Monitoring and Conserving Wildlife Communities across Northern Botswana

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ABSTRACT (ACADEMIC)

To develop effective conservation planning and mitigate biodiversity loss, standardized metrics for monitoring and assessing biodiversity are needed. This information is particularly vital in Botswana, where knowledge of many of the diverse wildlife populations is lacking. To address this knowledge gap, my dissertation research evaluated the distributions, densities, and ecology of the wildlife community in northern Botswana, with a focus on terrestrial carnivore species given their importance both ecologically and economically. My objectives were threefold: 1) estimate the distributions of the mammal community ($n = 44$ species) and evaluate community, group, and species-specific responses to anthropogenic and environmental variables, 2) test whether the presence of intraguild species or resource availability had a larger influence on the seasonal distributions of carnivore species, and 3) simultaneously estimate the population densities of 7 carnivore species. To accomplish these objectives, I completed a multi-year camera trap survey in a 1,154-km^2 study area and analyzed the data using occupancy models (single and multi- species) and spatially explicit capture-recapture models. Estimates of species richness ranged from 8 to 27 unique species, species had a mean occurrence probability of 0.32 (*95%* credible interval = 0.21–0.45), and estimated densities ranged from 1.8 aardwolves (*Proteles cristata*) to 12.7 spotted hyenas (*Crocuta crocuta*) per 100 km^2. The occupancy and richness of terrestrial mammals was negatively associated with human disturbance and in general, positively associated with open grasslands/floodplains. Carnivore species, specifically, tended to have greater species richness and larger population densities in open habitats than in closed. I also found carnivore distributions were positively associated with the detection rate of

intraguild competitors and predators, suggesting competitor/predator avoidance did not play a large role in shaping carnivore community structure. My research highlights the pivotal role protected areas and grasslands play in conserving wildlife populations in northern Botswana. Additionally, my research helps progress camera trap analyses from single to multi-species assessments. Broader application of this multi-species approach would likely result in a better understanding of wildlife and carnivore communities which in turn, may help inform management actions aimed at addressing the loss of wildlife populations globally.

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GENERAL AUDIENCE ABSTRACT

To conserve wildlife populations, information is needed on where species live, the resources (e.g., food, water, and shelter) they require, and how many there are. This information is particularly important in Botswana, where knowledge of many wildlife populations is lacking. To address this knowledge gap, my dissertation research evaluated the distributions, densities, and ecology of the wildlife community in northern Botswana, with a focus on carnivores given their importance both ecologically and economically. My objectives were threefold: 1) estimate the distributions of the mammal community ($n = 44$ species) and evaluate community, group, and species-specific responses to human and environmental variables, 2) test whether the presence of competitors/predators or resource availability had a larger influence on the seasonal distributions of carnivore species, and 3) estimate the population densities of 7 carnivore species. To accomplish these objectives, I completed a multi-year camera trap survey in a 1,154-km^2 study area and analyzed the data using advanced analytical techniques. I photographed 44 species of mammals and the estimated number of species per camera station ranged from 8 to 27. My estimated densities ranged from 1.8 aardwolves (*Proteles cristata*) to 12.7 spotted hyenas (*Crocuta crocuta*) per 100 km^2. Overall, mammal species were more likely to occupy grasslands and floodplains that were located further into protected areas (i.e., far from human disturbance). Open habitats seemed to be particularly important to carnivore species. In general, there were more carnivore species and these species had higher densities in open habitats than in closed. My results suggest carnivores did not avoid their competitors and predators by spatially separating themselves on the landscape, as has been found in the Serengeti. My research

highlights the pivotal role protected areas and grasslands play in conserving wildlife populations, and advances camera trap analyses from assessments of a single species to assessments of entire wildlife communities. My research approach is applicable to camera trap studies worldwide and broader application would likely result in a better understanding of wildlife and carnivore communities. This information, in turn, can help inform management actions aimed at addressing the loss of wildlife populations around the globe.

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Thank you to Dr. J. W. McNutt, the director of the Botswana Predator Conservation Trust (BPCT), for inviting me to collaborate with his organization and be based out of BPCT's field camp for the duration of my dissertation field work. I also thank Krystyna Golabek, Neil Jordan, Leanne Van der Weyde, Jessica Vitale, Hallie Walker, Geoff Gilfillan, Dix Kedikilwe, Briana Abrahms, and Kasim Rafiq at BPCT for their assistance with various parts of my dissertation field work and for becoming my lifelong friends and family. I would also like to thank the government of Botswana, the Ministry of the Environment, Wildlife and Tourism, and the Department of Wildlife and National Parks for permission to conduct this study (permit EWT 8/36/4 XXIII 44) in your breath-taking country, it was a dream come true.

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certainly not least, thank you to my family for your unwavering support and for encouraging my crazy career path, particularly my mom who has always pushed me to follow my dreams.

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ATTRIBUTION

Several people aided in my dissertation research and the resulting chapters/manuscripts. A brief description of their contributions is provided here:

Marcella J. Kelly, Ph.D., is my Ph.D. advisor and helped in the development of my research and study design. She also provided feedback throughout my Ph.D. and editorial comments on each manuscript.

Hugh S. Robinson, Ph.D., is on my Ph.D. committee. He helped in the development of my research, provided editorial comments on each manuscript, and procured camera traps from Panthera that were instrumental in the successful completion of my dissertation field work.

David A.W. Miller, Ph.D., is a professor at Penn State University. He provided guidance on the design of the camera trap survey, helped with the quantitative analyses, and contributed editorial comments on each manuscript.

Dr. "Tico" McNutt, Ph.D., is the director of the Botswana Predator Conservation, the organization I collaborated with for my dissertation research. He helped in the development of my research (ensuring it was pertinent to wildlife conservation in Botswana), allowed me to be based out of his field camp in Botswana for the duration of my field work, and provided editorial comments on each manuscript.

I. INTRODUCTION

Biodiversity loss, species-level extinction risks, and anthropogenic pressures on ecosystems are accelerating (Alkemade et al. 2009, Butchart et al. 2010). Biodiversity loss, specifically, could rank among the major drivers of ecosystem change in the 21st century, comparable to global change stressors such as ultraviolet radiation and climate warming (Hooper et al. 2012). These alarming trends resulted in The Convention on Biological Diversity developing a strategic plan, signed by 193 nations, aimed at conserving, restoring, and wisely using biodiversity. The infrastructure required to measure trends in abundance or changes in species distribution, however, is lacking thus limiting countries' ability to monitor progress towards achieving Convention goals (Ahumada et al. 2013; Schmeller et al. 2015). Additionally, the lack of rigorous data prevents the evaluation of species' responses to anthropogenic and environmental threats which, in turn, precludes effective conservation planning (Feeley and Silman 2011).

The conservation of carnivore species is of particular interest given their vulnerability to extinction and their impacts on ecosystems as a whole (Woodroffe and Ginsberg 1998, Ripple et al. 2014, Bauer et al. 2015). Nearly one-quarter of the world's 245 carnivore species are threatened with extinction and many more are experiencing population declines (Ginsberg 2001, Schipper et al. 2008, Ripple et al., 2014). Among the 31 largest carnivores, specifically, 19 are listed as threatened by the International Union for the Conservation of Nature (IUCN) and 24 are decreasing. African wild dogs (*Lycaon pictus*), tigers (*Panthera tigris*), and lions (*Panthera leo*), for example, have each disappeared from >80% of their historical range (Ripple et al. 2014, Bauer et al. 2015). Carnivores' vulnerability to extinction is a consequence of both intrinsic and extrinsic factors (Woodroffe and Ginsberg 1998, Bauer et al. 2015). Intrinsic factors can include

low population densities, low reproductive rates, high food requirements, and extensive area requirements (Woodroffe and Ginsberg, 1998, Cardillo et al. 2005). Extrinsic factors can include human-wildlife conflict, habitat loss and fragmentation, and prey loss (Creel 2001, Gittleman et al. 2001). Direct persecution by humans, for example, is often a major threat to carnivores as they are hunted for trophies, bushmeat, and for real or perceived threats to livestock and human life (Woodroffe and Ginsberg 1998). The unremitting decline of many of our world's carnivores is a threat to not only the species, but to the ecosystems in which they reside. Carnivore declines have reportedly led to changes in plant diversity, biomass, and productivity, which likely have extensive impacts on nearly all other species as well as ecological processes such as nutrient cycling, the frequency of wildfires, regulation of diseases, and carbon sequestration (Ripple et al. 2014). To curtail the decline of our world's remaining carnivore species, information on the distributions, demographics, and ecology of remaining carnivore populations is needed (Gros et al. 1996, Gaston and Fuller 2009, Pettorelli et al. 2010).

The wide ranging and elusive nature of many carnivore species makes them difficult to observe directly (Silver et al. 2004, Karanth et al. 2006, Balme et al. 2010). As a result, camera traps have become an increasingly common method for collecting standardized data on a diversity of carnivores (O'Brien et al. 2010, Ahumada et al. 2011, Burton et al. 2015, Steenweg et al. 2016). Remote sensing cameras detect passing animals using motion- and heat-sensing infrared technology, which allows them to collect data 24 hours per day without a human having to be present. Additionally, each photographic detection has corresponding metadata on the time, date, and location of the photograph, which allows human error to be minimized. This metadata also allows researchers to account for species' detection probabilities (i.e., the probability a species was present but went undetected; MacKenzie et al. 2002). As a result of

these features, camera traps have become a mainstream tool in conservation ecology and are now being used to evaluate species' distributions, occupancy, density, temporal activity patterns, movement, and population trends (O'Brien et al. 2010, Ahumada et al. 2013, Burton et al. 2015, Steenweg et al. 2016). Few studies, however, capitalize on the wealth of community information collected by camera traps as attention is typically focused on a single species such as tigers (Karanth and Nichols 1998, Karanth et al. 2006) or jaguars (*Panthera onca*; Silver et al. 2004, Soisalo and Cavalcanti 2006). This results in the majority of photos being discarded and additional, potentially valuable data being unused. Thus, multi-species assessments of camera trap data are needed. Multi-species assessments would result in considerable savings in money, time, and personnel costs, when compared to single species approaches, and a more comprehensive and efficient use of available data, which is critical for the many management agencies across the world where field data funding is limited (Zipkin et al. 2009).

With recent advancements in ecological modeling, multi-species assessments of camera trap data are now possible. Multi-species hierarchical occupancy models (Dorazio and Royle 2005), for example, can be used to evaluate the spatial ecology of entire wildlife communities. As occupancy models (MacKenzie et al. 2002), they account for imperfect detection by using temporally or spatially replicated data and as hierarchical models, they integrate data across species, permitting composite analyses of communities and individual species (Russell et al. 2009, Zipkin et al. 2009). Additionally, sharing data across species permits occupancy estimates for rare and elusive species, which would not have been possible using single species approaches (Zipkin et al. 2010). Multi-species hierarchical models can also be parameterized with variables hypothesized to influence the distributions of wildlife, allowing evaluation of how these variables affect wildlife communities or a specific species of concern (Russell et al. 2009). If

density is the parameter of interest, then spatially explicit capture-recapture (SECR; Efford et al. 2009, Royle et al. 2009) and spatial mark-resight (SMR; Sollmann et al. 2013, Rich et al. 2014) models can be used to simultaneously estimate the densities of multiple, sympatric species, including both fully and partially marked (i.e., identifiable to the individual-level using natural or artificial markings) species. When employing traditional capture-recapture approaches, study designs have to be tailored to the movements of an individual study species (Karanth and Nichols 1998, Sollmann et al. 2012). Spatial models, alternatively, directly incorporate the Cartesian coordinates of where individuals were photographed, making them much more robust to varying trap array sizes and distances between camera stations. As long as there is a large enough sample of individuals and spatial recaptures across a range of distances, spatial models make it possible to now use a single camera trap survey to simultaneously estimate the densities of multiple species (O'Brien and Kinnaird 2011, Sollmann et al. 2012, Sun et al. 2014).

My dissertation research pushed the envelope of population modeling by using camera trap data, in combination with these recent advances in ecological modeling, to evaluate northern Botswana's wildlife community (n = 44 species), with a focus on the carnivore guild. I chose to carry out my dissertation research in northern Botswana, where the Okavango Delta is located, because it has one of the highest diversities of carnivores found anywhere in Africa (Figure 1.1) and is a stronghold for many wildlife populations (Fig. 1.1; Gittleman et al. 2001). The large carnivore guild, which includes lions, cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), African wild dogs, spotted hyenas (*Crocuta crocuta*), and brown hyenas (*Hyaena brunnea*), is the most diverse assemblage of large (>15 kg) carnivores in the world (Dalerum et al. 2008). Accompanying the carnivores is a wide array of herbivores including high densities of African elephants (*Loxodonta africana*), Burchell's zebras (*Equus burchelli*), and impalas (*Aepyceros*

melampus). These wildlife populations may be under threat, however, as Botswana has recently

reported declining wildlife populations, increasing pressures from illegal hunting, and large scale

changes in land use and land management policies. The perceived loss of biodiversity is of

concern to the country as wildlife has both cultural and economic value; the wildlife-based

tourism industry is a large contributor to Botswana's Gross Domestic Product (World Travel and

Tourism Council 2015). In response to these reports, Botswana's Ministry of Environment,

Wildlife, and Tourism temporarily banned wildlife hunting, which generated $\geq$\$20 million per

year (Lindsey 2010), in early 2014. The Ministry also announced that they will be implementing

additional management actions targeted at conserving wildlife. To develop these actions,

information on Botswana's wildlife populations is needed.

Currently, there is no large scale monitoring of carnivores in Botswana and knowledge of

many wildlife species is lacking. My dissertation research addressed this knowledge gap by

evaluating the distributions, densities, and ecology of the wildlife community in northern

Botswana, with a focus on terrestrial carnivores. Specifically, I had three research objectives: 1)

quantify species richness, evaluate species' distributions, and elucidate community, group, and

species-specific responses to human disturbance and environmental variables, 2) test whether the

presence of intraguild species or resource availability had a larger influence on the seasonal

distributions of carnivore species, and 3) evaluate the utility of using a novel camera trap study

design and spatial models for estimating the population densities of multiple, sympatric

carnivore species. My research is among the first to use a single camera trapping array, in

combination with advanced statistical models, to evaluate the distributions of an entire wildlife

community and to simultaneously estimate the densities of multiple carnivore species. Broader

application of this framework would likely result in a more comprehensive and efficient use of

available camera trap data and a better understanding of terrestrial wildlife communities,

including the many carnivore species across the world that are experiencing population declines

and range contractions due to land-use change, fragmentation, and infrastructure development

(Ginsberg 2001, Schipper et al. 2008, Alkemade et al. 2009, Butchart et al. 2010, Ripple et al.

2014). Thus, in addition to providing needed information on the population dynamics and

ecology of Botswana's wildlife communities, my dissertation also provides a research

framework for multi-species assessments that is applicable to the growing number of camera trap

studies worldwide.

Figure 1.1. Meso- and large carnivore species endemic to northern Botswana including the A) aardwolf (*Proteles cristata*), B) bat-eared fox (*Otocyon megalotis*), C), black-backed jackal (*Canis mesomelas*), D) caracal (*Caracal caracal*), E) cheetah (*Acinonyx jubatus*), F) African civet (*Civettictis civetta*), G) honey badger (*Mellivora capensis*), H) leopard (*Panthera pardus*), I) lion (*Panthera leo*), J) serval (*Leptailurus serval*), K) spotted hyena (*Crocuta crocuta*), L) African wildcat (*Felis silvestris*), M) and African wild dog (*Lycaon pictus*).

Figure 1.1.

