0.95). Error bars show +SE.

Table 2.3. Model selection procedure for factors influencing impala site occupancy (Ψ) in the Limpopo National Park, Mozambique. Covariates considered are mopane shrubveld (MS), Lebombo hills (LH), combretum/mopane ruggedveld (CM), sandveld (SV), agro-pastoralist settlements (S) and water (W). Impala detectability (p) varies with method (Mm), pooled samples (Mp) and season (SN). Number of sites = 260.

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(S,MS,CM,SV)p(Mm,Mp,SN)	770.13	0.00	0.27	9	751.41
Ψ(S,CM,LH)p(Mm,Mp,SN)	771.05	0.92	0.17	8	754.48
Ψ(S,CM,LH,SV)p(Mm,Mp,SN)	771.71	1.58	0.12	9	752.99
Ψ(S,LH,SV)p(Mm,Mp,SN)	771.72	1.59	0.12	8	755.15
Ψ(S,CM,LH,W)p(Mm,Mp,SN)	773.03	2.90	0.06	9	754.31
Ψ(S,CM,LH,MS)p(Mm,Mp,SN)	773.08	2.95	0.06	9	754.36
Ψ(S,CM,SV,W)p(Mm,Mp,SN)	773.80	3.67	0.04	9	755.08
Ψ(S,CM)p(Mm,Mp,SN)	773.91	3.78	0.04	7	759.47
Ψ(S,CM,SV)p(Mm,Mp,SN)	775.54	5.41	0.02	8	758.97
Ψ(S,CM,MS)p(Mm,Mp,SN)	775.61	5.48	0.02	8	759.04
Ψ(S,CM,W)p(Mm,Mp,SN)	775.64	5.51	0.02	8	759.07
Ψ(S,CM,MS,SV)p(Mm,Mp,SN)	776.37	6.24	0.01	9	757.65
Ψ(.)p(Mm,Mp,SN)	795.81	25.68	0.00	5	785.57

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

Table 2.4. Covariates influencing impala site use ranked according to their relative contribution (summed model weights ∑w), β-coefficients and associated standard errors (SE).

Covariate	$\hat{\beta}$	**SE**	**∑w**
Agro-pastoralist settlements	**-1.569**	**0.385**	0.96
Combretum/Mopane	**-3.398**	**0.938**	0.85
Sandveld	**-1.894**	**0.672**	0.59
Lebombo hills	**1.511**	**0.558**	0.52
Mopane shrubveld	-1.229	0.654	0.36
Water	0.114	0.258	0.12

+/- sign indicates direction of influence; bold entries indicate robust impact (β ±1.96 x SE not overlapping zero) (MacKenzie *et al*., 2006).

Cheetah occupancy and detectability

Given presence in a grid cell, the probability of detecting cheetah on a single survey was <1, $\hat{p}$ = 0.295 (SE = 0.076) (Table 2.5). Accounting for detectability resulted in a model averaged (∑w >0.95) estimate of $\hat{\hat{\Psi}}$ = 0.395 (SE = 0.129), or cheetah occupied approximately 40% of a 2400 km^2 sample of potential habitat. This estimate is 16% higher than the naïve estimate (0.333) that fails to account for detection error. We mapped the variation in site occupancy estimates of cheetah across grid cells (Fig. 2.4).

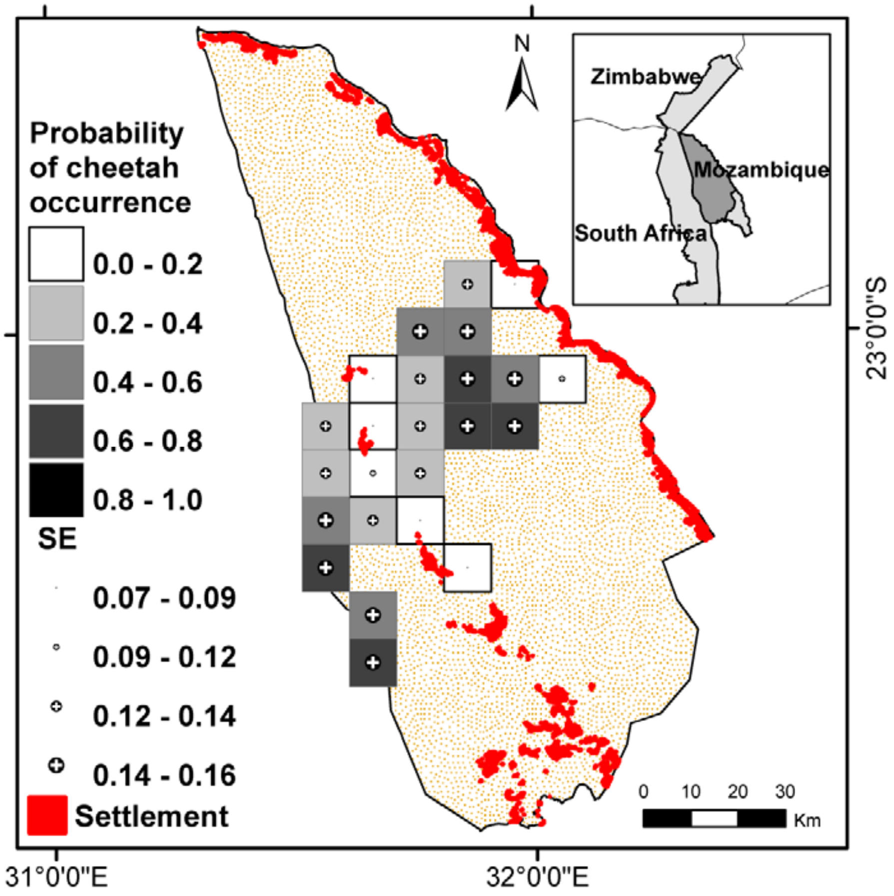

Figure 2.4. Spatial variation in site occupancy (Ψ) estimates of cheetah and associated standard errors (SE) in the Limpopo National Park, Mozambique. Estimates are based on the averaged model (∑w > 0.95) from 197 surveys. Probability of occurrence accounting for occurrence probability of preferred prey and agro-pastoralist use and accounting for variation in detection probability.

Table 2.5. Model selection procedure for factors influencing cheetah site occupancy (Ψ) obtained from 197 surveys of 24 (100 km^2) grid cells in the Limpopo National Park, Mozambique. Hypothesis considered are the influence of prey (P) agro-pastoralist settlements (S) and open-habitat patches (O). Cheetah detectability (p) varies with survey method (M). Ψ(.) assumes the parameter is constant. β coefficients for the variables direction and strength of influence on Ψ are also shown.

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2L**	**$\hat{\hat{\Psi}}$(SE)**	**$\hat{\hat{p}}$(SE)**	**$\hat{\beta}$(SE)**
Ψ(S) p(M)	113.27	0.00	0.69	4	103.16	0.40(0.13)	0.29(0.08)	**-1.60 (0.78)**
Ψ(P) p(M)	116.28	3.01	0.15	4	106.17	0.40(0.13)	0.30(0.08)	1.06 (0.63)
Ψ(.) p(M)	117.07	3.80	0.10	3	109.87	0.39(0.11)	0.30(0.08)	
Ψ(O) p(M)	119.61	6.34	0.03	4	109.50	0.39(0.15)	0.29(0.08)	-0.29 (0.48)
Ψ(.) p(.)	119.72	6.45	0.03	2	115.15	0.41(0.12)	0.29(0.06)	
Model Average						**0.40(0.13)**	**0.30(0.08)**	

Model AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2L); mean estimated occupancy ($\hat{\hat{\Psi}}$) and detectability ($\hat{\hat{p}}$) parameters; associated standard errors (SE). Bold entries for $\hat{\beta}$ indicate robust impact (β ± 1.96 x SE not overlapping zero) (MacKenzie *et al*., 2006).

There was considerable support for the hypothesis that human disturbance was a limiting factor of cheetah occurrence (ΔAICc<2; ∑w = 0.69%). Cheetah occurrence strongly decreased with proximity to settlements ($\hat{\beta}$ = -1.599, SE = 0.781; Fig. 2.5). Mean site occupancy was $\hat{\hat{\Psi}}$ = 0.558 (SE = 0.145) at sites that were >10 km from settlements (n = 13) compared to $\hat{\hat{\Psi}}$ = 0.179 (SE = 0.101) at sites that were <10 km from settlements (n = 11). Cheetah occurrence was greater in grid cells with greater impala occurrence (β = 1.062, SE = 0.630), however, there was less support for the prey hypothesis (ΔAICc = 3.01), which only slightly outperformed the constant model (ΔAICc = 3.80). There was little evidence that cheetah were limited by per cent openness at this spatial scale (ΔAICc = 6.34; $\hat{\beta}$ = -0.285, SE = 0.480). A goodness of fit test showed no evidence of lack of fit (p = 0.56) or overdispersion ($\hat{c}$ = 0.25).

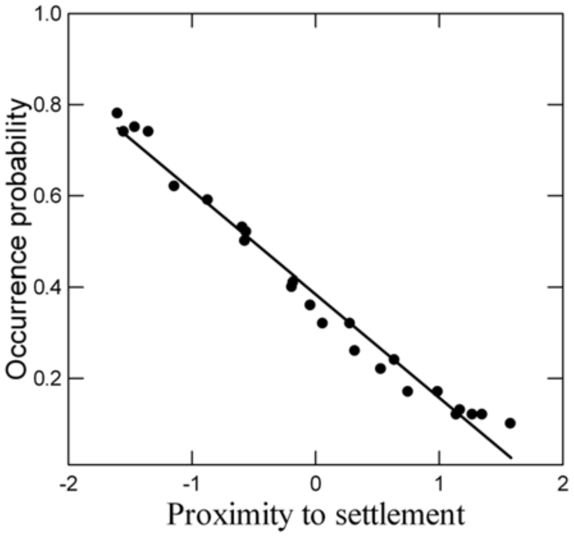

Figure 2.5. Influence of agro-pastoralist settlements use on the probability of cheetah occurrence. The variable proximity to settlement is normalized; Site occupancy estimates are based on the averaged model (∑w >0.95).

Based on the model averaged estimate of cheetah detectability (0.295) and our mean number of surveys per grid cell (8.21), the power of our survey was $1\text{-}(1\text{-}0.295)^{8.21} = 0.94$, that is, we can confirm cheetah absence with 94% certainty. Given cheetah presence in a 100 km^2 grid cell, the probability ($\hat{\bar{p}} = 0.431$, SE = 0.094) of detecting the species on a 3 km track survey was greater than on a 14 day camera-trap survey ($\hat{\bar{p}} = 0.195$, SE = 0.062). The power of track and camera surveys to detect cheetah at least once in an occupied grid cell is provided in Fig. 2.6. We estimate that 16 km (±SE = 12-22) of walking or 193 camera-trap nights (±SE = 141-292) are required to confirm cheetah absence in a given grid cell (with 95% certainty). The optimal number of grid cells to survey to achieve standard errors of 0.10, 0.075 and 0.05 (where $\Psi = 0.2\text{-}0.9$) was estimated to be 28, 50 and 113 sites, respectively (Fig. 2.7).

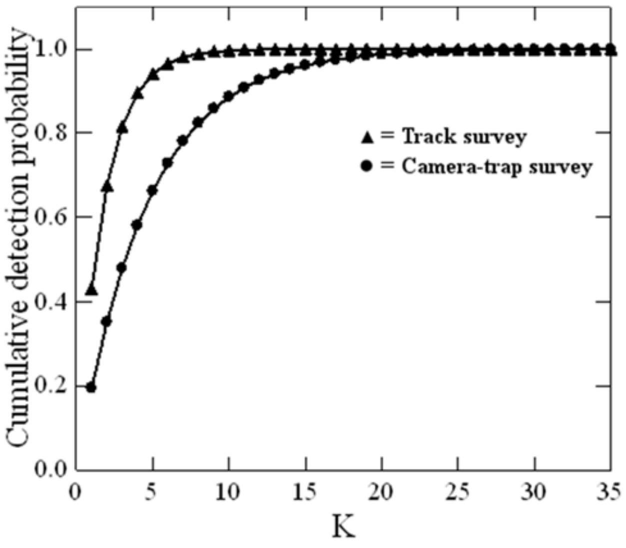

Figure 2.6. Probability of detecting cheetah at least once at 100 km^2 site that is in use after k surveys using different survey methodologies; where a camera-trap survey is a 14 day sample and a track survey is a (temporally replicated) 3 km transect. Detection probability estimates are based on the averaged model (∑w >0.95).

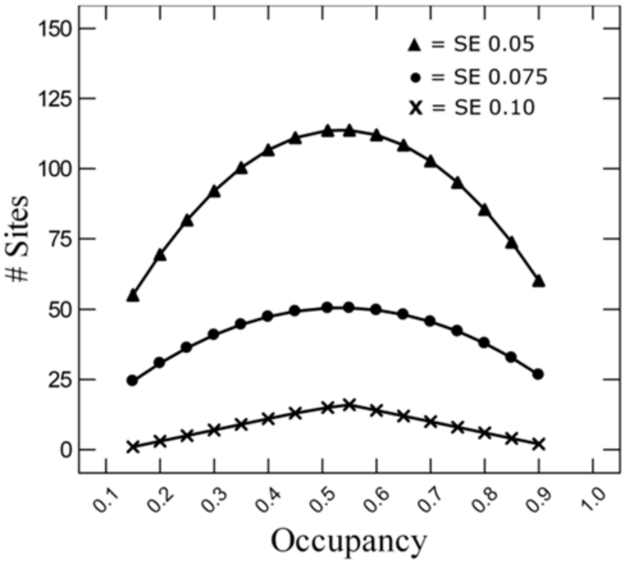

Figure 2.7. Total number of 100 km^2 grid cells to survey to achieve a given precision in the occupancy estimate as a function of occupancy probability. Curves are based on the averaged model (∑w >0.95) estimates of detectability and the estimated the minimum number of surveys required to be 95% certain of cheetah absence. The optimal number of sites to survey corresponds to value that can achieve a given precision at all occupancy rates.

Discussion

Informed conservation management of the cheetah requires reliable status assessments and inferences on their ability to utilize human-influenced landscapes. However, there are few quantitative data on cheetah population status or distribution and current estimates are primarily based on questionnaire surveys (Bashir *et al*., 2004). This study provides the first quantification of cheetah status in a recently established National Park in Mozambique, which is also the first for the country. Our results thus provide an important benchmark that future change can be measured against.

