Influence of bushmeat poaching and pastoralism on African lion *Panthera leo* (Linnaeus, 1758) ecology in rural Mozambique

By

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Submitted in partial fulfilment of the requirements for the degree

Magister Scientiae in Wildlife Management

Centre for Wildlife Management

Faculty of Natural & Agricultural Sciences

University of Pretoria

Pretoria

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October 2013

I, Kristoffer Everatt, 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.

2014-03-24

Signature **Date**

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SUMMARY

The African lion, *Panthera leo*, has suffered dramatic population and range declines over the last few decades and is listed as Vulnerable to extinction by the International Union for the Conservation of Nature. Quantification of the factors limiting the abundance and distribution of lions in human disturbed systems is critical if we wish to promote the conservation of the species beyond the sanctuaries of a limited number of reserves. From September 2011 - November 2012, I studied aspects of the population and habitat ecology of lions in the developing Limpopo National Park (LNP), Mozambique; a woodland savannah ecosystem supporting relatively low prey densities and inhabited by subsistence-agro-pastoralist-hunters.

Using call-up surveys I estimated a density of 0.99 lions/100 km^2 and a population abundance of 66 lions for the park. I compared this direct estimate of density with an indirect estimate derived from trophic scaling of available prey resources. The direct density estimate was less than 1/3 of the estimate derived from prey resources (3.05 lions/100 km^2). The observed disparity between the realized and potential densities of lions in LNP suggests the limiting influence of external top-down, anthropogenic pressures. I then used replicated detection/non-detection camera trap and track surveys to estimate the proportion of area occupied by lions, and hierarchical ranking of covariates to provide inferences on the relative contribution of prey resources and anthropogenic factors influencing lion occurrence. The proportion of area occupied by lions was $\Psi = 0.439$ (SE = 0.121), or approximately 44% of a 2400 km^2 sample of potential habitat. Although the occurrence of lions was strongly predicted by a greater probability of encountering prey resources, the greatest contributing factor to lion occurrence was a strong negative association with settlements. Altogether, these results describe a population of lions held below resource-based carrying capacity by anthropogenic factors, and highlight the limitations of trophic scaling for estimating predator populations exposed to anthropogenic pressures.

Following this, I investigated the habitat selection by lions at two spatial scales (temporary site use scale and home range scale) using site occupancy models and camera-trap and track surveys. I used hierarchical ranking of covariates to test the following hypotheses on habitat selection by an apex predator in a human disturbed system: 1) habitat use by lions should be most strongly predicted by bottom-up prey resources, 2) in a human disturbed system, habitat use by lions may also be predicted by top-down pressures, including both agro-pastoralism and bushmeat poaching. I also considered both the influence of the spatial scale examined and season on lion-habitat associations. Habitat use by lions was most strongly influenced by the occurrence of their preferred prey across both spatial scales and seasons. However, lions showed strong spatial avoidance of bushmeat poaching at the finer spatial scale and selected against agro-pastoralist use at the coarser scale. Restricting the analysis to a singular coarser scale would have greatly underestimated the impact of bushmeat poaching on the habitat ecology of lions. There was seasonal variation in the

relative contributions of all variables with a dramatic increase in the influence of bushmeat poaching during the dry season.

The results of this study agree with the trophic importance of prey resources to an apex predator but also demonstrate the limiting influence of top-down anthropogenic pressures on the ecology of lions. However, the results also suggest that provided with adequate prey and space, lions and subsistence-agro-pastoralist-hunters may be able to continue to persist in the same landscapes. This study provides the first empirical quantification of a population that future change can be measured against, and some of the few data on lion habitat ecology in human disturbed landscapes.

ACKNOWLEDGEMENTS

Without a doubt, the two people that I have to thank first and foremost are my wife, Leah and daughter, Eden. Thank you, Eden for being such a great bush kid. You have been such a great sport about the hot bumpy dusty drives, the spiders, the thorns, the hot showers on hot days and cold showers on cold days. But hey we had elephants at the waterhole, monkeys in the trees, hyenas whooping through the night, francolins and baboons for alarm clocks and the occasional mayhem of lions in the camp! Thank you, Leah, for being such an amazing partner on every front. I am so lucky to have a great life and research partner in one! You're also the one person I know that can get more excited than me about a faint track in the sand.

Thank you to the University of Pretoria, Wilderness Wildlife Trust, the Canada Student Grant Program, Great Canadian Wilderness Adventures and The Wipplinger Foundation for financial contributions to the project and to the Centre for Wildlife Management, Idea Wild, Twin Cities Eco-tourismo, Yokahama Tires and Acer for contributions of equipment. I am grateful to my academic advisor, Prof. Michael Somers, for facilitating the project and research through the Centre for Wildlife Management. Thank you to the National Director of Conservation Areas for granting us the research permits to conduct this work (005-2011/003-2012) and to Parque Nacional do Limpopo warden Baldeau Chande and project manager Antony Alexander for supporting the research. Thank you to Reinecke Janse van Rensburg, Lourence Swanepoel and Pieter Small for help with different aspects of the logistics and to Antony & Zorana Alexander and Lourence & Cory Swanepoel for hosting us when we made our trips out of the bush. I would also like to thank Graham & Danni Harman and Xonghile Game Reserve for hosting us during this final write up phase. Thank you to Jane Watson, Tom Jung and Marcella Kelly who have each provided me with guidance and mentoring over the years and helped to give me the skills I needed to do conduct scientific research.

I would like to thank both of my parents. My mother, who inspired in me a love for animals, would have really enjoyed seeing me become a biologist and return to Africa. I thank my father for inspiring in me a passion for wilderness, science and logic, which I think I have managed to combine quite well. Thank you, Dad and Gwen for all of your support on this venture. Thank you also Andreas and Carol for how much you have each supported us throughout this project. I want to thank all of my good friends in Canada who know how much I love the north and the mountains yet were supportive of this idea to sell the horses and dogs and head off to Africa.

And of course, a big thanks to the lions in the night and the wild African bush.

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CHAPTER 1: GENERAL INTRODUCTION

Ecology of lions

The lion, *Panthera leo*, first appeared in the fossil record approximately 3.5 million of years ago (Turner, 1997). As an apex predator of the African savannah, lions are naturally limited by bottom-up prey resources (Schaller, 1972; Van Orsdol *et al*., 1985; Carbone & Gittleman, 2002; Hayward *et al*., 2007) and may exert considerable influence on lower trophic levels (Sinclair *et al*., 2006; Estes *et al*., 2011; Tambling *et al*., 2012). Lions experience density dependence (Mosser *et al.,* 2009; Packer *et al*., 2013) and generally follow an optimal despotic distribution (Fretwell & Lucas, 1969; Mosser *et al.,* 2009). Prides maintain and defend territories ranging in size from 30 km^2 (Kissui *et al*., 2009) to 1 450 km^2 (Funston, 2011), with size inversely related to availability of fitness resources (Rich *et al*., 2012), including the availability of prey (Van Orsdol *et al*., 1985). Lions take a wide range of prey species; however, they show preferential selection for larger bodied prey (Hayward & Kerley, 2005) offering higher energetic returns (Scheel & Packer, 1995), which in forested savannahs in southern Africa include African buffalo, *Syncerus caffer*, giraffe, *Giraffa camelopardalis*, plains zebra, *Equus burchelli* and blue wildebeest, *Connochaetes taurinus* (Funston *et al*., 1998; Hayward & Kerley, 2005).

Status and conservation of lions in Africa

The current extinction crisis is characterized by a rapid global loss of mega-fauna resulting from pressures exerted by modern humans (Estes *et al*., 2011). The African lion has suffered significant population declines and range contractions in the last 20 - 50 years (IUCN, 2006; Riggio *et al.* 2012) as a result of persecution, habitat loss and fragmentation, prey depletion and disease (Ray *et al*., 2005; IUCN, 2006). Lions are now restricted to approximately 25%

of their historic range, with an estimated global population of 32 000 to 35 000 individuals. Of greatest concern is that populations continue to decline in numbers (Riggio *et al.* 2012) particularly those existing outside of fenced reserves (Packer *et al*., 2013).

As a large-bodied predator, lions are at inherent biological odds with the needs of humans (Treves & Karanth, 2003; Ogutu *et al*., 2005; IUCN 2006). Lions will often encounter and predate on domestic livestock, leading to direct retaliation (Woodroffe & Frank, 2005). Consequently, persecution by farmers and pastoralists has contributed significantly to the decline of lion populations and the reduction of lion range across Africa (Ogutu *et al*., 2005; IUCN, 2006; Kissui, 2008; Bauer *et al*., 2010; Riggio *et al.,* 2012).

Humans also impose pressure on lion populations through prey depletion and/or by-catch from 'bushmeat' hunting (wild meat). The unregulated hunting of bushmeat threatens biodiversity and ecosystem health across much of Africa (Wilkie *et al*., 2011). Despite the extensive ecological impacts of unregulated hunting, its effects can be disguised by the appearance of intact habitat; the "empty forest" syndrome (Redford, 1992; Wilkie *et al*., 2011). While bushmeat hunting is widespread across Africa (Lindsey *et al*., 2013) there are few data available on the influence of bushmeat hunting on lion populations (but see Becker *et al*., 2013).

Study area and population

This study was conducted in the developing Limpopo National Park (LNP), an approximately 8 000 km^2 area of woodland savannah plains located in south-western Mozambique. LNP forms a component of the Greater Limpopo Trans-frontier Park (GLTFP) with South Africa's Kruger National Park (KNP) and Zimbabwe's Gonarezhou National Park (Fig. 1.1). The predominant landscape type in LNP is sand plains ('sandveld') characterized by low woodlands and thickets of *Baphia massaiensis* and *Combretum apiculatum* and short-grass pans (depressions flooded for long periods) (Stalmans *et al*., 2004). Wildlife protection in LNP is currently limited and the park experiences considerable anthropogenic impact (*see below).* LNP is bordered to the west by KNP, characterized by high wildlife densities, while the southern, eastern and north-eastern boundaries are characterized by a near continuous band of agro-pastoralist human settlements (approximately 64 villages) along the banks of the Massingir Dam to the south and the Limpopo River to the east and north-east. There are additional smaller villages and agricultural areas situated at permanent pools along the seasonal Shingwedzi River that stretches north-south through the centre of the park. The human population living within the central portions of LNP is estimated at 6 500 with an additional 20 000 living in the eastern boundary villages (Huggins *et al*., 2003). The human residents of LNP practice subsistence agriculture, with maize being the primary crop, and grazing of livestock, including; sheep, *Ovis aries*, goats, *Capra aegagrus*, and cattle, *Bos primigenius*, (*pers. obs*.). The cattle population of LNP is estimated at greater than 20 000 (Stephensen, 2010). Residents also extract natural resources from the park including; fuel wood, honey, fish, illegal bushmeat, elephant, *Loxodonta africana*, ivory and white rhinoceros, *Ceratotherium simum*, horn (*pers. obs.; this study*) (Fig. 1.2).

Figure 1.1. Limpopo National Park, Mozambique (current park is dark green overlaid the original park boundary (light green)) in relation to the Kruger National Park in South Africa and Gonarezhou National Park in Zimbabwe (light green).

Figure 1.2. Images from the Limpopo National Park, Mozambique. Clockwise from top left: Woodland savannah and the seasonal Shingwedzi River; a short grass pan in the sandveld; a bushmeat hunter with snare; a free-ranging cattle herd; the village of Chimangue on the Shingwedzi River; a small herd of buffalo.

Wildlife populations in this region of Mozambique were largely decimated during the country's war of independence (1964 -1974) and subsequent civil war (1978 - 1992) (Hatton *et al*., 2001). The removal of portions of the South Africa-Mozambique border fence as part of the creation of the GLTFP (2000) has provided the opportunity for re-colonization or connection of wildlife in LNP (Hanks, 2000). However, wildlife population recovery in the park is currently hindered by poaching (*this study, pers. obs*.). This study documented 22 species of ungulates and 18 species of mammalian carnivores in the park (Table 1.1). The IUCN (2006) has identified the GLTFP as one of Africa's lion strongholds with an overall estimated population of 2 000 (Bauer & Van Der Merwe, 2004), of which approximately 1 684 are in KNP (Ferreira & Funston, 2010). An abundance estimate of 179 lions in LNP was derived from opinion-based surveys (Chardonnet *et al*., 2009); however, prior to this study there had been no rigorous attempt to quantify the population in LNP.

Table 1.1. Mammalian species (above 3.0 kg) recorded by this study using camera traps in the Limpopo National Park, Mozambique, from September 2011- November 2012.

Common name	**Species**	**Common name**	**Species**
African buffalo	*Syncerus caffer*	Lion	*Panthera leo*
Eland	*Tragelaphus oryx*	Leopard	*Panthera pardus*
Greater 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 hyena	*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*		
Suni	*Neotragus moschatus*	Side-striped jackal	*Canis adustus*
Klipspringer	*Oreotragus oreotragus*	Honey badger	*Mellivora capensis*
Common duiker	*Sylvicapra grimmia*	African Civet	*Civettictis civetta*
Giraffe	*Giraffa camelopardalis*	Large-spotted genet	*Genetta tigrina*
Warthog	*Phacochoerus africanus*	Banded mongoose	*Mungos mungo*
Bushpig	*Potamochoerus porcus*	Slender mongoose	*Herpestes sanguineus*
Hippopotamus	*Hippopotamus amphibius*	White-tailed mongoose	*Ichneumia albicauda*
White rhino	*Ceratotherium simum*		
Plains zebra	*Equus burchelli*		
Blue wildebeest*	*Connochaetes taurinus*	Savannah baboon	*Papio cynocephalus*
Elephant	*Loxodonta africana*	Vervet monkey	*Ceropithecus aethiops*
Aardvark	*Orycteropus afer*	Lesser bushbaby	*Gelago moholi*
Porcupine	*Hystrix africaeaustralis*	Greater bushbaby*	*Otolemur crassicaudatus*
Scrub hare	*Lepus saxatilis*		
Spring hare	*Pedetes capensis*		
Greater Cane-rat	*Thryonomys swinderianus*		

*Species observed only.

Why study lions in Limpopo National Park?

Many of Africa's remaining lion populations are thought to exist outside of formally protected areas (Ray *et al.,* 2005; Riggio *et al*. 2012), where they at risk of conflict with humans. Knowledge of the ecological requirements of lions in human disturbed systems in important for their conservation, however, there are few data on the habitat ecology of lions in such systems (*but see* Schuette *et al*., 2013) or on the influence of bushmeat hunting on lion ecology. LNP offers a unique natural laboratory where ecological interactions between free-roaming lions and subsistence agro-pastoralist-hunter communities can be investigated. While the population of lions in adjoining KNP has been investigated (*see* Funston *et al*., 1998; Funston *et al*., 2003; Ferreira & Funston, 2010), prior to this study there had been no empirical quantification of the population ecology of lions in LNP.

Thesis objectives

In 2011, I initiated a study on the population and habitat ecology of lions in LNP. I started the project in collaboration with Leah Andresen who simultaneously began research on the ecology of cheetah. Together these two studies constitute the first empirical investigation into predator ecology in this region of Mozambique. My primary research objectives were to provide empirical data on the status of lion in LNP, to determine whether the population is limited by bottom-up prey resources or top-down anthropogenic factors, and to determine the relative influence of ecological variables on lion resource use and non-use.