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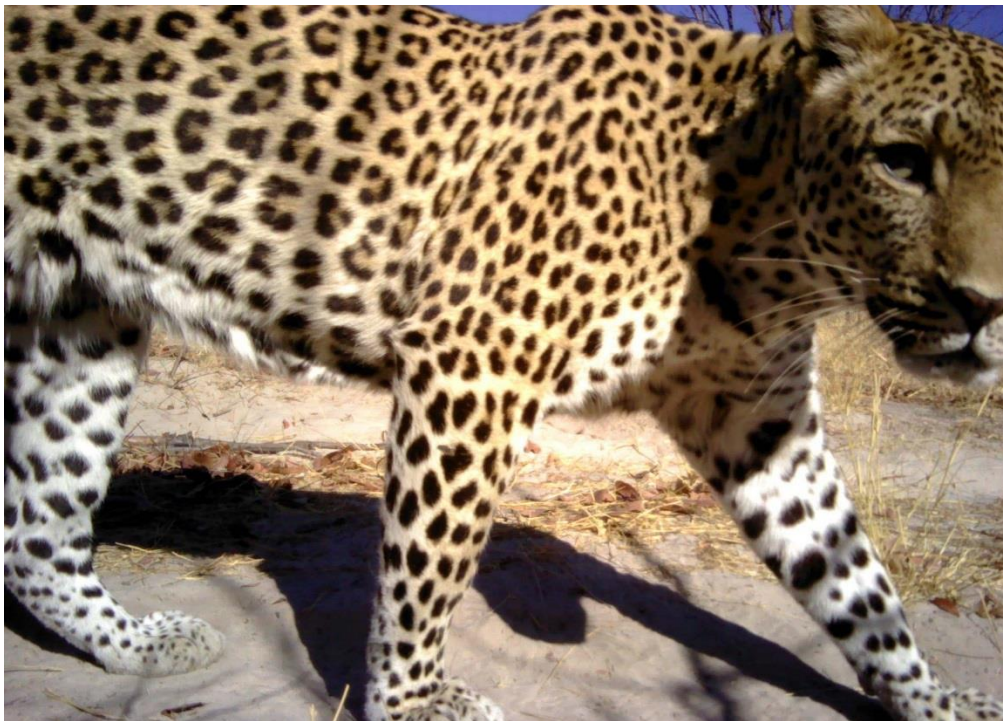
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II. USING CAMERA TRAPPING AND HIERARCHICAL OCCUPANCY MODELLING TO EVALUATE THE SPATIAL ECOLOGY OF AN AFRICAN MAMMAL COMMUNITY

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Abstract

Emerging conservation paradigms have shifted from single to multi-species approaches focused on sustaining biodiversity. Multi-species hierarchical occupancy modelling provides a method for assessing biodiversity while accounting for multiple sources of uncertainty. We analysed camera trapping data with multi-species models using a Bayesian approach to estimate the distributions of a terrestrial mammal community in northern Botswana and evaluate community, group, and species-specific responses to human disturbance and environmental variables. Groupings were based on two life-history traits: body size (small, medium, large, and extra-large) and diet (carnivore, omnivore, and herbivore). We photographed 44 species of mammals over 6607 trap nights. Camera station-specific estimates of species richness ranged from 8 to 27 unique species and species had a mean occurrence probability of 0.32 (*95%* credible interval = 0.21–0.45). At the community level, our model revealed species richness was generally greatest in floodplains and grasslands and with increasing distances into protected wildlife areas. Variation among species' responses was explained in part by our species groupings. The positive influence of protected areas was strongest for extra-large species and herbivores while medium-sized species actually increased in the non-protected areas. The positive effect of grassland/floodplain cover, alternatively, was strongest for large species and carnivores and weakest for small species and herbivores, suggesting herbivore diversity is promoted by habitat heterogeneity. Our results highlight the importance of protected areas and grasslands in maintaining biodiversity in southern Africa. We demonstrate the utility of hierarchical Bayesian models for assessing community, group, and individual species' responses to anthropogenic and environmental variables. This framework can be used to map areas of high conservation value and predict impacts of land-use change. Our approach is particularly applicable to the growing

number of camera trap studies worldwide and we suggest broader application globally will likely result in reduced costs, improved efficiency, and increased knowledge of wildlife communities.

Key-words: biodiversity, body size, camera trap, diet, grasslands, hierarchical Bayesian models, human disturbance, multi-species modelling, protected areas, species richness

Introduction

Prioritizing conservation actions, quantifying the impacts of management decisions, and designating protected areas are just a few of the challenging tasks faced by wildlife managers and conservationists. To address these tasks, surrogate species are often used (Carroll, Noss & Paquet 2001; Epps *et al.* 2011) such that by focusing on the requirements of the surrogate, the needs of an entire community are addressed (Lambeck 1997). This concept, however, is widely debated given that actions aimed at conserving a single species have positive and negative effects on a wealth of other non-target species (Simberloff *et al.* 1998; Wiens *et al.* 2008). As a result, emerging conservation and management paradigms favour multi-species vs. single species approaches where the objective is sustaining biodiversity and ecosystem functions (Yoccoz, Nichols & Boulinier 2001; Balmford *et al.* 2005).

Multi-species hierarchical occupancy models (Dorazio & Royle 2005), a recent advancement in community modelling, can be used to evaluate the spatial ecology of wildlife communities. As occupancy models (MacKenzie *et al.* 2002), they account for imperfect detection by using temporally or spatially replicated data collected in a time period during which populations are assumed to be geographically closed. As hierarchical models, they integrate data across species, permitting composite analyses of communities, species groups, and individual species (Russell *et al.* 2009; Zipkin, DeWan & Royle 2009). Sharing data across species leads to increased precision in estimates of species richness and species-specific occupancy, particularly for rare and elusive species (Zipkin *et al.* 2010). Multi-species hierarchical models can also be parameterized with variables hypothesized to influence the distributions of wildlife, allowing evaluation of how these variables affect wildlife communities, groups of species, or a species of concern (Russell *et al.* 2009).

The spatial ecology of wildlife is often shaped by human disturbance. Increasing human populations and the corresponding demand for land has resulted in land-use change, fragmentation, and infrastructure development being some of the greatest threats to biodiversity (Alkemade *et al*. 2009). One of the most prevalent forms of land-use change is conversion of wildlands to agriculture. Agricultural expansion has resulted in losses of 20–50% of forested land and 25% of grasslands globally (DeFries, Foley & Asner 2004). To combat the loss of wildlands and associated biodiversity, 12.7% of the Earth's land area has been designated as protected (Bertzky *et al*. 2012). The success of conserving biodiversity in these protected areas, however, is mixed (Western, Russell & Cuthill 2009; Craigie *et al*. 2010; Kiffner, Stoner & Caro 2013). In Kenya, for example, wildlife has declined at similar rates inside and outside of protected areas (Western, Russell & Cuthill 2009), whereas in Tanzania, species within protected areas fare better (Stoner *et al*. 2007). Land-use change may also lead to construction of artificial barriers such as roads and fences which can alter animal movements and fragment ecosystems (Forman & Alexander 1998; Hayward & Kerley 2009). The impacts of roads on wildlife vary widely, with increased human and vehicle activity often leading to increases in road mortality, edge effects, and both legal and illegal hunting pressure (Forman & Alexander 1998). The impact of fences, in contrast, depends on the type of fence and purpose (Hayward & Kerley 2009). Fences can minimize threats from humans and domestic animals but if erected with little regard to wildlife movements, the result can be mass-mortality of migrating ungulates (Hayward & Kerley 2009).

The spatial ecology of wildlife is also shaped by environmental features such as access to water, food availability, and vegetation cover. For example, occupancy of mammals often declines with increasing distance to permanent water (Pettorelli *et al*. 2010; Epps *et al*. 2011;

Schuette *et al*. 2013). Mesic habitats such as seasonal floodplains, however, tend to be

characterized by relatively tall, less nutritious grass species (Hopcraft *et al*. 2012), which could

result in grazing species preferring areas further from permanent water. The influence of

vegetation cover, alternatively, is likely to be species-specific (Estes *et al*. 1991). Within the

African carnivore guild, for example, black-backed jackals *Canis mesomelas* often avoid

floodplains and grasslands (Kaunda 2001) whereas servals *Leptailurus serval* prefer these land

covers (Pettorelli *et al*. 2010; Schuette *et al*. 2013).

A species' response to ecological variables may also be influenced by their life-history

traits. Theory suggests, for example, that larger-bodied species in trophic groups at the top of the

food chain (e.g. large carnivores) are more likely to decline than lower trophic guild species

under similar conditions (Gaston & Blackburn 1996; Davies, Margules & Lawrence 2000). Life-

history characteristics of species at high trophic levels, including low population densities, high

food requirements, and large home ranges, make them particularly vulnerable to persecution and

fluctuating environments (Gard 1984; Ripple *et al*. 2014). Large-bodied animals are also

targeted by trophy hunters (Packer *et al*. 2009) and bushmeat hunters (Fa, Ryan & Bell 2005).

Consequently, we would expect large-bodied species near the top of the food chain to show

greater sensitivity to anthropogenic and environmental changes.

In this study, we explore the utility of camera trap surveys and multi-species hierarchical

models to inform biodiversity management. We applied our multi-species approach to a

community of mammals in the Okavango Delta, Botswana – a World Heritage Site that is home

to abundant wildlife including some of Africa's most endangered mammals. Better

understanding of the spatial ecology of the mammal community will allow managers to more

fully balance gains against losses when managing the diversity of wildlife (Western *et al*. 2009;

Zipkin *et al*. 2009). Additionally, our research was motivated by the lack of broad-scale wildlife community studies. Community-level studies generally focus on a particular guild of species such as carnivores (Pettorelli *et al*. 2010; Schuette *et al*. 2013) or ungulates (Stoner *et al*. 2007; Western, Russell & Cuthill 2009; Kiffner, Stoner & Caro 2013). Our study is among the first to evaluate the distributions of all terrestrial mammals >0.5 kg, excluding rodents.

Our specific objectives were to quantify species richness, evaluate species' distributions, and elucidate community, group, and species-specific responses to human disturbance and environmental variables. We hypothesized: (i) species richness, group richness, and species-specific occupancy would be inversely related to human disturbance with large-bodied wildlife and carnivores expected to show the strongest relationships (Epps *et al*. 2011; Hopcraft *et al*. 2012; Schuette *et al*. 2013) and (ii) environmental conditions related to occupancy, in comparison with human disturbance, would be unique to each species and have weaker community and group-level effects. Our research aims to provide a better understanding of how environmental features and anthropogenic pressures are impacting species' distributions in southern Africa. Additionally, our analysis framework is applicable to the growing number of camera trap studies worldwide and could be applied to various land use related activities including mapping areas of high conservation value, predicting the effects of human development, and providing guidance for management strategies aimed at sustaining biodiversity.

Materials and methods

Study area

Our study was carried out in Ngamiland District of Northern Botswana, where the Okavango Delta and the northern reaches of the Kalahari Desert are located. The area (ca 550 km^2; 19˚31′S 23˚37′E) included a mixture of floodplains/grasslands, acacia woodland savannas, mopane *Colophospermum mopane* shrub and woodlands, and mixed shrublands. Our study site included the eastern section of Moremi Game Reserve, wildlife management areas NG33/34, and part of the livestock grazing areas of Shorobe (Fig. 2.1). Wildlife was fully protected within Moremi Game Reserve and partially protected within the wildlife management areas under a policy known as community-based natural resource management (Mbaiwa, Stronza & Kreuter 2011). Both areas were primarily used for photographic tourism. Moremi, however, was open to self-drive tourists and safari companies whereas the wildlife management areas were only accessible to Sankuyo community members and safari companies with leases in the area. Consequently, the game reserve had higher human activity ($\bar{x}$ = 6 vehicles per day per camera station) than the wildlife management areas ($\bar{x}$ = 2 vehicles per day per camera station). The wildlife management areas were separated from adjacent livestock grazing areas by an extensive 1.3-m high cable veterinary fence that was erected to prevent the transmission of foot-and-mouth disease from Cape buffalo *Syncerus caffer* to cattle (Keene-Young 1999). The fence aids in minimizing the impacts of human disturbance within the protected areas by helping to constrain livestock and humans to the livestock grazing areas. Carnivores and other wildlife species, however, commonly pass through the fence (Keene-Young 1999). Wildlife within the management and livestock areas could be legally killed when the animal posed a threat to human life or property (Republic of Botswana Conservation and National Parks Act 2001).

Camera trap survey

We deployed Panthera v4 incandescent-flash and Bushnell TrophyCam infra-red camera traps at 221 locations across our 550-km^2 study area between February and July 2015 (Fig. 2.1). We used 5-km^2 grid cells to guide the placement of cameras. To increase our probability of photographing wildlife, we placed cameras on sand roads because wildlife species including large predators, carrion feeders, and small mammals often use lightly-travelled roads as movement corridors (Forman & Alexander, 1998). We deployed two camera stations within each grid cell, one on the road closest to the predetermined centre point of each grid cell and the second on the road closest to a predetermined random point within each grid cell. We used a rotational system for camera deployment. We divided our study area into five, ~110 km^2 sub-areas and sequentially sampled each area for 30 nights. We deployed an average of 44 camera stations (i.e. 88 cameras) within each sub-area.

Each camera station included two opposing cameras mounted on trees. If there were no trees available, we mounted cameras on metal fence posts hammered into the ground. We secured cameras at knee height and positioned cameras to photograph flanks of passing animals. We programmed cameras to take three photos when triggered in the day with a delay of 30 seconds between photo events. At night-time, the infra-red cameras took three photos when triggered but the flash cameras could only take one photo every 15 seconds due to the flash having to re-charge. We checked cameras every 5–10 days to download photos, replace batteries, and ensure cameras were operational.

Covariates

We hypothesized the spatial distributions of wildlife may be influenced by two measures of human disturbance: human/vehicle capture rate and distance into the wildlife area. We did not

include distance to human development as the majority of human development was concentrated in the livestock area. To calculate human/vehicle capture rate, we determined the mean number of photo events of humans travelling by foot, donkey, horse, and vehicles per trap night for the respective camera station. Next, in ArcMap 10.3.1 (ESRI, CA, USA), we calculated distance into the wildlife area as the distance (km) from each camera station to the veterinary fence that separated wildlife and livestock areas. For camera stations within the livestock area, we gave distances a negative value to reflect how far removed they were from the wildlife area.

In addition to human disturbance, we hypothesized environmental variables including vegetation cover and distance to water may influence spatial distributions of wildlife. To quantify vegetation cover, we used a habitat map created by Bennitt, Bonyongo & Harris (2014). The dominant vegetation cover included floodplains/grasslands and mopane shrub and woodlands. For each of these vegetation covers, we calculated percentage cover within a 1-km buffered area surrounding each camera station. A 1-km buffer size provides information on the general conditions surrounding the camera station applicable to our suite of variably sized species. Floodplains/grasslands and mopane were highly correlated (Pearson $r = -0.76$) so we only retained floodplains/grasslands for our analyses. We estimated distance to water by calculating the distance (km) from each camera station to the nearest permanent water source including rivers, ponds, lagoons, and large pans. We were unable to account for seasonal water sources.

Finally, we hypothesized human/vehicle capture rate, road density, and vegetation density may influence a species' probability of being photographed. To calculate road density, we georeferenced all roads and calculated road density for the area immediately surrounding each camera station (i.e. 250-m buffered area) in ArcMap. To measure vegetation density

around camera stations, we took two photographs at knee height, pointed at 90º and 270º in relation to the road. We took these photos at the camera station, 50 m up the road and 50 m down the road for a total of six photos per station. We then digitally placed a 13×15 grid over each photo and counted the number of grid cells that were $\geq 50\%$ covered by forbs, shrubs, or trees. We divided this count by the total number of grid cells and used the mean value across the six photos as our estimate of vegetation density for the respective camera station.

Modeling framework

We used multi-species hierarchical occupancy modelling (Dorazio & Royle 2005) to estimate the probability species i occurred within the area sampled by a camera station during our survey period (i.e. occurrence), while accounting for incomplete detection (MacKenzie *et al*. 2002). Specifically, we defined occurrence, $z_{i,j}$, as a binary variable where $z_{i,j} = 1$ if camera station j was within the range occupied by species i and 0 otherwise. We assumed $z_{i,j}$ was a Bernoulli random variable, $z_{i,j} \sim \mathrm{Bern}(\psi_{ij})$, where ψ_{ij} is the probability that species i occurred at camera station j. Distinguishing the true absence of a species from the non-detection of a species (i.e. species present but not photographed) requires spatially or temporally replicated data. We treated each trap day as a repeat survey at a particular camera station resulting in ~30 sampling occasions per camera station. We estimated the probability of observing species i at camera station j on trap day k conditional on the site being occupied as $x_{i,j,k} \sim \mathrm{Bern}(p_{i,j,k} * z_{i,j})$ where $p_{i,j,k}$ was the detection probability of species i at camera station j during trap day k, given species i was truly present at camera station j (MacKenzie *et al*. 2002).