This study has demonstrated the feasibility of quantifying cheetah status in a location with limited infrastructure using an occupancy modelling approach that explicitly accounts for species detectability. The use of replicated detection/non-detection surveys enabled us to estimate the probability of detecting cheetah and to provide an unbiased estimate of occurrence that can be used to compare status across different sites and as a basis for long-term monitoring. Given presence, the probability of detecting cheetah on a single survey was <1 ($p = 0.295$). By accounting for detectability, we estimate that cheetah occupy approximately 40% of a 2400 km^2 sample of potential habitat. This estimate is 16% higher that the naïve estimate that fails to account for detection error. Failing to account for detectability in distributional assessments of cheetah is problematic because it can lead to populations being overlooked that require conservation interventions and misleading inferences on factors influencing their occurrence.

Knowledge of the survey effort required to provide robust occupancy estimates is critical for the design of ecological studies that seek to inform conservation plans. Our study demonstrates the value of using detectability estimates to construct robust survey design for monitoring cheetah occurrence. The power of a study to detect a decline in occupancy corresponds to the number of surveys required to infer absence (MacKenzie & Royle, 2005). Based on our results, 16 km of walking or 193 camera-trap nights are required to confirm cheetah absence at a given 100 km^2 grid cell (with 95% certainty) in LNP. We recommend surveying 50 or 113 grid cells to achieve a standard error of 0.075 or 0.05 in the occupancy estimate (Fig. 2.7). This may be most logistically feasible using spatially replicated track surveys (Karanth *et al*., 2011) given the limited accessibility.

An occupancy approach is advantageous because it permits comparison between studies that differ in their survey methodologies, thereby allowing researchers to employ the method(s) that are best suited for their location and study objectives. That unequal sampling across sites can be accounted for is logistically advantageous when accessibility is limited. Robust occurrence estimates require sufficiently high detection probabilities (i.e., >0.15) (MacKenzie *et al*., 2002). In our study, the probability of detecting cheetah using either method was adequate; however, track surveys out-performed camera surveys: Given presence in a 100 km^2 grid cell, the probability of detecting cheetah was 55% greater on a 3 km track survey than on a 14 day camera-trap survey. Incorporating scent-marking sites helped us to achieve an adequate detection rate; however, incorporating these sites may cause dependency between sampling occasions. Cheetahs visit scent-marking sites frequently (Caro, 1994) and therefore once a surveyor knows where one is located the probability of detecting cheetah on subsequent surveys is increased. We suggest following a ‘partial removal design’ (MacKenzie *et al*., 2006), halting surveys at scent-marking sites after cheetah have been detected.

We selected grid cells to be slightly smaller than home ranges to reduce the likelihood of over-estimating the proportion of area occupied by cheetah. We acknowledge that sampling adjacent cells may have introduced spatial dependency; however, we aimed to reduce spatial autocorrelation by selecting grid cells that were approximate to home range size. Previous authors have raised concern that cheetah's tendency to temporarily cluster around resources may result in biased estimates (Bashir *et al*., 2004). Future studies might consider multi-scale models (Mordecai *et al*., 2011) or sampling in a checkerboard fashion for addressing spatial dependency.

Our results demonstrate that cheetah can persist in landscapes impacted by cultivation and livestock. However, we found that both cheetah and their preferred prey were strongly negatively influenced by proximity to agro-pastoralist human settlements (Tables 2.3-2.5). Cheetah occurrence was low in the core area of the park that contains villages and near agro-pastoralist communities along the eastern park boundary (Fig. 2.4). These results indicate spatial avoidance of agro-pastoralist settlements, which may be a result of persecution. Alternatively, cheetah may be avoiding settlement areas due to harassment and/or kleptoparasitism from packs of free-ranging domestic dogs. LNP is presently undergoing resettlement of communities from the core area of the park (*pers. comm*. LNP Park Management) and it can be anticipated that cheetah will expand into these areas. A robust occupancy monitoring program in LNP could be achieved by conducting 16 km (±12-22) of track surveys within 50 grid cells (Fig. 2.7). Replicating occupancy surveys over time will permit the estimation of vital rates such as local extinction and colonization probabilities.

The status of cheetah in LNP has positive implications for other nearby protected areas in Mozambique (e.g., Banhine and Zinave National Parks) where cheetah are thought to have been extirpated but status is unknown (IUCN/SSC, 2007). Our study has shown that cheetah can persist in an agro-pastoralist landscape characteristic of these areas. As occupied range, LNP has the potential to facilitate cheetah recolonization to other locations and to prevent genetic impoverishment by providing connectivity to populations in South Africa. On the other hand, that cheetah exhibited low occurrence along the eastern park boundary may be indicative of edge effects (Woodroffe & Ginsberg, 1998), and therefore the ability for cheetah to exploit potential corridor areas needs to be assessed. Landscape-scale occupancy surveys could be used to identify meta-populations, which if coupled with prey occurrence models and anthropogenic information could permit the delineation of important corridors and suitable locations for reintroductions (Hebblewhite *et al*., 2011).

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CHAPTER THREE

Investigating cheetah habitat selection and species co-occurrence patterns in a human-impacted woodland savannah

Abstract

A sound understanding of the ecological requirements of carnivores in human-disturbed systems is essential for effective conservation planning. Few studies have investigated cheetah ecology in human-impacted systems, yet these landscapes form a large portion of the cheetah's remaining range. In this study, we used replicated detection/non-detection surveys and occupancy models to investigate cheetah habitat selection at two spatial scales in a human-impacted landscape in Mozambique. Cheetahs avoided settlement areas across both spatial scales; however, these features contributed considerably more to home range level use. More determining, however, was a strong spatial avoidance of sites with greater bushmeat poaching site use across both spatial scales. Moreover, cheetah exhibited a greater spatio-temporal avoidance of bushmeat poachers and their dogs then they did of lions, suggesting that humans were the greater competitor in the study system. Open habitat patches with dense edges, a landscape feature facilitating prey capture, were strongly determining at the temporary use scale, and contributed considerably more to cheetah site selection than prey occurrence. Cheetahs were negatively correlated with prey occurrence at the temporary patch scale, but we failed to find support for the hypothesis that this was due to interspecific competition with lions. Two-species occupancy models revealed that cheetah may elicit a strong behavioural response in their prey, manifesting as spatial avoidance. Our study provides some of the few data on cheetah habitat use in systems

impacted by human hunting and agro-pastoralism; conditions that may characterize many cheetah populations across Africa.

Introduction

Knowledge of carnivore ecology in human-modified environments is important for species conservation management (Mitchell & Hebblewhite, 2012). Formally protected areas may not be large enough to support viable large carnivore populations indefinitely (Woodroffe & Ginsberg, 1998), and many populations persist in human-disturbed landscapes (e.g., Athreya *et al*., 2013; Schuette *et al*., 2013).

Few studies have investigated cheetah (*Acinonyx jubatus*) ecology in human modified environments (*but see below*) yet these landscapes form a large portion of the cheetah's remaining range (Durant *et al*., 2008). While cheetah habitat use has been investigated in commercial game and cattle ranches in Namibia (Marker, 2002; Muntifering *et al*., 2005; Marker *et al*., 2008), there are even fewer data available on the impacts of rural subsistence living on cheetah (*but see* Maddox, 2003). While often associated with grassland plains (e.g., Caro, 1994; Durant *et al*., 2004), cheetah were once widely distributed (Turner, 1997), and inhabit a diverse range of more densely vegetated habitats (Purchase & du Toit, 2000; Mills, Broomhall & du Toit, 2004; Bisset & Bernard, 2005). Cheetah exhibit greater hunting success when prey form small group sizes (FitzGibbon, 1990) and tend to exploit the most common antelopes within their preferred weight range (23-56 kg) (Hayward *et al*., 2006). However, cheetahs have been shown to avoid areas of higher prey densities where their competitors, lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), are more abundant (Durant, 1998). That cheetah exploit common prey species and are able to utilize comparatively low prey density systems may contribute to their ability to persist in human-modified environments.

The proximate reasons for why an organism selects one habitat over another are ultimately driven by evolutionary processes relating directly to the organisms survival and reproduction (Hall, Krausman & Morrison, 1997; Krebs, 2009). Considering that prey is a primary component of a carnivore's habitat, any attempt at understanding carnivore habitat use should include a measure of these resources. While surrogates for prey resources such as vegetation cover and rainfall may be easily obtainable, these can perform poorly in systems where humans deplete prey (Mitchell & Hebblewhite, 2012).

The cost of prey capture for a predator is inherently great and features that facilitate prey catch-ability are key habitat components (Mitchell & Hebblewhite, 2012). Cheetahs exhibit a highly specialized rapid pursuit hunting strategy (Wilson *et al*., 2013), requiring both cover for stalking (Fitzgibbon, 1990; Caro, 1994) and suitable terrain for short high-speed chases (Bertram, 1979). In densely vegetated regions where there is no lack of cover, cheetahs are known to situate their territories to include more open habitats and to prefer open areas with denser habitat edges for hunting (Purchase & du Toit, 2000; Mills *et al*., 2004), even if these areas support lower prey densities (Broomhall, Mills & du Toit, 2003; Bisset & Bernard, 2007). Similarly, in the bush-encroached farmlands of Namibia, cheetahs were shown to select for sites with greater sighting visibility and grass cover, where prey densities were lower (Muntifiering *et al*., 2005). These patterns have led to the conclusion that cheetah habitat selection may be determined more by hunting requirements than by prey density (Hunter, 1998; Muntifering *et al*., 2005; Bisset & Bernard, 2007). The importance of prey catch-ability features over prey density in carnivore ecology has also been evidenced by studies of other large felids including lion

(Hopecraft, Sinclair & Packer, 2005), leopard (*Panthera pardus*) (Balme, Hunter & Slotow, 2007), and cougar (*Puma concolor*) (Laundre & Loxterman, 2006).

Competition and predation also influence species habitat selection (Krebs, 2009). Interspecific competition is common in natural systems and can also exert major influence on population size (Palomares & Caro, 1999; Krebs, 2009). Over time, species evolve competitive ability by becoming more efficient resource users and by developing mechanisms to reduce competition over resources. Theoretical models of competition indicate that between similar species, one may be displaced or both may reach stable equilibrium, where the species with less competitive ability may be held at a lower density than the other. Non-equilibrium communities exist when disturbance intervals (i.e., fire, land clearing, predation and disease) are shorter than recovery times (Krebs, 2009).

Cheetah and lion are large felids that have co-occurred for the past 3.5 million years (Turner, 1997) and there are numerous examples of mechanisms thought to facilitate species coexistence. For instance, cheetahs have evolved a highly specialized hunting strategy (Turner, 1997; Wilson *et al*., 2013) and the two species differ in their temporal patterns (Pienaar, 1969; Hayward & Slotow, 2009) and prey preferences (Hayward *et al*., 2006). Nevertheless, being of much smaller stature (Estes, 1992), cheetahs suffer from interspecific competition including kleptoparasitism (Caro, 1994) and intraguild predation (Laurenson, 1994). In the Serengeti plains of Tanzania, cheetahs experience lower reproductive success when lion densities are higher (Kelly *et al*., 1998), and exhibit avoidance behaviour to reduce competition (Durant, 1998; 2000). However, in less open habitats where there is increased cover for concealment, interspecific competition is thought to be reduced (Mills *et al*., 2004; Bisset & Bernard, 2007).

An important aspect of habitat selection is the effect of scale on its interpretation (Johnson, 1980; Orians & Wittenberger, 1991). The selection of habitats can be seen as a hierarchical biological process; where animals first select for the home ranges, and then for patches where daily resource use decisions are made (Johnson, 1980). Habitat selection can be scale-dependent if the fitness-related value of habitats differs between levels (e.g., Rettie & Messier, 2000; Dickson & Beier, 2002; McLoughlin *et al*., 2002; Ciarniello *et al*., 2007). Rettie & Messier (2000) suggested that factors influencing selection at coarser spatial scales (e.g., home ranges) may be most limiting to species fitness, whereas less-important limiting factors may contribute to daily selection patterns at finer spatial scales (e.g., patches within home ranges).

Detection/non-detection surveys can be used to quantify species habitat selection because attributes of used versus unused sites can be compared to make inferences about suitability (Mitchell & Hebblewhite, 2012). However, failure to account for detection probability (i.e., false absences) can lead to biased inferences (MacKenzie *et al*., 2002; 2006). Failure to account for detection error has been shown to produce distorted species-habitat relationships (Gu & Swihart, 2004), which can be particularly problematic when species detectability itself is related to site characteristics (MacKenzie *et al*., 2006). Fortunately, these problems can largely be overcome with the use of site occupancy models, which derive a detection probability from replicated detection/non-detection surveys (MacKenzie *et al*., 2002). Occupancy models permit site and survey specific variation in detectability to be accounted for while estimating the probability of site use with the hierarchical ranking of covariates. The development of occupancy models negate the need to rely on assumptions of equal detectability with the use of detection/non-detection data, thereby permitting more robust inferences to be made on species site use. Two-species occupancy models can be used to investigate co-occurrence patterns while accounting for individual species detection probabilities and habitat correlates, thereby providing robust inferences on species interactions (MacKenzie, Bailey & Nichols, 2004).

In this study, we used an occupancy modeling approach to investigate cheetah habitat selection in a human-impacted woodland savannah in southwestern Mozambique. Cheetah site selection was examined at two spatial scales that cheetah can be expected to make resource use decisions; 'temporary patch use' and 'home range' level sites. The following hypotheses were tested 1) landscape features facilitating prey capture are most determining at the temporary patch use scale, but also contribute at a home range scale, 2) prey catch-ability features contribute more to cheetah site use than greater prey occurrence across spatial scales, 3) anthropogenic factors contribute to cheetah habitat use at both spatial scales.

Following this, we used two-species occupancy models (MacKenzie, Bailey & Nichols, 2004) to investigate the co-occurrence patterns of cheetahs and lions at a fine spatial scale in a non-equilibrium community. Our goals were to compare how each species responds to prey and human pressure, and investigate how these factors contribute to their co-occurrence. While accounting for detectability of each species, a test for statistical independence was performed to determine if cheetah site use was conditional on the presence of lions. Following this, individual species response to increased prey occurrence and human pressure were compared. In addition, we test two predictions for co-occurrence patterns related to prey and human pressure 1) cheetah occurrence should be lower at sites with greater occurrence of their preferred prey because lion site use is also higher at these sites and interspecific competition should increase, 2) both cheetah and lion should be negatively influenced by anthropogenic factors, but cheetah occurrence should be higher at sites with greater human pressure given lion absence because interspecific competition should decrease. Lion population densities were low (0.99/100km^2) in the study area due to top-down anthropogenic pressure (Everatt, 2013). Considering this, we used spatial and temporal data to test the hypothesis that competition (i.e., avoidance behaviour) with humans was greater than competition with lions in a human-dominated woodland savannah.