Thesis organization

This thesis was written with the intention that the two main chapters be submitted for publication in peer-reviewed journals. My goal is that chapters 2 and 3 be co-authored with Leah Andresen and Michael Somers, and so I use the plural "we" in these chapters. Although both of these chapters are written as stand-alone papers, they each relate to the overall objectives of the thesis; to quantify the factors limiting lions in LNP and contribute to our understanding lion ecology in human-impacted systems.

In Chapter 2 I provide base line data on the status of lions in Limpopo National Park (LNP). I compare a direct density estimate from call-ups with an estimate derived from trophic scaling. I use hierarchical modelling of covariates to provide inferences on the relative influences of top-down and bottom-up factors on the occupancy of lions. I discuss the bias associated with trophic scaling in a human influence system, and the relative influence of bottom-up versus top-down pressures on the occurrence of lions. My results suggest a population of lions held below carrying capacity by anthropogenic pressures.

In Chapter 3 I investigate the multi-scale habitat selection of lions in LNP using site occupancy models and detection/non-detection data obtained from camera-trap and track surveys. I determine the relative influence of prey resources, landscape features facilitating prey capture, agro-pastoralist pressure and bushmeat hunting on habitat selection by lions at the temporary site use scale and home range scale, and between seasons. I discuss the influence of scale on our understanding of lion-habitat relationships. I present quantitative data on the importance of prey resources and the limiting influence of human pressures on habitat use by lions.

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CHAPTER 2: TROPHIC SCALING AND OCCUPANCY ANALYSIS REVEALS A LION POPULATION LIMITED BY ANTHROPOGENIC PRESSURE IN THE LIMPOPO NATIONAL PARK, MOZAMBIQUE

Abstract

The African lion, *Panthera leo*, has suffered drastic population and range declines over the last few decades and is listed by the IUCN as Vulnerable to extinction. Conservation management requires reliable population estimates, however these data are lacking for many of the continent's remaining populations. It is possible to estimate lion abundance using a trophic scaling approach. However, such inferences assume that a predator population is subject only to bottom-up regulation, and are thus likely to produce biased estimates in systems experiencing top-down anthropogenic pressures. Here we provide baseline data on the status of lions in a developing National Park in Mozambique that is impacted by humans and livestock. We compare a direct density estimate using call-ups with an estimate derived from trophic scaling. We then use replicated detection/non-detection surveys to estimate the proportion of area occupied by lions, and hierarchical ranking of covariates to provide inferences on the relative contribution of prey resources and anthropogenic factors influencing lion occurrence. Direct density estimates were less than 1/3 of the estimate derived from prey resources (0.99 lions/100 km^2 vs. 3.05 lions/100 km^2). The proportion of area occupied by lions was $\Psi = 0.436$ (SE = 0.127), or approximately 44% of a 2400 km^2 sample of potential habitat. Although lions were strongly predicted by a greater probability of encountering prey resources, the greatest contributing factor to lion occurrence was a strong negative association with settlements. Finally, our empirical abundance estimate is approximately 1/3 of a published abundance estimate derived from opinion surveys. Altogether, our results describe a lion population held below resource-based carrying capacity by anthropogenic factors, and highlight the limitations of trophic scaling and opinion

surveys for estimating predator populations exposed to anthropogenic pressures. Our study provides the first empirical quantification of a population that future change can be measured against.

Introduction

The African lion, *Panthera leo*, has suffered dramatic population and range declines over the last few decades and is currently listed by the IUCN (2012) as vulnerable to extinction. Conservation management of the species requires reliable population estimates, however, these data are lacking for many of the continent's remaining populations; particularly those existing outside of formally protected areas that are exposed to human pressure (Riggio *et al.*, 2012; Packer *et al.*, 2013). Quantifying the status of such populations is critical if we wish to promote the conservation of the species beyond the sanctuaries of a limited number of reserves (Packer *et al.*, 2013).

Filling the niche of apex predator on the African savannah, lions are naturally limited by bottom-up prey resources and experience density dependence (Schaller, 1972). The ecological limitations of being carnivorous include upper limits on predator density, where the relationship between predator biomass to prey biomass (averaged across all Carnivora) follows a ratio of 0.009/1 (Carbone & Gittleman, 2002). An association between lion density and lean prey density has been documented (Van Orsdol *et al.*, 1985) and can be exploited to estimate lion density from prey density data (Hayward *et al.*, 2007). However, demographic inferences based on trophic scaling assume that a predator population is subject only to bottom-up regulation, and are thus likely to produce biased estimates in systems with considerable top-down anthropogenic pressure (Carbone & Gittleman, 2002; Treves *et al.*, 2009). Lion populations in human influenced landscapes are susceptible to a variety of direct top-down pressures including; persecution in defence of livestock (Ogutu *et al*., 2005), targeted poaching (Bauer *et al*., 2003), by-catch of bushmeat hunting (Becker *et al*., 2013) over exploitation by trophy hunting (Packer *et al*., 2009) and disease (Kissui & Packer, 2004). The limiting effects of these top-down pressures may be felt by a population while being masked by an intact prey base (Kissui & Packer, 2004; Kiffner *et al*., 2009).

Comparing the observed differences between a realized density and potential density estimate based on estimates of prey biomass of an apex carnivore can provide evidence of non-density dependence, whereby variables other than resources are limiting a population (Hayward *et al*., 2007). Such comparisons are becoming increasingly important as Africa's rising human population exerts top-down pressures on predator populations both inside and outside of protected areas (Woodroffe & Ginsberg, 1998; Woodroffe & Frank, 2005).

Here we investigate the status of lion in the developing Limpopo National Park (LNP) in Mozambique; a region where population data are lacking. LNP forms a component of one of Africa's Lion Conservation Units (Greater Limpopo LCU) and is contiguous with a protected population in the Kruger National Park (KNP) in South Africa (Riggio *et al*., 2012; IUCN, 2006). Unlike KNP, however, LNP is occupied by humans and livestock, and unregulated human hunting (hereafter referred to as bushmeat poaching) is not uncommon (*this study*). Prior to this study the only estimate of the lion population in LNP was derived from an opinion survey (Chardonnet *et al*., 2009). Previous authors have suggested that the use of opinion surveys can be inherently biased and produce overestimates of lion populations and should therefore be verified against empirical data (Riggio *et al*., 2012). The goal of this study was to provide empirical data on the status of lion in LNP, and to determine whether the population is limited by bottom-up prey resources or top-down anthropogenic factors. We compare a direct density estimate (realized density) obtained from a call-up survey (Ferreira & Funston, 2010) with an indirect density estimate obtained from trophic scaling (potential density) (Hayward *et al*., 2007). In addition, we employ replicated detection/non-detection surveys and an occupancy modelling technique that explicitly accounts for detectability (MacKenzie *et al.*, 2002) to estimate the proportion of area occupied by lion across a 2400 km^2 study area and to provide robust inferences on the factors limiting lion occurrence. We hypothesized that the lion population in LNP is currently limited by top-down anthropogenic pressures including subsistence-agro-pastoralism and bushmeat poaching. Our study provides the first empirical quantification of a population that future change can be measured against.

Methods

Study area and population

This study was conducted in the LNP in south-western Mozambique, which forms a component of the Greater Limpopo Trans-frontier Park (GLTFP) with South Africa's KNP and Zimbabwe's Gonarezhou National Park. LNP is framed to the west by KNP, characterized by formal protection and high wildlife densities, and to the east, north-east and south by a near continuous band of agro-pastoralist settlements situated along the banks of the Limpopo River and Massingir Dam. There are additional smaller settlements situated along the Shingwedzi River that stretches north-south through the centre of the park. The human population living within the central portions of LNP is estimated at 6,500 (2003) with an additional 20,000 living in the eastern boundary settlements (Huggins *et al*., 2003). The cattle, *Bos primigenius*, population within LNP has been estimated at over 20, 000 from 2010 aerial counts (Stephensen, 2010). LNP officially covers 11 000 km^2 (Peace Parks Foundation, Stellenbosch), although excluding cultivated areas and a section to the extreme south that has been separated by a recently erected wildlife barrier fence, reduces the effective area of the park to 6, 708 km^2 (Fig. 2.1). There is limited infrastructure, including roads or tourist facilities. Wildlife populations in Mozambique were largely decimated during 22 years of war (1964-1974; 1980-1992) (Hatton *et al*., 2001). Subsequent removal of portions of the South Africa-Mozambique border fence as part of the creation of the GLTFP (2000) has provided the opportunity for re-colonization of wildlife into LNP (Hanks, 2000). However, wildlife population recovery continues to be hindered by anthropogenic pressures including livestock husbandry, bushmeat poaching and poaching for elephant, *Loxodonta africana*, ivory and rhinoceros, *Ceratotherium simum*, horn (camera-trap data*, this study*). The IUCN (2006) has identified the region as one of Africa's lion strongholds with an overall estimated population of 2000, of which approximately 1684 are in KNP (Ferreira & Funston, 2010). An abundance estimate of 179 lions in LNP was derived from opinion based surveys (Chardonnet *et al*., 2009); however, prior to this study there had been no rigorous attempt to quantify the population.

The study area is comprised of woodland savannah plains with four distinct landscapes situated in approximate north-south orientation. These include: 1) sand plains characterized by low woodlands and thickets on deep sandy soils, the absence of well-defined drainage lines and the presence of 'pans' (seasonally flooded depressions), 2) combretum/mopane rugged veld characterized by tall shrublands and woodlands on clay soils, 3) mopane shrubveld characterized by thickets, short woodland and tall grasslands on calcareous soils, and 4) Lebombo hills characterized by short woodlands on undulating hills of stony, rhyolite soils (Stalmans *et al*., 2004). The region receives an annual average 500 mm of rain, with the majority occurring between October and March (Gertenbach, 1980).

Survey design

Call-ups

To estimate lion density, a call-up survey was conducted during June and July 2012 *as per* Ferreira and Funston's (2010) census of lions in KNP. Call-ups surveys employ a probability model to estimate lion abundance based on response counts to an auditory lure (Mills *et al*., 2001). Demographically specific response probabilities, as well as a response radius needed to determine the effective area surveyed are estimated using calibration experiments (Ferreira & Funston, 2010). Such calibration experiments were not possible in LNP due to low lion densities and insufficient road networks. We therefore assumed that the probabilities of lion response and response radius in LNP would be comparable to those in the adjoining and contiguous KNP.

To ensure the safety of the researchers when luring lions, we conducted call-ups from the back of a vehicle (Ferreira & Funston, 2010), which restricted our access to large portions of LNP that are not vehicle accessible. Given these constraints, we selected 43 call-up stations for sampling, located along all available roads, tracks and drivable routes. Although large portions of LNP were not accessible, the chosen call-up stations incorporated important environmental strata present in the park, including; 1) the most productive wildlife areas of the park (specifically areas of greater African buffalo, *Syncerus caffer*, abundance, based on aerial survey data (Stephensen, 2010)), 2) a representative range of distances from human settlement areas, 3) a representative range of distances from the KNP boundary, and 4) major bio-physical features including the Limpopo River and distinguishing landscape types (Fig. 2.1). Call-up stations were located a minimum of 5 km apart and sites were chosen to have relatively good visibility. In addition, call-up stations were located a minimum of 3 km from settlement boundaries or areas of high pastoralist use to avoid causing lion-human conflict.

Occupancy

We used an occupancy modelling approach that explicitly accounts for the probability of detection (MacKenzie *et al*., 2002) to estimate the proportion of area occupied by lion and provide inferences on the ecological factors limiting their occurrence. Site occupancy models use replicated detection/non-detection surveys to estimate a detection probability (p) and derive unbiased estimates of species occurrence (Ψ). We make the following assumptions of an occupancy model for the estimator (Ψ) to be interpreted as the proportion of area occupied: 1) Sites are closed to changes in occupancy (i.e., are either occupied *by the species* or not for the survey duration, 2) Species are not falsely identified, 3) Detections are independent, and 4) Heterogeneity in occupancy or detection probability are modelled using covariates (MacKenzie *et al*., 2002). To estimate the proportion of area occupied by lion, sample units (sites) were defined as 10 km x 10 km grid cells, which are comparable to estimated lion home ranges in the adjoining KNP (approximately 100 km^2) (Funston *et al*., 2003). We considered this size large enough to reduce spatial autocorrelation between sites, but conservative enough to assume that entire grid cells were occupied at sites where lions were detected (and thus reduce the chance of over-estimating the proportion of area occupied by lion). Our study design was constrained by lack of accessibility of large portions of LNP and the associated logistics of repeatedly accessing grid cells. Given these limitations, we selected 24 grid cells to be surveyed such that the resulting area followed a gradient of major bio-physical and anthropogenic features present in LNP (i.e., distinguishing landscapes, KNP boundary, drainage lines, and human settlements) and thus incorporated important strata (Fig. 2.1).

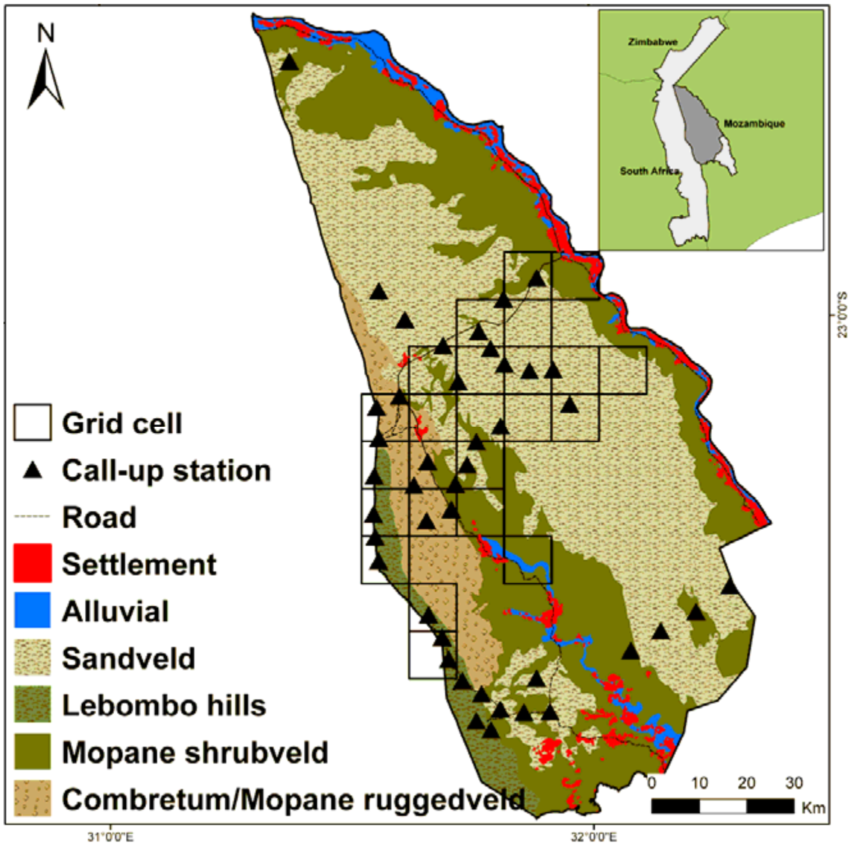

Figure 2.1. Survey effort in the Limpopo National Park (LNP), Mozambique. LNP is bounded to the west by the Kruger National Park in South Africa, characterized by formal protection and high wildlife densities, and to the east by the Limpopo River, characterized by agro-pastoralist settlements. Surveyed grid cells (100 km^2) and call-up stations shown overlaid across a gradient of landscape types and human impact. Inset map: Location of LNP (dark grey) in relation to the Greater Limpopo Trans-frontier Park (light grey), including the region to the south of LNP which has been recently seperated by a wildlife barrier fence, and to Zimbabwe and South Africa.