We incorporated site-level characteristics affecting species-specific occurrence and detection probabilities using a generalized linear mixed modelling approach (Dorazio & Royle

2005; Russell *et al*. 2009). We followed the protocol of Zipkin, DeWan & Royle (2009) and

Zipkin *et al*. (2010) of fitting a single model with a limited number of covariates for which there

was a strong *a priori* justification. The occurrence probability for species *i* at camera station *j*

was specified as:

$$\text{logit}(\psi_{ij}) = \alpha 0_i + \alpha 1_i(\text{human/vehicle trap rate})_j + \alpha 2_i(\text{wildlife area})_j + \alpha 3_i(\text{floodplains/grasslands})_j$$

$$+ \alpha 4_i(\text{water})_j,$$

and detection probability as:

$$\text{logit}(p_{ij}) = \beta 0_i + \beta 1_i(\text{road density})_j + \beta 2_i(\text{vegetation density})_j + \beta 3_i(\text{human/vehicle trap rate})_j$$

We standardized all covariates to have a mean of 0 and standard deviation of 1. Therefore, the

inverse logit of $\alpha 0_i$ and $\beta 0_i$ are the occurrence and detection probabilities, respectively, for

species *i* at a camera station with average covariate values. Remaining coefficients ($\alpha 1_i$,.., $\alpha 4_i$,

and $\beta 1_i$,..,$\beta 3_i$) represent the effect of a one standard deviation increase in the covariate value for

species *i*. A species' abundance can significantly affect detection probabilities, often resulting in

strong, positive correlations between occupancy and detection (Royle & Nichols 2003). As a

result, we modelled among species correlation (ρ) between $\alpha 0_i$ and $\beta 0_i$ by specifying the two

parameters to be jointly distributed (Dorazio & Royle 2005; Kéry & Royle 2008).

   We linked species-specific models using a mixed modelling approach. We assumed

species-specific parameters were random effects derived from a normally distributed,

community-level hyper-parameter (Zipkin *et al*. 2010). Hyper-parameters specify the mean

response and variation among species within the community to a covariate (Kéry & Royle 2008).

Specifically, for our community model, the α coefficients were modelled as $\alpha_i \sim \text{normal}(\mu_\alpha, \sigma^2_\alpha)$

where μ_α is the community-level mean and σ^2_α is the variance (Chandler *et al*. 2013). We also

hypothesized body size and diet may influence how a species responds to the respective

covariates. Thus, we divided species into body size groups based on mean body mass for males

and females (Estes 1991). Groups included extra-large ($\geq$ 200kg), large (50–200kg), medium

(20–50kg), and small ($<$ 20kg) sized species (see Appendix 2.A in Supporting Information). The

diet groups included carnivores, herbivores, and omnivores (Estes 1991). To assess group-level

effects, we allowed α coefficients to be species-specific and governed by a group-level and

community-level hyper-parameter. For our group models, α coefficients were modelled as

functions of the community-level mean, group-level mean (body size or diet group), and species-

specific effect for the respective covariate.

We estimated posterior distributions of parameters using Markov chain Monte Carlo

(MCMC) implemented in JAGS (version 3.4.0) through program R (R2Jags; Plummer 2011).

We generated three chains of 50 000 iterations after a burn-in of 10 000 and thinned by 50. For

priors, we used a uniform distribution of 0 to 1 on the real scale for $\alpha 0_i$ and $\beta 0_i$ and uniform from

0 to 10 for σ parameters. We used a normal prior distribution with a mean of 0 and standard

deviation of 100 on the logit-scale for the remaining covariate effects ($\alpha 1_i$,.., $\alpha 4_i$ and $\beta 1_i$,..,$\beta 3_i$).

We assessed convergence using the Gelman-Rubin statistic where values $<$1.1 indicated

convergence (Gelman *et al*. 2004).

During each iteration, the model generates a matrix of camera station and species-specific

z values (i.e. an occupancy matrix) where as previously stated, $z_{i,j} = 1$ if camera station j was

within the range occupied by species i and 0 otherwise. To estimate species richness at camera

station j, we summed the number of estimated species (i.e. instances where $z_i = 1$ for camera

station j) during iteration x. We then repeated this process for each of the 50 000 iterations and

used these values to generate a probability distribution representing camera station-specific

species richness (Zipkin *et al*. 2010). We calculated group-level richness similarly, the only

difference being that we restricted the estimate to species belonging to the respective group. As an example, the complete specification for the diet group model and how we calculated species and group richness is presented in Appendix 2.B.

Results

We recorded 8668 detections of 44 species of mammals during our 6607 trap nights. Body size groups included 12 small, 11 medium, 11 large, and 10 extra-large species (Appendix 2.A). Diet groups included 21 carnivores, 18 herbivores, and 5 omnivores (Appendix 2.A). Brown hyaenas *Hyaena brunnea* (n = 3) and cheetahs *Acinonyx jubatus* (n = 3) were photographed least often while African elephants *Loxodonta africana* (n = 1665) and impalas *Aepyceros melampus* (n = 900) were photographed most often.

Community-level and group-level summaries

Our camera station-specific estimates of species richness ranged from 8 (95% credible interval = 5–12) to 27 (95% CI = 24–32) unique species (Appendix 2.C), with a mean of 17 (95% CI = 14–20). Species richness was generally greater in the game reserve ($\bar{x}$ = 20, 95% CI = 17–24) and wildlife management area ($\bar{x}$ = 17, 95% CI = 14–21) than within the livestock grazing area ($\bar{x}$ = 13, 95% CI = 10–16). Overall, species had lower detection probabilities in areas with high road density, vegetation density, and human/vehicle trap rates (Table 2.1). Between the human disturbance variables, distance into the wildlife area had the largest impact on community-level species richness, with richness increasing as the camera station's distance into the wildlife area increased (Table 2.1; Fig. 2.2). This positive relationship was most evident for small species,

extra-large species, and herbivores (Table 2.2; Fig. 2.2). Mean richness of medium-sized species

(5–25 kg) and omnivores, conversely, increased in livestock areas (Table 2.2; Fig. 2.2).

Between the environmental variables, percentage cover of floodplains/grasslands had the

greater impact on community-level species richness, with richness generally increasing as

floodplain/grassland cover increased (Table 2.1; Fig. 2.2). Floodplains/grasslands had the

strongest influence on richness of large species followed by carnivores and omnivores, and the

weakest influence on richness of small species and herbivores (Table 2.2; Fig. 2.2). The richness

of all species groups were only weakly related to the camera station's distance from permanent

water (Table 2.1, 2.2). Among these relationships, distance to permanent water had the largest

influence on richness of extra-large species and omnivores with richness increasing close to

permanent water (Table 2.2). The 95% CIs for community-level and many group-level covariate

effects overlapped zero (Table 2.1, 2.2), suggesting high variability among species and species

groups. This result was not unexpected, given the diversity of species. Gelman-Rubin statistics

indicated convergence for all parameters.

Species-level summaries

The mean probability of occurrence across all species and camera stations was 0.32 (95% CI =

0.214–0.451) but this varied dramatically among species, ranging from 0.97 for elephants to 0.04

for brown hyaenas and cheetahs. Daily detection probabilities also varied greatly among species,

ranging from 0.01 to 0.27. Variation among species in occurrence and detection probabilities

was correlated, so that species occurring more widely were photographed on a greater proportion

of days at individual camera stations ($\rho = 0.39$, 95% CI = 0.126–0.882). Species-specific

estimates of occurrence, detection and covariate effects are presented in Appendix 2.A.

Of the 44 species photographed, 20 were significantly (i.e. 95% CI did not overlap zero) related to distance into the wildlife area (14 positively and 6 negatively) and 23 to percentage cover of floodplain/grassland (15 positively and 8 negatively; Fig. 2.3). In contrast, occurrence of only seven and one species were significantly related to the trapping rate of humans/vehicles and distance to permanent water, respectively (Appendix 2.A). As expected, precision of estimates was lower for species with limited numbers of detections, leading to diffuse posterior distributions for their estimates of covariate effects.

Discussion

Our research highlights the importance of protected areas and grasslands in maintaining biodiversity in southern Africa (Millenium Ecosystem Assessment 2005; Biggs *et al*. 2008; Craigie *et al*. 2010). We found overall species richness was generally greater in floodplains and grasslands and areas located further into protected wildlife areas (Table 2.1; Fig. 2.2). Our results support regional conservation initiatives focused on grasslands as this biome is vulnerable to future land-use pressures (Biggs *et al*. 2008) and benefits a broad diversity of species, including large-bodied animals that are often threatened by hunting pressure (Fa, Ryan & Bell 2005; Packer *et al*. 2009). Additionally, over a quarter of the world's grasslands have already been lost (DeFries, Foley & Asner 2004) and the remaining grasslands are threatened by woody encroachment (Ratajczak, Nippert & Collins 2012). Our results also highlight the importance of protected wildlife areas, particularly to small and large-bodied species, herbivores, and carnivores. While the effectiveness of protected areas is mixed (Western, Russell & Cuthill 2009; Craigie *et al*. 2010; Kiffner, Stoner & Caro 2013), we found livestock areas had lower levels of species richness and that species richness increased with distance into protected areas.

These results are consistent with the trend of agriculture growth and habitat loss functioning as primary threats to biodiversity worldwide (Millenium Ecosystem Assessment 2005).

In northern Botswana, wildlife and livestock areas are separated by the veterinary fence. The fence is positive in that in constrains livestock to the grazing areas, thus serving as an important tool in minimizing the negative impacts of human disturbance within the protected areas. The fence, however, is negative in that it is only permeable to some wildlife species (e.g. carnivores). When it was erected, for example, it cut-off migratory routes of wildebeests *Connochaetes taurinus* and zebras *Equus burchelli* and disturbed the movement patterns of additional ungulate species (Hayward & Kerley 2009). If the fence, as a physical boundary, was the underlying cause of increased species richness in wildlife areas, then we would expect species richness to be nearly constant between the core and edge of wildlife areas (Kiffner, Stoner & Caro 2013). Our results showing species richness increasing with distance from the fence, however, (Fig. 2.2) suggest other spatial factors such as land use and human–wildlife conflict (e.g. poaching and retaliatory killings) are likely to be contributing drivers of this edge effect (Woodroofe & Ginsberg 1998). Results presented here suggest management of human activities on both sides of protected area borders is essential for minimizing edge effects (Woodroffe & Ginsberg 1998).

The weak effects of human/vehicle trap rates and water accessibility on community-level species richness were surprising (Table 2.1). The human/vehicle trap rate results likely reflect that most of our study area was used by tourists or tourism operators, all of whom seek out areas with abundant wildlife. This human disturbance may have had minimal impact on nocturnal species given tourism activities were generally restricted to daylight hours (i.e. via Game Reserve permit rules). Distance to permanent water had a weak effect on species richness in this

study, in contrast with other studies in Africa (Pettorelli *et al*. 2010; Epps *et al*. 2011; Schuette *et al*. 2013). We found wildlife to be more evenly distributed across the landscape in relation to water availability perhaps because (i) our study took place during the end of the wet season and beginning of the dry season when water was less of a limiting resource, (ii) we were unable to account for ephemeral water sources and (iii) selection of high quantities of grass in wet areas vs. grass with higher nutrition in dry areas is species-dependent (Hopcraft *et al*. 2012).

In addition to community-level effects, our multi-species approach allowed us to evaluate how specific groups of species were influenced by human and environmental factors. If managers wish to focus their efforts on conserving herbivores, for example, our research suggests protected areas and heterogeneity in vegetation types promote herbivore diversity. Similar to overall species richness, we found herbivore richness increased with distance into wildlife areas (Table 2.2; Fig. 2.2). The influence of grassland and floodplain cover, however, was highly variable (Fig. 2.2). Species that are predominantly grazers, such as zebras and impalas, were more likely to use grasslands and floodplains where their food source was abundant. We found small ungulates including steenbok *Raphicerus campestris* and bush duikers *Sylvicapra grimmia*, however, had a negative relationship with grasslands and floodplains. These small grazers may select for mixed shrub and mopane-dominated areas because they are adapted to selecting high-quality components of grass allowing them to forage in low biomass areas (Wilmshurst, Fryxell & Colucci 1999).

Our research can also be used to predict which groups of species or individual species would be most impacted by increasing levels of human disturbance in and outside of protected areas. As hypothesized, we found extra-large species like giraffes *Giraffa camelopardalis* and roan antelopes *Hippotragus equinus* were most sensitive to human disturbance where the

probabilities of using an area increased with distance into the wildlife area (Table 2.2, Fig. 2.2).

The groups of species that would likely be unaffected or positively affected by increasing levels

of human disturbance were omnivores and medium-sized species (Fig. 2.2), such as the African

civet *Civettictis civetta* and jackal species (Fig. 2.3). Medium-sized omnivores tend to be

generalists that can use a wide array of landscapes and thrive even after extensive human

modification (Roemer *et al*. 2009).

Reliable methods for evaluating biodiversity are key to making informed conservation

and management decisions (Pettorelli *et al*. 2010; Zipkin *et al*. 2010). Equally important is the

need to understand how top–down (e.g. humans) and bottom–up (e.g. vegetation cover) factors

influence diversity (Elmhagen & Rushton 2007). Our research demonstrates the utility of

camera trap surveys and hierarchical models for assessing community, group, and individual

species' responses to both anthropogenic and environmental variables. Our study did, however,

have some potential limitations. First, our sequential sampling of sub-areas may have violated

the model's assumption of geographic closure (MacKenzie et al. 2002). A simulation study

based on estimated occupancy and detection probabilities from our pilot season, however, found

this sampling design balanced precision of occupancy estimates with survey effort. Second,

because we only included camera station-specific covariates, we were unable to account for

species-specific measures of predation and competition, which are known to influence species'

distributions (Caro and Stoner 2003). Lastly, we sampled on sand roads to maximize detection

probabilities (Forman and Alexander 1998). If cameras had been placed randomly, we believe

the photographic rates of many wildlife species, particularly carnivores, would have been

prohibitively low. However, if any species avoided roads, then our sampling design may have

resulted in their true occupancy being underestimated.

Our multi-species approach provides a method for using detection/non-detection data to estimate and evaluate species' occupancy and richness that should reduce money, time, and personnel costs, which are critical for many management agencies across the world where field data funding is limited (Zipkin *et al.* 2009). Camera trap surveys are an ideal field method for community studies on terrestrial species because they photograph every species that passes in front of them. Few studies, however, capitalize on this wealth of community information as attention is typically focused on a single species or guild of species (Stoner *et al*. 2007; Pettorelli *et al*. 2010; Schuette *et al*. 2013). Unlike traditional community analyses, our multi-species approach allowed us to retain species identity while properly accounting for multiple sources of uncertainty (Kéry & Royle 2008; Zipkin *et al*. 2010). Many of the species in our study had low detection probabilities which, if left unaccounted for, would have resulted in underestimates of species richness and affected estimates of our ecological variables (Zipkin *et al*. 2010). Additionally, our multi-species approach allowed us to integrate data across species using the community-level hyper-parameter (Dorazio & Royle 2005; Russel *et al*. 2009; Zipkin, DeWan & Royle 2009). This permitted us to complete a comprehensive assessment of all wildlife species and resulted in increased precision of species-specific occupancy probabilities, particularly for species that were rarely photographed. We suggest that broader application of this approach to camera trap studies worldwide will likely result in a more comprehensive and efficient use of available data and a better understanding of the spatial ecology of all species within the terrestrial wildlife community.

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Table 2.1. Mean ($\bar{x}$) and 95% credible interval (95% *CI*) estimates of the community-level hyper-parameters hypothesized to influence the probability of use (α) and detection (β) of 44 mammal species in northern Botswana, 2015

Community-level hyper-parameter		$\bar{x}$	95% *CI*	
$\alpha 1_i$	Human/vehicle trap rate	0.19	-0.049	0.489
$\alpha 2_i$	Dist. into wildlife area	0.27	-0.002	0.547
$\alpha 3_i$	Floodplain/grassland	0.16	-0.142	0.439
$\alpha 4_i$	Dist. to permanent water	-0.02	-0.133	0.092
$\beta 1_i$	Road density	-0.06	-0.142	0.015
$\beta 2_i$	Vegetation density	-0.16	-0.247	-0.066
$\beta 3_i$	Human/vehicle trap rate	-0.05	-0.134	0.019

Table 2.2. Mean ($\bar{x}$) and 95% credible interval (95% *CI*) estimates of the group-level hyper-parameters hypothesized to influence the probability 44 mammal species used the area sampled by our camera stations in northern Botswana, 2015. Body size groups included small (S = < 5 kg), medium (M = 5–25 kg), large (L = 25–200 kg) and extra-large (XL = ≥ 200 kg) species and diet groups included omnivores (Omn), carnivores (Carn) and herbivores (Herb).