Materials and Methods

Study area

This study was located in the Limpopo National Park (LNP) in southwestern Mozambique, which forms a key component of the Great Limpopo Transfrontier Park. The Kruger National Park (KNP) in South Africa forms the western boundary, characterized by formal protection and high wildlife densities. LNP supports comparatively lower prey densities (Stephenson, 2010) and there is limited enforced wildlife protection and infrastructure. The Limpopo River forms the eastern boundary, characterized by near-continuous agro-pastoralist settlements with an estimated human population of 20,000. There are eight additional communities situated within the park boundary, inhabited by approximately 6,500 humans (Huggins *et al*., 2003) (Fig. 3.1). Park residents practice subsistence agriculture, free-grazing of livestock and unregulated hunting of bushmeat with snares, traps, bows and arrows, spears and packs of domestic dogs (*Canis lupus familiaris*) (*this study*).

The predominant landscape in LNP is sandveld, which is comprised of short woodlands of *Terminalia sericea*, *Combretum apiculatum* and *Pogonarthria squarrosa* and thickets of *Baphia massaiensis*. The sandveld landscape is characterised by sandy substrates, the presence of 'pans' (seasonally flooded depressions) and the absence of well-defined drainage lines. The region has a warm arid climate with annual precipitation of <450 mm falling primarily during November-April, and a mean annual temperature > 18°C (Stalmans *et al.,* 2004).

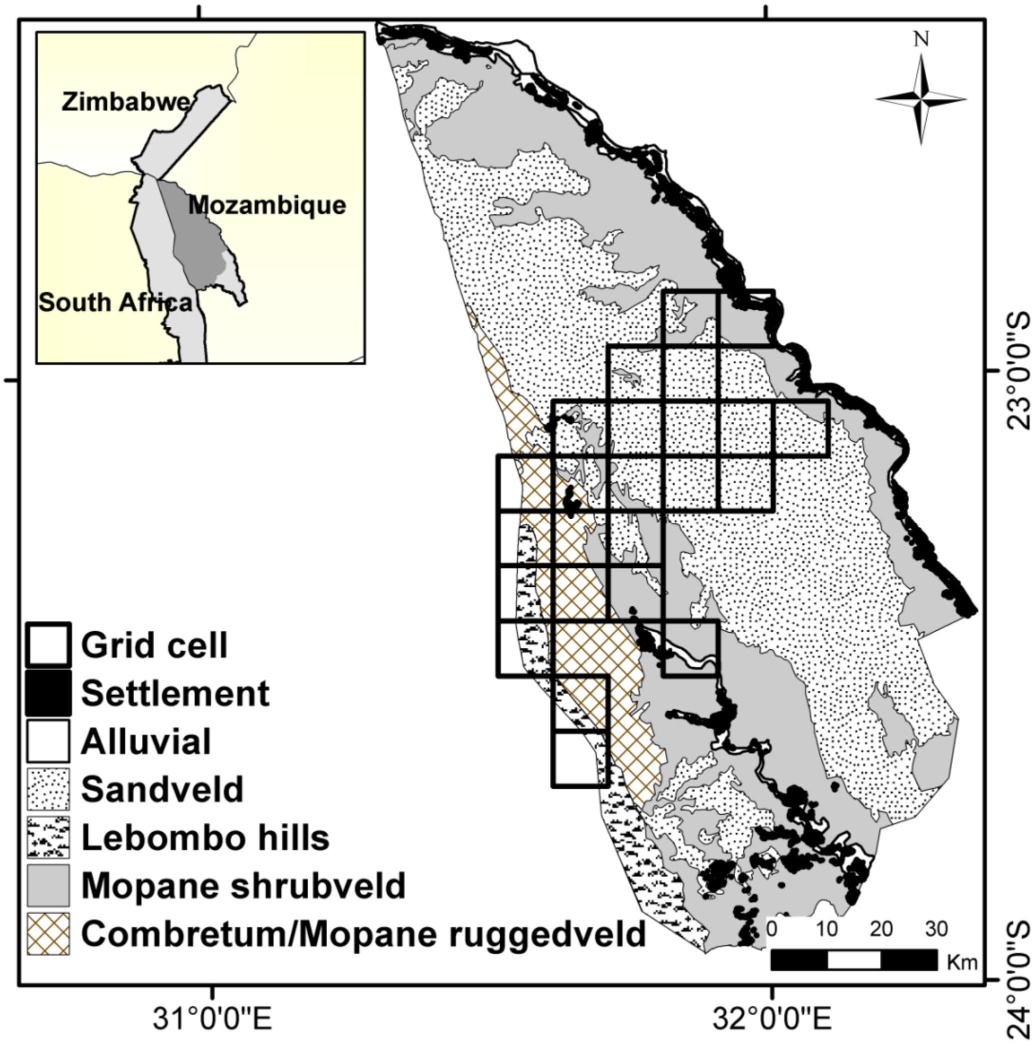

Figure 3.1. Study area with surveyed grid cells. The Limpopo National Park (LNP) in Mozambique is bordered by the South Africa international boundary and the Kruger National Park, and to the east by the Limpopo River, characterized by rural subsistence agro-pastoralist settlements. Surveyed grid cells overlaid across a gradient of distinguishing features including settlement areas, major rivers (Alluvial) and landscapes. Inset map: Location of LNP (dark grey) in relation to the Greater Limpopo Transfrontier Park (light grey) and to Zimbabwe and South Africa. The light grey region to the south of LNP has been recently separated with a wildlife barrier fence (Shape file: gltp_lnpLandscapes, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch).

Survey design and field methodology

An occupancy modelling technique (MacKenzie *et al*., 2002) was used to investigate environmental factors influencing cheetah habitat selection at ‘home range’ (i.e., second order) and ‘resource patch use’ (i.e., third order) spatial scales (Johnson, 1980) in a human-disturbed, woodland savannah landscape. Cheetah home ranges in KNP have been estimated at 125-195 km^2 (Broomhall *et al*., 2003). Considering this, we designated home range level sample units as 100 km^2 grid cells, reasoning that this size was biologically meaningful to the scale that cheetahs make home range level resource use decisions in the study area. For the temporary resource patch use spatial scale, we designated sample units as 1 km sites, reasoning that this scale was biologically representative of the temporary patches where cheetahs make resource use decisions relating to their fitness including prey searches and competitor avoidance.

We make the following assumptions of an occupancy model, where the estimator (Ψ) is defined as *probability of site use* (MacKenzie *et al*., 2006): 1) Detections are independent; 2) Species are never falsely identified; 3) Heterogeneity in occupancy and detection probabilities are modelled with covariates. We note that the closure assumption could be relaxed because the parameter of interest was probability of site use (MacKenzie *et al*., 2006).

Detection/non-detection surveys for cheetah were conducted simultaneously at two spatial scales (100 km^2 grid cells and 1 km sites) using temporally replicated track surveys conducted along transects and photographic data collected from remote camera-traps. Sampling occurred continuously over a 15 month period (September 9, 2011-November 26, 2012), which permitted us to account for variation in cheetah habitat selection and detectability (p) between wet and dry seasons. A subset of these data was used in an evaluation of occupancy as a state variable for monitoring cheetah (Chapter 2).

The survey area was selected by placing a matrix of 100 km^2 grid cells across a topographical map and selecting 24 grid cells such that they were representative of a gradient of landscape types, distinguishing features and settlement areas present in LNP (Fig. 3.1). Sampling occasions ($\bar{x}$ = 17) of 100 km^2 grid cells were represented by temporally replicated 3 km transects ($\bar{x}$ = 8 per grid cell, replicates separated by $\geq$14 days) and 14 day camera-trap surveys ($\bar{x}$ = 13 per grid cell). Of the 24 grid cells, 23 were sampled with cameras ($\bar{x}$ = 192 camera-trap nights/grid cell) and 23 were sampled with track surveys ($\bar{x}$ = 23 km/grid cell). Note that the occupancy model accounts for unequal sampling across sites (MacKenzie *et al*., 2002). Transects and camera stations were established opportunistically along game trails and small dirt tracks while attempting to optimize spatial representation of grid cells ($\bar{x}$ = 3 camera stations, x = 3 transects) and ensure comparable representation of distinguishing landscapes and distances from human settlements. To maintain an order of randomness, grid cells were subdivided into quadrants and one quadrant was randomly selected from each grid cell for obligate sampling. Due to logistical constraints two cells were sampled in only one quadrant while the rest were sampled in $\bar{x}$ = 3 quadrants.

Detections were represented by unambiguously identified cheetah tracks or photographs. In an effort to maintain assumptions of sample independence, occasions/detections were pooled when a camera-trap had sampled 14 days prior to a track survey within the same quadrant.

At a finer spatial scale, sampling occasions ($\bar{x}$ = 4) of 1 km sites (n = 260) were represented by temporally replicated 1 km transects (both 3 km segments and discrete locations) and/or by 14 day camera-trap sampling intervals (n = 184 sites sampled by transects, n = 48 sampled by transects and a camera-traps, n = 28 sampled by camera-traps). For sites that were sampled by both methods, occasions/detections were pooled when a camera-trap had sampled 14 days prior to a track transect.

Surveys were conducted to maximize the detection (MacKenzie *et al*., 2006) of cheetahs, sympatric carnivores and other mammalian fauna. Transects were walked on suitable substrate along game trails and small dirt roads during early morning or late afternoon hours. Sections of trail with poor substrate (i.e., gravel) were excluded and resumed where conditions improved. On each (1 km) transect where cheetah tracks were detected, a representative track was recorded with a GPS, given a unique identification number and photographed with a metric ruler. Unambiguously identified detections of lion were also recorded in this manner.

To increase the probability of detecting cheetah, researchers opportunistically searched for landscape features cheetah may use to scent mark (i.e., prominent objects such as termite mounds, rock piles, and fallen-trees) (Caro, 1994). Considering that cheetahs were exhibiting a behavioural response at scent marking sites and thus multiple detections would be a violation of model independence, we followed a 'partial removal design', removing multiple sampling occasions/detections at transects/camera stations that included scent-marking sites (MacKenzie *et al*., 2006).

Identification of covariates

To investigate cheetah habitat selection in a human-disturbed woodland savannah landscape, a simple set of variables (covariates) that may influence survival and reproduction was considered (Table 3.1). Since cheetahs are obligate carnivores, a key component of their habitat includes prey availability and factors that facilitate prey capture (Mitchell & Hebblewhite, 2012). Cheetah recruitment has been positively correlated to the abundance of their preferred prey (Durant, Kelly & Caro, 2004). The principal prey species of cheetah in this region of Africa are impala (*Aepyceros melampus*) (Pienaar, 1969; Hayward *et al*., 2006), which are a non-migratory, comparatively abundant, mid-sized antelope (Estes, 1992).

To quantify the impact of prey availability on cheetah habitat selection, an impala occupancy model was used; based on detection/non-detection surveys conducted during September 9, 2011-October 13, 2012 (Chapter 2). The model was based on 1268 surveys (n = 602 temporally replicated 1 km transects, n = 666 seven day camera-trap intervals; $\bar{x} = 5$ sampling occasions/site) of the same (n = 260) 1 km sites, from 360 camera-trap detections and 154 sightings of impala along transects (maximum value = 1). The model considered covariates to account for variation in nutritional content of vegetation, surface water availability and human disturbance (*for details see* Chapter 2). Site (n = 260) values were taken as the model averaged probability of impala site use. For 100 km^2 sites, values were extracted from a 30 x 30 m resolution map of the inverse weighted distance of impala $\widehat{\bar{\Psi}}$ using Spatial Analyst Tool in ArcGIS 9.3.1. We assume that the probability of impala site use is representative of an encounter probability for cheetahs' primary prey.

We identified two covariates that may be representative of the landscape structure providing suitable prey capture for cheetah; open habitat patches and drainage lines. Patches of open habitat were considered a suitable landscape structure for prey capture because in woodland habitats, open patches of land (i.e., pans or other natural short-grass clearings) provide both a high edge/area ratio that may be utilized for concealment and suitable terrain for high-speed chase (Fig. 3.2). Site values were extracted from a raster layer of landscape cover classified as 'bare' or 'grassland' (GLTF Landcov_Banhine, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch) using Spatial Analyst Tool in ArcGIS 9.3.1. Values were taken as the number of 30 m x30 m pixels within 1) grid cells (100 km^2 sites) and 2) a 50 m buffer placed around each transect or camera station (1 km sites) (for sites sampled with both a transect and a camera station, data were extracted from the buffer of the corresponding transect). Drainage lines were considered a suitable landscape structure for prey capture because these features are often bordered by dense vegetation and game trails adjacent to open clearings. Site values were extracted from a landscape raster layer (as above) classified as 'rivers' for $100km^2$ and 1 km sites (as above).

Cheetah site selection in LNP may also be influenced by various anthropogenic factors including prey depletion (which should be represented by our prey occurrence model), persecution, and loss of cover from cultivation and over-grazing of livestock (Durant *et al.*, 2008). Considering that these pressures should be greatest closest to human settlements, a covariate based on the proximity to these areas was considered. Proximity was calculated as the mean Euclidean distance of each 30 m x 30 m pixel in a grid cell (100 km^2 sites) or buffer (1 km sites, as above) to the nearest human settlement. Data were extracted from a raster layer of landscape cover classified as 'village' (GLTF Landcov_Banhine, 2010; WGS 1984; Peace Parks Foundation, Stellenbosch) using Spatial Analyst Tool in ArcGIS 9.3.1.