Lions are territorial felids, where males disperse from their natal range between the ages of 27-36 months (Smuts *et al*., 1978). To reduce the chance that a grid cell would become permanently vacated or colonized by the species over the survey period, we restricted our sampling duration to five months (May 7 to October 13, 2012). We employed two sampling methodologies; track surveys and camera-trapping. Sample occasions were represented by temporally replicated 3 km transects (replicates separated by more than 14 days) and 14 day camera-trap samples; considering this a reasonable amount of time to assume sample independence. Detections were represented by unambiguously identified lion tracks or photographs. Camera-traps and transects were located to maximize spatial representation of grid cells with a mean of two camera stations and two track transects per grid cell. To impose an order of randomness, each cell was divided into quadrants and one was randomly selected for obligate sampling. Due to logistical constraints, three cells were sampled in only one quadrant each, while the rest were sampled in two to four quadrants. Multiple surveys within the same quadrants were separated by more than 14 days. Of the 24 grid cells, 20 were sampled with camera-traps with a mean of 90 camera-trap nights per grid cell (range: 28 – 224 camera trap nights/grid cell) and 23 were sampled with track surveys with a mean of 13 km walked per grid cell (range: 6 – 30 km/grid cell). Unequal sampling across sites is accounted for in the occupancy model (MacKenzie *et al*., 2002).

We identified three predictor variables (covariates) that may explain the occurrence of lions in a human disturbed landscape, considering both bottom-up resources and top-down anthropogenic pressures. The covariates investigated were; preferred prey resources, bushmeat poaching and agro-pastoralist use (Table 2.1).

Table 2.1. Covariates expected to influence the proportion of area occupied by lion.

Covariate	**Relationship to lion fitness**	**Description**	**Sampling range**
Buffalo	Availability of preferred prey	Probability of buffalo site use (encounter probability)	0.1 – 0.6 mean = 0.4
Bushmeat poaching	Targeted or accidental snaring	Probability of bushmeat poaching site use (encounter probability)	0.1 – 1.0 mean = 0.6
Settlement	Persecution in defense of livestock	Proximity to agro-pastoralist settlements (km)	2.0 - 20.8 mean = 11.1

Considering that lions select home ranges based on characteristics that may change seasonally (i.e., buffalo or bushmeat poaching occurrence), we collected covariate data over the course of a year, from September 2011 to October 2012. To quantify the influence of preferred prey availability for lions we developed a probability of use model for buffalo; the most common preferred prey species of lions in the region (Funston *et al*., 1998; Hayward & Kerley, 2005). We made the assumptions of an occupancy model (as above), but note that the closure assumption could be relaxed because here we interpreted our estimator (Ψ) as the *probability of site use* (MacKenzie *et al*., 2006 pg. 105). We developed the buffalo occupancy model based on replicated detection/non-detection surveys using camera-traps. Data was collected from 82 camera stations; each considered a buffalo sampling site. Buffalo sites were located to maximize spatial representation of lion grid cells with a mean of three buffalo sites per lion grid cell. Active camera stations were located more than 4 km apart. Sampling occasions were represented by 14 day camera-trap intervals.

Buffalo spatial use is influenced by the nutritional quality (nitrogen levels) of vegetation, water availability and predation risk (Winnie *et al*., 2008). To describe buffalo site use, we used six landscape covariates that account for variation in vegetation communities and underlying geology, surface water availability and anthropogenic disturbance. Covariates included; mopane shrubveld, sandveld, Lebombo hills, combretum/mopane rugged veld, distance to KNP boundary, distance to permanent water and distance to human settlements (Table 2.2).

Table 2.2. Covariates expected to influence buffalo site use.

Covariate	**Relationship to Buffalo fitness**	**Description**	**Number of sites/ Sampling range**
KNP	Protected population	Proximity to KNP border (km)	0.0 - 50.0 mean = 21.9
Mopane shrubveld	Nutritional variation	Shrublands and thickets on calcerous soil	n = 11
Combretum/mopane rugged veld	Nutritional variation	Woodlands and shrublands of on clay soils	n = 17
Lebombo hills	Nutritional variation	Short woodlands and shrublands on rhylolite soils	n = 11
Sand plains	Nutritional variation	Short woodlands and thickets on sandy soils	n = 41
Water	Water availability Nutritional variation	Proportion of site (50 m buffer) overlapping a drainage line	0.0 -1.0 mean = 0.1
Settlement	Direct persecution and competion with cattle	Proximity to agro-pastoralist settlement (km)	0.5 – 22.7 mean = 11.7

Landscape covariates were extracted from a raster layer (Peace Parks Foundation Stellenbosch). All GIS analysis was done using the Spatial Analysis Toolbox in ArcGIS 9.3.1. (www.esri.com). The final mean buffalo occurrence covariate values were extracted for each of the 24 lion grid cells from a continuous (30 m resolution) Inverse Distance Weighted raster layer built from the weighted average occupancy estimates for each of the 82 buffalo sites. We assumed that our buffalo occupancy model is representative of a preferred prey encounter probability for lions.

We used a similar approach (as above) to quantify the impact of bushmeat poaching on lion occurrence. A bushmeat poaching occupancy model was built from photographic data of humans carrying snares, spears or bows, domestic hunting dogs, *Canis lupus familiaris*, and spotted hyenas, *Crocuta crocuta*, with snares around their necks or with obvious snare wounds. While it could be argued that spotted hyenas may have been snared far from the camera station where they were photographed, it is noted that in the two cases where we included these data, the individual spotted hyenas were photographed regularly at the same station and we discovered snare sets in the vicinity of the camera station. Data were collected from 82 camera stations (as above) each considered a bushmeat poaching sampling site, with a mean of three bushmeat sites per lion grid cell. Sampling occasions were represented by 14 day camera-trap intervals. We make the assumptions of an occupancy model (as above), but again note that the closure assumption could be relaxed because we interpret our estimator (Ψ) as the *probability of site use*.

We identified six covariates that could account for heterogeneity in bushmeat poaching site use based on optimal foraging theory; considering risk, effort and reward to hunters (Alvard, 1993; Rowcliffe *et al*., 2004). Covariates included; ranger patrols, distance from villages, distance from tracks/trails, proximity to waterholes and rivers, the relative abundance of bushmeat and the relative biomass of bushmeat (Table 2.3).

Table 2.3. Covariates expected to influence bushmeat poaching site use.

Covariate	**Relationship to bushmeat poaching**	**Description**	**Sampling range**
Bushmeat abundance	Availability of bushmeat	Relative abundances of bushmeat obtained from aireal count data (23) including: Impala, *Aepyceros melampus* Kudu, *Tragelaphus strepsiceros* Nyala, *Tragelaphus angasii* Waterbuck, *Kobus ellipsiprymnus* Buffalo, *Sycerus caffer*	1.2 – 8.4 mean = 3.6
Bushmeat biomass	Profitability of bushmeat	Relative biomass (kg/site) of above bushmeat points multiplied by ¾ adult female weight (7)	70 – 3 079 mean = 437
Track	Ease of access	Proximity (km) to tracks/trails measured in ArcGIS	0.0 – 3.4 mean = 0.3
Water	Increased probabilty of encountering bushmeat	Proximity (km) to rivers measured in ArcGIS	0.0 – 9.3 mean = 3.7
Settlement	Proximity decreases energetic costs of meat retrieval	Proximity (km) to settlements measured in ArcGIS	0.5 – 22.7 mean = 11.7
Ranger patrol	Risk of arrest, fines or dogs destroyed	Proximity (km) to road measured in ArcGIS	0.0 – 22.9 mean = 7.7

We considered 'bushmeat' as species that were observed in snares over the course of this study. Site specific relative abundance of bushmeat was estimated from a continuous raster layer built from raw data (237 points) from the most recently available (2010) fixed-wing aerial survey. The aerial survey used a total area count strip-transect method, sampling every third transect (Stephensen, 2010). Relative bushmeat biomass was measured as the relative abundance of each species multiplied by ¾ average female weights of the species (Hayward *et al*., 2007). During the survey period, patrol effort in LNP was limited and primarily restricted to monthly patrols of the main roads (park management *pers. com*). Considering that bushmeat poachers may avoid these areas, we used proximity to main roads as a proxy for patrol effort. Proximity to tracks/trails, main roads, rivers, and settlements were measured from a landscape raster (Peace Parks Foundation, Stellenbosch) using the Spatial Analysis tool in ArcGIS 9.3.1. Considering that the cameras were disguised and used infra-red flashes (data collection below), we could think of few covariates to explain heterogeneity in detection. However we experienced 10 camera thefts over the course of the study, primarily along tracks (*versus* natural landscape features), and therefore considered that tracks may influence detectability. The final mean bushmeat poaching occurrence covariate values were extracted for each of the 24 lion grid cells from a continuous (30 m resolution) Inverse Distance Weighted raster layer built from the weighted average occupancy estimates for each of the 82 bushmeat poaching sites. We assume that our occurrence probability model for bushmeat poaching is representative of an encounter probability for lions. To quantify the impact of agro-pastoralism on lion occurrence, we considered the mean Euclidean distance (from each 30 m pixel in a grid cell) to a settlement boundary. We accounted for heterogeneity in lion detectability between survey methodologies using a survey-specific covariate. We did not attempt to model differences in detectability between camera brands in any of our occupancy models, considering trigger speed and detection zones between camera brands comparable (below).

Data collection

Call-ups

At each station, a four minute recording of a buffalo calf distress call was broadcast twice followed by two minutes of silence for a total period of 60 minutes. The call was recorded onto a SD card and broadcast thru a 12 volt 100 watt amplifier (Stewart PA100-MP3, Sonora, USA), powered by the vehicle's battery, and two 40 Watt horn speakers with driver units (Show TC-40P, Kyung Gi-Do, Korea). The call was broadcast at full volume from the speakers mounted 180° from each other, 3 m off of the ground on a steel tripod placed 20 m from the vehicle. The speakers were rotated 90° one time after 30 min to provide 360° coverage. We scanned for eye shine at three to five minute intervals using a spotlight (Lightforce SL240 Blitz, Hindmarsh, Australia) with a red filter, and listened for animal movements during the periods of silence. We recorded the number of adult and sub-adult lions and the presence or absence of cubs (Ferreira & Funston, 2010).

Camera-traps

To maximize the probability of detecting lions, camera stations were deployed at waterholes and on dirt tracks, game trails, and river edges used for travel by carnivores. Digital motion-activated cameras with infra-red flashes were used (15 Reconyx HC500 (Wisconsin, USA) (trigger time of 0.97 seconds, detection zone approximately 24 m), 7 Spy Point Tiny-W2 (Québec, Canada) (trigger time of 0.91 seconds, detection zone approximately 17 m), 10 Bushnell Trophy Cam (Beijing, China) (trigger time of 0.66 seconds, detection zone approximately 18 m) (www.trailcampro.com)). Risk of theft and vandalism required us to put substantial effort into concealing the cameras, including setting them on overhanging branches 4 to5 m above trails, or hidden at ground level. Each camera was enclosed in a steel box, secured using cable locks and camouflaged with vegetation. Vegetation that could falsely trigger the cameras was removed with care to reduce human attention to the site.

Track transects

Track transects were conducted on foot due to the lack of road networks. Track transects followed a main path of travel, (i.e., track, trail or river edge), and were conducted by KE and LA in early morning or late afternoon hours where substrate was adequate for tracking. The detection or non-detection of lion tracks was recorded for each 3 km transect sample.

Minimum number alive and mortalities

In addition, we determined the minimum number of individual lions alive (with identification based on sex, age and distinguishing scars (Whitman & Packer, 2007)) and recorded the minimum number of lion mortalities within the study area (i.e., the area encompassed by the 24 grid cells and call-up stations; Fig. 2.1).

Analytical methods

Call-ups

The abundance of lions was estimated from call-up data using a probabilistic approach first developed by Mills *et al*. (2001) for spotted hyenas and refined for lions by Ferreira and Funston (2010). Probabilities and response radius were borrowed from Ferreira and Funston's (2010) calibration experiments in KNP; each station was assumed to have sampled an area of 57.7 km^2.

Trophic scaling

To estimate the ecological carrying capacity of lions in LNP, we used Hayward *et al*.'s (2007) regression model relating the density of lions to the biomass of preferred prey species. Prey biomass was calculated using ¾ of the adult female weight (Hayward *et al*., 2007) of each species considered preferred prey by lions (Hayward & Kerley, 2005) and available in LNP, including; buffalo, blue wildebeest, *Connochaetes taurinus*, giraffe, *Giraffa camelopardalis*, and plains zebra, *Equus burchelli*, multiplied by species minimum counts obtained from 2010 aerial survey of LNP (Stephensen, 2010).

Occupancy models

Site occupancy (Ψ) and probability of detection (p) were estimated using maximum likelihood functions (MacKenzie *et al*., 2006) and the single season option in the program PRESENCE Version 5.5 (Hines, 2006). Continuous site covariates were standardized on a z-scale. We tested for collinearity between variables using a cut-off of $r = 0.5$. Models were ranked based on Akaike Information Criterion (AIC), using AICc adjusted for small sample size, with the sample size set at the number of sampling sites. Models with a ΔAICc < 2 were considered to be strongly supported. We considered a candidate set of all models ΔAICc < 7 whose combined weights $\geq$0.95 (i.e., 95% confidence set), excluding models that did not reach numerical convergence. AICc weights were used to determine the weight of evidence for each model, and were summed for each covariate in the 95% confidence set (Burnham & Anderson, 2002). Variables with high summed model weights were considered more important in explaining heterogeneity in occupancy. The direction of influence of covariates was determined by the sign of the β-coefficients (MacKenzie *et al*., 2006). Covariates were considered to have strong or robust impact if $\beta \pm 1.96 \times SE$ did not include zero. A weighted model averaging technique was used to calculate overall estimates of $\bar{\hat{\psi}}$ and $\bar{\hat{p}}$ (MacKenzie & Bailey, 2004). A goodness of fit test using 10, 000 bootstrap samples and a Pearson’s chi-squared statistic was performed on the most saturated model (MacKenzie & Bailey, 2004).

Buffalo occupancy model

A detection/non-detection matrix was constructed for each of 82 buffalo sites, recording a ‘1’ or ‘0’ where buffalo were detected or not, respectively. The covariates combretum/mopane rugged veld and sand plains were found to be correlated (r = -0.5), as were KNP and sand plains (r = 0.7) and KNP and Lebombo hills (r = -0.6) and were not included in the same models. To determine the factors that best describe buffalo occurrence, we compared all possible (non-correlated) combinations of occupancy covariates (60 models).

Bushmeat poaching occupancy model

Following the same procedure as above, a detection/non-detection matrix was constructed for each of 82 bushmeat poaching sites, recording a ‘1’ or ‘0’ where bushmeat poaching was detected or not, respectively. The covariates ranger patrol and settlement were found to be correlated (r = 0.7) and were not included in the same models. First, we evaluated the covariate track to describe heterogeneity in bushmeat hunting detection probability. We included the covariate for track in all subsequent analysis; this model was strongly supported and ranked higher than the model that assumed detectability was constant (ΔAICc = 20.44). To determine the factors that best describe bushmeat poaching occurrence, we compared all possible (non-correlated) combinations of occupancy covariates (47 models).