Body Size Group				Diet Group			
Group	$\bar{x}$	95% *CI*		Group	$\bar{x}$	95% *CI*	
Human/vehicle trap rate							
S	0.46	-0.035	1.127	Omn	0.59	-0.419	1.698
M	0.04	-0.472	0.659	Carn	0.38	-0.045	0.875
L	0.40	-0.112	1.067	Herb	0.02	-0.477	0.453
XL	-0.11	-0.831	0.441				
Distance into the wildlife area (km)							
S	0.36	-0.069	0.806	Omn	-0.43	-1.213	0.314
M	-0.31	-0.752	0.110	Carn	0.22	-0.166	0.582
L	0.21	-0.266	0.664	Herb	0.53	0.141	0.944
XL	0.90	0.410	1.398				
Floodplain/grassland (% cover)							
S	-0.07	-0.619	0.484	Omn	0.39	-0.444	1.244
M	0.18	-0.375	0.723	Carn	0.33	-0.111	0.751
L	0.64	0.052	1.220	Herb	-0.11	-0.575	0.333
XL	-0.17	-0.782	0.453				
Distance to water (km)							

S	0.16	-0.043	0.354	Omn	-0.27	-0.595	0.034
M	-0.09	-0.293	0.105	Carn	0.08	-0.090	0.247
L	-0.01	-0.220	0.223	Herb	-0.05	-0.216	0.133
XL	-0.19	-0.418	0.033				

Figure Captions

Figure 2.1. Our study area including the eastern section of Moremi Game Reserve, wildlife management areas NG33/34, and livestock grazing areas in Shorobe, Botswana.

Figure 2.2. Mean, site-specific estimates of overall species richness and the richness of diet and body size (small < 5kg, medium 5–25 kg, large 25–200 kg and extra-large ≥ 200 kg) groups of species in relation to (a) the camera station's distance into a protected wildlife area (negative values indicate camera was in a livestock area) and (b) grassland/floodplain cover. Camera trap survey took place in Ngamiland District, Botswana, 2015.

Figure 2.3. Standardized beta (specified as α in model) coefficients, and 95% credible intervals, for the influence of distance into the wildlife area (a) and floodplain/grassland cover (b) on the probability a species used an area during our camera trap survey in northern Botswana, 2015. Species are arranged in body size groups including small (< 5kg), medium (5–25 kg), large (25–200 kg) and extra-large (≥ 200 kg)

Figure 2.1.
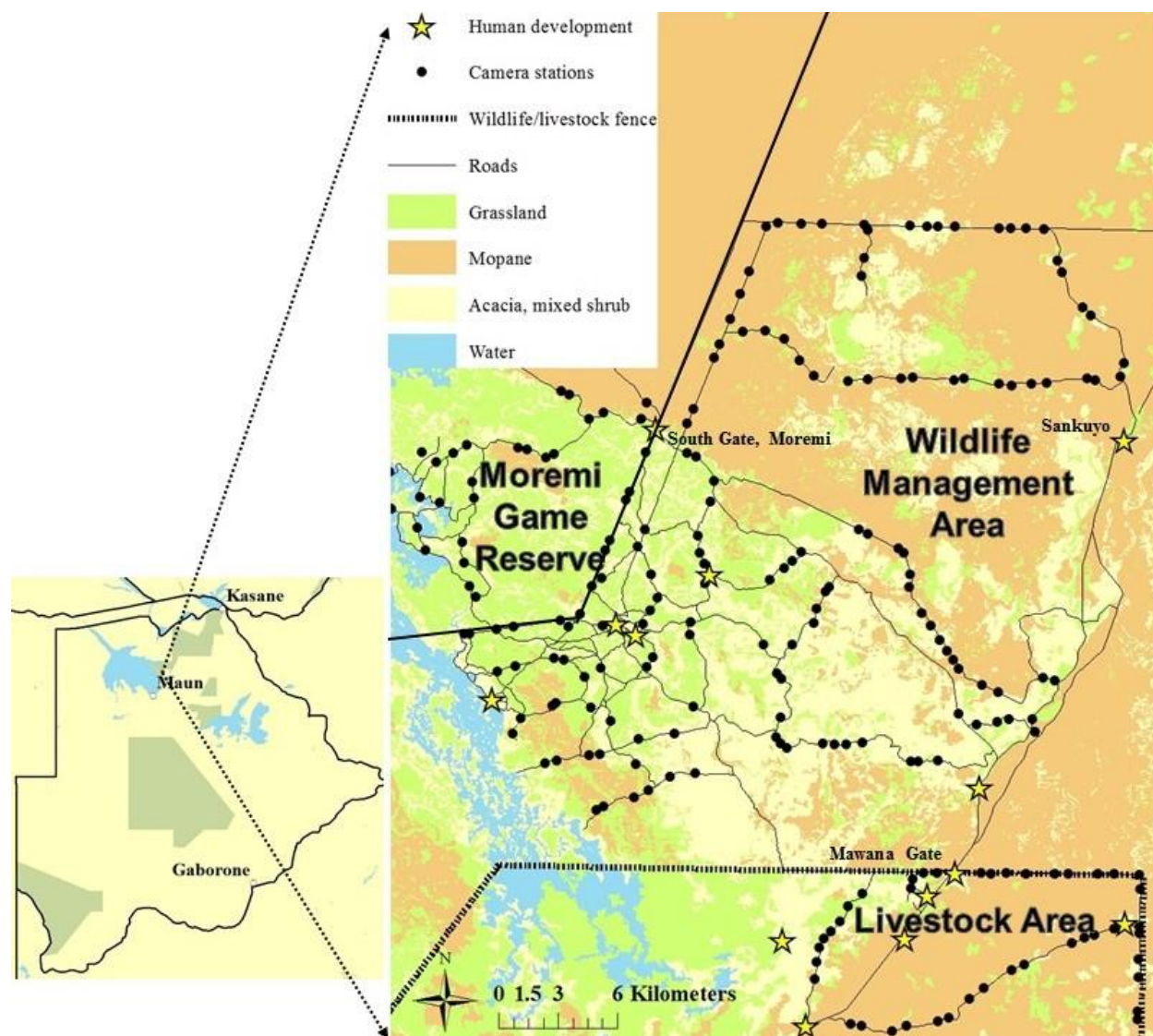
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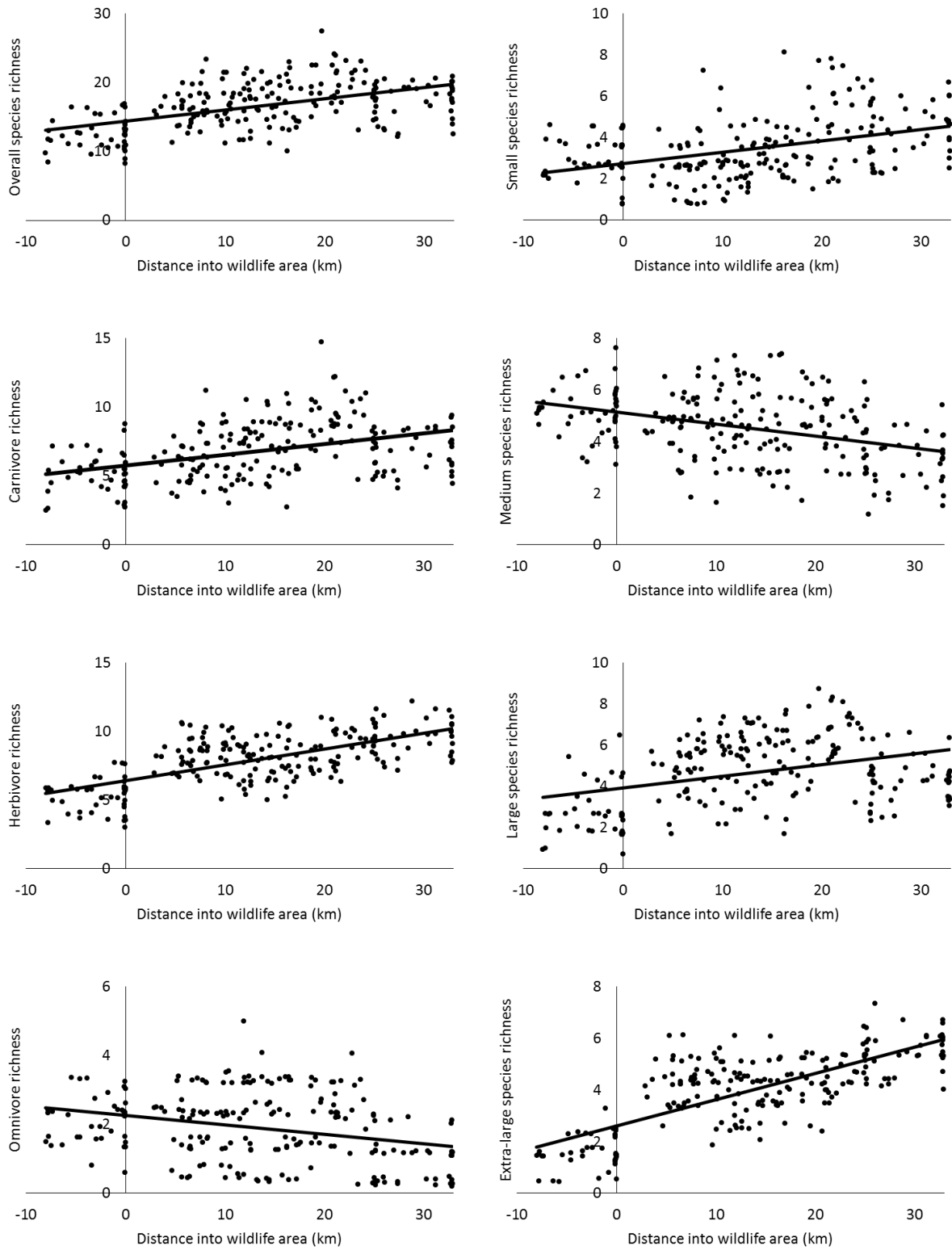
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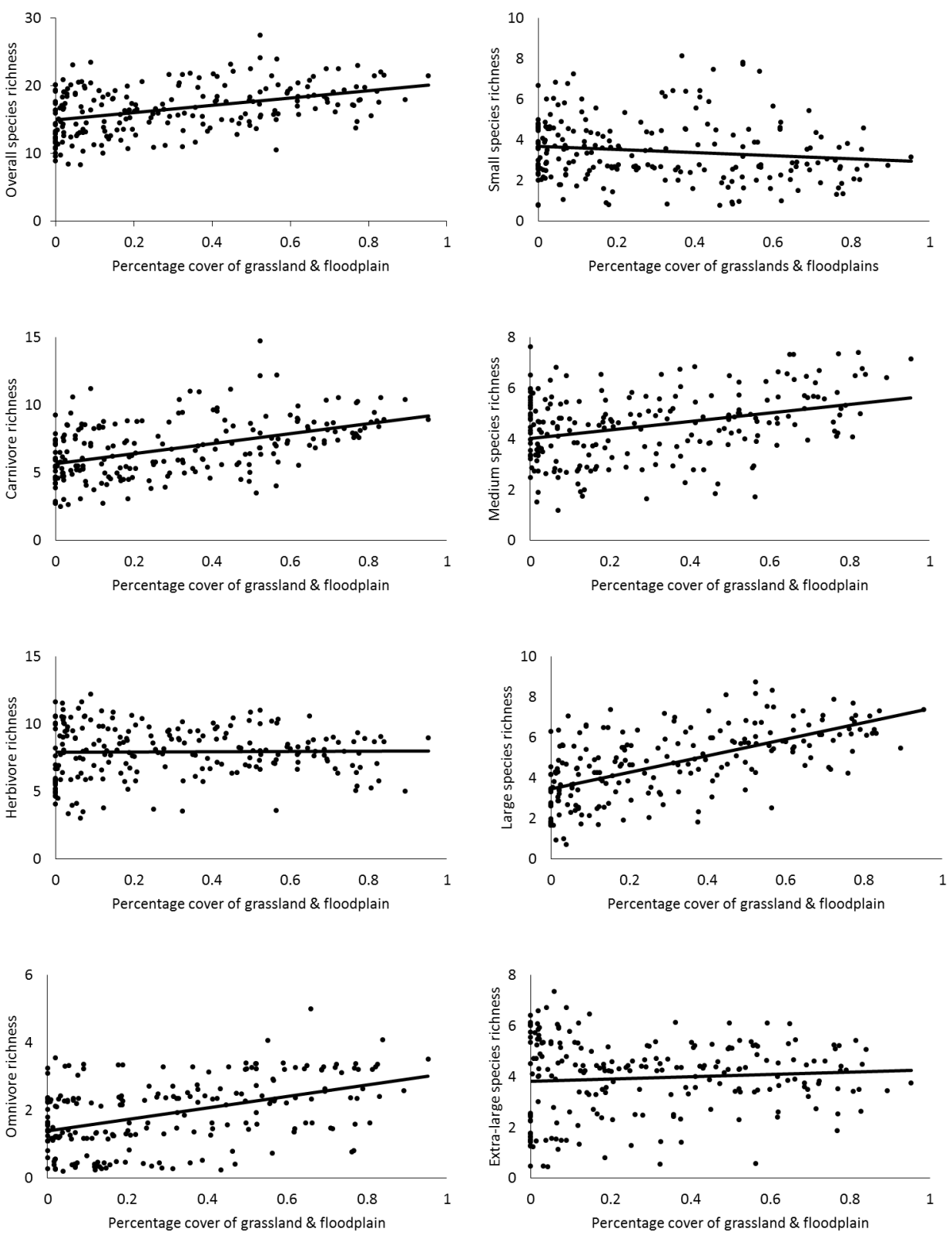
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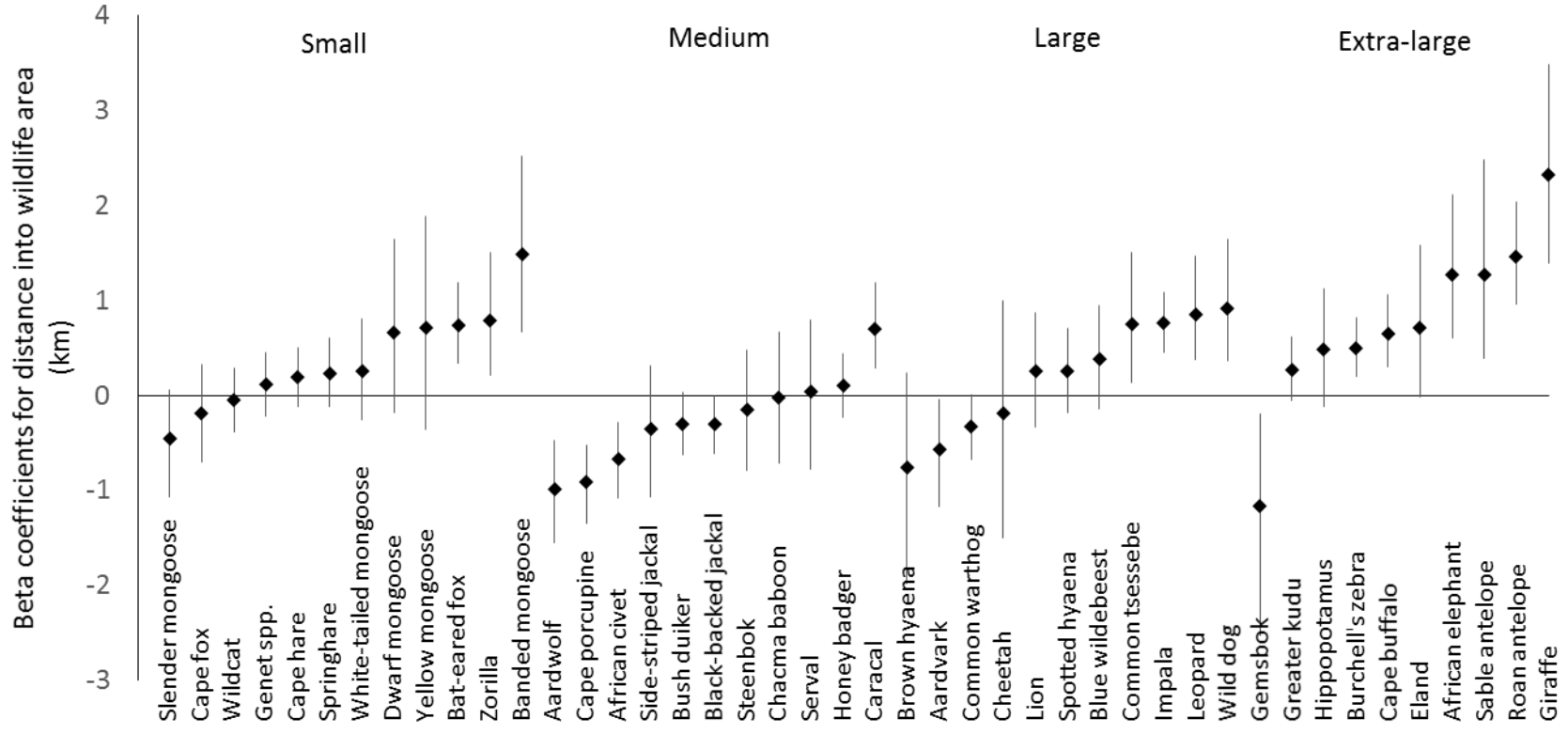
Figure 2.3b.
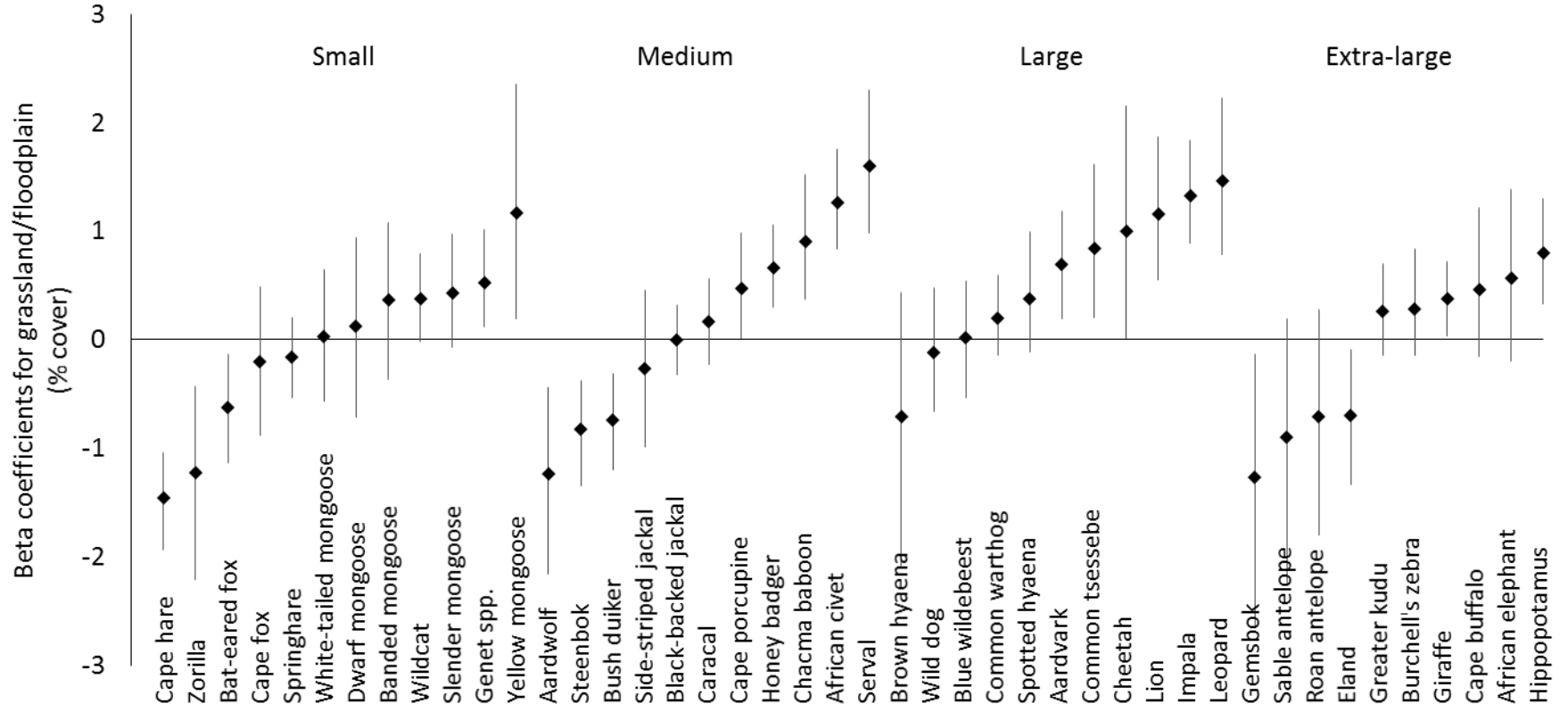
Supporting Information