Although anthropogenic pressures may be concentrated around settlement areas in LNP, human hunters are known to travel to areas with greater prey abundance accompanied by packs of domestic hunting dogs (Everatt, 2013). Considering that cheetah may suffer from exploitive or interference competition with bushmeat poachers and their dogs, we predicted that cheetah would spatially avoid areas with greater probability of bushmeat poaching use. To quantify the impact of this potential competitor on cheetah, we used a bushmeat poaching occupancy model; developed by Everatt, (2013) for the study area based on detection/non-detection surveys conducted during September 9, 2011-October 13, 2012. Following the same sampling protocols as for cheetah (*Survey design and field methodology*), Everatt (2013) developed a model from 375 sampling occasions (where sampling occasions were represented by 14 day camera-trap intervals; $\bar{x}$ = 5 sampling occasions/site) across 82 camera-trap sites, from photographic detections of human hunters (n = 89), domestic dogs (n = 66) and snared mammalian fauna (n = 21). The model considered covariates based on risk, effort and reward to hunters, including; ranger patrols, distance from villages, trails, proximity to water, prey abundance and prey biomass (*for details see* Everatt, 2013). Covariate values were extracted from a 30 x 30 m resolution map of the inverse weighted distance of bushmeat poaching site use, using Spatial Analyst Tool in ArcGIS 9.3.1. We assume that the probability of bushmeat poaching site use is representative of an encounter probability for cheetah.

Cheetah habitat selection may also be influenced by increased presence of their competitor; lion (Durant, 1998). Lions persist at low densities in the study area and during the time of this study occupied approximately 46% of the study area (Everatt, 2013). Considering that lions occur at low population densities and that the habitat provides cover for concealment from lions, we predicted that competition with humans (i.e., combined anthropogenic pressures) would be more determining of cheetah site use than competition with lions. To quantify the impact of lion occurrence on cheetah habitat selection, we used a lion occupancy model; developed by Everatt, (2013) for the study area based on detection/non-detection surveys conducted during September 9, 2011-October 13, 2012. Following the same sampling protocols as for cheetah (*Survey design and field methodology*), Everatt (2013) developed lion site use models for the same 100 km^2 and 1 km sites used in this study. The lion site use model for 100 km^2 sites (n = 24) was based on 515 surveys (n = 326, 14 day camera-trap intervals; $\bar{x}$ = 14 sampling occasions/site; n = 189, 3 km track transects, $\bar{x}$ = 8 sampling occasions/site). The lion site use model for 1 km sites (n = 260) was based on 998 sampling occasions (n = 360, 14 day camera-trap intervals; $\bar{x}$ = 2 sampling occasions/site; n = 638, 3 km track transects, $\bar{x}$ = 2 sampling occasions/site). Models were built from 239 lion detections (n = 101 camera-trap, n = 138 track). Similar to this study, lion site use models considered covariates based on prey occurrence, prey catch-ability features, bushmeat poaching occurrence and proximity to agro-pastoralist settlements (*for details see* Everatt, 2013). Site values were taken as the model averaged probability of lion site use. We assume that the probability of lion site use is representative of an encounter probability for cheetah.

Table 3.1. Predictor variables for cheetah habitat selection, their relationship to cheetah fitness, data unit, type and source and values.

Covariate ID	Habitat component	Relationship to cheetah fitness	Unit (Data type/ source)	Range of Values (Mean) Temporary patch use	Range of Values (Mean) Home range level use
P	Prey†	Availability of prey	Probability of site use (Field data‡)	0.08-0.92 (0.46)	0.11-0.79 (0.44)
O	Open patches with dense edge	Facilitates capture of prey (concealment & high-speed chase)	% (GIS)φ	0.00-1.00 (0.13)	0.81-5.85 (2.63)
D	Drainage lines	Facilitates capture of prey	% (GIS)φ	0.00-1.00 (0.10)	-
S	Agro-pastoralist settlements	Risk of injury or death, loss of cover, loss of prey	km (GIS)φ	0.20-24.51 (10.87)	2.01-20.41 (11.17)
B	Interspecific competition: Bushmeat poaching	Risk of injury or death, loss of prey	Probability of site use (Field data*)	0.00-1.00 (0.63)	0.07-1.00 (0.55)
L	Interspecific competition: Lions	Risk of injury or death, kleptoparasitism	Probability of site use (Field data*)	0.00-1.00 (0.20)	0.01-0.84 (0.26)

†Cheetah's preferred prey species (impala, *Aepyceros melampus*) (Hayward *et al*., 2006).
‡Taken from occupancy model (Chapter 2).
φ GLTF Landcov_Banhine raster layer. WGS 1984. Peace Parks Foundation, Stellenbosch.
*Taken from occupancy model, Everatt, (2013).

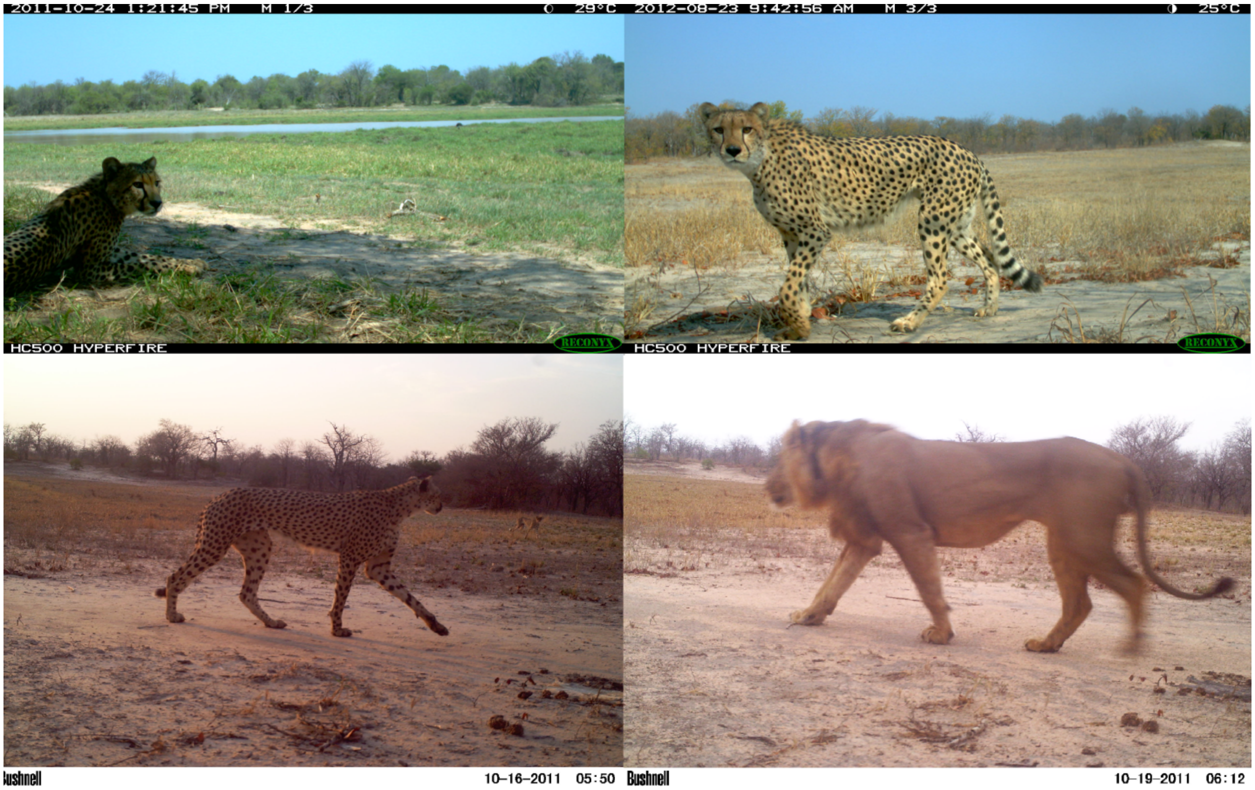

Figure 3.2. Sites characteristic of 'open habitat patches' modelled as a landscape structure for cheetah prey capture; offering dense edge habitat for concealment and suitable terrain for high speed chases. Top images show cheetah at different sites and bottom images show cheetah and lion at the same site.

Sampling occasion-specific covariates were constructed to account for differences in cheetah detectability between survey methodologies and wet and dry seasons, respectively (MacKenzie *et al*., 2006). Considering that detectability of tracks may be higher in areas with greater bare surface area, we included the covariate open habitat patches as a site covariate for detection probability.

Due to the low number of sites at the home range level (n = 24), the number of occupancy covariates was reduced to five, excluding the covariate 'drainage lines' (Table 3.1). Interactions between cheetah and lion were investigated using two-species occupancy models at the temporary patch use scale (n = 260, 1 km sites).

Identification of covariates: species interaction models

Non-random patterns of species co-occurrence may be the result of species specific habitat preferences (MacKenzie *et al*., 2006). To isolate these relationships we considered site covariates for each species accounting for their unique principal prey species as well as anthropogenic factors that may influence their fitness (Table 3.2). The goal was to compare how the two species respond to prey and human pressure, and investigate how these factors contribute to their co-occurrence. Similar to the prey covariate, an occupancy model of lion's principal prey, buffalo (*Syncarus caffer*) (Hayward & Kerley, 2005), developed by Everatt, (2013) was used. The model was based on 1268 surveys (n = 602 temporally replicated 1 km transects, n = 666, 7 day camera-trap intervals; $\bar{x}$ = 5 sampling occasions/site) of the same 1 km sites (n = 260), from 86 camera-trap detections and 15 sightings of buffalo along transects (maximum value = 1). The model considered landscape covariates based on vegetation communities and underlying geology, in addition to the proximity to water and to agro-pastoralist settlements (*for details see* Everatt, 2013). Site values were taken as the model averaged probability of buffalo site use. To determine whether lion were selecting for areas with greater impala occurrence, the covariate 'cheetah prey' was included in the lion occupancy models. Variation in species detectability with season, survey methodologies and open habitat patches was accounted for using sampling occasion-specific covariates (as above).

Table 3.2. Predictor variables for cheetah and lion two species occupancy models, their relationship to species fitness, their unit, data type, source and values.

Covariate ID	Habitat component	Relationship to species fitness	Unit (Data type/ source)	Range of Values (Mean)
CP	(Cheetah) Prey†	Availability of prey	Probability of site use (Field data)	0.08-0.92 (0.46)
LP	(Lion) Prey‡	Availability of prey	Probability of site use (Field data*)	0.04-0.64 (0.41)
S	Agro-pastoralist settlements	Risk of injury or death, loss of cover, loss of prey	% (GIS)ᵠ	0.20-24.51 (10.87)
B	Interspecific competition: Bushmeat poaching	Risk of injury or death, loss of prey	Probability of site use (Field data*)	0.00-1.00 (0.63)

†Cheetah's preferred prey species (impala, *Aepyceros melampus*) (Hayward *et al*., 2006)
‡Lion's primary preferred species (buffalo, *Syncarus caffer*) (Hayward & Kerley, 2005)
*Taken from occupancy model of Everatt, (2013).
ᵠGLTF Landcov_Banhine raster layer. WGS 1984. Peace Parks Foundation, Stellenbosch.

Data analysis

Occupancy model

Cheetah site use (Ψ) was estimated using a maximum likelihood approach that implicitly accounts for detectability (p) (MacKenzie *et al*., 2002). For each spatial scale, detection matrices for each site were constructed, recording a '1' for detection and '0' for non-detection for each sampling occasion (i.e., sampling occasions represented by pooled samples received a single '1' if cheetah were detected by either track or camera surveys, or by both methods). To account for differences in sampling methodologies, an occasion-specific matrix was constructed, recording a '1' for track surveys and '0' for camera surveys (excluding pooled sampling occasions). Following this, a second occasion-specific matrix was constructed, recording a '1' for sampling occasions represented by both a camera and a track survey, and a '0' for occasions represented by only one survey method. Finally, an occasion-specific matrix was constructed, recording a '1' or '0' for surveys conducted during wet (November 1-April 30) or dry (May 1-October 31) seasons, respectively. Covariates were assessed for correlation using a Pearson's r test (with $r = 0.5$ as the cut-off value) (Green, 1979) and continuous data were normalized using z-transformation. Variables found to be correlated were not included in the same models. All the following analyses were implemented in the program PRESENCE ver. 4.4 (Hines, 2006). Cheetah site use of 100 km^2 and 1 km sites were analyzed separately using single season occupancy models. Each analysis was conducted in two stages; covariates for p were first considered, in univariate and multivariate combinations, holding Ψ constant (.). Following this, covariates for Ψ were considered, in all possible (non-correlated) combinations, including all detection covariates that emerged in a 95% confidence set ($\sum w > 0.95$) in all models for Ψ. Goodness of fit of the general model was checked using Pearson's chi-square statistic and 10,000 bootstrap samples (MacKenzie & Bailey, 2004).

Model selection

Akaike Information Criterion adjusted for small sample sizes (AICc) was used to rank the relative support for different models in order of parsimony, with the effective sample size defined conservatively as the number of sites. AICc weights (w) were used to assess the weight of evidence for each model. Unless a single model emerged with a $w>0.9$, site level occupancy estimates, and the overall probability of site use were obtained using a model-averaging technique from a 95% confidence set ($\sum w > 0.95$) of models with good support ($\Delta AICc<7$) Models with $\Delta AICc<2$ were considered to be more strongly supported (Burnham & Anderson, 2002). AICc weights were summed for each covariate in the final model set ($\sum w > 0.95$), and covariates with high summed model weights were considered more influential at explaining cheetah site use (Burnham & Anderson, 2002). We examined the β coefficient values/signs to determine the strength and direction of influence for each covariate in the final model set. Covariates were considered to have strong or robust impact if their β-coefficients were significant ($\beta \pm 1.96 \times SE$ not overlapping 0) (MacKenzie *et al*., 2006).

Testing species interactions

A general likelihood based framework that explicitly accounts for species detectability was used to quantify interactions between cheetah and lion at the 'temporary resource patch' scale. Models were built from track data of cheetahs and lions collected along (1 km) temporally replicated transects and camera-trap data (as above). Species-specific detection matrices for each site ($n = 260$) were constructed (as above). Maximum likelihood estimates for parameters were estimated using a single season, two-species occupancy model (MacKenzie *et al*., 2004). We used the alternate parameterizations because these perform better when covariates are incorporated (MacKenzie *et al*., 2006; Richmond, Hines & Beissinger, 2010). The alternate parameterizations for two-species occupancy models can be used to estimate individual species detection probability (p^A, p^B) and the conditional parameter Ψ^{BA}, which in this study is the probability a site will be used by cheetah (B) given that lion (A) are present and Ψ^{Ba}, the probability a site will be used by B given that A is absent.