Lion occupancy model

A detection/non-detection matrix was constructed for each of 24 lion grid cells, recording a ‘1’ or ‘0’ where lion were detected or not, respectively. Following this, a survey-specific matrix was constructed to account for differences between the two sampling methods, recording a ‘1’ for cameras and a ‘0’ for tracks. To determine whether top-down anthropogenic factors or bottom-up prey resources were limiting the lion population in LNP, we compared a simple set of three univariate models to the model that accounts for variation in lion detection with survey method.

Results

We recorded a minimum of 34 lions in the study area between September 2011 and November 2012. These included 22 individuals identified from the camera trapping survey, four additional individuals identified only from the call-up survey, six additional individuals that we opportunistically observed and an additional two individuals that were photographed by a park contractor. The overall sex ratio was 0.9 females to 1.0 male. We recorded five lion mortalities, all human-caused (Fig. 2.2), in the study area during September 2011 to November 2012.

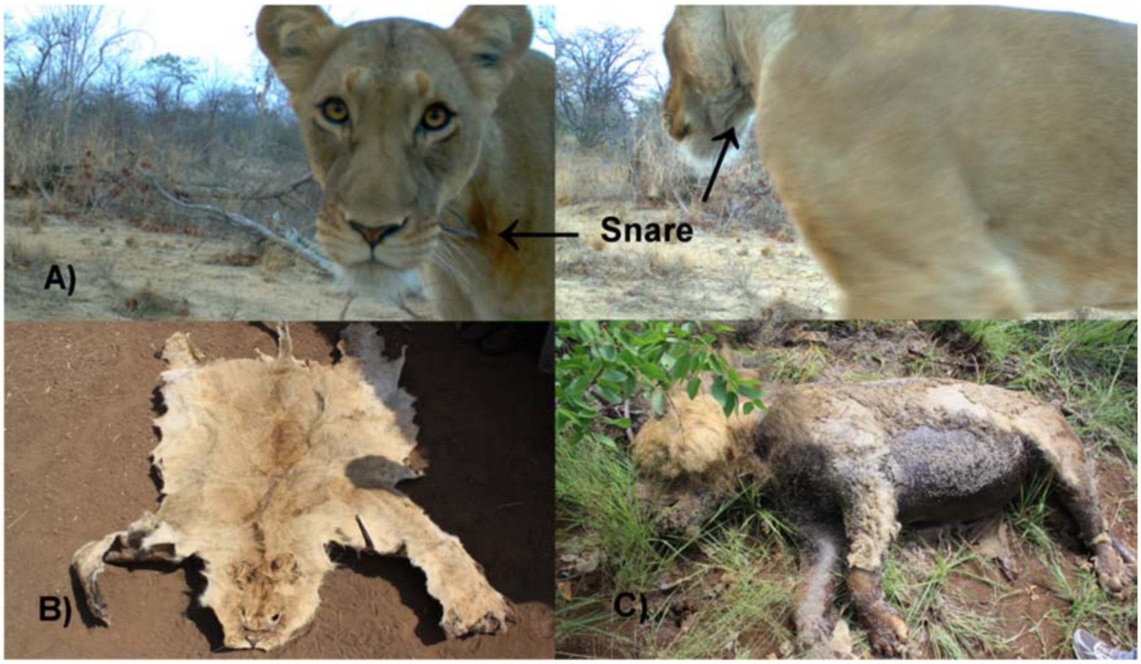

Figure 2.2. Examples of persecution of lions documented in Limpopo National Park during the study. A) Female photographed with a snare, likely as by-catch of bushmeat poaching. B) Sub-adult male killed in a snare set in retaliation of livestock depredation. C) Adult male shot for unknown reasons.

Call-ups density estimate

We recorded 13 lion responses at five of the 43 call-up stations, providing a mean of 0.27 lions per sample (Fig. 2.3). Lions were easily distinguished from sympatric species (i.e. spotted hyena and leopard, *Panthera pardus*), and lion eye shine was readily detectable, including through relatively thick vegetation. We estimated the effective area surveyed to include 1 852 km^2, which represents approximately 28 % of the potential lion habitat in LNP (calculated using published response radius (Ferreira & Funston, 2010) and excluding a 2 km buffer around cultivated areas). Respondents included five adult males, seven adult females and one cub. Two of the responding groups of lions (3 x adult females and 3 x adult females) were counted at adjoining stations on consecutive nights. Ferreira and Funston (2010) attempted to account for possible bias caused by double counting lions by developing a probability of repeat response; however in five trials they did not record any repeat responses. We attempted to account for bias induced by the possibility of double sampling the three lionesses by calculating abundance both with and without the second group and taking the average of the two. This provided an abundance estimate of 66.2 and an overall density estimate of 0.99 lions/100 km^2 in LNP (excluding the areas covered by a 2 km buffer around cultivation). We were unable to calculate variance for these estimates.

Indirect density estimate

Aerial count data of 475 points of preferred prey (Stephensen, 2010) produced an average available biomass estimate of 50.07 kg/km^2. Trophic scaling of the available biomass produced a density estimate of 3.05 lions per 100 km^2. This estimate is more than three times greater than that produced from the call-up survey.

Buffalo site use

Buffalo were detected on 105 sampling occasions (collapsed from 1 264 independent photo events). The final data set consisted of 369 sampling occasions, with a mean of five sampling occasions per buffalo site. The weighted average probability of detecting buffalo where they occurred on a single survey was $\bar{\hat{p}} = 0.368$ (SE = 0.041).The summary of model selection procedure is provided in Table 2.4. Buffalo site use was considerably higher closer to the KNP border and further from settlements, and considerably lower in the mopane shrubveld. Buffalo site use was also generally higher in closer proximity to water and lower in the combretum/mopane rugged veld. Site level occupancy estimates ranged from 0.008 to 0.887 with a weighted average of 0.416 (SE = 0.084). There was no evidence lack of fit (p = 0.09) or over-dispersion ($\hat{c} = 1.43$).

Table 2.4. Summary of model selection procedure for factors influencing buffalo site use (Ψ) across 82 sites in the Limpopo National Park, Mozambique.

Models	**ΔAICc**	***w***	**K**	**-2l**
Ψ(K+M+C)p(.)	0.00	0.134	5	264.43
Ψ(K+V)p(.)	0.03	0.132	4	266.73
Ψ(K+V+C)p(.)	0.32	0.114	5	264.75
Ψ(K+V+M)p(.)	0.54	0.102	5	264.97
Ψ(K+M+C+V)p(.)	0.62	0.098	6	262.72
Ψ(K+M)p(.)	0.79	0.090	4	267.49
Ψ(K+M+C+W)p(.)	1.31	0.067	6	263.41
Ψ(K+W+V)p(.)	1.57	0.061	5	266.00
Ψ(K+C+V+W)p(.)	1.73	0.056	6	263.83
Ψ(K+M+C+V+W)p(.)	2.02	0.049	7	261.73
Ψ(K+W+M)p(.)	2.33	0.042	5	266.76
Ψ(.)p(.)	9.58	0.001	2	280.65

Covariates considered include; distance to KNP (K), mopane shrubveld (M), combretum/mopane rugged veld (C), distance to settlements (V), distance to water (W), Lebombo hills (L), and sand plains (S), Ψ(.) assumes site use is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood value.

Bushmeat poaching site use

Camera-traps recorded 89 events of humans carrying bows, snares, or spears, 66 domestic hunting dog events and 21 events of mammals carrying snares or with snare wounds. These data were collapsed into 47 bushmeat poaching detections. The final data set consisted of 375 sampling occasions, with mean of five sampling occasions per bushmeat sampling site. Model averaged estimates showed that the probability of detecting bushmeat poaching at a site where it occurs was low ($\bar{\hat{p}}$ = 0.165, SE = 0.027) (Table 2.5). Site level occupancy estimates ranged from 0.000 to 0.994 with a weighted average of 0.799 (SE = 0.050).

Table 2.5. Summary of model selection procedure for factors influencing bushmeat poaching site use (Ψ) across 82 sites in the Limpopo National Park, Mozambique.

Models	**ΔAICc**	***w***	**K**	**-2l**
Ψ(B+A+V)p(T)	0.00	0.648	6	244.34
Ψ(B+A)p(T)	2.93	0.150	5	249.60
Ψ(B+A+T+V)p(T)	4.27	0.077	7	246.22
Ψ(B+A+T)p(T)	4.52	0.068	6	248.86
Ψ(B+A+R)p(T)	5.05	0.052	6	249.39
Ψ(.)p(T)	9.33	0.006	3	260.48

Covariates considered are relative bushmeat abundance (A), and biomass (B) and proximity to tracks (T), settlements (V), and water (W), and ranger patrol effort (R). Detectability (p) varies with tracks (T).

Ψ(.) assumes occupancy is constant, ΔAICc is the difference in AICc values between each model with the lowest AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood value.

Bushmeat poaching site use increased strongly with the relative abundance of bushmeat but decreased with the relative biomass of bushmeat (Table 2.6). These results indicate use of sites with a relatively higher abundance of the smaller-bodied antelopes that we considered (i.e., impala). Bushmeat poaching site use was also considerably higher closer to tracks/trails and settlements and lower along the main road. There was no evidence lack of fit (p = 0.79) or over-dispersion ($\hat{c}$ = 0.44).

Table 2.6. β- coefficient estimates for covariates influencing bushmeat poaching site use ($\bar{\hat{\psi}}$) in order of their summed model weights (∑w).

Occupancy Covariate	**∑ w (%)**	***β* coefficient**	**SE**
Bushmeat abundance	99.4	429.632*	3.588
Bushmeat biomass	99.4	-134.160*	3.493
Settlement	72.5	16.460*	3.559
Tracks	38.0	15.250*	6.502
Ranger patrol	5.0	-0.348	0.724

* Indicates covariate has robust impact (*β* ± 1.96 x SE not overlapping 0).

Lion occupancy

A total camera-trapping effort of 1 845 camera-trap nights resulted in 26 lion detection events (collapsed from 218 photographs of lions) from 10 of 38 camera stations in seven grid cells.

A total of 303 km of track surveys were walked, resulting in 33 lion track events in nine grid cells. The final data set consisted of 206 sampling occasions with a mean of nine sampling occasions per lion grid cell. The weighted average probability of detecting lions where they occurred on a single survey was relatively high; $\bar{\hat{p}}$ = 0.274 (SE = 0.066). The weighted average estimate of the proportion of area occupied by lion was $\bar{\hat{\psi}}$ = 0.439 (SE =0.121) (Table 2.7), or lion occupied approximately 44% of the 2 400 km^2 survey area. The spatial distribution of lion occurrence in the study area is provided in Fig. 2.3.

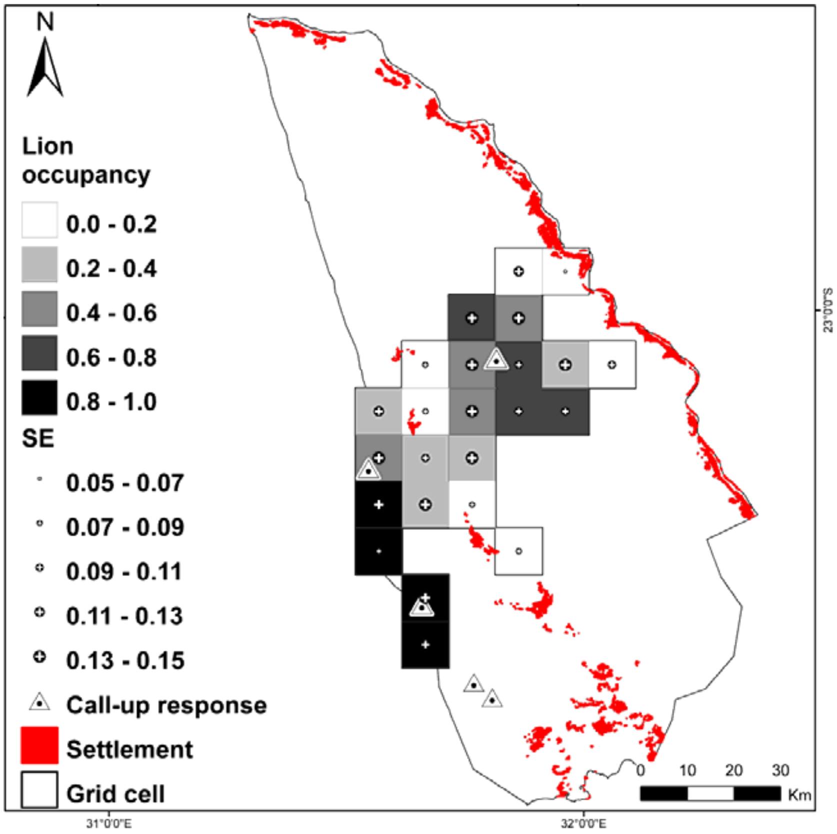

Figure 2.3. Spatial distribution of lion site occupancy and locations of call-up detections in the Limpopo National Park, Mozambique. Occupancy estimates are based on the averaged model ($\sum w > 0.95$) from 206 (mean = 9/grid cell) surveys of 24 (100 km^2) grid cells. Call-up detections are from a total of 43 stations.

In agreement with our hypothesis, there was evidence that lions are limited by anthropogenic pressure in LNP. The greatest contributing factor (*w* = 63%) to lion occurrence was a strong negative association with agro-pastoralist settlements; (β = -2.02, SE = 0.93) (Table 2.7). Mean site estimates were $\bar{\hat{\psi}}$ = 0.182 (SE = 0.098) at sites less than 10 km from settlements (10 sites) and $\bar{\hat{\psi}}$ = 0.591 (SE = 0.129) at sites equal to or greater than 10 km from settlements (14 sites). There was also support for the hypothesis that lions were limited by prey resources (*w* = 33%). Lions were strongly positively associated (β = 6.59, SE = 2.93) with sites where they had a greater probability of encountering buffalo (Table 2.7). Mean site estimates were $\bar{\hat{\psi}}$ = 0.609 (SE = 0.124) at sites with greater than 50% buffalo occupancy (five sites) and $\bar{\hat{\psi}}$ = 0.343 (SE = 0.113) at sites with less than 50% buffalo occupancy (19 sites). We found no support for the hypothesis that lions were limited by bushmeat poaching at the spatial scale examined (ΔAICc = 7.79), however, lions did tend to occur less at sites with a greater probability of encountering bushmeat poaching (Table 2.7). There was no evidence of lack of fit (p = 0.52) or over-dispersion ($\hat{c}$ = 0.49).

Table 2.7. Model selection procedure for factors influencing lion occupancy ($\bar{\hat{\psi}}$) across 24 ($100km^2$) sites in the Limpopo National Park, Mozambique. β-coefficient estimates for covariates strength and direction of influence are also shown.