Additional supporting information:

Appendix 2.A. Species-specific probabilities of occurrence, probabilities of detection and the effects of anthropogenic and habitat covariates.

Appendix 2.B. Hierarchical group model JAGS code.

Appendix 2.C. Camera station-specific estimates of species richness, including overall community, carnivore, omnivore, herbivore, small (< 5kg), medium (5–25kg), large (25–200kg), and extra-large (>200kg) species richness.

III. CARNIVORE DISTRIBUTIONS IN BOTSWANA SHAPED BY RESOURCE AVAILABILITY AND THE PRESENCE OF INTRAGUILD COMPETITORS/PREDATORS

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Abstract

The compositions of ecological communities are shaped by the interplay between interspecific

interactions and species' habitat and food requirements. The influence of interspecific

interactions is particularly widespread within carnivore guilds, where species must balance the

trade-off between resource acquisition and potentially costly encounters with intraguild

competitors/predators. We tested whether the presence of intraguild species or resource

availability had a larger influence on the seasonal distributions of 10 carnivore species in

northern Botswana. Specifically, we deployed 132 camera stations across a 330 km^2 area during

the 2014 dry season and 2015 wet season. For each species and season, we developed

occupancy models based on resource availability (i.e., prey, vegetation, and water) and on

intraguild species (i.e., photographic detection rates of intraguild competitors and predators). We

then used k-fold cross-validation to assess the relative predictive ability of each model.

Carnivore distributions were generally negatively associated with dense vegetation and contrary

to expectations, positively associated with the detection rate of intraguild species. This suggests

competitor/predator avoidance did not play a large role in shaping the carnivore community in

northern Botswana, which differs from other systems, and may be attributed to differences in

habitat, carnivore densities, and prey availability. The predictive ability of our resource

availability vs. intraguild species models differed between seasons and among species. Leopard

distributions, for example, were best predicted by resource availability during the dry season and

by the presence of intraguild species in the wet season. The majority of seasonal distributions

were best predicted by the presence of intraguild species or a combination of both resource

availability and intraguild species. As environments continually change, studies similar to ours

are pertinent as they can be used to monitor distributions of wildlife communities and to better

understand the relative importance of the diversity of ecological processes impacting wildlife communities.

Key words: camera trap, carnivore, community dynamics, intraguild species, occupancy modeling, seasonal distributions

Introduction

Carnivore populations have declined globally due to increasing human populations, widespread habitat loss, and declining prey populations (Gittleman *et al.*, 2001; Ripple *et al*., 2014; Bauer *et al*., 2015). African wild dogs (*Lycaon pictus*), tigers (*Panthera tigris*), and lions (*Panthera leo*), for example, have each disappeared from >80% of their historical range (Ripple *et al*., 2014; Bauer *et al*., 2015). As the extent and quality of wildlife habitat erodes, information on the distributions of remaining carnivore populations is needed to facilitate informed conservation actions aimed at mitigating declines (Pettorelli *et al*., 2010). Such information is especially pertinent for mammalian carnivores as they are wide ranging, sensitive to environmental and land use changes, and generally exist at low densities, making them particularly vulnerable to local extinctions (Woodroffe & Ginsberg, 1998; Bauer *et al*., 2015).

The composition of carnivore communities is shaped by the interplay between competitive interactions, and species' habitat and food requirements (Rosenzweig, 1966; Holt, 1984). Competitive interactions, both direct (i.e., interference) and indirect (i.e., exploitative), are particularly widespread within the carnivore community, influencing individual behavior, population dynamics, and community structure (Rosenzweig, 1966; Palomares & Caro, 1999; Caro & Stoner, 2003). Typically, competition increases as carnivore species become more similar in habitat selection, diet, activity pattern, and body size (Rosenzweig 1966). Predation and interspecific killing (i.e., killing without eating), alternatively, are more likely among carnivore species with body sizes that differ by a factor of 2-5.4 and with overlapping diets (Donadio & Buskirk, 2006). The potential for intraguild interactions can result in spatial and temporal niche partitioning among species, with subordinate species often changing their habitat use to less optimal areas in an effort to minimize encounters with dominant species (Creel &

Creel, 1996; Durant, 1998; Berger & Gese, 2007). This can result in top predators matching the distributions of their prey, while subordinate predators balance the trade-off between resource acquisition and risk of aggression and kleptoparasitism from larger predators (Palomares & Caro, 1999; Heithaus, 2001). In East Africa, for example, cheetahs (*Acinonyx jubatus*) and wild dogs, both subordinate competitors, occurred in areas with lower prey densities than areas frequented by lions and spotted hyena (*Crocuta crocuta*), the dominant competitors (Creel & Creel, 1996; Durant, 1998).

When modeling intraguild interactions and community dynamics, it is also vital to account for species' decisions regarding habitat use, as habitat selection plays an important role in determining population dynamics and community structure (Brown, Laundré & Gurung, 1999; Heithaus, 2001). Prey density, for example, has been found to be a fundamental driver of carnivore densities and distributions (Carbone & Gittleman, 2002; Hayward, O'Brien & Kerley, 2007) as has water availability, with carnivore occupancy often increasing close to permanent water sources (Pettorelli *et al*., 2010; Epps *et al*., 2011; Schuette *et al*., 2013). Vegetation cover and productivity may also influence carnivore distributions, often due to its relationship with prey abundance (Pettorelli *et al*., 2005).

The mammalian carnivore community in northern Botswana is one of the most diverse and complex assemblages of carnivores in Africa (Gittleman *et al*., 2001; Caro & Stoner, 2003). The strength and frequency of interactions within this diverse carnivore guild likely varies based on resource availability, the respective species' resource requirements, and their rank within the intraguild dominance hierarchy (Rosenzweig, 1966; Palomares & Caro, 1999; Heithaus, 2001; Caro & Stoner, 2003). Seasonality may also play a role as the region has distinct wet and dry

seasons, resulting in pronounced differences in vegetation which in turn, can influence prey availability (Bartlam-Brooks, Bonyongo & Harris, 2011).

In this study, we tested whether the presence of intraguild species or resource availability had a stronger influence on the seasonal distributions of 10 carnivore species in northern Botswana. Specifically, for each species and season, we developed occupancy models based on variables pertaining to resource availability (i.e., prey biomass, vegetation cover, vegetation productivity, and water availability) and to the presence of intraguild species (i.e., detection rate of intraguild competitors and predators). We then used k-fold cross-validation to assess the relative predictive ability of each model. The presence of intraguild species may have a larger influence on carnivore distributions than resource availability if, for example, carnivores were avoiding intraguild competitors and predators through spatial partitioning (Durant, 1998; Berger & Gese, 2007). We expected the distributions of carnivores to have a stronger, negative association with the presence of dominant predators, as encounters with these species have a higher associated risk than encounters with competitors (Donadio & Buskirk, 2006). Resource availability, alternatively, may have a larger influence on carnivore distributions than intraguild species if, for example, resources were limited or the species was at the top of the dominance hierarchy. Overall, we predicted the distributions of large carnivores would be predominantly influenced by resource availability whereas the distributions of meso-carnivores would be influenced by both resource availability and the presence of intraguild species (Palomares & Caro, 1999; Heithaus, 2001). Our research aims to provide a better understanding of the relative importance of the diversity of ecological processes impacting wildlife communities.

Materials and methods

Study area

Our study was carried out in Ngamiland District of northern Botswana. The area (ca 550 km^2; 19˚31′S, 23˚37′E; elevation ca 950 m) included a mixture of floodplains/grasslands, acacia woodland savannas, mopane shrub (*Colophospermum mopane*) and woodlands, and mixed shrublands. Our study site included the eastern section of Moremi Game Reserve and parts of wildlife management areas NG33/34 (Fig. 3.1). Wildlife was fully protected within Moremi Game Reserve and partially protected within the wildlife management areas. Both areas were used for photographic tourism (i.e., no hunting or livestock grazing). The region has two distinct seasons, with rain (~300 – 600 mm/year) falling almost exclusively during the wet season which generally lasts from November to April.

Camera trap survey

We deployed Panthera v4 incandescent-flash and Bushnell TrophyCam infra-red camera traps at 132 locations across a 330 km^2 area between August and November 2014 (dry season) and again between February and May 2015 (wet season). We used 5-km^2 grid cells (i.e., 2.24 x 2.24 km) to guide the placement of cameras and ensure systematic coverage of the entire study area. We placed all cameras on sand roads to increase our probability of photographing carnivores given that large predators and carrion feeders often use lightly-traveled roads as movement corridors (Forman & Alexander, 1998). If cameras had been placed randomly or on the extensive network of game trails, we believe our detection rates would have been prohibitively low. We deployed two camera stations within each grid cell, one on the road closest to the predetermined center point of each grid cell and the second on the road closest to a predetermined random point within each grid cell. We used a rotational system for camera deployment to increase our spatial

coverage where we divided our study area into three, ~110 km^2 sub-areas and sequentially

sampled each area for 30 nights. We deployed an average of 44 camera stations (i.e., 88

cameras) within each sub-area.

Each camera station included two opposing cameras mounted on trees, offset by 0.5-1 m.

If there were no trees available, we mounted cameras on metal fence posts hammered into the

ground. We secured cameras at knee height and positioned the cameras to photograph flanks of

passing animals. We programmed cameras to take three photos at each trigger event in the

daytime with a delay of 30 seconds between trigger events. At nighttime, the infra-red cameras

took three photos when triggered but the incandescent-flash cameras could only take one photo

every 15 seconds due to the flash having to re-charge. For each station, we combined

information from the 2 opposing cameras using the time/date stamps on the photographs

Covariates

We hypothesized resource availability including relative prey availability, vegetative cover,

water, and vegetation productivity (i.e., Enhanced Vegetation Index- EVI) may influence the

seasonal occupancy patterns of carnivore species. We tested for correlations ($r > 0.6$) among

these covariates using Pearson correlation coefficients. To represent relative prey availability,

we used a species-specific surrogate. For each camera station, we estimated the kilograms of

prey biomass per trap night by multiplying the number of independent detections of a prey

species by its average adult body mass (based on Estes, 1991) and standardized this value by

sampling effort (i.e., number of days the camera station was active). Independent detections of a

prey species were defined as photo events separated by ≥30 minutes unless different individuals

could be distinguished (e.g., eight individuals in a single photo would be 8 events). We then

summed biomass values for each prey species of the respective carnivore to obtain our camera station and species-specific estimates of prey biomass. We included prey weighing < 5kg for African civets (*Civettictis civetta*), wildcats (*Felis silvestris*), and servals (*Leptailurus serval*), < 20 kg for black-backed jackals (*Canis mesomelas*), caracals (*Caracal caracal*), and honey badger (*Mellivora capensis*), < 100 kg for leopards (*Panthera pardus*), 10 – 60 kg for wild dogs, and ≥ 100 kg for lions and spotted hyenas. The prey species included for each carnivore were based on Estes (1991) and kill site data from the Botswana Predator Conservation Trust (unpublished data). We used this measure of relative prey availability, as compared to estimates of prey occupancy, because it provided more detailed information regarding how frequently a prey species used the area surrounding a camera station.

The dominant land covers found within our study area included open floodplains/grasslands and densely vegetated mopane shrub and woodlands. The two land cover types are negatively correlated so we only included one land cover type, mopane, in our analysis. We used a land classification map (Bennitt, Bonyongo & Harris, 2014) to calculate percent mopane cover within a 1km buffered area surrounding each camera station. A 1km buffer size provides information on the general conditions surrounding the camera station applicable to our suite of variably sized species. We estimated distance to water by calculating the distance (km) from each camera station to the nearest permanent water source. Lastly, we also included season-specific estimates of EVI. By measuring infrared reflectance, this satellite-derived measure provides information on the spatial and temporal distribution of vegetation productivity (Pettorelli *et al*., 2005). We downloaded monthly 30m resolution MODIS EVI data sets from the USGS and NASA land processes distributed active archive center (https://lpdaac.usgs.gov/). We

used the median values from August through October to represent the dry season and the median values from February through April for the wet season.