The analysis was conducted in two stages (as above); first determining the covariates that best explain lion *p* using a single season (single species) model, and then including these covariates in all subsequent (two species) models (covariates for cheetah *p* at this spatial scale were determined in the previous analysis). Following this, factors that may cause statistical dependency between cheetah and lion were investigated using the "Ψ^{Ba}" parameterization, which estimates the conditional co-occurrence parameters, Ψ^{BA} and Ψ^{Ba}. First, a set of simple models was constructed that allowed covariates to influence species Ψ independently (i.e., constraining the interaction parameters to $\Psi^{BA} = \Psi^{Ba}$) in univariate and multivariate combinations. These models were then compared to a set of models where covariates were allowed to influence the conditional co-occurrence probabilities Ψ^{BA}/ Ψ^{Ba}. Models were evaluated based on (model selection) criteria stated above. The level of species co-occurrence between two species can be quantified using a species interaction factor (φ) which is a ratio of how much more or less two species co-occur than would be expected if the species distributions were independent. $\varphi = 1$ indicates independence, $\varphi>1$ indicates species co-occur more often than would be expected by chance and $\varphi<1$ indicates species co-occur less often than would be expected by chance (MacKenzie *et al.*, 2004; 2006). The Ψ^{Ba} parameterization does not estimate φ directly, and was thus calculated using (MacKenzie *et al.*, 2006):

$$\varphi = [\Psi BA/(1-\Psi BA]/[\Psi Ba/(1-\Psi Ba)]$$

Temporal activity patterns of cheetah, lion and bushmeat hunters were graphed. The estimate of temporal overlap (Δ; where 0 is no overlap and 1 is complete overlap) was calculated by taking the minimum of the two (species pair) activity patterns at each hour.

Results

A total survey effort of 646 km of transects and 5535 camera trap nights resulted in 48 sets of cheetah tracks and 161 cheetah photographic events in eight (100 km^2) grid cells. A total of seven cheetah scent marking sites were located by researchers in four grid cells. After excluding multiple sampling occasions at scent marking sites and pooling sampling occasions at double sampled sites, the final data set consisted of 431 sampling occasions for the 100 km^2 (hereafter 'home-range') level analysis and 879 sampling occasions for the 1 km (hereafter 'temporary patch') level analysis. Twelve adult cheetahs were identified (by their unique spot patterning) in the study area using photographic data obtained from camera-traps (Table 3.3). We note that this is the minimum number of individual animals sampled in this study.

Temporary patch use

At the temporary patch use (1 km) spatial scale, models incorporating the influence of open habitat patches, season and method on cheetah detectability (*p*) were strongly supported (ΔAICc<2), and ranked higher than the model that assumes *p* was constant (ΔAICc = 5.81)

Table 3.3. Minimum number of cheetah in the Limpopo National Park, Mozambique photographed by 12 of 89 camera-trap stations located over a 2400 km^2 study area during September, 2011-November, 2012.

Social Unit	**Adults**	**Dependent adolescents (12-18 mo)**			**Cubs**
		Female	**Male**	**Unknown sex**	**<1 yr**
Lone Female	3				
Female with cub(s)	4	1	1	5	1
Lone Male	3				
Male coalition	2				

(Table 3.4). Given presence, cheetahs were easier to detect in open habitat patches ($\hat{\beta}$ = 0.286, SE = 0.094) in the wet season $\widehat{\beta}$ = 0.410, SE = 0.318). Based on these results, these covariates for *p* were retained in all subsequent analysis for cheetah site use (Ψ). The covariates 'prey' and 'lions' were both found to be negatively correlated with 'settlements' (r = -0.72, r = -0.60) and were not included in the same models. At the temporary site use level, seven models emerged showing good support (ΔAICc<7) and so model averaging was used to obtain the final parameter estimates (Table 3.5). The probability of detecting cheetah on a single survey at a site where they occurred was $\hat{\bar{p}}$ = 0.163 (SE = 0.055). A goodness of fit test for the global model: $\Psi(P,O,D,S,B,L)$, $p(M,O,SN)$ did not show evidence for lack of fit (p = 0.54) or over-dispersion ($\hat{c}$ = 0.75).

At this spatial scale, the factors contributing most to the probability a site would be used by cheetah were bushmeat poaching (∑w = 0.97) and open habitat patches (∑w = 0.95) (Fig. 3.3). Cheetah exhibited a strong avoidance of sites with a greater probability of bushmeat poaching ($\hat{\beta}$ = -3.780, SE = 1.133) and a strong selection for sites with greater openness ($\bar{\beta}$ = 0.782, SE = 0.393). There was considerably less support for the other covariates (Table 3.6). The sign of the β-coefficients suggest (in order of their relative contribution) that cheetah tended to avoid sites with a greater occurrence probability of their preferred prey and lions and select sites closer to drainage lines that were further from settlements.

Table 3.4. Model selection procedure for factors influencing cheetah detectability (p) at (n = 260) 1 km sites in the Limpopo National Park, Mozambique. Covariates considered are method (M), open habitat patches (O) and season (SN). Cheetah site use (Ψ) is held constant (.)

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(.)p(O)	370.83	0.00	0.27	3	364.74
Ψ(.)p(O,SN)	371.01	0.18	0.25	4	362.85
Ψ(.)p(M,O)	371.04	0.21	0.24	5	360.80
Ψ(.)p(M,O,SN)	372.44	0.68	0.19	6	360.11
Ψ(.)p(.)	371.51	5.81	0.01	2	372.59
Ψ(.)p(SN)	376.64	6.51	0.01	3	371.25
Ψ(.)p(M)	377.34	6.55	0.01	4	369.22
Ψ(.)p(M,SN)	377.38	7.37	0.00	5	367.96

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

Table 3.5. Model selection procedure for the influence of covariates on determining cheetah site use (Ψ) of (n = 260) 1 km sites in the Limpopo National Park, Mozambique. Covariates considered are prey (P), open habitat patches (O), drainage lines (W), agro-pastoralist settlements (S), bushmeat poaching (B) and lions (L). Detectability (p) varies with method (M), season (SN) and open habitat patches (O). For comparison, the constant model (.) is shown.

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(B,O),p(M,SN,O)	341.21	0.00	0.37	8	324.64
Ψ(B,O,P),p(M,SN,O)	342.67	1.46	0.18	9	323.95
Ψ(B,O,L), p(M,SN,O)	343.28	2.07	0.13	9	324.56
Ψ(B,O,W),p(M,SN,O)	343.33	2.12	0.13	9	324.61
Ψ(B,O,S),p(M,SN,O)	343.36	2.15	0.13	9	324.64
Ψ(B,O,P,W,L),p(M,SN,O)	347.00	5.79	0.02	11	323.94
Ψ(B,P,L),p(M,SN,O)	347.68	6.47	0.01	9	328.96
Ψ(.),p(M,SN,O)	372.44	31.23	0.00	6	360.11

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL).

Table 3.6. β-coefficients, associated standard errors (SE) and *a priori* prediction for covariates influence on cheetahs selection of 1 km sites (n = 260) in order of their summed model weights (∑*w*), in the Limpopo National Park, Mozambique. β-coefficients for the variables direction and strength of influence on cheetah site selection are also shown.

Covariate	**B**	**SE**	**∑*w***	***a priori* prediction**
Bushmeat	**-3.780**	**1.133**	0.97	-
Open patches	**0.782**	**0.393**	0.95	+
Prey	-1.185	1.420	0.21	-
Lion	-0.359	1.212	0.17	-
Water	0.103	0.625	0.15	+
Settlement	-1.284	0.903	0.13	-

Bold entries indicate robust impact (β ± 1.96 x SE not overlapping 0) (MacKenzie *et al.*, 2006).

The results supported the second hypothesis; prey catch-ability features contributed more to cheetah site use than prey occurrence at the temporary patch use scale (∑w = 1.10 versus ∑w = 0.21). The results also supported the third hypothesis; anthropogenic features contributed considerably to cheetah site use (∑w = 1.09) (Table 3.6, Fig. 3.3).

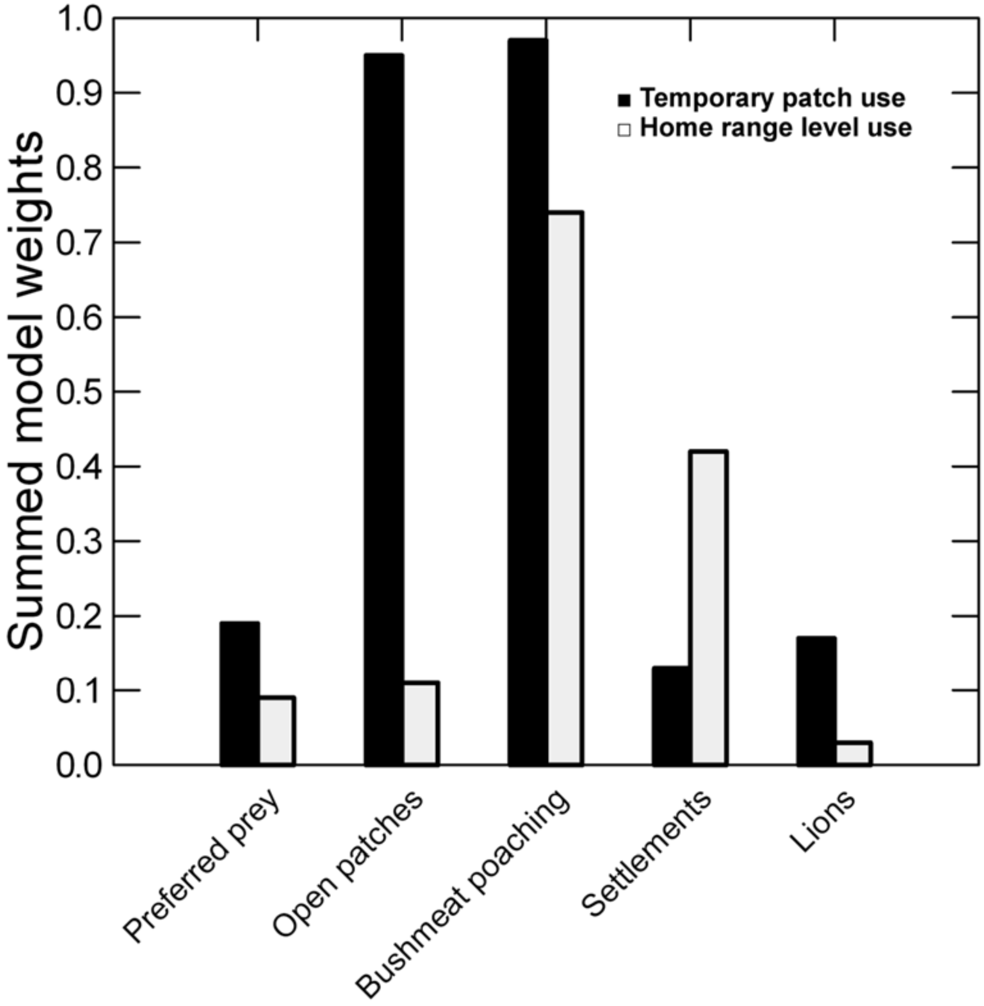

Figure 3.3. Factors contributing to cheetah site use at multiple spatial scales in the Limpopo National Park, Mozambique. Variables with high summed (AICc) model weights are more influential of cheetah site use. Estimates are based on the averaged model ($\sum w>0.95$). n = 260 temporary use (1 km) sites; n = 24 home range level (100 km^2) sites.

Home range level use

At the home range level (100 km^2) spatial scale, the models incorporating the influence of method, season and open habitat patches on cheetah detectability (p) showed good support ($\Delta AICc<7$; $\sum w>0.95$), and ranked higher than the model that assumes p was constant ($\Delta AICc$ = 10.97) (Table 3.7). Based on these results, these covariates for p were retained in all subsequent analyses for cheetah site use (Ψ). The covariates 'prey' and 'settlements' were found to be highly correlated (r = -0.82), as were 'lions' and 'settlements' (r = -0.69) and 'lions' and 'open habitat patches' (r = 0.54) and were not included in the same models. Ten models emerged showing good support (ΔAICc<7; ∑w>0.95) and so model averaging was used to obtain the final parameter estimates (Table 3.8). The probability of detecting cheetah on a single sampling occasion in a grid cell where they occurred was $\widehat{p}$ = 0.238 (SE = 0.069). A goodness of fit test for the global model: *Ψ(P,O,S,B,L), p(M,O,SN)* did not show evidence for lack of fit (p = 0.28) or over-dispersion ($\hat{c}$ = 0.40).

The most contributing factor of cheetah site use at the home range level was bushmeat poaching (∑w = 0.74), followed by agro-pastoralist settlements (∑w = 0.42) (Fig. 3). Cheetahs showed strong avoidance of sites with a greater probability of bushmeat poaching ($\widehat{\beta}$ = -5.144, SE = 2.397). There was considerably less support for the other covariates (Table 3.9). The sign of the β-coefficients suggest (in order of their relative contribution) that cheetah tended to avoid agro-pastoralist settlements and select for sites with a greater percentage of open habitat patches and higher prey and lion use.

The results supported the first hypothesis; cheetah presence was determined more by features facilitating prey capture at the temporary use scale than at the home range scale, (∑w = 0.95 versus ∑w = 0.11, considering only 'open habitat patches' because the 'drainage line' covariate could not be used at the home range scale). Prey catch-ability features contributed considerably less to cheetah site use at the home range scale and the impact was not robust. It is worth noting here that the covariates 'drainage lines' and 'open habitat patches' were highly correlated at the home range scale (r = 0.77), thus the impact of this covariate was likely accounted for. The results supported the second hypothesis; prey catch-ability features contributed more to cheetah site use than prey occurrence at the home range scale (∑w = 0.11 versus ∑w = 0.09), however, the differences are not considerable (Fig. 3.3). Finally, the results supported the third hypothesis; anthropogenic features contributed considerably to cheetah site use (∑w = 1.16), and were more influential than the other factors that were considered (∑w = 0.23) (Fig. 3.3, Table 3.9).

Table 3.7. Model selection procedure for factors influencing cheetah detectability (p) at 100 km^2 sites (n = 24) in the Limpopo National Park, Mozambique. Covariates considered are method (M), open habitat patches (O) and season (SN). Cheetah site use (Ψ) is held constant (.)