Models	**ΔAICc**	***w***	**K**	**-2l**	$\bar{\hat{\psi}}$	**(±SE)**	$\bar{\hat{p}}$	**(±SE)**	***β*-coefficient**	**SE**
Ψ(V)p(M)	0.00	0.627	4	129.97	0.441	0.119	0.274	0.066	-2.02*	0.93
Ψ(P)p(M)	1.27	0.332	4	131.24	0.433	0.125	0.276	0.065	6.59*	2.93
Ψ(.)p(M)	6.23	0.028	3	139.11	0.458	0.120	0.268	0.066		
Ψ(B)p(M)	7.79	0.013	4	137.76	0.462	0.167	0.267	0.066	-2.92	2.58
Model Average					0.439	0.121	0.274	0.066		

Covariates considered include; settlement (V), buffalo (preferred prey) (P) and bushmeat poaching (B). Detectability (p) varies with method (M). Estimates of $\bar{\hat{\psi}}$ and $\bar{\hat{p}}$ and associated standard errors (SE). Ψ(.) assumes lion occupancy is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood.

* Indicates covariate has robust impact (β ± 1.96 x SE not overlapping 0).

Discussion

The influence of prey, bushmeat poaching and pastoralism on lions

In agreement with our hypothesis, our results indicate that the lion population in LNP is limited by top-down anthropogenic pressures. Comparing our direct density estimate with the estimate obtained from trophic scaling indicates that the lion population in LNP is currently at less than 1/3 of its carrying capacity based on prey resources. As an apex predator, lions are naturally limited by bottom-up prey resources (Schaller, 1972; Van Orsdol *et al*., 1985; Carbone & Gittleman, 2002; Hayward *et al*., 2007) and therefore the observed disparity between realized and potential densities suggests the influence of external top-down, anthropogenic pressures. Additionally, during the survey we documented five lions snared or shot by bushmeat poachers or pastoralists (Fig. 2.2), which compared to our minimum count of 34 lions, suggests a relatively high rate of human-caused mortality in the park. The hypothesis of top-down anthropogenic pressures limiting the lion population in LNP is further supported by the observed relationships between lion occupancy and the explanatory covariates investigated.

In agreement with known species relationships (Hayward & Kerley, 2005), there was strong support for the hypothesis that lions were bottom-up limited by prey resources. Nevertheless, there was slightly more support for the top-down limiting hypothesis; the greatest predictor of lion occurrence in LNP was a strong negative correlation with agro-pastoralist settlements. Persecution by farmers and pastoralists has contributed significantly to the decline of lion populations and the reduction of lion range across Africa (IUCN, 2006; Bauer & Sogbohossou, 2010; Riggio *et al*., 2012) and it is therefore not surprising that the pastoralism covariate carried the greatest weight in explaining lion occurrence in a region impacted by humans and livestock. We estimate that lions occupy only approximately 44%

of our 2 400 km^2 sample area in LNP and note that the distribution of their occurrence suggests lion may be suffering from persecution around agro-pastoralist settlement areas. A further interpretation of the ranking of the covariates is that lions in LNP are demonstrating a behavioural mechanism, spatial avoidance, which facilitates co-existence with subsistence agro-pastoralist communities that may have developed over an extensive period of co-evolution with similar human pressures. This interpretation suggests that provided with adequate prey and space, lions may be able to share the landscape with agro-pastoralist people. However, there may not be enough prey or space for the continued co-existence of lions and humans in many parts of Africa, and it is for this reason that relatively large tracts of potential lion habitat are so important. Interestingly, our analysis indicated that lion occurrence was not significantly influenced by bushmeat poaching activities. We caution, however, against the interpretation that lion populations are not limited by the pressures of bushmeat poaching. In order to estimate the proportion of area occupied by lion, we examined the influence of variables on lion occurrence at the home-range spatial scale only. While bushmeat poaching did not appear to influence lion occurrence at this scale, the same relationship may not hold at smaller spatial scales (Ciarniello *et al.*, 2007). We suggest that further research should consider the influence of scale when investigating the limiting effects of anthropogenic pressures on lions. It is also important to note that while the level of bushmeat poaching present in LNP may not influence the probability that a home range sized sample unit is occupied by the species, it may, however, influence the local abundance of lion.

Determining abundance of lions in a human disturbed landscape

Our study provides the first empirical data on a lion population exposed to anthropogenic disturbance in a developing National Park in Mozambique. Prior to this study, the only population estimate available for lion in LNP was derived from an expert opinion survey, which produced an estimate of 179 individuals (Chardonnet *et al.*, 2009). Our results suggest that the actual number of lions in the park is approximately one third of their estimate. Our estimate of 66 lions in LNP excludes the region south of the wildlife barrier fence (Fig. 2.1), and is based on the assumption that the areas within 2 km of cultivation cannot be considered suitable lion habitat. If we applied our call-up density estimate of 0.99 lions per 100 km^2 to the full 11 000 km^2 area of the park as drawn on a government map without consideration to human disturbance, than our abundance estimate for LNP would increase to 108 lions. However, we feel that this would be a gross overestimate of the actual population. Our call-up survey sampled approximately 28 % of the available lion habitat in LNP, however, we do acknowledge the possible bias in extrapolating our density estimate across areas of the park that were not sampled due to lack of vehicle accessibility. We attempted to account for variability that may arise in lion densities by sampling from important environmental strata including the full range of distances from human settlements and the KNP boundary as well as distinguishing landscape types. It is still possible that we may be underestimating lion densities if areas inaccessible by vehicle have lower human impact (i.e., lower cattle grazing and bushmeat poaching) and therefore higher lion densities. However, neither cattle grazing nor bushmeat poaching are road dependent in LNP; both activities are conducted by people that walk long distances using trail networks (camera-trap data, *this study*). Therefore, based on our knowledge of the park, we believe that the distance from a road should be of less consequence to the effects of these anthropogenic factors on lion density than is the distance from a human settlement. By sampling across a representative range of distances from human settlements in LNP we feel that we were able to account for variation in lion density that may arise from variation in human pressures. A further consideration is that the 2010 aerial surveys reported relatively low ungulate abundance, including low buffalo abundance, in the two large un-sampled areas in the park. The majority of buffalo were found along the unpopulated stretches of the Shingwedzi River valley and close to the KNP border (Stephensen, 2010); areas that we were able to include in our sample. It is therefore unlikely that the lion density in either of the un-sampled areas would be significantly higher than the average density for the areas that we were able to sample. Despite the limitations of our study design, our estimate comprises the only empirical population data on lions in LNP and thus is the most reliable estimate available. In light of the overall lack of empirical data on lion populations in this region and across much of Africa (Riggio *et al*., 2012) and the declining conservation status of the species (Riggio *et al*., 2012; Henschel *et al*., 2014) we believe that our initial estimates are a valuable contribution to the conservation management of lions in the region.

A possible bias in our trophic scaling estimate could have arisen because our estimates are based on aerial prey data obtained in 2010 (Stephensen, 2010) and prey populations may have since changed. However, we reasoned that the competing forces of bushmeat poaching activities reducing ungulate populations and natural immigration from KNP augmenting ungulate populations should dampen these changes. Furthermore, a repetition of the aerial survey was conducted in 2013 and preliminary results indicate that the total count and location of buffalo herds remained approximately the same (LNP management *pers. com*).

Density estimates based on trophic scaling assume that a predator population is subject only to bottom-up regulation. With increasing human disturbance, simple bottom-up regulatory systems are likely becoming increasingly rare across Africa and much of the world (Cardillo *et al*., 2004; Estes *et al*., 2011). While estimating lion densities using trophic scaling may be a practical means of acquiring empirical population data, the failure to account for top-down anthropogenic pressure can result in overestimations of predator populations. Such overestimates can lead to erroneous status assessments and populations going overlooked that require conservation attention. A trophic scaling approach for estimating lion abundances may therefore have limited usefulness in human-impacted systems (Carbone & Gittleman, 2002).

Management implications

Our results indicate the lion population in LNP is currently held below carrying capacity by anthropogenic factors. That lion were strongly negatively associated with settlement areas suggests lion may be suffering mortality due to persecution and/or spatially avoiding these sites (Figs. 2.2 & 2.3). Furthermore, a negative association with settlements along the Limpopo River may be indicative of edge effects (Woodroffe & Ginsberg, 1998). The long term development plan for LNP includes the re-settlement of the central settlements to areas along the Limpopo River (Huggins *et al*., 2003). Reduction of human-impact in the core of the park may permit the lion population to increase towards a prey-based carrying capacity and increase their proportion of area occupied. However, increasing human density along the Limpopo River may decrease landscape permeability for lions between the Kruger-Limpopo system and other areas of the Greater Limpopo LCU (i.e., Gonarezhou National Park in Zimbabwe and Banhine and Zinave National Parks in Mozambique), thus compromising the viability of a potential meta-population.

Altogether, our results have important conservation implications when placed in context of the Greater Limpopo LCU. We expect that both the population and range estimates of IUCN (2006), Chardonnet *et al*. (2009) and Riggio *et al.* (2012) for the Mozambican component are unrealistically optimistic and that the lion population is likely highly fragmented and require conservation interventions. We suggest that landscape-scale, spatially replicated occupancy surveys (Karanth *et al*., 2011), could be extended across the Greater Limpopo LCU to identify sub-populations, potential corridors and limiting factors, which if coupled with demographic data could be used to assess the viability and conservation needs of a lion meta-population (Hebblewhite *et al*., 2011; Barber-Meyer *et al*., 2012).

Acknowledgements

We thank the Parque National do Limpopo for supporting this research and the Director of National Conservation Areas Mozambique for granting us the research permits (005-2011/003-2012) to conduct this study. We thank Eden Everatt for help and enthusiasm in the field. We thank John Goodrich and two reviewers whose comments greatly improved the manuscript.

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CHAPTER 3: THE INFLUENCES OF PREY, PASTORALISM AND BUSHMEAT POACHING ON HABITAT USE BY LIONS.

Abstract

A biologically meaningful definition of species habitat considers the resources that relate directly to species fitness, describing *why* an animal is found where it is in addition to where an animal is found. As an apex predator, the habitat of African lions, *Panthera leo*, is primarily determined by bottom-up prey resources; however, increasing anthropogenic pressures may alter these relationships. Using camera traps and track surveys in the Limpopo National Park, Mozambique, we collected detection/non-detection data of lions and their prey and combined these with spatial data on agro-pastoralist land use and landscape features and occurrence data of bushmeat poaching activities. We used hierarchical modeling within an occupancy framework to determine the relative influence of ecological variables, specifically of bottom-prey resources and top-down anthropogenic pressures, on resource use and non-use by lions at two spatial scales and across two seasons. Habitat use by lions was most strongly influenced by the occurrence of their preferred prey across both spatial scales and seasons. However, lions showed strong spatial avoidance of bushmeat poaching at the finer spatial scale and selected against agro-pastoralist use at the coarser scale. Restricting our analysis to a singular coarser scale would have greatly underestimated the impact of bushmeat poaching on the ecology of lions. Landscape features that facilitate prey catch-ability were always less determining than prey availability. There was seasonal variation in the relative contributions of all variables with a dramatic increase in the influence of bushmeat poaching during the dry season. The results of this study agree with the trophic importance of prey resources but also

demonstrate the limiting influence of top-down anthropogenic pressures on habitat selection by lions.

Introduction

A biologically meaningful definition of species habitat considers the resources that relate directly to species fitness (Morrison, 2001; Mitchell & Hebblewhite, 2012). Habitat should therefore describe *why* an animal is found where it is in addition to where an animal is found (Mitchell & Hebblewhite, 2012). Habitat selection can be seen as a hierarchical process (Johnson, 1980; Schaefer & Messier, 1995), involving behavioral choices that span a continuum of time, space and ecological processes (Mitchell & Hebblewhite, 2012). The scale of these processes can range from species distribution or persistence, through home ranges and lifetimes, to temporary use of resource patches, and finally, to discreet feeding sites (Johnson, 1980; Schaefer & Messier, 1995; Mitchell & Hebblewhite, 2012). Species' individual fitness needs may differ with spatial scale (Schaefer & Messier, 1995; Rettie & Messier, 2000; Ciarniello *et al.,* 2007) with variables that are more limiting to fitness should influence habitat selection at coarser scales (Holling 1992; Rettie & Messier, 2000). Considering this, inferences of species-habitat relationships are then only biologically applicable to the scale in question (Wiens, 1989; McLoughlin *et al*., 2002; Hobbs, 2003; Boyce, 2006; Ciarniello *et al.,* 2007; Mitchell & Hebblewhite, 2012) and importance of habitat components may be masked when investigations are limited to a singular scale (Dickson & Beier, 2002).

The contemporary distribution of the African lion, *Panthera leo*, is largely associated with the remaining extent of intact savannah (IUCN, 2012; Riggio *et al.,* 2012). At a home-range scale, lions may select for areas with relatively higher densities of large bodied ungulates (Schaller, 1972; Van Orsdol *et al*., 1985), and may select against areas with increased threat of human persecution (Ogutu *et al*., 2005, but see; Woodroffe & Frank, 2005). Lion foraging success requires a combination of prey availability and suitable cover from which to attack (Schaller, 1972; Funston *et al*., 1998; Mosser *et al.,* 2009). At the finest scale of habitat use, lions may forgo locations with higher prey densities in exchange for locations with preferred hunting features, even if such habitats support lower prey densities (Mosser *et al.,* 2009; Davidson *et al*., 2013); selecting for prey catch-ability over prey availability. Stalking and ambush cover are less limiting to lions in forested savannahs (Funston *et al.,* 1998; Hopcraft *et al*., 2005), than to lions on open plains (Hopcraft *et al.,* 2005; Mosser *et al.,* 2009). In forested systems prey catch-ability may be more closely related to prey availability (Hopcraft *et al.,* 2005; Boer *et al.,* 2010). While there have been numerous in-depth studies of lion-habitat relationships (see; Schaller, 1972; Funston *et al.,* 1998; Hopcraft *et al.,* 2005; Mosser *et al.,* 2009; Boer *et al.,* 2010; Riggio *et al*., 2012), many of these studies investigated only habitat selection at the finest (kill site) spatial scale or at the largest distribution scale (but see Davidson *et al*., 2013). Many of Africa's lion populations are spatially restricted by human impact to the extent that habitat selection at distributional and home range scales may largely be imposed. Selection at these scales is most artificial in the context of the smaller fenced reserves of South Africa. Few studies have investigated habitat ecology of free-ranging lions existing outside of well protected reserves (Ray *et al*., 2005, but see Schuette *et al.,* 2013) or determined the influence of anthropogenic disturbance on lion habitat use. Persecution by humans or competition with humans for resources can alter "natural' species-habitat relationships among members of the carnivore guild (Hebblewhite & Merril, 2008). For instance, anthropogenic disturbance influences home range level habitat selection for cougars, *Felis concolor*, (Dickson & Beier, 2002), wolves, *Canis lupus*, (Rich *et al*., 2012) and tigers, *Panthera tigris*, (Barber-Meyer *et al*., 2012). It reasons that lion-habitat associations found in protected reserves may also differ from areas where lions exist within the context of subsistence agro-pastoralism and bushmeat hunting.