We also hypothesized the presence of intraguild species, as represented by the detection rate of intraguild competitors and predators, may influence the occupancy patterns of carnivore species. For each season and camera station, we standardized the number of independent detections (photo events separated by ≥30 minutes) of a carnivore species by sampling effort. For each of our study's target carnivores, we then summed the camera station-specific values for the intraguild species designated as competitors or dominant predators. Species that were similar in weight and diet were designated as competitors and species that were ≥ twice the size of the target carnivore were designated as dominant predators.

Finally, for detectability, we hypothesized that seasonal vegetation density and vehicle activity may influence a species' probability of being photographed (i.e. detection probability). To measure the vegetation density of the area immediately surrounding the camera station during each season, we took photographs at knee height, one pointed at 90º and the other at 270º in relation to the road. We took these photos at the camera station, 50m up the road and in 50m down the road. We then digitally placed a 13 x 15 grid over each photo and determined the proportion of grid cells that were ≥ 50% covered by forbs, shrubs, or trees and averaged this across the six photos as our estimate of vegetation density for the respective camera station. To represent human/vehicle activity, we determined the mean number of photo events of vehicles per trap night for the respective camera station.

Modeling framework

We fit standard single season, single species occupancy models in a Bayesian framework to estimate the seasonal distributions of all meso- and large carnivores in our study area (Dorazio & Royle, 2005; MacKenzie *et al.*, 2005). We treated each trap day as a repeat survey at a particular camera station, resulting in ~30 sampling occasions per camera station. We did not use a multi-season model because we wanted to limit the number of parameters and because our research was focused on occupancy probabilities, as compared to local colonization and extinction probabilities. We evaluated four models per species per season, a null (i.e., included detection covariates only), resource availability, intraguild species, and all-inclusive (i.e., all covariates combined) occurrence model. We limited our analysis to these four models given our objective was testing whether resource availability or the presence of intraguild species had a larger influence on the seasonal distributions of carnivores. Our resource availability occurrence (ψ) model for the respective species at camera station j was specified as:

$$\text{logit}(\psi_j) = \alpha 0 + \alpha 1(\text{prey availability})_j + \alpha 2(\text{mopane cover})_j + \alpha 3(\text{water})_j + \alpha 4(\text{EVI})_j$$

the intraguild species occurrence model was specified as:

$$\text{logit}(\psi_j) = \alpha 0 + \alpha 1(\text{competitors})_j + \alpha 2(\text{predators})_j$$

and the detection (p) model associated with all occurrence models was:

$$\text{logit}(p_j) = \beta 0 + \beta 1(\text{vegetation density})_j + \beta 2(\text{human/vehicle activity})_j$$

We standardized all covariates to have a mean of 0 and standard deviation of 1. Therefore, the inverse logit of $\alpha 0$ and $\beta 0$ are the occurrence and detection probabilities, respectively, for the species at a camera station with average covariate values. Remaining coefficients ($\alpha 1, \ldots, \alpha 2$ or $\alpha 4$ and $\beta 1$) represent the effect of a one standard deviation increase in the covariate value. .

We estimated posterior distributions of parameters using Markov chain Monte Carlo (MCMC) implemented in JAGS (version 3.4.0) through program R (R2Jags; Plummer, 2011).

We generated 3 chains of 100,000 iterations after a burn-in of 20,000 and thinned by 10. We

used non-informative priors including a uniform distribution of 0 to 1 on the real scale for $\alpha 0$ and

$\beta 0$ and uniform from 0 to 10 for standard deviation parameters. We used a normal prior

distribution with a mean of 0 and standard deviation of 100 on the logit-scale for the remaining

covariate effects. We assessed convergence using the Gelman-Rubin statistic where values <1.1

indicated convergence (Gelman *et al.*, 2004).

We used k-fold cross-validation to assess the relative predictive ability of each of the occupancy

models (Boyce *et al.*, 2002; Hooten & Hobbs, 2015). We divided the data into 5 randomly

chosen subsets; subsets (i.e., data from the same camera stations) were kept consistent for all

species- and season-specific analyses. We fit the occupancy model 5-times, each time leaving

out one of our data subsets and calculating total deviance for our set-aside data using our

parameter estimates from the leave-in data. The model (i.e., null, resource availability, intraguild

species, or combined) with the lowest summed deviance for all 5 subsets was considered to have

the best model fit.

Results

We photographed the 10 carnivore species included in our study 1,935 times during our 3,384

trap nights in the 2014 dry season and 1,768 times during our 3,949 trap nights in the 2015 wet

season (Fig. 3.2). With the exception of leopards, carnivores were photographed more often in

the dry season than in the wet or at similar rates between seasons (Fig. 3.2). Spotted hyenas

were photographed most often and servals least (Fig. 3.2). We found spotted hyenas were the

most widely distributed carnivores during both seasons ($\psi \geq 0.9$) whereas black-backed jackals

and servals had more restricted distributions ($\psi < 0.5$; Fig. 3.2). African civets and honey

badgers were the only species to show differences (i.e., 95% credible intervals, CI, did not overlap) in their estimated occupancy probabilities between seasons, with distributions becoming more restricted in the wet season (Fig. 3.2).

The direction and strength of covariate effects from our models pertaining to resource availability and the presence of intraguild species varied between seasons for many of the species (Table 3.1). Caracals and honey badgers, for example, had stronger, positive and negative associations with mopane cover, respectively, in the wet season. Among the covariates, mopane cover had a significant impact (i.e., 95% CI did not overlap zero) on the greatest number of species, with the majority of species being less likely to occupy mopane dominated habitats (Table 3.1). In contrast, the occupancy probabilities of most species were not influenced by relative prey availability (Table 3.1). Contrary to expectations, our intraguild species model revealed that carnivores were generally positively associated with intraguild species, particularly competitors (i.e., species that were similar in weight and diet; Table 3.1).

We found that species differed in which occurrence model best predicted the respective carnivore distribution (Table 3.2). During the dry season, our combined model best predicted the distributions of lions and spotted hyena. When comparing just the resource availability and intraguild species models, however, we observed a consistent pattern across large carnivore species where resource availability better predicted species' distributions than the detection rate of intraguild competitors and predators (Table 3.2). In contrast, during the wet season, the intraguild species model best predicted distributions of leopards, spotted hyenas and African wild dogs, where species were positively associated with the detection rates of intraguild competitors and predators (Table 3.2). Similarly, the relative influence of intraguild species and/or resource availability on the distributions of meso-carnivores varied between seasons. The

intraguild species model best predicted the distributions of the majority of meso-carnivores in the dry season while the combined model was generally the best predictive model in the wet season (Table 3.2).

Discussion

Coexistence and exclusion among intraguild carnivores can be influenced by dietary overlap and competitive ability relative to sympatric species (Durant, 1998; Heithaus, 2001; Donadio & Buskirk, 2006). Many community models of intraguild predation, however, ignore species' decisions regarding habitat use despite the important role resource availability plays in shaping intraguild interactions, population dynamics and community structure (Brown *et al*., 1999; Heithaus, 2001; Carbone & Gittleman, 2002). Our research examined the influence of both the presence of intraguild species and resource availability on the seasonal distributions of 10 carnivore species in northern Botswana. In Botswana, and elsewhere in Africa, many members of the diverse carnivore guild compete for similar prey species (Estes, 1991; Caro & Stoner, 2003; Hayward *et al*., 2007) resulting in a strong dominance hierarchy where larger members of the guild have been observed killing or harassing smaller members and stealing their kills (Caro & Stoner, 2003). Theory suggests this will result in the top predators matching the distributions of their resources while the subordinate predators balance the trade-off of resource acquisition and risk (Palomares & Caro, 1999; Heithaus, 2001). Temporal partitioning has been suggested as a mechanism for coexistence within the carnivore guild yet in our study area, large carnivores have extensive temporal overlap (Cozzi et al. 2012). Overall, our research found the majority of seasonal carnivore distributions were best predicted by either the detection rate of intraguild species or a combination of both resource availability and intraguild species. Contrary to theory, we found carnivores were generally positively associated with the presence of intraguild species

and that the wet season distributions of three top predators (i.e., leopards, spotted hyenas and African wild dogs) were best predicted by the detection rate (i.e., there was a positive association) of intraguild competitors and predators.

The generally positive associations we found among carnivore species differ from areas such as the Serengeti, where subdominant carnivores can be limited by and often times locally excluded from prey-rich areas by competition with dominant carnivores (Durant, 1998; Creel & Creel, 1996). Previous studies have found that the negative effects of intraguild predation are reduced in structured habitats (Janssen *et al*., 2007). For example, spotted hyenas are more likely to detect and steal wild dog kills in open areas where visibility is good than in thickly vegetated areas (Gorman *et al*., 1998). Thus, the divergent evidence of competitor/predator avoidance in the two systems may be attributed to extreme differences in habitat (i.e., the densely vegetated woodland savanna of the Okavango Delta versus the short grass plains of the Serengeti). The influence of intraguild competitors/predators has also been found to vary dependent on species' densities, with reduced rates of intraguild predation when species occur at low densities (Holt & Polus, 1997; Heithaus, 2001; Caro & Stoner, 2003). Therefore, we also suggest that differences between the two systems may be attributed to carnivore densities. Lion densities in the Serengeti, for example, average ~0.118 lions km^{-2} (Cusack *et al*., 2015), more than double that of our study area (~0.053 lions km^{-2}; Cozzi *et al*., 2013). Carnivore densities in our study area may be below the threshold at which competitor/predator avoidance begins shaping community structure (Holt & Polus, 1997; Palomares & Caro, 1999; Caro & Stoner, 2003). Lastly, the strength and frequency of intraguild interactions varies based on resource availability (Rosenzweig, 1966; Palomares & Caro, 1999; Heithaus, 2001; Caro & Stoner, 2003).

If prey resources were plentiful in our study area, the influences of intraguild competition and predation may have been minimized.

Inferring ecological interactions from our observed patterns of occupancy is challenging as other factors such as the placement of camera traps or our measure of prey availability could influence the observed patterns (MacKenzie *et al*., 2005). We sampled on sand roads to maximize detection probabilities (Forman & Alexander, 1998). If any species avoided roads, however, then our sampling design may have resulted in their true occupancy being underestimated. Our estimates of prey availability were based on prey detection rates from the camera trap surveys and were found to influence the distributions' of a small number of species when compared to photographic trapping rates of intraguild competitors and predators. This suggests detections of intraguild species did a better job representing the distributions of resources (e.g., prey) on the landscape than our estimated measure of prey availability as it is unlikely species actively sought areas occupied by other carnivores, with the possible exception of carrion feeding species (e.g., black-backed jackals and spotted hyenas). Our measure of prey availability did not account for the vulnerability of prey to predation or small mammals and insects, which are a critical part of many meso-carnivore diets (Estes, 1991). We recommend future studies better account for prey availability, potentially through independent field methods such as distance sampling and small mammal trapping, in order to improve model inferences.

In general, we found seasonal occupancy patterns of most carnivore species were influenced by a unique combination of resource availability and detection rates of intraguild species. Among the resources included, mopane cover had the largest influence on species' distributions where species were generally less likely to occupy areas dominated by mopane shrub and woodlands. This is consistent with previous studies reporting greater biodiversity of

African mammals in grassland savannas (Oindo & Skidmore, 2002; Rich *et al*., 2016). In contrast with previous studies (Pettorelli *et al*., 2010; Epps *et al*., 2011; Schuette *et al*., 2013), we found no evidence that permanent water was a significant predictor of carnivore distributions. This is likely because we were unable to account for smaller pans and seasonal, ephemeral water sources. Lastly, we found vegetation productivity, as measured by EVI, was negatively related to lion, honey badger, and wildcat occupancy in the dry season and black-backed jackal occupancy in both seasons. The negative association is likely because at high levels of productivity there is increased production of woody species which can result in reduced plant diversity and primary production of grass (Oindo & Skidmore, 2002). This, in turn, may result in lower occupancy of the many prey species that select for open grasslands and floodplains (Rich *et al*., 2016).

The composition of ecological communities is shaped by the interplay between competitive interactions and species' habitat and food requirements (Rosenzweig, 1966; Holt, 1984). Supporting this, our research found that close to half of the seasonal carnivore distributions were best predicted by models that accounted for both resource availability and the presence of intraguild species. The generally positive associations that we found among intraguild species suggests competitor/predator avoidance did not play a large role in shaping carnivore community structure in northern Botswana. In the future, however, this may change. As Botswana becomes hotter and drier and human development increases (Hulme *et al*., 2001), carnivore densities and vegetation structure will likely change, both of which could influence the strength of intraguild interactions (Holt & Polus, 1997; Gorman *et al*., 1998; Caro & Stoner, 2003; Janssen *et al*., 2007). As environments continually change, studies similar to ours are pertinent as they can be used to monitor distributions of wildlife communities and elucidate the

combined influences of resource availability and the presence of intraguild species. A comprehensive knowledge of how wildlife responds to dynamic ecosystems will enable managers to better predict how system changes may impact carnivore communities, leading to proactive instead of reactive management decisions and more informed conservation planning (Pettorelli *et al*., 2010).

Acknowledgments

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Table 3.1. Covariate effects and the corresponding standard errors on carnivore species' probabilities of occupancy during the dry season of 2014 (August – November) and wet season of 2015 (February – April) in Ngamiland District, Botswana.

	Species	Resource availability model				Intraguild interactions model	
		Mopane	EVI	Water	Prey	Competitors	Predators
DRY SEASON — Large carnivores	Leopard	-0.7 (0.72)	0.3 (0.53)	-0.3 (0.33)	1.1 (1.15)	1.2 (1.01)	0.5 (0.48)
	Lion	-2.2 (0.91) *	-1.1 (0.67) *	-0.9 (0.54)	0.5 (0.62)	-0.4 (0.27)	·
	Spotted hyena	0.9 (0.82)	0.2 (0.96)	-0.5 (0.59)	1.4 (1.21)	0.9 (0.74)	
	Wild dog	-1.3 (1.32)	0.8 (1.16)	-0.6 (0.99)	1.2 (2.79)	1.1 (1.01)	0.4 (1.20)
Meso-carnivores	BB jackal[a]	-1.0 (0.43) *	-2.1 (0.73) *	-0.5 (0.37)	0.0 (0.36)	1.0 (0.35)*	0.1 (0.24)
	Caracal	0.4 (0.32)	0.1 (0.34)	0.2 (0.35)	0.1 (0.27)	0.1 (0.35)	1.4 (0.77)*
	Civet	-1.3 (0.33) *	0.1 (0.29)	-0.3 (0.27)	0.0 (0.25)	-0.7 (0.41)*	0.6 (0.44)
	Honey badger	0.2 (0.58)	-1.0 (0.56) *	-0.7 (0.48)	2.2 (1.13) *	0.5 (0.39)	0.1 (0.37)
	Serval	-2.2 (0.61) *	-0.4 (0.39)	-0.8 (0.48)	-0.6 (0.34)	1.3 (0.53)*	0.6 (0.56)
	Wildcat	-0.3 (0.40)	-1.9 (0.64) *	2.3 (1.07) *	-0.1 (0.35)	1.5 (0.79) *	0.0 (0.29)

WET SEASON	**Large carnivores**	Leopard	-1.0 (0.88)	0.5 (0.84)	0.1 (0.81)	2.3 (2.32)	1.5 (1.65)	3.3 (1.47) *
		Lion	-2.3 (0.89) *	-0.8 (0.79)	0.3 (0.66)	2.3 (1.62) *	1.2 (1.21)	.
		Spotted hyena	0.0 (0.37)	0.1 (0.34)	-0.2 (0.38)	1.8 (0.84) *	2.2 (0.86) *	
		Wild dog	1.3 (1.20)	-0.8 (0.82)	1.5 (1.11)	1.7 (1.50)	0.2 (0.69)	1.3 (0.62) *
	Meso-carnivores	BB jackal[a]	-0.6 (0.28) *	-1.0 (0.28) *	1.1 (0.35) *	0.4 (0.28)	0.4 (0.23) *	0.1 (0.20)
		Caracal	0.9 (0.89) *	-0.5 (0.31)	-0.1 (0.52)	-0.1 (0.49)	0.2 (0.43)	-0.3 (0.29)
		Civet	-1.7 (0.35) *	-0.5 (0.29)	-0.5 (0.30)	0.1 (0.27)	1.5 (0.45) *	-0.1 (0.23)
		Honey badger	-0.7 (0.25) *	-0.1 (0.21)	0.1 (0.23)	-0.0 (0.22)	1.5 (0.45) *	-0.1 (0.23)
		Serval	-5.2 (4.63) *	-0.6 (1.20)	-0.8 (1.41)	4.5 (7.48)	3.9 (1.61) *	-0.2 (0.56)
		Wildcat	-0.3 (0.36)	0.3 (0.31)	0.2 (0.33)	0.8 (0.64)	1.5 (0.73) *	0.3 (0.31)

[a] BB jackal = black-backed jackal

*95% credible interval did not overlap 0.0

Table 3.2. Comparison of deviance statistics (Δ deviance, model with lowest deviance value has best model fit) for models used to predict carnivore occupancy (ψ) probabilities during the 2014 dry season and 2015 wet season in Ngamiland District, Botswana. We compared null (no ψ covariates), resource availability (ψ covariates = mopane, prey, water, EVI), intraguild interactions (ψ covariates = detection rate of intraguild competitors and predators), and combined (ψ covariates = all covariates) models.