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(.),p(M)	189.24	0.00	0.69	4	179.13
Ψ(.),p(M,SN)	192.21	2.97	0.16	5	178.88
Ψ(.),p(M,O)	192.43	3.19	0.14	5	179.10
Ψ(.),p(M,O,SN)	195.77	6.53	0.03	6	178.83
Ψ(.),p(.)	200.21	10.97	0.00	2	195.64
Ψ(.),p(SN)	202.71	13.47	0.00	3	195.51
Ψ(.),p(O)	202.78	13.54	0.00	3	195.58
Ψ(.),p(O,SN)	205.57	16.33	0.00	4	195.46

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

Table 3.8. Model selection procedure for the influence of covariates on cheetah site use (Ψ) of 100 km^2 sites (n = 24) in the Limpopo National Park, Mozambique. Covariates considered are prey (P), open habitat patches (O), lions (L), agro-pastoralist settlements (S) and bushmeat poaching (B). Detectability (p) varies with method (M), season (SN) and open habitat patches (O).

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(B),p(M,SN,O)	191.57	0.00	0.34	7	170.57
Ψ(B,S),p(M,SN,O)	192.23	0.66	0.24	8	166.63
Ψ(S), p(M,SN,O)	193.66	2.09	0.12	7	172.66
Ψ(B,P),p(M,SN,O)	194.95	3.38	0.06	8	169.35
Ψ(B,O),p(M,SN,O)	195.43	3.86	0.05	8	169.83
Ψ(.),p(M,SN,O)	195.77	4.20	0.04	6	178.83
Ψ(S,O),p(M,SN,O)	195.80	4.23	0.04	8	170.20
Ψ(B,L),p(M,SN,O)	196.14	4.57	0.03	8	170.54
Ψ(P),p(M,SN,O)	196.67	5.10	0.03	7	175.67
Ψ(B,S,O),p(M,SN,O)	197.47	5.90	0.02	9	166.61

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

Table 3.9. β-coefficients, associated standard errors (SE) and *a priori* prediction for covariates influence on cheetahs selection of 100 km^2 sites (n = 24) in order of their summed model weights (∑*w*), in the Limpopo National Park, Mozambique. β coefficients for the variables direction and strength of influence on cheetah site selection are also shown.

Covariate	**β**	**SE**	**∑*w***	***a priori* prediction**
Bushmeat	**-5.144**	**2.397**	0.74	-
Settlement	-1.555	0.983	0.42	-
Open patches	0.633	0.803	0.11	+
Prey	4.069	3.932	0.09	+
Lion	0.424	2.418	0.03	-

Bold entries indicate robust impact (β ± 1.96 x SE not overlapping 0) (MacKenzie *et al*., 2006).

Species interactions

Lions were detected at 36% of the sampled sites on 97 sampling occasions. Models incorporating the influence of method, season and open habitat patches on lion detectability (*p*) showed good support ($\sum w > 0.95$; ΔAICc<3), and ranked higher than the model that assumes *p* was constant (ΔAICc = 6.08) (Table 3.10). Based on these results, these covariates for *p* were retained in all subsequent analyses for lion site use (*Ψ*) and its influence on cheetah occurrence (Ψ^{BA}, Ψ^{Ba}). The covariates 'cheetah prey' and 'settlements' were found to be highly correlated (as noted above), as were 'lion prey' and 'settlements' (r = -0.53) and were not included in the same models. A goodness of fit test for the global model for lion site use: *Ψ(LP, CP, B, S), p(M,O,SN)* did not show no evidence for lack of fit (p = 0.17) or over-dispersion ($\hat{c}$ = 1.31).

Table 3.10. Model selection procedure for factors influencing lion detectability (p) at (n = 260) 1 km sites in the Limpopo National Park, Mozambique. Covariates considered are method (M), open habitat patches (O) and season (SN). Lion site use (Ψ) is held constant (.)

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(.),p(M)	547.66	0.00	0.40	4	539.50
Ψ(.),p(M,O)	548.26	0.60	0.30	5	538.02
Ψ(.),p(M,SN)	549.72	2.06	0.14	5	539.48
Ψ(.),p(M,O,SN)	550.30	2.64	0.11	6	537.97
Ψ(.),p(.)	553.74	6.08	0.02	2	549.69
Ψ(.),p(O)	553.95	6.29	0.02	3	547.86
Ψ(.),p(SN)	555.77	8.11	0.00	3	549.68
Ψ(.),p(O,SN)	556.00	8.34	0.00	4	547.84

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

The model selection procedure for lion and cheetah co-occurrence models are provided in Table 3.11. The results are somewhat ambiguous regarding whether cheetah site selection was independent or conditional on the presence of lions. Both conditional and unconditional models had similar support (ΔAICc<2). However, the summed Akaike weights for models that assumed independence between cheetah and lion site use were higher than those that assumed cheetah site use was conditional on lion presence (0.58 versus 0.38). Cheetah and lion each showed strong avoidance of sites with greater bushmeat poaching; however, cheetah exhibited a greater negative response (Table 3.12, Fig 3.4). Lions and cheetahs differed in their response to their preferred prey; lions showed a strong selection for sites with greater buffalo site use, whereas cheetahs tended to avoid sites with greater impala site use (Table 3.12).

Although the majority of evidence is in support of independent site selection by cheetah and lion, there was evidence of statistically dependent associations ($\sum w = 0.38$). The mean probability of cheetah occurrence, averaged over the models that assumed site use was conditional on the presence of lions, was greater at sites where lion were absent ($\hat{\bar{\Psi}} = 0.476$, SE = 0.102) than at sites where lion were present ($\hat{\bar{\Psi}} = 0.340$, SE = 0.087). The species interaction factor was estimated at $\varphi = 0.57$, indicating spatial avoidance.

Table 3.11. Two species occupancy models examining interactions between cheetah (B) and lion (A) in Limpopo National Park, Mozambique. Ψ^{A}, Ψ^{B} are independent species site use parameters and Ψ^{BA}, Ψ^{Ba} are species B parameters conditional on the presence or absence of A. Covariates include lions preferred prey (LP), cheetahs preferred prey (CP), agro-pastoralist settlements (S) and bushmeat poaching (B). Species detectability (p) varies according to method (M), season (SN) and open habitat patches (O). For comparison, the constant (.) models are shown.

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
$\Psi^{A}(LP,B),\Psi^{B}(CP,B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	868.77	0.00	0.27	16	834.53
$\Psi^{A}(LP,B),\Psi^{BA},\Psi^{Ba}(CP,B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	869.32	0.55	0.21	17	832.79
$\Psi^{A}(LP,B),\Psi^{B}(B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	869.58	0.81	0.18	15	837.61
$\Psi^{A}(LP,B),\Psi^{B}(S,B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	870.82	1.62	0.12	16	836.15
$\Psi^{A}(LP,B),\Psi^{BA},\Psi^{Ba}(B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	871.81	2.05	0.10	16	836.58
$\Psi^{A}(LP,B),\Psi^{BA},\Psi^{Ba}(S,B),p^{A}(M,SN,O),p^{B}(M,SN,O)$	874.73	3.04	0.06	17	835.28
$\Psi^{A}(LP),\Psi^{BA},\Psi^{Ba}(B,CP),p^{A}(M,SN,O),p^{B}(M,SN,O)$	876.39	5.96	0.01	16	840.49
$\Psi^{A}(.),\Psi^{BA},\Psi^{Ba}(.),p^{A}(M,SN,O),p^{B}(M,SN,O)$	913.60	44.83	0.00	13	886.12
$\Psi^{A}(.),\Psi^{B}(.),p^{A}(M,SN,O),p^{B}(M,SN,O)$	920.83	52.06	0.00	12	895.57

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL).

Table 3.12. β-coefficients and associated standard errors (SE) for covariates influence on lion and cheetah site use from two-species occupancy models in the Limpopo National Park, Mozambique.

	Lion		**Cheetah**	
Covariate	**β**	**SE**	**β**	**SE**
Bushmeat	**-2.232**	**0.788**	**-4.752**	**1.671**
Prey*	**5.657**	**1.565**	-3.469	1.832
Settlement			-0.808	0.572

Bold entries indicate robust impact (β ± 1.96 x SE not overlapping 0) (MacKenzie *et al*., 2006).
*Species preferred prey

In support of the first hypothesis, cheetah site use was lower at sites with greater impala site use (Table 3.12), and there was some evidence in support of models that showed cheetah site use was higher at sites with greater impala site use given that lions were absent (∑w = 0.22). However, there was also evidence in support of models with the 'cheetah prey' covariate being independent (∑w = 0.27), suggesting cheetah were negatively associated with their preferred prey for reasons other than lion presence. Furthermore, the highest ranking model incorporating the 'cheetah prey' covariate for explaining lion site use was not supported (ΔAICc = 16.98) and the sign of the β-coefficient was negative (β = -0.594, SE = 0.997), providing evidence that lion presence was not higher at sites with greater impala site use. In sum, while the results indicate that cheetah were negatively associated with (1 km) sites with greater impala occurrence (Table 3.12), there is insufficient evidence to conclude that interspecific competition with lions was the cause of the negative correlation, although there was some evidence that cheetah were experiencing reduced interspecific competition when lions were absent at these sites.

In support of the third hypothesis; cheetah and lion each exhibited a strong negative response to bushmeat poaching (Fig. 3.4), and there was support (∑w = 0.38) for models that showed cheetah site use appeared to be higher at sites with bushmeat poaching given that lion were absent (Fig.3.5). However, there was more evidence that cheetah's avoidance of sites with greater bushmeat poaching was independent of lion presence (∑w = 0.58). In sum, the majority of evidence indicates that cheetah and lion were independently avoiding areas with a greater probability of bushmeat poaching, and there was evidence that cheetah were experiencing reduced interspecific competition when lions were absent at these sites.

Finally, the results support the hypothesis that cheetah were experiencing greater competition with humans than with lions. Cheetah showed strong avoidance of sites with greater bushmeat poaching use at both spatial scales (Tables 3.6 & 3.9), and anthropogenic pressures contributed considerably more to cheetah site use than lion occurrence did at both the temporary patch use (∑w = 1.09 versus ∑w= 0.21) and the home range spatial scales (∑w = 1.16 versus ∑w = 0.23) (Tables 3.6 & 3.9, Fig.3.3). Further analysis using two-species occupancy models provided evidence that cheetahs occurred statistically less often than would be expected at sites where lions occurred (φ = 0.57, ∑w = 0.38), however, there was more support for models that indicated that cheetah site selection was independent of lion site use (∑w = 0.58) (Table 3.11). Finally, the results indicate that cheetah temporally overlapped slightly more with lions than with bushmeat poachers (and their dogs) in the study area (Δ = 0.66 versus Δ 0.53; Fig. 3.6). These results suggest that cheetah may have shifted their temporal activity patterns to be more nocturnal, thereby reducing contact with humans.

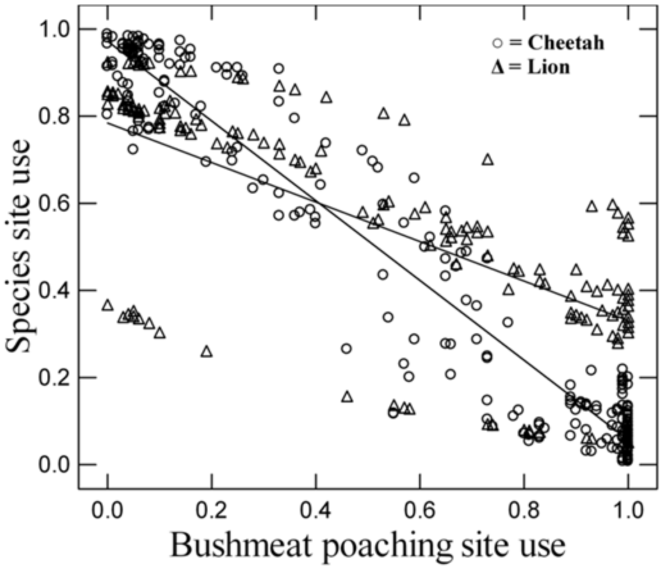

Figure 3.4. Influence of bushmeat poaching on the probability of site use by cheetah and lion. The variable bushmeat poaching is based on an occupancy model of human hunters, domestic hunting dogs and snared mammalian fauna (Everatt, 2013). Estimates are based on the averaged model (∑w≥0.95). Number of (1 km) sites = 260.

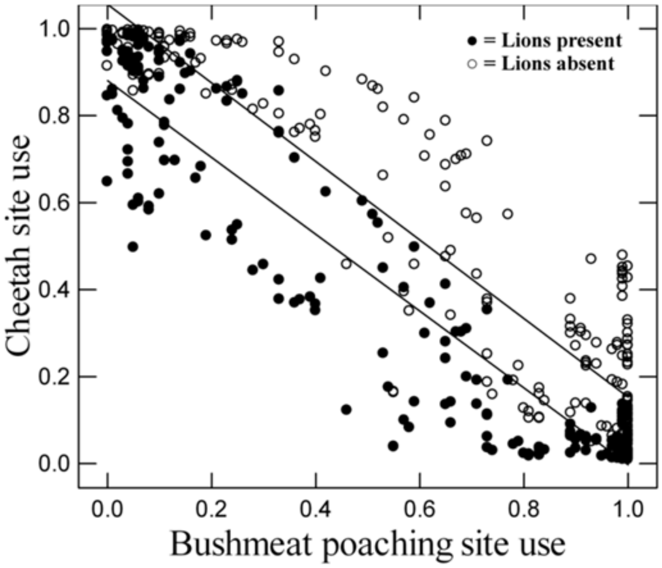

Figure 3.5. Influence of bushmeat poaching on the probability of site use by cheetah, conditional on the presence or absence of lions. The variable bushmeat poaching is based on an occupancy model of human hunters, domestic hunting dogs and snared mammalian fauna (Everatt, 2013). Estimates are based on the averaged model (∑w≥0.95). Number of (1 km) sites = 260.