This study aimed to determine the relative influence of ecological variables on lion resource use and non-use (Mitchell & Hebblewhite, 2012). Only environmental variables that were thought to relate directly to the fitness of lions were considered, including prey availability and catch-ability and anthropogenic disturbances including subsistence agro-pastoralism and bushmeat poaching (Mitchell *et al*., 2002; Mitchell & Hebblewhite, 2012). A site occupancy modeling approach was applied (Mackenzie *et al.,* 2002) using detection/non-detection data obtained from camera traps and replicated track surveys. Occupancy models are considered an ideal approach for investigating species habitat use and non-use because they explicitly account for survey and site level species detectability (Mackenzie *et al.,* 2006; Baldwin & Bender, 2008; Mitchell & Hebblewhite, 2012). To quantify the impact of prey availability and bushmeat poaching on site use by lions, separate occupancy models were built for each of these covariates. We predicted that habitat use by lions would follow general patterns documented elsewhere, being primarily determined by bottom-up prey resources but also expected that anthropogenic pressures may influence habitat use by lions in this study system. We made the following specific hypotheses regarding habitat selection by an apex predator in a human disturbed system: 1) habitat use by lions should be most strongly predicted by bottom-up prey resources, 2) in a human disturbed system, habitat use by lions may also be determined by top-down pressures, including both agro-pastoralism and bushmeat poaching. In addition we examined the influence of spatial scale and season on the relative contribution of variables in describing habitat selection by lions and predicted that landscape features that may facilitate prey capture, including; river edges, drainages and water holes, should be more important at a finer spatial scale.

Methods

Study area and population

This study was conducted in the developing Limpopo National Park (LNP) in southwestern Mozambique, which forms a component of the Greater Limpopo Trans-frontier Park (GLTFP) with South Africa's Kruger National Park (KNP) and Zimbabwe's Gonarezhou National Park (Fig. 3.1). LNP is bordered to the west by KNP and to the east, north-east and south by a near continuous band of agro-pastoralist settlements along the banks of the Limpopo River and Massingir Dam. There are additional smaller agro-pastoralist settlements situated along the Shingwedzi River that stretch north-south through the centre of the park. The human population is estimated at 6 500 (in 2003) in central LNP and 20 000 living in the eastern boundary villages (Huggins *et al.,* 2003), together grazing over 20 000 head of cattle, *Bos primigenius,* (Stephensen, 2010).

Wildlife populations in this region of Mozambique were largely decimated during 28 years of war (1964-1992) (Hatton *et al*., 2001), however, the removal of portions of the South Africa-Mozambique border fence as part of the creation of the GLTFP in 2000 has provided the opportunity for re-colonization (Hanks, 2000) in LNP. The park is currently inhabited by 22 species of ungulates (this study, Fig. 1.1). At the time of this study, the lion population in LNP was estimated at 66 individuals or a density of 0.99 lions / 100 km^2 (Chapter 2).

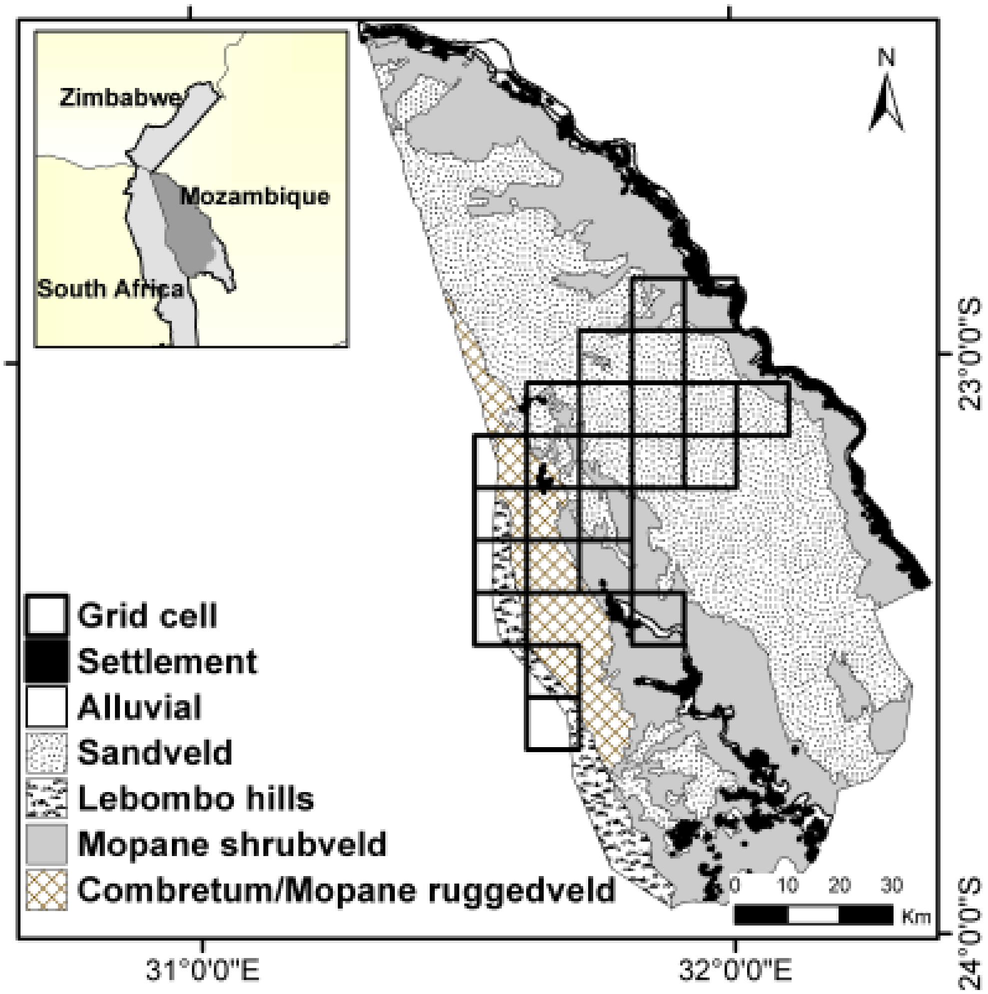

Figure 3.1. Location of survey area within Limpopo National Park (LNP), Mozambique. LNP is bordered to the west by the Kruger National Park (KNP) in South Africa, characterized by formal protection and high wildlife densities, and to the east by the Limpopo River, characterized by agro-pastoralist settlements. Surveyed grid cells (100 km^2) shown overlaid across a gradient of landscape types and human impact. Inset map: Location of LNP (dark grey) in relation to the Greater Limpopo Trans-frontier Park (light grey), including the region to the south of LNP which has been recently seperated by a wildlife barrier fence, and to Zimbabwe and South Africa.

LNP is comprised of woodland savannah plains. Four distinguishing landscapes are recognized, situated in approximate north-south orientation. These include: 1) sand plains characterized by low woodlands, thickets and grass covered pans, 2) combretum/mopane rugged veld, characterized by tall shrubland and woodlands, 3) mopane shrubveld on calcareous soil characterized by thickets, short woodland and tall grasslands, and the 4) Lebombo hills characterized by low woodlands on stony, rhyolite soils with rocky outcrops (Stalmans *et al.,* 2004). The region receives an annual average 500 mm of rain, with the majority occurring between October and March (Gertenbach, 1980).

Survey design

It is possible to examine habitat selection at multiple spatial scales using sampling windows of differing, biologically relevant, sizes (Nams *et al*., 2006; Baldwin & Bender, 2008; Sunarto *et al*., 2012). In this study, we examined habitat selection by lions at two spatial scales; a temporary site use scale and a home range scale (i.e., equivalent to Johnson's (1980) second and third order of habitat selection). At the temporary site use scale, we defined sites as approximately 1 km^2 areas, sampled by a camera station and/or a 1 km track transect. We reasoned that sampling at this scale was biologically meaningful to the scale at which lions make temporary resource use decisions. In order to examine habitat selection at the home range scale, we defined sites as 100 km^2 grid cells, which are similar in size to estimated home range size of lions in the adjoining and contiguous KNP (Funston *et al*., 2003). While lions in LNP may have relatively larger home ranges in response to lower prey densities, we reasoned that 100 km^2 grid cells were nevertheless biologically meaningful to the scale at which lions make third order habitat selection decisions. Our study design was constrained by lack of accessibility of large portions of LNP. Given these constraints, we selected 24 grid cells to be surveyed such that the resulting area sampled a gradient of important bio-physical and anthropogenic features present in the park, including; distinguishing landscapes, KNP boundary and human settlements (Fig. 3.1). Replicated detection/non-detection camera trap and spoor surveys were conducted across the 2400 km^2 study area from September 9, 2011 to November 26, 2012. The following assumptions of an occupancy model were made, where the estimator (Ψ) was defined as the *probability of site use*; 1) species were not falsely identified, 2) detections were independent, and 3) heterogeneities in occupancy or detection probabilities were modelled using covariates, noting that the closure assumption could be relaxed because the parameter of interest was site use (MacKenzie *et al*., 2006). Detections were represented by unambiguously identified photographs of lions and/or tracks made by lions. Survey methodologies were non-invasive and it was therefore assumed that detections were independent (but see further below). To account for variation between sampling methodologies and between wet and dry seasons, survey-specific detection matrices were constructed (MacKenzie *et al*., 2006).

Home range scale

Sampling occasions (mean = 21.6 / grid cell) were represented by 189 temporally replicated 3 km transect samples (replicates separated by ≥ 14 days) and 326, 14 day camera-trap samples. Within the confines of access, sampling sites were located to maximize spatial representation of grid cells (mean = 3.4 camera stations/ grid cell, mean = 3.2 track transects / grid cell). Of the 24 grid cells, 23 were sampled with camera-traps (mean = 14 samples / grid cell, range = 3 – 30 samples / grid cell) and 23 were sampled with track surveys (mean = 8 samples / grid cell, range = 2 – 16 samples / grid cell). We note here that unequal sampling across sites is accounted for within an occupancy model (MacKenzie *et al*., 2002). In an effort to meet the assumption of independence between sampling occasions at the home range scale, detections were pooled (within grid cells) when a camera-trap had sampled anytime 14 days prior to a track transect.

Temporary site use scale

Sample occasions (mean = 3.6 / site) were represented by 998 temporally replicated 1 km transects (232 sites; 638 samples) (replicates separated by ≥ 14 days) and 14 day camera-trap samples (82 sites; 360 samples). Of the total 260 sites surveyed, 184 sites were sampled only by transects, 48 were sampled by transects and camera-traps, and 28 sampled only by camera-traps. For sites surveyed by both methods within the same 14 day interval, sampling occasions/detections were pooled.

Identification of covariates

To explain habitat selection by lions in a human disturbed landscape, we used five predictor variables (covariates) that may influence the fitness of lions. These included: availability of preferred prey, availability of alternate prey, landscape features that facilitate prey capture (i.e., riparian areas), relative bushmeat poaching and relative agro-pastoralist use (Table 3.1).

Table 3.1. Covariates expected to influence lion habitat use.

Covariate	**Key**	**Fitness value to lion**	**Description**	**Sampling range: Temporary site**	**Sampling range: Home range**
Preferred Prey	PP	Availability of preferred prey	Probability of buffalo site use	0.1 – 0.5 mean = 0.4	0.1 - 0.6 mean = 0.4
Alternate Prey	AP	Availability of alternate prey	∑ Probability of warthog and impala site use	0.1 – 1.7 mean = 1.0	0.2 – 1.5 mean = 0.9
Bushmeat Poaching	B	Targeted or accidental snaring	Probability of bushmeat poaching site use	0.0 – 1.0 mean = 0.6	0.1 – 1.0 mean = 0.6
Village	V	Persecution in defense of livestock	Proximity to agro-pastoralist settlements (km)	0.1 – 24.5 mean = 10.9	2.0 – 20.4 mean = 11.2
Riparian	R	Landscape feature facilitating prey capture	Amount of riparian area in site (# 30 x 30 m pixels)	0.0 – 2.7 mean = 0.1	0.0 – 928.1 mean = 315.3

Lions exhibit a strong preference for larger bodied prey including Africa buffalo, *Syncerus caffer*, (Hayward & Kerley, 2005). To quantify the influence of preferred prey availability on lion habitat, we used a probability of occurrence model for buffalo that was developed by Everatt (Chapter 2) for the same survey area during September 2011 to October 2012. Other species that lions are known to preferentially select for, including; giraffe, *Giraffa camelopardalis*, plains zebra, *Equus burchelli*, and blue wildebeest, *Connochaetes taurinus*, (Hayward & Kerley, 2005), were excluded from the analysis because they occurred at markedly low densities in the study area (Stephensen, 2010).

The buffalo probability of site use occupancy model was developed from 369 sampling occasions of 82 sampling sites (mean = 5 sampling occasions / site). Six landscape covariates, accounting for variation in vegetation communities, underlying geology, surface water availability, topography and anthropogenic disturbance were used to describe heterogeneity in buffalo site use (for more details, see Chapter 2).

To quantify the influence of alternate prey availability for lions, we used combined probability of occurrence models for warthog, *Phacochoerus africanus*, and impala, *Aepyceros melampus*, (Hayward & Kerley, 2005) developed for the same survey (as above). A warthog occupancy model was built from replicated detection/non-detection surveys using camera-trap data collected from 82 sites located across the study area during September 2011 to October 2012. Twenty-three lion grid cells were surveyed for warthogs (mean = 3.6 camera sites / lion grid cell). Active camera stations were located ≥ 4 km apart. Sampling occasions (n = 797; mean = 9.7 / site; range = 2 - 22) were represented by seven day intervals. We made the assumptions of an occupancy model (as above), but again note that the closure assumption was relaxed because the parameter of interest was *probability of site use* (MacKenzie *et al*., 2006). Warthog spatial use is influenced by the nutritional quality of vegetation, water availability and predation risk (Estes, 1991). To describe heterogeneity in warthog site use, we used six landscape covariates, accounting for variation in vegetation communities, underlying geology, surface water availability, topography and anthropogenic disturbance (Table 3.2). An impala occurrence model for the study area was borrowed from

Andresen *et al.,* (2014). We assume that the probability of prey occurrence (i.e., site use) is biologically representative of an encounter probability for lions.

To quantify the influence of bushmeat poaching on lion-habitat, we used a bushmeat poaching occupancy model developed by Everatt (Chapter 2). The probability of bushmeat poaching occurrence across the study area was estimated from 375 sampling occasions represented by 14 day camera-trap intervals across 82 sites (mean = 5 / site). The model considered six covariates that could account for heterogeneity in bushmeat poaching site use based on optimal foraging theory; including risk, effort and reward to hunters. These included; ranger patrols, distance from settlements, trails, proximity to waterholes and rivers, bushmeat abundance and bushmeat biomass (*for more details see* Chapter 2).

Agro-pastoralist use was measured as the mean Euclidean distance to a settlement edge per 30 m x 30 m pixel in a grid cell (home range analysis) or in a buffer (50 m diameter) placed around each camera station or track transect (temporary site use analysis) from a landscape raster (Peace Parks Foundation, Stellenbosch). For temporary site use sampling sites that were sampled by both methods the buffer values were extracted from the corresponding transect.

We considered riparian areas as a proxy for landscape features that facilitate prey capture (Hopcraft *et al.*, 2005), measured as the number of 30 m x 30 m pixels (per grid cell or buffer) overlapping either river (including drainage lines) or water (including pans) raster layers (Peace Parks Foundation, Stellenbosch). Analyses were made using the Spatial Analysis tool in ArcGIS 9.3.1. (www.esri.com).

Heterogeneity in detection probabilities were accounted for using survey-specific sampling covariates to account for variation between wet (November to April) and dry (May to October) seasons and sampling methodologies.

Table 3.2. Covariates expected to influence occurrence of warthog.