		Large carnivores				Meso-carnivores					
		Leopard	Lion	Spotted hyena	Wild dog	Black-backed jackal	Caracal	African civet	Honey badger	Serval	Wildcat
2014 Dry Season	Null	6.03	35.89	4.22	0.00	2.13	0.56	8.82	1.45	8.55	1.35
	Resource availability	0.00	15.49	0.34	1.06	2.41	5.54	0.00	9.93	1.73	3.39
	Intraguild interactions	4.42	30.25	3.02	5.05	0.00	0.00	7.66	0.00	0.00	1.35
	Combined	0.38	0.00	0.00	4.99	8.45	6.58	12.80	29.69	5.17	0.00
2015 Wet Season	Null	1.91	7.22	5.85	1.89	21.61	1.51	40.93	13.69	80.95	5.85
	Resource availability	0.69	0.32	4.36	3.90	2.57	1.37	7.13	7.77	34.20	10.51
	Intraguild interactions	0.00	6.67	0.00	0.00	13.85	3.19	25.91	53.61	0.00	0.00
	Combined	0.25	0.00	0.24	0.22	0.00	0.00	0.00	0.00	25.56	8.56

Figure Captions

Figure 3.1. Our camera trap survey was carried out in the eastern section of Moremi Game

Reserve and wildlife management areas NG33/34, Botswana, 2014-2015.

Figure 3.2. Mean estimated probabilities of occupancy, corresponding 95% credible intervals,

and raw numbers of independent photo detections for meso- and large carnivores during camera

trap surveys in Ngamiland District, Botswana during the 2014 dry season and 2015 wet season.

Figure 3.1.
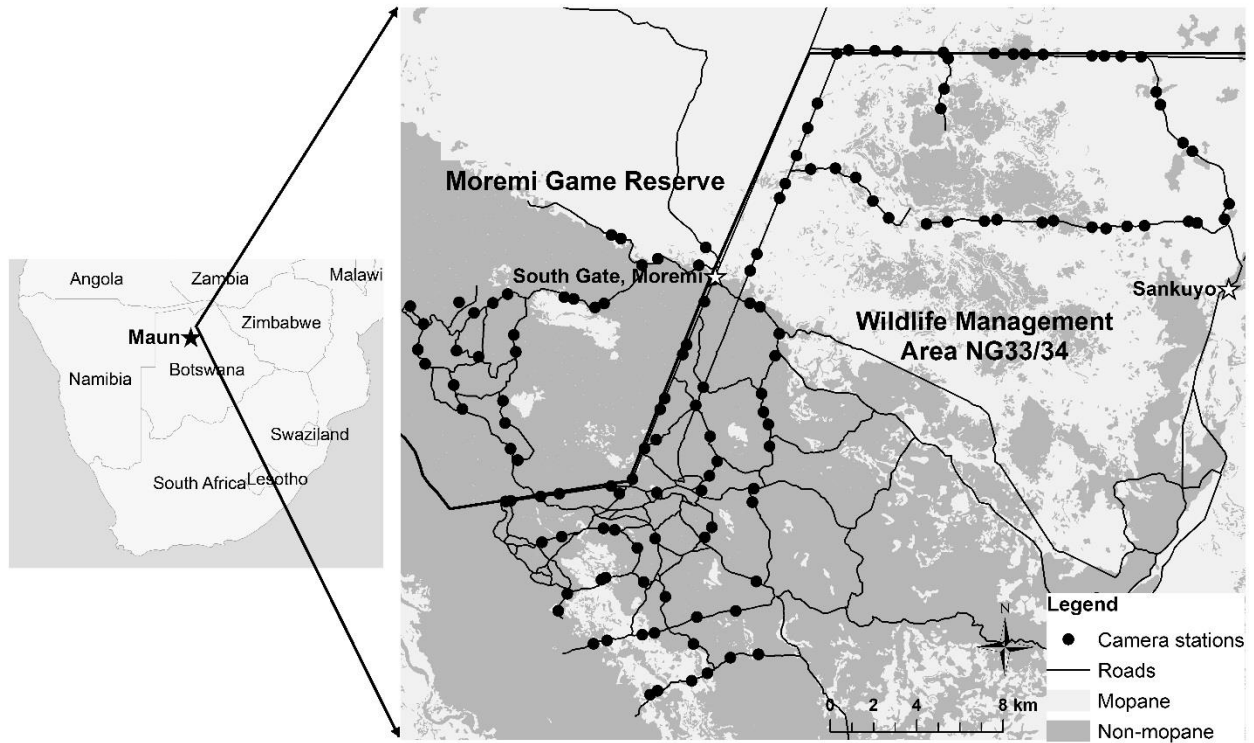
Figure 3.2.
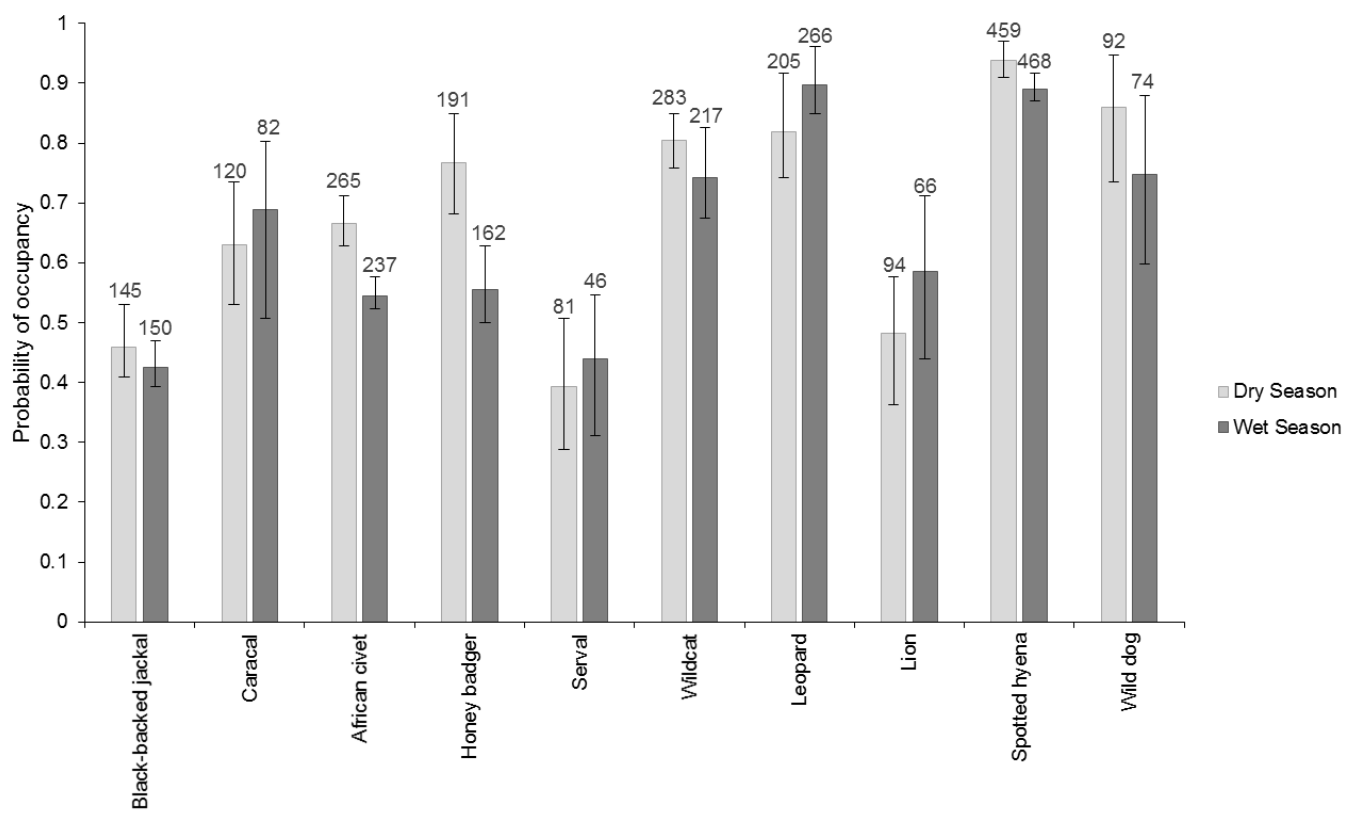
IV. MODELING DENSITIES OF SYMPATRIC SPECIES: A MULTISPECIES PHOTOGRAPHIC CAPTURE-RECAPTURE APPROACH

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Abstract

Abundance and density of wildlife populations are fundamental parameters needed for

management and conservation planning. Information on carnivore populations, however, is

often scarce due to their wide ranging and elusive nature. Camera trap surveys, in combination

with capture-recapture techniques, have consequently emerged as an increasingly common

method for estimating the density of carnivore species that have uniquely identifiable

individuals. Our research expanded this approach from single to multispecies assessments.

Specifically, we evaluated the utility of using a novel camera trap study design and newly

developed capture-recapture techniques for simultaneously estimating the population densities of

7 carnivore species in Botswana. We deployed camera traps at 221 locations across a 1,154-km^2

area. We sequentially rotated cameras through the study area to increase spatial coverage and

spaced cameras at a range of distances to recapture individuals at multiple camera stations and

adequately reflect movements of small to wide-ranging species. To estimate density for species

where a subset of the population was uniquely identifiable and species where every individual

was identifiable, we used, respectively, spatially explicit capture-recapture models with and

without unresolved sightings (i.e., photographs only identifiable to the species-level). Lastly, we

accounted for varying levels of habitat suitability by modeling density as a function of habitat,

specifically, whether the habitat was dominated by mopane shrub and woodlands. Our approach

allowed us to simultaneously generate estimates of density for 7 carnivore species with estimates

ranging from 1.8 aardwolves/100 km^2 to 12.7 spotted hyenas/100 km^2. Densities were generally

higher in non-mopane habitats than in mopane. Our research is the first to use a single camera

trap survey, designed to collect spatial capture-recapture information on a diversity of carnivores,

and newly developed spatial models to estimate densities of both fully- and partially-marked

species, while accounting for differential habitat use. Given the recent emergence of

conservation paradigms focused on sustaining biodiversity, progressing from single to

multispecies photographic capture-recapture assessments is timely. Additionally, broader

application of our approach to camera trap studies worldwide would likely result in a better

understanding of elusive carnivore communities which is critical to the conservation of the many

carnivore species experiencing population declines.

Key words: camera trap, carnivore, mark-resight, multispecies, population density, sampling

design, spatially explicit capture-recapture

Introduction

Abundance and density of wildlife populations are fundamental quantities in ecology as they are key, baseline parameters needed for management and conservation planning (Efford et al. 2009, Royle et al. 2009). Information on population dynamics of carnivores, however, is often scarce as carnivores range over wide areas and their elusive nature makes them difficult to count directly (Silver et al. 2004, Karanth et al. 2006, Balme et al. 2010). As a result of these challenges, camera traps have become an increasingly common tool for indirectly surveying carnivores. Camera traps do not require human observers, operate 24 hours per day, and photograph everything that passes in front of them, making them an ideal tool for monitoring carnivore communities in remote places (O'Brien et al. 2010).

When individuals can be identified based on natural (e.g., pelage pattern) or artificial (e.g., ear tag or radio-collar) markings, camera traps provide a method for obtaining large amounts of individual-level information over expansive areas with moderate effort (Karanth and Nichols 1998, Silver et al. 2004). Capture histories detailing when and at which camera stations individuals were photographed can then be analyzed using capture-recapture techniques to estimate population abundance and density (Otis et al. 1978, Williams et al. 2002, Efford et al. 2004, Royle and Young 2008). To date, however, density estimation using photographic capture-recapture techniques has almost exclusively focused on single, uniquely identifiable species such as tigers (*Panthera tigris*, Karanth and Nichols 1998, Karanth et al. 2006) and jaguars (*Panthera onca*; Silver et al. 2004, Soisalo and Cavalcanti 2006). Given the recent emergence of conservation and management paradigms focused on sustaining biodiversity (Yoccoz et al. 2001, Balmford et al. 2005), a multispecies photographic capture-recapture

approach that informs the management and conservation of wildlife communities, as opposed to individual species, is needed.

Photographic capture-recapture techniques have been limited to individual species as traditionally, study designs had to be tailored to the movements of the respective species (Karanth and Nichols 1998, Dillon and Kelly 2007, Maffei and Noss 2008, Sollmann et al. 2012). For example, when employing non-spatial capture-recapture approaches it is recommended that trap arrays are at least 3-4 times the size of an individual home range and that cameras are spaced close enough to ensure no individual within the study area has a zero probability of capture (Karanth and Nichols 1998, Maffei and Noss 2008). This precludes simultaneously estimating the densities of multiple species with differing home range sizes and movement patterns (O'Brien and Kinnaird 2011). Spatially explicit capture-recapture (SECR) models, alternatively, are much more robust to varying trap array sizes and spacing, relative to animal movement, because they directly incorporate the locations of where individuals were photographed (Sollmann et al. 2012, Sun et al. 2014). SECR models assume the probability of an individual being photographed at a camera station is a decreasing function of the distance between the camera station and the individual's activity center (Borchers and Efford 2008, Royle et al. 2009). This detection function includes two parameters: $g0$, the detection probability when a camera station is located on an activity center and σ, a spatial scale parameter related to an individual's home range radius (Borchers and Efford 2008, Royle and Young 2008). Estimating $g0$ and σ requires that some individuals are photographed at multiple camera stations. As long as there is a large enough sample of individuals and spatial recaptures across a range of distances, spatial models exhibit low bias and remain relatively precise (Sollmann et al. 2012, Sun et al.

2014). This flexibility makes it possible to now design camera trap surveys aimed at estimating

densities of multiple species simultaneously (O'Brien and Kinnaird 2011, Sollmann et al. 2012).

Photographic capture-recapture techniques are also generally limited to individually

identifiable species. Recently, however, spatial mark-resight models have been developed to

address this limitation (Sollmann et al. 2013, Rich et al. 2014, Efford *in press*). Spatial mark-

resight models estimate densities of partially marked populations (e.g., from natural marks such

as scars and ear nicks or from artificial marks) by incorporating spatial information and data

from marked, unmarked, and marked but not identifiable individuals into a single model

(Sollmann et al. 2013, Rich et al. 2014). When analyzing spatial mark-resight models using a

Bayesian approach, encounter histories are treated as partially latent as only a portion of the

population is uniquely identifiable (Chandler and Royle 2013, Sollmann et al. 2013). In the

recently developed maximum likelihood approach, alternatively, sightings of marked but not

identifiable and unmarked individuals can be pooled into 'unresolved' sighting occasions (Efford

in press). This classification may be preferable as it is often difficult to distinguish whether a

photo is of a marked but not identifiable or an unmarked animal (e.g. photo is blurry, photo only

includes a tail, photographed animal is walking away from the camera). When modeling

unresolved sightings, the expected values for these aggregated counts are a function of covariate

and detection parameters at the respective camera station (Efford *in press*). The unresolved

sightings do not contribute to the detection histories of marked animals, rather, they inform

spatial trends in density and detection (Efford *in press*).