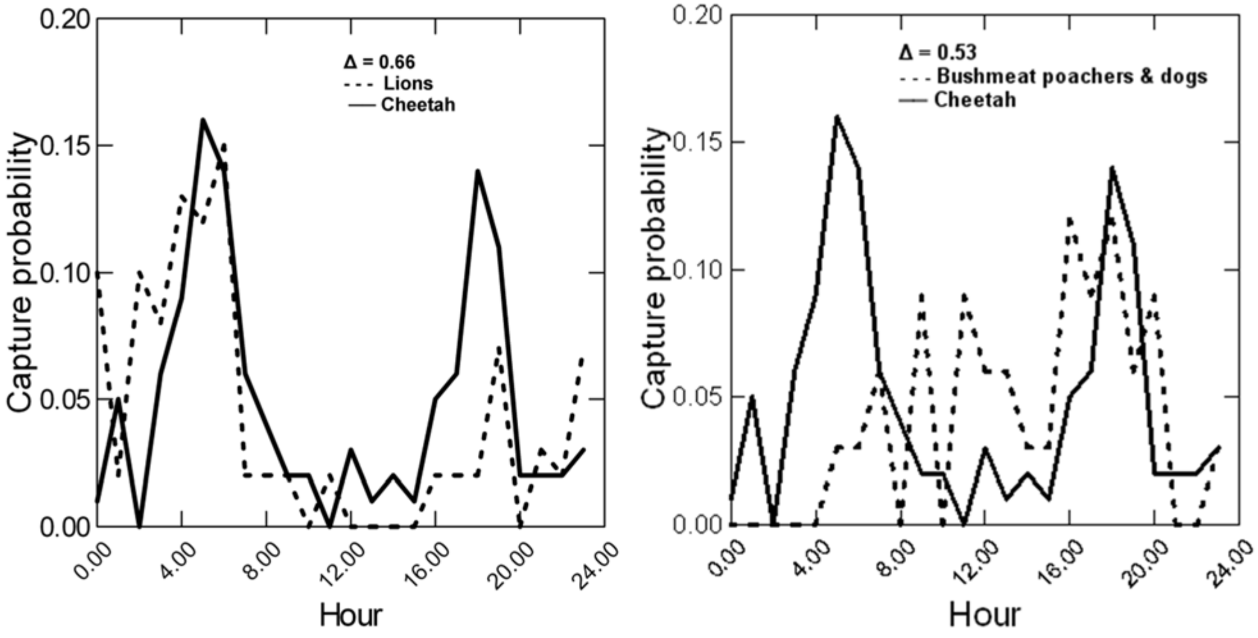

Figure 3.6. Temporal overlap between cheetah and lion (left) and between cheetah and bushmeat poachers and domestic hunting dogs (right). The estimate of temporal overlap (Δ; where 0 is no overlap and 1 is complete overlap) is defined as the area under the curve, calculated by taking the minimum of the two activity patterns at each hour. Data were obtained from photographic events of cheetah (n = 161), lion (n = 60) and bushmeat poachers (accompanied by domestic dogs) (n = 87), from 89 camera-trap stations located across a 2400 km^2 study area in the Limpopo National Park, Mozambique during September, 2011- November, 2012.

We performed subsequent analyses to better understand the mechanisms behind the observed negative association between cheetah and their preferred prey (at the temporary patch use scale) and determine whether predation risk was a contributing factor. Two-species occupancy models were used to test whether cheetah and impala site use was independent or showed evidence of statistically dependent interactions (following the procedures described in *Data analysis*, above). The following two hypotheses were tested to explain the negative association between cheetah and impala: 1) cheetah site use is conditional on impala presence, and 2) impala site use is conditional on cheetah presence.

The impala and cheetah data were collected for the same 1 km sites (n = 260) over the same survey period (see *identification of covariates*, above). Considering that impala detectability along transects may vary with seasonal changes in vegetative growth and be greater in open areas, the covariates 'season' and 'open habitat patches' were included as sampling covariates. Models incorporating the influence of method, season and open habitat patches on impala detectability (*p*) were strongly supported (ΔAICc<2), and ranked higher than the model that assumes *p* was constant (ΔAICc = 12.77) (Table 3.13). Based on these results, these covariates for *p* were retained in all subsequent analysis for impala site use (*Ψ*).

Table 3.13. Model selection procedure for factors influencing impala detectability (p) 1 km sites (n = 260) in the Limpopo National Park, Mozambique. Covariates considered are method (M), season (SN) and open habitat patches (O). Impala site use (Ψ) is held constant (.)

Model	**AICc**	**ΔAICc**	**w**	**k**	**-2LL**
Ψ(.),p(M)	819.18	0.00	0.37	4	811.02
Ψ(.),p(M,SN)	819.50	0.32	0.30	5	809.26
Ψ(.),p(M,O)	820.13	0.95	0.19	5	809.89
Ψ(.),p(M,SN,O)	820.62	1.44	0.14	6	808.29
Ψ(.),p(SN)	831.32	12.14	0.00	3	825.23
Ψ(.),p(.)	831.95	12.77	0.00	2	827.90
Ψ(.),p(SN,O)	833.28	14.10	0.00	4	825.12
Ψ(.),p(O)	833.79	14.61	0.00	3	827.70

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL). (.) assumes the parameter is constant.

For each hypothesis, we fit eight models for species independent and conditional site use, considering the constant models (.) and models that included covariates that previous analysis revealed were determinant (∑w ≥95) of cheetah *Ψ* (bushmeat poaching, Table 3.6) and impala *Ψ* (proximity to agro-pastoralist settlements, Chapter 2). The model selection procedures for cheetah and impala co-occurrence models are provided in Table 3.14. The results did not support the first hypothesis; the model that assumed cheetah occurrence was independent of impala presence was strongly supported (ΔAICc<2, w = 0.74) and out-performed the model that assumed cheetah site selection was conditional on impala presence (ΔAICc = 2.11, w = 0.26) (Table 3.14). The mean probability of cheetah site use was slightly lower when impala were present ($\hat{\hat{\Psi}}$= 0.322, SE = 0.073) than when impala were absent ($\hat{\hat{\Psi}}$ = 0.359, SE = 0.088), however the species interaction factor was fairly close to 1, (φ = 0.85), suggesting weak spatial avoidance and that cheetah presence was largely independent of impala site use. These results indicate that the observed negative association between cheetah and impala at temporary use patches (Tables 3.6 & 3.12) cannot be attributed to cheetahs' avoidance of impala.

The results supported the second hypothesis; the model that assumed impala occurrence was conditional on cheetah presence was strongly supported (w >0.99) and greatly out-performed the model that assumed impala site selection was independent of cheetah (ΔAICc = 12.55) (Table 3.14). The mean probability of impala site use was considerably lower when cheetah were present ($\hat{\hat{\Psi}}$ = 0.282, SE = 0.117) than when cheetah were absent ($\hat{\hat{\Psi}}$ = 0.720, SE = 0.084). The species interaction factor was estimated at φ = 0.15, indicating strong spatial avoidance. These results indicate that the observed negative association between cheetah and impala at the temporary patch use scale (Tables 3.6 & 3.12) is due to impala spatially avoiding cheetah.

Table 3.14. Two species occupancy (Ψ) models examining interactions between cheetah and their preferred prey (impala) in Limpopo National Park, Mozambique. Models are grouped according to hypotheses. Ψ^{A}, Ψ^{B} are independent species site use parameters and Ψ^{BA}, Ψ^{Ba} are species B parameters conditional on the presence or absence of A. Covariates considered include bushmeat poaching (B) and agro-pastoralist settlements (S). Species detectability varies according to method (M), season (SN) and open habitat patches (O). For comparison, the constant (.) models are shown.

Hypothesis	**Model**	**AICc**	**ΔAICc**	**w**	**K**	**-2LL**
Cheetah (B)	$\Psi^{A}(S), \Psi^{B}(B), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1212.36	0.00	0.74	14	1182.65
site use is	$\Psi^{A}(S), \Psi^{BA}, \Psi^{Ba}(B), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1214.47	2.11	0.26	15	1182.50
conditional on	$\Psi^{A}(.), \Psi^{B}(.), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1256.71	44.35	0.00	12	1231.45
impala (A)	$\Psi^{A}(.), \Psi^{BA}, \Psi^{Ba}(.), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1258.43	46.07	0.00	13	1230.95
Impala (B)	$\Psi^{A}(B), \Psi^{BA}, \Psi^{Ba}(S), p^{A}(M,SN,O), p^{B}(M,SN,O)$	993.74	0.00	1.00	15	961.77
site use is	$\Psi^{A}(B), \Psi^{B}(S), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1006.27	12.55	0.00	14	976.56
conditional on	$\Psi^{A}(.), \Psi^{BA}, \Psi^{Ba}(.), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1031.17	37.43	0.00	13	1003.69
cheetah (A)	$\Psi^{A}(.), \Psi^{B}(.), p^{A}(M,SN,O), p^{B}(M,SN,O)$	1033.29	39.57	0.00	12	1008.08

AICc values; the relative difference in AICc values between each model and the model with the lowest AICc (ΔAIC); AICc model weights (w); the number of parameters in the model (k); twice the negative log-likelihood (-2LL).

Discussion

A sound understanding of carnivore habitat selection in human-disturbed landscapes is important for species conservation planning and management. Although humans alter landscapes and place increasing pressure on protected areas (Caro & Scholte, 2007; Wittemyer *et al*., 2008) there are few data available on how carnivores select habitats in human-modified systems. This study investigated fitness-related factors that may influence cheetahs' selection of habitats at multiple spatial scales in a human-disturbed system in Mozambique. The results show that cheetah habitat selection was scale dependent; that is, the influence of prey and competitor occurrence, prey catch-ability features, and anthropogenic pressures varied considerably with scale in the system.

Prey availability versus prey catch-ability

The results from this study support the theories that landscape features facilitating prey capture are a limiting factor for cheetah (Caro, 1994; Hunter, 1998; Broomhall *et al*., 2003; Muntifering *et al*., 2005; Bisset & Bernard, 2007).   Open habitat patches with dense edges were strongly determining and contributed considerably more to cheetah site selection than prey occurrence at the temporary patch use scale (Fig. 3.3). Cheetah were negatively associated with their preferred prey at temporary patches, but tended to select for home range level sites that had greater prey occurrence (Tables 3.6 & 3. 9). The prey occurrence model used in this study can be seen as the probability that cheetah will encounter their preferred prey. It should be noted that this study did not measure prey abundance but rather prey site use, however, occurrence and abundance may often be related, since occurrence is simply the locations where abundance is >0 (MacKenzie *et al*., 2006).

The specialized cheetah prey capturing technique is highly efficient in terms of capture success, but limiting in that it requires suitable terrain for the high speed chase needed to topple prey (Bertram, 1979; Turner, 1997). Moreover, cheetah require a combination of cover for stalking and open line of sight to spot prey from an adequate distance necessary to build chase momentum (Caro, 1994). The open habitat patches modeled in this study offer vantage points (i.e., termite mounds or fallen trees on the perimeter of open patches) for spotting prey, densely vegetated edges for concealed stalking, and suitable terrain (i.e., few obstructions) for high-speed chase (Fig. 3.2). That cheetah showed stronger selection for patches of open habitat than prey occurrence indicates that cheetah's daily use patterns were determined more by prey catch-ability than by prey availability. Cougars may select home range sizes to include a necessary minimum amount of edge habitat required for hunting (Laundre & Loxterman, 2006). Similarly, Broomhall *et al*., (2003) suggested that suitable habitat structure for hunting may influence cheetah home range size. While this study did not investigate home range sizes, the results do indicate that prey catch-ability features also contribute to cheetah site use at a coarse scale.

Altogether these findings have important management implications. Open patches in LNP are discrete locations scattered across a woodland continuum, and comprise a small proportion of the landscape (9.8%) Similarly, Hunter (1998) found that cheetah in the Phinda reserve selected open patches for hunting, a feature which comprised only 8.6% of the landscape. Open habitat patches may facilitate the ability of cheetah to persist in woodland habitats where their hunting strategy would be otherwise compromised. Moreover, since competition with sympatric predators is less severe in more densely vegetated habitats (Mills *et al*., 2004; Bisset & Bernard, 2007) than in open grassland plains (Laurenson, 1994; Kelly *et al*., 1998), cheetah recruitment in more closed habitats may be greater (assuming no significant external pressures such as human persecution, e.g., Marker, 2002). It is therefore possible that landscapes offering higher edge/area ratios could sustain greater cheetah population densities because minimum home range area requirement may be reduced in response to greater abundance of optimal hunting sites and increased concealment from competitors.

Predation and competition

This study failed to find support for the hypothesis that cheetah were negatively associated with prey due to interspecific competition with lions. Overall, interspecific competition with lions did not appear to be a major determining factor of cheetah site selection in LNP. Cheetahs were influenced more by prey catch-ability features, anthropogenic factors and prey occurrence than by lion occurrence across spatial scales (Fig. 3.3). Two-species occupancy models were used to explore the influence of prey on cheetah and lion co-occurrence patterns at the temporary patch scale. Cheetah and lion differed in their response to their preferred prey; lions were strongly positively associated with buffalo whereas cheetahs were negatively associated with impala (Table 3.12). As predicted, there was evidence that cheetah site use was greater given that lions were absent, however, there was slightly more support for models that showed cheetah were independently negatively associated with their prey (Table 3.11). Moreover, lions were not positively correlated with impala occurrence, indicating that cheetah did not have a greater than normal chance of interacting with lion at sites with greater impala occurrence. In sum, there is insufficient evidence to conclude that cheetahs were avoiding their prey due to lion presence. Another likely explanation for the observed negative association may be avoidance by impala due to a behavioural response to predation risk by cheetah (Caro, 2005).

To better understand the mechanisms behind the observed negative association between cheetah and their preferred prey, this study used *post-hoc* analysis to determine whether the results could be explained by predation risk. We used two-species occupancy models to test for statistically dependent associations (i.e., avoidance) between cheetah and impala, accounting for individual species detectability and determining habitat correlates. The model assuming that cheetah site use was dependent on impala site use received little support and was out-ranked by the model that assumed their site use was independent. Conversely, the model showing that impala site use was dependent on cheetah site use received strong support, and the species interaction factor indicated strong spatial avoidance (Table 3.14). These results provide evidence that impala were spatially avoiding sites with greater cheetah occurrence, indicating that the observed negative association between cheetah and their prey was due to a strong behavioural response on behalf of impala.

Predation risk is a major contributing factor to species distributions (Krebs, 2009). Cheetahs exhibit preferential selection for certain prey species (Hayward *et al*., 2006) and a markedly high capture success rate (Bertram, 1979; Turner, 1997). This study showed that impala exhibited strong spatial avoidance of temporary resource patches where cheetah site use was greater, likely as a behavioural response to predation risk. These results contrast to that of Thaker *et al*., (2011), which showed that impala exhibited only a weak spatial avoidance of cheetah at the landscape scale. However our study differed from Thaker *et al*., (2011) in scale (i.e., second versus third order selection) (Johnson, 1980), which may indicate a scale dependency of these species-habitat relationships (Rettie & Messier, 2000). It is interesting that Muntifering *et al*., (2005) also found a negative correlation to cheetah and their prey in a landscape where lion and spotted hyaena had been eradicated (and therefore interspecific competition could be excluded as the causational factor). Muntifering *et al*., (2005) suggested that the observed correlation was due to cheetah selecting for hunting requirements over prey density; however, this interpretation does not fully explain the negative association between cheetah and their prey. While the results from this study support the conclusion that hunting requirements (i.e., habitat structure) are limiting to cheetah, our results also provide evidence that cheetah may elicit strong spatial avoidance behaviour in their prey.