Covariate	**Fitness value to warthog**	**Description**	**Sampling effort**
Mopane shrubveld	Nutritional variation	Shrublands and thickets of *Colophospermum mopane* on calcerous soil	12 sites
Combretum/ mopane rugged veld	Nutritional variation	Woodlands and shrublands of *Combretum spp*. and *Colophospermum mopane* on clay soils	17 sites
Lebombo hills	Nutritional variation	Short woodlands and shrublands of *Combretum apiculatum* on rhylolite soils	11sites
Sand plains	Nutritional variation	Short woodlands and thickets of *Baphia massaiensis* and *Combretum apiculatum* on sandy soils	42 sites
Water	Water availability Nutritional variation	Proximity to rivers measured in ArcGIS (km)	0.0 – 9.3 mean = 3.7
Village	Direct persecution	Proximity to settlements measured in ArcGIS (km)	0.5 – 22.7 mean = 11.7

Data collection

Data were collected during September 9, 2011, to November 26, 2012. To maximize the probability of detecting lions, digital motion-activated cameras were deployed on dirt tracks, game trails and along river edges. Cameras used included; 15 Reconyx HC500 (Wisconsin, USA), 7 Spy Point Tiny-W2 (Québec, Canada) and 10 Bushnell Trophy Cam (Beijing, China). Due to the presence of illegal hunting activities in the area, substantial effort was made to conceal the cameras to avoid theft; including setting them on overhanging branches above trails, or hidden beneath logs or debris at ground level. Each camera was enclosed in a steel box, secured using cable locks and camouflaged with glued on vegetation. Vegetation that could cause false triggers was removed, while being careful to avoid attracting human attention to the site. In some cases a visual lure (a small piece of torn plastic) was placed opposite the station to draw human attention away from the hidden camera. Track transects were conducted on foot due to the lack of road networks. Transects followed a path of travel, (i.e., track, game trail or river edge), and were conducted in early morning or late afternoon hours where substrate was adequate for tracking. Sections of trail with poor substrate (e.g., rock) were excluded and the survey resumed where the substrate improved. The detection or non-detection of lion tracks was recorded for each (1 km) transect sample.

Analytical methods

Site occupancy (Ψ) and detection probability (p) were estimated using maximum likelihood functions (MacKenzie *et al.,* 2006) and the single season option in the program PRESENCE Version 5.5 (Hines, 2006). Continuous site covariates were standardized on a z-scale and all covariates were tested for collinearity using a cut-off of $r = 0.5$. Covariates found to be correlated were not included in the same models. Models were ranked based on Akaike Information Criterion (AIC), using AICc adjusted for small sample size, with the sample size set as the number of sampling sites. Models with a ΔAICc < 2 were considered to have strong support. We considered a candidate set of all models ΔAICc < 7 whose combined weights $\geq$ 0.95 (i.e., 95 % confidence set). AICc weights were used to determine the weight of evidence for each model, and were summed for each covariate in the 95 % confidence set (Burnham & Anderson, 2002). Variables with high summed model weights were considered more important in explaining heterogeneity in occupancy. The direction of influence of individual covariates was determined by the sign of the β-coefficients (MacKenzie *et al.,* 2006). Covariates were considered to have strong or robust impact if $\beta \pm 1.96 \times SE$ from the top ranking model were not overlapping zero. A weighted model averaging technique was used to calculate overall parameter estimates (Burnham & Anderson, 2002). A goodness of fit test using 10 000 bootstrap samples and a Pearson's chi-squared statistic was performed on the most saturated model (MacKenzie & Bailey, 2004).

Prey occupancy model

A detection/non-detection matrix was constructed for each site (n = 82), recording a '1' or '0' where warthog were detected or not detected, respectively. Similarly, a season (wet *versus* dry) specific matrix was built to account for differing detection probabilities throughout the year (1 = November - April, 0 = May - October). First, covariates describing heterogeneity in warthog detection probability were evaluated. The detection covariate for season was included in all the following analysis; the model with this covariate was strongly supported (ΔAICc < 2) and ranked higher than the model that assumed detectability was constant. Following this, we compared all possible combinations of occupancy covariates (63 models). Final covariate values were extracted as mean warthog site use from a continuous (30 m x 30 m resolution) raster layer using the Spatial Analysis toolbox in ArcGIS 9.3.1.

Lion occupancy models

A detection/non-detection matrix was constructed for each site, recording a '1' or '0' where lion were detected or not detected, respectively, for each spatial scale. Following this, two survey-specific matrices were constructed for each analysis to account for differences in detectability between the two sampling methods used. In the first matrix a '1' was recorded where the method 'track' was employed and a '0' where cameras were employed. In the second matrix a '1' was recorded where each method was used and data were pooled, and a '0' where only one method was used. The overlap of the two matrices therefore accounted for three sampling possibilities at each site; tracks only, pooled tracks and camera and by default camera only. Additionally, season specific (wet *versus* dry) matrices were constructed (as above).

To account for variation in lion detection probability (p) the covariates 'track' and 'pooled' (hereafter referred to as 'method' or "M") and 'season' were included in all models describing lion site use (Ψ). All possible (non-correlated) combinations of occupancy covariates (Table 3. 3) were considered for each analysis (home range scale = 11 models, temporary site use scale = 16 models). Following this, an additional two analyses were performed to describe lion site use at the temporary site use scale in wet (November - April) (145 sites) and dry (May - October) (210 sites) seasons.

Table 3.3. Results of Pearson's *r* correlation test from lion occupancy models.

Home range		**Temporary Site Use**	
Covariates	***r***	**Covariates**	***r***
B+P	0.000	B+P	0.000
B+AP	-0.386	B+AP	-0.363
B+W*	0.561	B+W	0.254
B+V	0.373	B+V	-0.431
P+AP*	0.702	P+AP*	0.544
P+W	0.235	P+W	0.137
P+V*	-0.695	P+V*	0.526
AP+W	-0.039	AP+W	0.051
AP+V*	-0.943	AP+V*	0.895
W+V	-0.069	W+V	-0.055

* indicates covariates that are correlated using a cut-off of r = 0.5 and were therefore not combined in models.

Results

Warthog site use

The model selection procedure for warthog site use is provided in Table 3.4. Model averaged estimates showed that the probability of detecting warthogs at a site where they occur was $\bar{p} = 0.336$ (SE = 0.035). Site level estimates ranged from 0.008 (SE = 0.011) to 0.771 (SE = 0.004). Site use by warthogs increased strongly with distance from villages (Table 3.5). There was no evidence lack of fit (p = 1.10) or over-dispersion ($\hat{c} = 0.20$).

Table 3.4. Summary of model selection procedure for factors influencing warthog site use (Ψ) across 82 sites in the Limpopo National Park, Mozambique. Covariates considered include; distance from villages (V), combretum/mopane rugged veld (C), distance from water (W), sand plains (SP) and mopane shrubveld (M). Detectability (p) varies with season (S).

Models	**ΔAICc**	***w***	**K**	**-2l**
Ψ(V)p(S)	0.00	0.267	4	538.42
Ψ(V+C)p(S)	0.20	0.241	5	536.35
Ψ(V+W+C)p(S)	1.12	0.152	6	534.94
Ψ(V+SP)p(S)	1.60	0.120	5	537.75
Ψ(V+W)p(S)	1.67	0.116	5	537.82
Ψ(V+M)p(S)	1.96	0.100	5	538.11
Ψ(.)p(S)	38.84	0.000	3	579.47

Ψ(.) assumes site use is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood value.

Table 3.5. β- coefficient estimates for covariates influencing warthog site use (Ψ) in order of their summed model weights (∑w).

Occupancy Covariate	**∑ model w (%)**	**β**	**SE**
Village	99.6	-2.95*	0.77
Combretum/Mopane rugged veld	39.4	0.61	0.52
Water	26.8	1.39	1.05
Sand plains	12.0	-0.79	1.00
Mopane shrubveld	10.0	-0.57	1.02

* Indicates covariate has robust impact (β ± 1.96 x SE not overlapping 0).

Lion habitat use

A survey effort of 5335 camera trap nights and 638 km of track surveys resulted in 101 lion photographic events (from 664 lion photos) and 138 lion track events. After pooling sampling occasions, the final data set consisted of 957 sampling occasions at the temporary site use scale and 251 sampling occasions at the home range scale.

Nineteen individual lions were identified from camera trap images in the survey area and included in the subsequent habitat use analysis. The model selection procedure for site use by lions at two spatial scales is provided in Table 3.6 and for site use by lions across two seasons in Table 3.7.

Table 3.6. Summary of model selection procedure for factors influencing the occurrence (Ψ) of lions at the temporary site use scale and at the home range scale. Covariates considered include; occurrence probability of preferred prey (P), occurrence probability of alternate prey (AP), occurrence probability of bushmeat poaching (B), distance from villages (V) and proportion of riparian area (W).

Models	**ΔAICc**	***w***	**K**	**-2l**
Temporary site use				
Ψ(P+B)p(M)	0.00	0.574	6	539.79
Ψ(P+B+R)p(M)	1.08	0.334	7	538.76
Ψ(P)p(M)	4.27	0.068	5	546.15
Ψ(P+R)p(M)	6.33	0.024	6	546.12
Ψ(.)p(M)	29.18	0.000	4	573.14
Home range level use				
Ψ(P)p(M+S)	0.00	0.372	6	151.44
Ψ(V)p(M+S)	2.47	0.108	6	153.91
Ψ(P+R)p(M+S)	2.89	0.088	7	150.27
Ψ(R)p(M+S)	3.45	0.066	6	154.89
Ψ(.)p(M+S)	3.52	0.064	5	158.57
Ψ(AP)p(M+S)	3.54	0.063	6	154.98
Ψ(P+B)p(M+S)	3.58	0.062	7	150.96
Ψ(AP+R)p(M+S)	4.18	0.046	7	151.56
Ψ(R+V)p(M+S)	4.21	0.045	7	151.59
Ψ(B+R)p(M+S)	5.50	0.024	7	152.88
Ψ(P+B+R)p(M+S)	5.72	0.021	8	148.50

Detectability (p) varies with method (M) and season (S). Ψ(.) assumes site use is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood value.

Table 3.7. Summary of model selection procedure for factors influencing the occurrence (Ψ) of lions at the temporary site use scale during wet season and dry season. Covariates considered include; occurrence probability of preferred prey (P), occurrence probability of alternate prey (AP), occurrence probability of bushmeat poaching (B), distance from villages (V) and proportion of riparian area (W).

Models	**ΔAICc**	***w***	**K**	**-2l**
Temporary site use (Wet)				
Ψ(P)p(M)	0.00	0.412	5	222.59
Ψ(P+R)p(M)	0.95	0.256	6	221.36
Ψ(P+B)p(M)	2.11	0.143	6	222.52
Ψ(P+B+R)p(M)	3.13	0.086	7	221.33
Ψ(V)p(M)	3.35	0.077	5	225.94
Temporary site use (Dry)				
Ψ(P+B)p(M)	0.00	0.725	6	302.05
Ψ(P+B+R)p(M)	1.94	0.275	7	301.85

Detectability (p) varies with method (M) and season (S). Ψ(.) assumes site use is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, K is the number of parameters in the model, and −2l is twice the negative log-likelihood value.

Habitat selection at the temporary site use scale.

The model averaged probability of detecting lions where they occurred at the temporary site use scale was $\bar{\hat{p}}$ = 0.230 (SE = 0.038). The greatest contributing factors to site use by lions at this scale were the probability of occurrence of their preferred prey and the probability of occurrence of bushmeat poaching (∑w = 99.9 % and ∑w = 90.8 %, respectively). Lions showed a strong selection for sites with a greater probability of occurrence of their preferred prey (β = 8.62, SE = 2.49) and a strong avoidance of sites with a greater probability of occurrence of bushmeat poaching (β = -1.50, SE = 0.63). In addition, lions generally selected for sites with a greater proportion of riparian areas (Table 3.8; Fig. 3.2). There was no evidence lack of fit (p = 0.41) or over-dispersion ($\hat{c}$ = 0.44).

Habitat selection at the home range scale.

The model averaged probability of detection lions where they occurred at the home range scale was $\bar{\hat{p}}$ = 0.304 (SE = 0.095). The covariate preferred prey was strongly supported and the greatest contributing factor to site use by lions at this spatial scale; the only model that emerged with a ΔAICc < 2.00 was the univariate model Ψ(P)p(M+S) (Table 3.6). Lions showed a strong selection for sites with a greater probability of occurrence of their preferred prey (β = 9.82, SE = 4.73). In addition, lions generally selected for sites with a greater proportion of riparian areas that were further from villages with a greater probability of occurrence of alternate prey and lower probability of occurrence of bushmeat poaching (Table 3.8; Fig. 3.2). There was no evidence lack of fit (p = 0.22) or over-dispersion ($\hat{c}$ = 1.20).

Table 3.8. β- coefficient estimates for covariates influencing site use (Ψ) by lions in order of their summed model weights (∑w) for the temporary site use scale and the home range scale.

Occupancy Covariate	**∑ model w (%)**	**β**	**SE**
Temporary site use			
Preferred Prey	99.9	8.62^*	2.49
Bushmeat Poaching	90.8	-1.50^*	0.63
Riparian	35.9	0.56	0.46
Home range use			
Preferred Prey	57.6	9.82*	4.73
Riparian	20.4	0.57	0.62
Villages	16.8	-1.12	0.64
Alternate Prey	10.7	2.51	1.57
Bushmeat Poaching	7.0	-1.13	1.69

* Indicates covariate has robust impact (β ± 1.96 x SE not overlapping 0).

Table 3.9. β- coefficient estimates for covariates influencing site use (Ψ) by lions in order of their summed model weights (∑w) for the temporary site use scale in the wet season and in the dry season.

Occupancy Covariate	**∑ model w (%)**	**β**	**SE**
Temporary site use Wet Season			
Preferred Prey	89.7	7.43*	2.83
Riparian	34.2	0.32	0.31
Bushmeat Poaching	22.9	0.28	1.05
Villages	7.7	-7.51	4.08
Temporary site use Dry Season			
Preferred Prey	99.9	17.59*	5.51
Bushmeat Poaching	99.9	-3.43*	0.92
Riparian	27.5	0.13	0.29

* Indicates covariate has robust impact (β ± 1.96 x SE not overlapping 0).

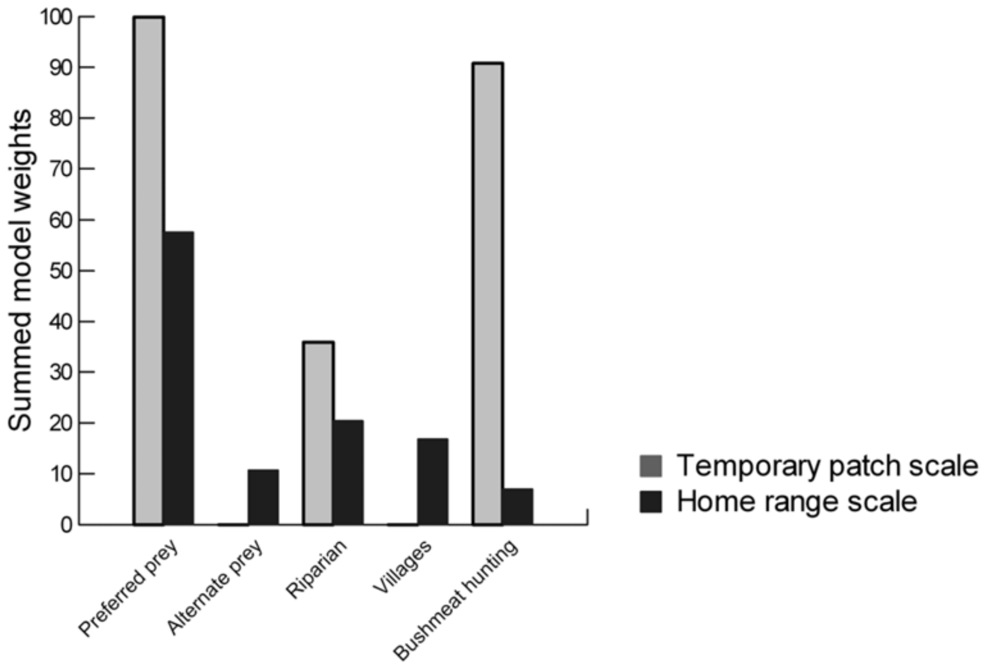

Figure 3.2. Relative contribution of covariates influencing habitat use by lions at temporary site use scale (n = 260, 1 km sites) and home range scale (n = 24, 100 km^2 sites) in the Limpopo National Park, Mozambique.