Anthropogenic pressure

There are few data on the impact anthropogenic pressure on cheetah habitat selection. Muntifering *et al*., (2005) investigated the influence of bush encroachment on fine-scale habitat use by cheetah on commercial game and cattle ranches in Namibia. Pettorelli *et al*., (2008) found that cheetah selected against sites that were closer to human settlements bordering the Serengeti National Park. This study attempted to quantify the impact of rural agro-pastoralist settlements and bushmeat poaching on cheetah site use; conditions that could be considered characteristic of much of cheetahs remaining range outside of commercial farmlands and formally protected areas. Anthropogenic factors contributed to cheetah site selection at both spatial scales, and contributed more to cheetahs' use of home range level sites than the other fitness related factors considered (i.e., prey occurrence, competitor occurrence and prey catch-ability features combined) (Fig. 3.3). Since factors contributing to site selection at the coarsest scale should be most limiting to species fitness (Rettie & Messier, 2000), these results indicate that cheetah were most limited by anthropogenic pressures in the system. Cheetahs avoided settlement areas across spatial scales; however, these features contributed considerably more to home range level use. These results indicate that cheetah coexistence with humans in LNP was facilitated by their avoidance of areas with greater cultivation and livestock grazing at a coarse level and less so by local avoidance.

This study is the first to quantify the impact of bushmeat poaching on cheetah ecology. Interestingly, selection against sites with greater occurrence probability of bushmeat poaching was strongly determining for cheetah across both spatial scales. That selection against these sites varied little with scale emphasizes the importance of this limiting factor (Rettie & Messier, 2000) on cheetah site use. Bushmeat poachers and their accompanying dogs are mobile hunters that travel on routes used by carnivores, and select for areas with greater mid-sized antelope abundance (Everatt, 2013). Cheetah may avoid these sites due to risk of human persecution and/or kleptoparasitism from packs of domestic dogs.

Durant (1998) proposed that cheetah seek out 'competition refugia' as a mechanism for coexistence with lion and spotted hyaena. Similarly, the results of this study indicate that cheetah seek competition refugia from bushmeat hunters and their dogs. Habitat selection can be seen as a behavioural response to factors influencing individual fitness (Rettie & Messier, 2000). Cheetahs have evolved alongside humans hunting with bows, spears, snares and dogs, and it is probable that they have developed mechanisms for coexistence. This study showed that cheetahs spatially (Tables 3.6 & 3.9) and temporally (Fig. 3.6) avoid human hunters similar to how they avoid other competitors (Durant, 1998; 2000).

Considering that lions occur at low population densities in the study area and that the habitat provides suitable cover, it was predicted that competition with humans (i.e., combined anthropogenic pressures) would be more determining of cheetah site use than competition with lions. Two species occupancy models were used to investigate cheetah and lion co-occurrence patterns and test for statistical dependency. The results provided evidence that cheetah were spatially avoiding lion, however, there was more support for models that found cheetah site use was not conditional on the presence of lions (Table 3.11); that is, given each species detectability and individual habitat preferences, there was no strong evidence that cheetahs were found less often than would be expected at sites where lion were present.

Both species showed strong avoidance of sites with greater bushmeat poaching; however, cheetah exhibited the greater negative response (Fig. 3.4). There was evidence that cheetah site use was higher at sites with bushmeat poaching given that lions were absent, indicating that cheetah may exhibit lower tolerance of human pressure when lions are also present (Fig. 3.5). Altogether, however, it appears that competition with humans was greater than competition with lions in the system; anthropogenic pressures contributed considerably more to cheetah site use than lion occurrence did across spatial scales (Tables 3.6 & 3.9, Fig. 3.3). This was further supported by evidence of a greater temporal avoidance of bushmeat hunters and their dogs than of lions (Fig. 3.6). Avoidance behaviour can be interpreted as an adaptation to reduce competition and increase individual fitness (Krebs, 2009). That cheetah shifted their typical crepuscular activity patterns (Hayward & Slotow, 2009) to be more nocturnal, thus overlapping more with lions and less with bushmeat hunters, suggests that in this system, human hunters and packs of hunting dogs were more of a threat to individual cheetah fitness than were lions. Future investigations into co-occurrence patterns between cheetah and humans using two-species occupancy models could provide insight into potential competitive interactions and the ability for cheetah to persist in to different human pressures. A deeper understanding cheetah ecology in human-disturbed systems can inform conservation strategies and increase our capacity to prevent the global loss of wild cheetah populations.

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CHAPTER FOUR

General Discussion

The use of site occupancy models for targeted monitoring of cheetah

Cheetah conservation management is hindered by a lack of reliable data on their conservation status throughout large portions of their remaining range. This study has demonstrated the feasibility of quantifying cheetah occurrence and limiting factors using detection/non-detection data and an occupancy modelling technique. I conducted my study in a location with limited infrastructure where population data were lacking; conditions that characterize much of cheetahs remaining range. With the use of replicated detection/non-detection surveys, I was able to estimate the probability of detecting cheetah directly, thereby providing an unbiased estimate of occurrence that can be used to compare status across different sites and as a basis for long-term monitoring. Failing to account for detectability in status assessments of cheetah (i.e., the use of indices of abundance) is problematic because it can lead to populations being overlooked that require conservation interventions and misleading inferences on factors influencing their occurrence. The use of site occupancy models was also advantageous because it permitted the simultaneous provision of data on factors influencing the occurrence of cheetah. A targeted monitoring approach that seeks to understand *why* organisms occur *where* they do in addition to collecting population data is an efficient use of conservation resources and can provide the necessary information for adaptive management (Yoccoz, Nichols & Boulinier, 2001).

Based on the results from this study, I suggest that track and/or camera-trap surveys coupled with site occupancy models are an appropriate technique for assessing the status of less known cheetah populations, and have the potential to become widely used for ecological investigations and monitoring programs. When designing occupancy surveys, it is important to consider the population parameter of interest (i.e., proportion of area occupied versus site use) and the biology of the species, and how these relate to model assumptions. I found that cheetah detectability was 55% greater on (3 km) track surveys than on (14 day) camera-trap surveys, and suggest that replicated track surveys are an efficient means of collecting empirical data on less-known cheetah populations. I see much potential in the use of spatially replicated sign surveys (Hines *et al*., 2010) for large-scale status assessments (e.g., Karanth *et al*., 2011) of cheetah. This approach is logistically advantageous because it uses sections of trail as replicates, and therefore does not require grid cells to be revisited. A landscape-scale approach could be used to identify meta-populations (Karanth *et al*., 2011), evaluate corridor use (Barber-Meyer *et al*., 2013) and potential areas for re-introductions (Hebblewhite *et al*., 2011). Site occupancy models can be used in meta-population viability analysis (Linkie *et al*., 2006); estimating the vital processes of local extinction and colonization and factors that determine patch persistence (Sjögren-Gulve & Hanski, 2000).

The ecological requirements of cheetah in human-dominated landscapes

This study provides some of the few data on cheetah ecology in human-impacted landscapes, and is the first to quantify the impact of human-hunters and domestic dogs on cheetah habitat selection. Knowledge of the ecological requirements of cheetah in disturbed systems is important for their conservation management because we can use this information to promote coexistence. By accounting for detection error, I was able to distinguish between factors influencing detection and occurrence simultaneously, and thus provide robust inferences on cheetah habitat selection. Similarly, two-species occupancy models permitted me to provide robust inferences on interactions with conspecifics while accounting for individual species detection probabilities and habitat correlates. I found that cheetah habitat selection was scale dependent; that is, the influence of prey availability, prey catch-ability, lion occurrence and human disturbance factors varied between temporary patch use and home range scales.

Open habitat patches with dense edges, a landscape feature facilitating prey capture, were strongly determining at the temporary use scale, and these features contributed more to cheetah site selection than prey occurrence at both spatial scales. Open habitat patches may facilitate the ability of cheetah to persist in woodland habitats where their hunting strategy would be otherwise compromised. Moreover, since competition with sympatric predators is thought to be reduced in more densely vegetated habitats (Mills *et al*., 2004), cheetah recruitment in these environments may be greater. I propose that landscapes offering higher edge/area ratios may sustain greater cheetah population densities because minimum home range area requirements may be reduced in response to greater abundance of optimal hunting sites and increased concealment from competitors.

My results showed that cheetah generally selected for areas with greater impala occurrence at a coarse scale, but were negatively associated with impala at a fine scale. I failed to find support, however, for the hypothesis that cheetah were avoiding areas of greater prey occurrence due to interspecific competition with lions (as has been documented in the Serengeti plains by Durant, 1998). Overall, interspecific competition with lions did not appear to be a major determining factor of cheetah site selection in LNP; cheetahs were influenced more by prey catch-ability features, prey occurrence and anthropogenic factors than by lion occurrence across spatial scales. Two-species occupancy models indicated some spatial avoidance of lion by cheetah, but there was more support for models that indicated cheetah site use was independent of lion presence. These results are somewhat unsurprising considering that lions occur at low densities in the study area and the habitat offers cover for concealment. I used two-species occupancy models to further explore the negative association between cheetah and their prey, which revealed a strong spatial avoidance of cheetah by impala. These results suggest that cheetah can elicit a strong behavioural response in their prey.

Considering that factors limiting species fitness should be most limiting at a coarser scale (Rettie & Messier, 2000), my results indicate that cheetah were most limited by anthropogenic pressures in the study system; these factors contributed more to cheetah site use than the other fitness related factors considered (at the 'home range' scale). Cheetahs avoided settlement areas across both spatial scales; however, these features contributed considerably more to home range level use. More determining, however, was a strong spatial avoidance of sites with greater bushmeat poaching site use across both spatial scales. These results indicate coexistence with agro-pastoralist hunters in the study area was facilitated by spatial avoidance of settlements and bushmeat poaching use areas at a coarse scale and additionally by spatial avoidance of human hunters at a finer scale. My results supported the hypothesis that competition with humans was greater than competition with lions in the study system; cheetah exhibited greater spatial and temporal avoidance of humans and domestic dogs than of lions. These results indicate that cheetah seek 'competition refugia' (Durant, 1998) from human hunters and their dogs similar to how they avoid other competitors. Future investigations into co-occurrence patterns between cheetah and humans using two-species occupancy models could provide insight into potential competitive interactions and the ability for cheetah to persist in landscapes exposed to different human pressures. A deeper understanding of the mechanisms facilitating coexistence between cheetah and humans can inform conservation strategies and increase our capacity to prevent the global loss of wild cheetah populations.

Management implications

This study provides the first quantification of cheetah occurrence and limiting factors in a region of Mozambique where cheetah were thought to have been extirpated, and an important benchmark that future change can be measured against. My results show that despite being impacted by human hunting, cultivation and pastoralism, cheetah occupied approximately 40% of the 2400 km^2 study area. The results indicate that anthropogenic factors are limiting the population more than biotic factors. LNP is presently undergoing resettlement of communities from the core area of the park and I anticipate that this will result in an expansion of cheetahs' distribution. In Chapter 2, I provide recommendations for future monitoring. Overall, my results show that LNP can be considered recovered range, which has positive implications for other nearby protected areas in Mozambique (e.g., Banhine and Zinave National Parks) where cheetah are thought to have been extirpated but status is unknown (IUCN/SSC, 2007). LNP is strategically important habitat for cheetah because it has the potential to serve as a 'gateway' for recolonization other locations and to prevent genetic impoverishment by providing connectivity to populations in South Africa.

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APPENDIX I

Biodiversity of mammals (> 3 kg) documented in the Limpopo National Park, Mozambique. Data were obtained from 89 camera-trap stations and 5535 camera-trap nights during 2011-2012.

Common name	**Species**	**Common name**	**Species**
Buffalo	*Sycerus caffer*	Lion	*Panthera leo*
Eland	*Tragelaphus oryx*	Leopard	*Panthera pardus*
Kudu	*Tragelaphus strepsiceros*	Cheetah	*Acinonyx jubatus*
Nyala	*Tragelaphus angasii*	Caracal	*Felis caracal*
Bushbuck	*Tragelaphus scriptus*	Serval	*Felis serval*
Impala	*Aepyceros melampus*	African wild cat	*Felis libyca*
Waterbuck	*Kobus ellipsiprymnus*	Spotted hyaena	*Crocuta crocuta*
Roan	*Hippotragus equinus*	Aardwolf	*Proteles cristatus*
Sable*	*Hippotragus niger*	African wild dog	*Lycoan pictus*
Oribi*	*Ourebia ourebi*	Bat-eared fox	*Otocyon megalotis*
Steenbok	*Raphicerus campestris*	Black-backed jackal	*Canis mesomelas*
Sharpe's grysbok	*Raphicerus sharpei*	Side-striped jackal	*Canis adustus*
Suni	*Neotragus moschatus*	Honey badger	*Mellivora capensis*
Klipspringer	*Oreotragus oreotragus*	African Civet	*Civettictis civetta*
Common duiker	*Sylvicapra grimmia*	Large-spotted genet	*Genetta tigrina*
Giraffe	*Giraffa camelopardalis*	Banded mongoose	*Mungos mungo*
Warthog	*Phacochoerus africanus*	Slender mongoose	*Herpestes sanguineus*
Bushpig	*Potamochoerus porcus*	White-tailed mongoose	*Ichneumia albicauda*
Hippopotamus	*Hippopotamus amphibius*		
White rhino	*Ceratotherium simum*	Savannah baboon	*Papio cynocephalus*
Plains zebra	*Equus burchelli*	Vervet monkey	*Ceropithecus aethiops*
Elephant	*Loxodonta africana*	Lesser bushbaby	*Gelago moholi*
Aardvark	*Orycteropus afer*	Greater bushbabay*	*Otolemur crassicaudatus*
Porcupine	*Hystrix africaeaustralis*		
Scrub hare	*Lepus saxatilis*		
Spring hare	*Pedetes capensis*		
Greater cane-rat	*Thryonomys swinderianus*		

*indicates species was only observed