Temporary site use wet season.

The model averaged probability of detecting lions where they occurred at the temporary site use scale in the wet season was $\bar{p}$ = 0.202 (SE = 0.058). The greatest contributing factor to site use by lions in the wet season was preferred prey (Table 3.9; Fig. 3.3). Lions also generally selected for sites offering a greater proportion of riparian areas, a lower occurrence probability of bushmeat poaching and sites that were further from villages (Fig. 3.3). There was no evidence lack of fit (p = 0.36) or over-dispersion ($\hat{c}$ = 0.88).

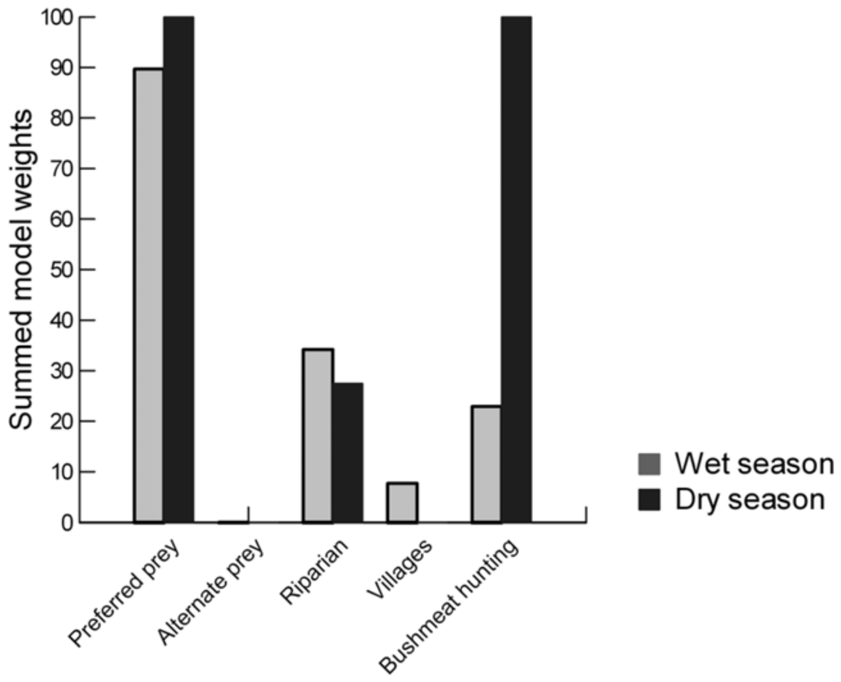

Figure 3.3. Relative contribution of covariates influencing habitat use by lions at the temporary site use scale during wet (November - April) (n = 145, 1 km sites) and dry (May - October) (n = 210, 1 km sites) seasons of 2011 - 2012 in the Limpopo National Park, Mozambique.

Temporary site use dry season.

The model averaged probability of detection lions where they occurred at the temporary site use scale in the dry season was $\bar{p}$ = 0.302 (SE = 0.063). The greatest contributing factors to site use by lions in the dry season were preferred prey and bushmeat poaching (Table 3.9; Fig. 3.3). Lions showed a strong positive selection for sites with a greater probability of occurrence of their preferred prey (β = 17.59, SE = 5.51) and a strong avoidance of sites with a greater probability of bushmeat poaching (β = -3.43, SE = 0.92) and generally selected for sites with greater proportion of riparian areas (Fig. 3.3). There was no evidence lack of fit (p = 0.70) or over-dispersion ($\hat{c}$ = 0.30).

Discussion

This study presents some of the few data on habitat use by lions in a human disturbed landscape. We tested the hypotheses that; as an apex predator, habitat use by lions would be most predicted by bottom-up prey resources, and alternatively, that in a human disturbed landscape, habitat use by lions would be predicted by top-down anthropogenic pressures. In addition, we examined the importance of scale when assessing the influences of variables on the habitat selection by lions.

Habitat use by an apex carnivore is most determined by bottom-up prey resources

In agreement of our first hypothesis, habitat use by lions in LNP was most strongly influenced by the occurrence of their preferred prey (buffalo). The importance of this variable was indicated by the weight of evidence for models containing the buffalo covariate and by the strong positive influence of this covariate at the coarser home range spatial scale. That the buffalo covariate was strongly determining across both spatial scales emphasizes the importance of this component of lion-habitat (Rettie & Messier, 2000). These results suggest that lions in LNP are making behavioural choices to select habitat at the home range scale to include the limited distribution of buffalo herds in the park and then further selecting areas at a finer spatial scale that would increase the probability of encounter with buffalo.

The observed strong association between habitat use by lions and available prey resources is characteristic of apex predator ecology; where habitat selection is limited more by bottom-up food resources than by top-down predation (Krebs, 2009; Mitchell & Hebblewhite, 2012). For instance, food resources were the primary predictor of habitat use at the second order scale for grizzly bears, *Ursus arctos*, in the Canadian Arctic (McLoughlin *et al*., 2002) and tigers in the Russian Far East (Miquelle *et al*., 1999). In contrast, predation risk by wolves was the primary predictor of second order habitat selection by caribou, *Rangifer tarundus*, in northern Canada (Rettie & Messier, 2000) and predation risk by lions was the primary predictor of second order habitat selection of zebra, giraffe and wildebeest on a reserve in South Africa (Thaker *et al*., 2011). The almost singular importance of prey resources to the habitat selection by lions at the home range scale may be considered the ‘natural’ trophic based species-habitat relationship (Van Orsdol *et al*., 1985; Estes *et al*., 2011).

Habitat use by lions is also influenced by human disturbances

This study found that lions showed strong spatial avoidance of sites with a greater probability of bushmeat poaching occurrence at a finer spatial scale and also tended to select against areas with higher proportions of agro-pastoralist use at the home range scale. Such relationships support our alternative hypothesis that habitat selection by lions in a human disturbed system is influenced by top-down anthropogenic pressures. It is therefore likely that both hypotheses are true. That is, while the ecology of an apex predator predicts that its selection of habitat should be determined by bottom-up prey resources, in the context of contemporary human pressures, habitat use by lions is now also determined by top-down anthropogenic pressures. Interestingly, there was no evidence of selection by lions against the agro-pastoralist variable at the finer temporary site use scale. This may suggest that avoidance of this pressure at the coarser home range scale negated the need for avoidance at the finer scale. It should be noted that while the strength of influence of the pastoralist covariate was not statistically significant, the overall density of lions in this system is below the resource-based carrying capacity, suggesting a top-down limiting influence on the population (Chapter 2). In addition, Everatt (Chapter 2) found that agro-pastoralism was the most important variable describing lion occupancy at the home range scale when only considering dry season data, indicating a seasonal variation in its influence on lion ecology.

During the dry season, bushmeat hunting was a strong negative predictor of habitat selection by lions at the third order scale, equaling the influence of prey resources. This study provides the first quantitative measure of the influence of bushmeat poaching on lion-habitat, and suggests that the effects of this pressure on the ecology of lions may be widely overlooked. The proximate causes for the influence of bushmeat poaching on habitat selection by lions may include prey depletion as well as direct persecution in the form of accidental or targeted snaring (see Chapter 2 and Becker *et al*., 2013). By modeling prey occurrence directly, however, we could isolate these variables, thus indicating that the bushmeat poaching covariate was most likely describing direct persecution of lions (*see also* Chapter 2). That bushmeat poaching was more influential at the finer spatial scale may be because the spatial occurrence of these activities change constantly and are widely distributed, making them potentially more difficult for lions to predict. The dramatic increase in the influence of bushmeat poaching during the dry season could be attributed to increased rates of human hunting and/or increased concentration of human hunting near dry season water points, making them more predictable to lions.

Figure 3.4. Habitat use by lions in LNP was influenced by a combination of bottom-up prey resources (buffalo) and by top-down anthropogenic pressures including pastoralism and bushmeat poaching.

Our results demonstrate the scale dependency of ecological relationships for lions. In LNP, the importance of the preferred prey covariate spanned the domain of both spatial scales examined, emphasizing the importance of this prey base to lion-habitat. Interestingly, however, the relative limiting influences that the anthropogenic variables had on the habitat use by lions varied with the spatial scale examined. Recognizing the hierarchical nature of habitat selection and the scale dependency of variables on species fitness is important for effective conservation management. Ciarniello *et al*. (2007) demonstrated how delineating protected areas for grizzly bears based on habitat selection at a third order selection would have excluded important landscape features whose selection only became evident at the home range scale. Similarly, this study has demonstrated how considering habitat selection of lions only at the second order selection would have greatly underestimated the impact of bushmeat poaching.

While the relationships found by this study between anthropogenic variables and habitat selection by lions describe negative top-down limiting effects that humans can have on lions, they may also describe mechanisms of co-existence (i.e., spatial avoidance) that lions may have developed towards human presence. However, most importantly these results demonstrate the strong importance of prey resources to lion-habitat in a human disturbed system, and the less known influence of bushmeat poaching on the ecology of lions.

Lions, like other apex carnivores, are extinction prone in part due to inherent conflicts between their biological requirements and those of expanding human populations (Woodroffe, 2000; Cardillo *et al*., 2004). As Africa's rising human population exerts increasing top-down influence on lions outside of, and within, protected areas (Woodroffe & Ginsberg, 1998; Packer *et al*., 2013) quantifying the effects of these pressures on the ecology of lions becomes increasingly critical to the conservation management of the species. This study provides data on the habitat selection of lions in a human disturbed landscape. Our results demonstrate that prey resources continue to represent the principal limiting factor to lion-habitat in a human disturbed system; although the limiting pressures exerted by bushmeat poaching can be equally important. These results suggest that the potential for future coexistence between free-roaming lions and subsistence agro-pastoralist-hunters may be dependent on maintaining a suitable prey base and sufficient space for lions to spatially avoid human activities.

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CHAPTER 4: FINAL DISCUSSION

We are in a time that has been described as being the Earth's sixth mass-extinction (Wake & Vredenburg, 2008). However, unlike previous mass-extinction events, the current crisis comes at the hand of humankind (Estes *et al*., 2011). Large carnivores have been particularly affected by humanity's rapid population growth and rampant habitat degradation due to their large space requirements and conflicts with humans (Ray *et al*., 2005). As Africa's rising human population exerts increasing top-down influence on lions outside of, and within, protected areas (Woodroffe & Ginsberg, 1998; Packer *et al*., 2013) quantifying the effects of these pressures on the ecology of lions becomes increasingly critical to the conservation management of the species.

During September 2011 to November 2012, I studied aspects of the ecology of lions sharing a landscape with subsistence agro-pastoralist-hunter-gatherer people in the Limpopo National Park (LNP), Mozambique. My research objectives were to provide empirical data on the status of lion in LNP, to determine whether the population is limited by bottom-up prey resources or top-down anthropogenic factors, and to determine the relative influence of ecological variables on lion resource use and non-use.

Using call-up surveys I produced an initial density estimate of 0.99 lions/100 km^2 and an abundance estimate of 66 lions for LNP. This number is considerably lower than a reported "guestimate" of 179 lions made for the same area (Chardonnet *et al.*, 2009). (It is also notably more accurate than qualitative answers I got when I asked local rangers, such as; there are "plenty lions" or "too many lions").

I compared this direct estimate of density with an indirect estimate derived from trophic scaling of available prey resources. The direct density estimate was less than 1/3 of the estimate derived from prey resources (3.05 lions/100 km^2). As an apex predator, lion populations are naturally limited by bottom-up prey resources (Schaller, 1972; Van Orsdol *et al*., 1985; Carbone & Gittleman, 2002; Hayward *et al*., 2007). The observed disparity between the realized and potential densities of lions in LNP therefore suggests the limiting influence of external, top-down, anthropogenic pressures.

Following this, I used replicated detection/non-detection data from camera trap and track surveys to estimate the proportion of area occupied by lions, and hierarchical ranking of covariates to provide inferences on the relative contribution of prey resources and anthropogenic factors influencing lion occurrence. Lions occupied approximately 44% of a 2400 km^2 sample of potential habitat. While lions were strongly predicted by a greater probability of encountering prey resources, the greatest contributing factor to lion occurrence was a strong negative association with settlements. Although the proportion of area occupied is not directly reflective of density (MacKenzie *et al*., 2006), these results suggest that anthropogenic pressures associated with human settlements may explain the observed differences between the potential and realized population densities of lions in LNP.

Altogether, my results describe a lion population that is held below resource-based carrying capacity by top-down anthropogenic factors. My results highlight the limitations of trophic scaling suggested by Carbone and Gittleman (2002) and agree with the criticism of Riggio *et al*. (2012) on the use of opinion surveys when estimating predator populations exposed to anthropogenic pressures. Trophic relationships are becoming increasingly disrupted by anthropogenic disturbance across Africa and much of the world (Estes *et al*., 2011). Contrasting trophic-based density estimates of lions with direct density estimates can be a useful means of identifying systems where lions are limited by top-down anthropogenic pressures (Hayward *et al*., 2007).

Following this, I determined the relative influences of ecological variables on the habitat selection by lions in LNP. I used hierarchical modeling within an occupancy framework to test the specific hypotheses regarding habitat selection by an apex predator in a human disturbed system that: 1) habitat use by lions should be most strongly predicted by bottom-up prey resources, 2) in a human disturbed system, habitat use by lions may also be predicted by top-down pressures, including both agro-pastoralism and bushmeat poaching. I also considered the influence of the spatial scale examined and season on lion-habitat associations. Habitat use by lions was most strongly influenced by the occurrence of their preferred prey (buffalo) across both spatial scales and seasons. However, lions showed strong spatial avoidance of bushmeat poaching at the finer spatial scale and selected against agro-pastoralist use at the coarser scale. Restricting the analysis to a singular coarser scale would have greatly underestimated the impact of bushmeat poaching on the ecology of lions. Landscape features that facilitate prey capture were always less determining than prey availability. There was seasonal variation in the relative contributions of all variables with a dramatic increase in the influence of bushmeat poaching during the dry season. My study presents some of the first quantifications of the impacts of bushmeat poaching on lion ecology.

There is debate as to whether the continued co-existence between lions and humans in Africa can only be facilitated by a tall fence separating one species from the another (Creel *et al.,* 2013; Packer *et al.,* 2013). My results suggest that provided with adequate prey and space, lions and subsistence-agro-pastoralist-hunters may be able to persist in the same landscapes.

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