The goal of our research was to use a single camera trap survey, designed to collect

spatial capture-recapture information on a diversity of carnivores, and newly developed spatial

models to estimate densities of both fully and partially marked species, while accounting for

differential habitat use. We applied our approach to a community of 7 carnivore species in the Okavango Delta, Botswana. To adequately sample the carnivore populations, we developed a novel camera trapping study design where 1) we sequentially rotated cameras through the study area to increase our spatial coverage and 2) we spaced cameras across a range of distances to capture the movements of species ranging in size from aardwolves (~11 kg; *Proteles cristata*) to lions (~200 kg; *Panthera leo*; Table 4.1). To estimate the densities of both fully marked and partially marked populations, we used SECR models with and without unresolved sightings (Efford *in press*; Borchers and Efford 2008). Lastly, our study area was a mosaic of habitat types with varying levels of suitability for the respective carnivore species (Rich et al. 2016). Thus, we modeled density as a function of the two major habitat types: densely vegetated mopane (*Colophospermum mopane*) shrub and woodlands and the more open non-mopane areas, which consisted primarily of floodplains and grassland savannas.

Methods

Study area

Our study was carried out in Ngamiland District of Northern Botswana, where the Okavango Delta is located. The area (ca 550 km^2; 19°31′S 23°37′E) has one of the highest diversities of carnivores ($n = 24$) found anywhere in Africa (Gittleman et al. 2001). Habitat types include, primarily, floodplains, savanna grasslands and mopane shrub and woodlands. Our study site included the eastern section of Moremi Game Reserve, wildlife management areas NG33/34, and part of the livestock grazing areas of Shorobe (Fig. 4.1). The wildlife management areas were separated from adjacent livestock grazing areas by an extensive 1.3-m high cable veterinary fence. The fence constrains livestock to the grazing areas but remains permeable to carnivores and many other wildlife species (Keene-Young 1999). The game reserve and wildlife

management areas were used primarily for photographic tourism and the livestock area was used

for cattle grazing.

Camera trap survey and photo classification

We deployed Panthera v4 incandescent-flash and Bushnell TrophyCam infra-red camera traps at

221 locations across our 1,154-km^2 study area between February and July 2015 (Fig. 4.1). Our

target species included 7 meso- and large carnivores (Table 4.1). Given predators and carrion

feeders often use lightly-travelled roads as movement corridors (Forman and Alexander 1998),

we placed cameras on sand roads to increase our probability of photographing carnivores. We

used 5-km^2 grid cells to guide the placement of cameras. We deployed two camera stations

within each grid cell, one on the road closest to the predetermined center point of each grid cell

and the second on the road closest to a predetermined random point within each grid cell. This

resulted in camera stations being separated by a mean of 735m with the distance to the nearest

neighbouring camera station ranging from 212m to 1661m (Fig. 4.2). This survey design

ensured that we were able to estimate the spatial scale parameter, σ, for species that varied in the

relative extent of their movements. This was consistent with the recommendation that camera

stations are spaced closer than twice the estimated value of σ (Sollmann et al. 2012, Sun et al.

2014). Having camera stations separated by a range of distances increased both our likelihood of

spatial recaptures (i.e. individuals caught at multiple locations) and our likelihood of adequately

reflecting the scale of species' movement as needed by the SECR models.

We used a rotational system for camera deployment that allowed us to extend our spatial

coverage. We divided our study area into five sub-areas and sequentially sampled each area for

30 nights. We deployed an average of 44 camera stations within each sub-area. Camera stations

included two opposing cameras mounted on trees or, if no trees were available, on metal fence posts that we hammered into the ground. We secured cameras at knee height and positioned cameras to photograph flanks of passing carnivores. We programmed cameras to take three photos when triggered in the day with a delay of 30 seconds between photo events. At night-time, the infra-red cameras took three photos when triggered but the flash cameras could only take one photo every 15 seconds due to the flash having to re-charge. We checked cameras every 5–10 days to download photos, replace batteries, and ensure cameras were operational.

We identified photographic detections of spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), African civets (*Civettictis civetta*), servals (*Leptailurus serval*), and aardwolves to the individual-level using pelage patterns. If we could not identify a photo to the individual level (e.g., image was blurry), we classified the photo as an unresolved sighting. We used WildID (Bolger et al. 2011) to help identify leopards, civets, and servals by pelage patterns; the remaining species were identified by eye. The behavior and space use of many felids differs between sexes (Sollmann et al. 2011). Thus, for leopards, we also distinguished males from females using secondary sexual traits and estimated density for males and females separately. We identified detections of lions to the individual level using natural markings such as ear nicks, whisker spot patterns, scars, and radio-collars (a subset of the population was collared). As with other species, if we could not identify a lion to the individual level, we labelled the photo as an unresolved sighting. Lastly, we identified whether the lion was an adult male (i.e., likely to be a territory holding male), sub-adult male, or female. We restricted our analysis to individuals that appeared to be ≥ 2 years of age.

Spatial models

We collapsed daily camera trapping data from our 6-month survey period into 20 sampling occasions such that one occasion consisted of a 7-8 day sampling period. We then created capture history and camera trap input files for each individually identifiable carnivore species for use in package secr (Efford 2016). Species-specific capture histories were matrices in which each photographic detection was a vector including the individual identification, sampling occasion, and camera station of the respective detection. The camera trap input file provided camera stations' Cartesian coordinates and sampling histories for each of the 20 sampling occasions; a 1 indicated the camera station was active and a 0 it was not. The trap input file also had camera station-specific estimates of vegetation density (see Rich et al. 2016 for details). Lastly, we made an input file for photographic detections classified as unresolved. The models do not permit resolved and unresolved sightings in the same sampling occasion. Therefore, we created 5 additional sampling occasions, one corresponding to each of our five sub-areas (from the rotational deployment of cameras). The input file then provided a count of the number of unresolved sightings at each camera station during each of the 5 sampling occasions. The capture history, camera trap, and when appropriate, unresolved sightings files were then joined into a large detection matrix where every detection is georeferenced to a trap location.

For individually identifiable species, we assumed the number of photographic detections of individual i at camera station j during sampling occasion k, y_{ijk}, was a Poisson random variable with a mean encounter rate λ_{ijk} (Borchers and Efford 2008, Royle et al. 2009). We modeled the mean encounter rate using a half-normal detection kernel where the shape of the kernel is dependent on $g0$ and σ. We included vegetation density as a covariate for $g0$ as it is negatively related to the detection probability of mammals in northern Botswana (Rich et al. 2016). When appropriate, we modeled unresolved sightings as a Poisson variate that had its own baseline

encounter rate, *g*0, but shared σ and spatial distribution parameters with other sampling occasions (Efford *in press*).

Density was a derived parameter, calculated by dividing *N*, the number of activity centers, by the area of *S*, the state space (Borchers and Efford 2008, Royle et al. 2009). The state space is an area large enough to include the activity centers of all individuals exposed to trapping. To define *S,* we used buffers surrounding our camera station grid ranging in size from 5km to 25km depending on species-specific estimates of σ (Table 4.2). We modeled density as a function of habitat and had a separate density parameter for the two major habitat types: mopane and non-mopane. To quantify vegetation cover, we used a habitat map created by Bennitt et al. (2014). To develop maximum likelihood density estimates, we fit an inhomogeneous Poisson density by maximizing the full likelihood using the secr package (Efford 2016) implemented in program R (vs 3.2.2). We then calculated density for the entire study area by calculating the area weighted mean density based on habitat; 48% of the study area was covered by mopane shrub and woodlands.

Results

We recorded 1,765 photographic detections of our 7 focal carnivore species over 6,607 trap nights. Spotted hyenas were photographed most often while aardwolves were photographed least (Table 4.1). Among the marked species, we identified the largest numbers of individual spotted hyenas, African civets, and leopards and the smallest numbers of aardwolves, servals, and lions (Table 4.1). Large, male felids (i.e., leopards and lions) and African wild dogs had the highest recapture rates (Table 4.1). For all species, we photographed at least some individuals at multiple camera stations (Table 4.1). Among the species where all or a subset of individuals

were uniquely identifiable, African civets and lions were the only species where greater than one-third of the photographic detections were classified as unresolved. When unresolved photos constitute less than 1/3 of the data, they contribute very little to the model and are better left ignored (Efford *in press*). Consequently, we only included unresolved sightings when estimating the densities of civets and lions.

We were able to use our single camera trapping grid to estimate the densities of each of the 7 carnivore species, including species residing at both high and low densities (Table 4.2, Fig. 4.3). With the exception of aardwolves, carnivore densities were higher in non-mopane areas than in mopane areas (Table 4.2). Spotted hyenas (12.7/100 km^2) and African civets (13.3/100 km^2) had the highest estimated densities compared to aardwolves (1.8/100 km^2) and lions (1.9/100 km^2), which had the lowest (Table 4.2). Estimated density was 0.00 for servals in mopane areas and aardwolves in non-mopane areas due to low detection rates of these species in the respective habitat type. Male leopards and African civets had the highest estimated baseline encounter rate $g0$ and wild dogs and spotted hyenas had the largest estimated movement parameter σ. Estimates of $g0$ and σ were higher for male leopards than for females, supporting our decision to model male and female leopards separately. For lions, however, the estimated movement parameter was similar for adult male lions ($\sigma = 3.8$) and young male lions and females ($\sigma = 4.2$) so we opted to model all lions together.

Discussion

An understanding of population densities is needed to mitigate wildlife declines and to implement effective conservation measures. Carnivore population characteristics, in addition to their generally cryptic and elusive nature, make them difficult to count directly. Consequently,

information on population densities is lacking for many carnivore species across the world (Silver et al. 2004, Pettorelli et al. 2010, Balme et al. 2010). Our research demonstrates the utility of using a single camera trap array, in combination with spatial models, to simultaneously estimate the densities of multiple, sympatric carnivores. Our density estimates for leopards, wild dogs, civets, servals, and aardwolves are the first published population density estimates for these species in Botswana. For our camera trap survey, we maximized the number of spatial recaptures of individuals from each of our study species by spacing cameras across a range of distances. To estimate densities we implemented SECR models with and without unresolved sightings to estimate the densities of species where every individual or only a subset of individuals was uniquely identifiable. This multispecies approach is applicable to camera trap studies worldwide and can be used to gain fundamental insights into the population status and habitat use of entire carnivore communities as compared to single carnivore species. This information is particularly pertinent to the conservation of carnivores considering one-quarter of the world's 245 carnivore species are threatened with extinction and many more are experiencing population declines (Ginsberg 2001, Schipper et al. 2008, Ripple et al. 2014).

In contrast to our multispecies approach, photographic capture-recapture techniques almost exclusively focus on estimating the density of a single, uniquely identifiable species, particularly large felids (Karanth and Nichols 1998, Silver et al. 2004, Sollmann et al. 2011). When employing non-spatial capture-recapture techniques, density estimates are strongly influenced by the size of the trap array and the spacing of traps relative to individual movements (Dillon and Kelly 2007, Maffei and Noss 2008, Sollmann et al. 2012). As a result, species with differing home range sizes, movement patterns, and spatial distributions cannot be sampled simultaneously (O'Brien and Kinnaird 2011). Spatial density estimators, alternatively, are a

relatively new class of models that directly incorporate the spatial nature of the sampling process, allowing them to 1) account for differences among individuals in capture probability due to spatial location, 2) directly estimate density, and 3) perform well across a range of camera study designs and animal movements (Borchers and Efford 2008, Sollmann et al. 2012, Sun et al. 2014).

Spatial models are robust to varying trap array sizes and spacing, but their ability to produce reliable estimates of animal movement and density depends on the number of individuals photographed and the number of spatial recaptures (i.e., photographic detections of an individual at multiple camera stations). It is therefore recommended that the extent of the sampling array is on scale with the target species' home range (Efford et al. 2009, Sollmann et al. 2012). We sampled across a 1,154-km^2 study area to expose a large number of individuals to our camera trap survey. This study area size was larger than the size of a wild dog territory (~ 605 km^2), the carnivore species known to have the largest home range size in our study region. We were able to sample such a large area because of our rotational system for camera deployment. This design obtained an adequate number of spatial recaptures while allowing us to sample an area five times larger than if cameras had remained stationary for the entire survey duration. Despite sampling a large area, we still had a relatively small number of photographic detections for two of our study species, serval and aardwolf. In an effort to increase detections for some of the mesocarnivores, it may be advisable to deploy camera stations on and off road. We sampled on sand roads to maximize detection probabilities (Forman and Alexander 1998) because we believed the photographic rates of carnivores would have been prohibitively low if we had deployed cameras randomly or on game trails. However, if species like servals and aardwolves avoided roads, then our sampling design likely resulted in their densities being underestimated.

To ensure an adequate number of spatial recaptures, it is also recommended that camera stations are spaced closer than twice the estimated value of σ, the spatial scale parameter (Sollmann et al. 2012, Sun et al. 2014). Our camera stations were spaced much closer together ($\bar{x}$ = 734m) than the minimum recommended spacing of 2400m (based on twice the estimated σ value for serval, the species with the smallest σ estimate; Table 4.2). Camera station spacing ranged from 212-1661m and our estimates of σ for the 7 carnivore species ranged from 1200-4800m. By having a high density of camera stations spaced at a range of distances, we were able to recapture individuals from each of our study species at multiple camera stations and adequately reflect both the large movements of African wild dogs and the shorter movements of servals. It is possible camera stations could have been spaced wider, but the 95% confidence intervals for $g0$ and σ show that there was residual variation in these parameters, particularly for species with a limited number of detections. Having a lower density of trapping points within the sampled area may have further reduced precision in parameter estimates (O'Brien and Kinnaird 2011).

Our camera trap sampling design allowed us to collect enough information to estimate the densities of 7 carnivore species, each with differing home range sizes and movement patterns. Our overall estimates of carnivore densities ranged from 1.8 aardwolf/100 km^2 to 12.7 spotted hyenas/100 km^2. Lions and spotted hyenas are the only carnivore species with published estimates of density in the Okavango Delta (Cozzi et al. 2013). We provide the first published population density estimates for leopards, wild dogs, civets, servals, and aardwolves in Botswana. Our estimates of 10.3 and 14.9 spotted hyenas/100 km^2 in mopane and non-mopane habitat, respectively, are slightly lower than previous estimates (mopane: 12.3 hyenas/100 km^2, floodplains: 16.9 hyenas/100 km^2) but previous estimates fall within our 95% confidence

intervals. Our estimate of 1.9 lions/100 km^2, alternatively, was substantially lower than the previous estimate of 5.8 lions/100 km^2. Cozzi et al. (2013) estimated lion and hyena densities, however, using calling stations. Converting call station responses to population estimates may be limited by the researcher's ability to estimate the proportion of animals that respond, and by accurately calculating the distance from which the species responds to the calling station (Midlane et al. 2015). Consequently, differences in estimated densities are likely attributed to the differing sampling and estimation techniques and not to an actual decline in the study area's lion population.

Although wild dog densities have not been estimated explicitly in northern Botswana, our estimates of 1.1 and 3.6 wild dogs/100 km^2 in mopane and non-mopane habitats, respectively, seem reasonable based on known pack sizes (3 - 14) and home range sizes (337 - 999 km^2) in the area (Pomilia et al. 2015). No density estimates were available for the aardwolf in southern Africa for comparison but our estimates of civet and serval densities were comparable to other density estimates in the region (7.5 – 14.2 civets/100 km^2, 4.3 – 9.3 servals/100 km^2; Amiard 2014, Ramesh and Downs 2013). Our estimated density of 2.5 and 6.8 leopards/100km^2 in mopane and non-mopane habitat, respectively, also fell within the range of estimated leopard densities in southern Africa although previous estimates of leopard density have been based on spoor surveys or non-spatial capture-recapture techniques (Boast and Houser 2012, Balme et al. 2010). Our estimated sex ratio for leopards was approximately 2 female leopards for every 1 male. This aligns with research in eastern Botswana where the territory sizes of female leopards were approximately half the size of a male leopard (Steyn and Funston 209). We had a median of 2 recaptures per female leopard compared to 5 recaptures per male leopard supporting that the

behavior and space use of felids differs between sexes and should be accounted for when estimating density (Sollmann et al. 2011).

In addition to estimating density, the flexibility of spatial models also allows inferences to be drawn about the processes governing locations of individuals (Sollmann et al. 2011). We assumed activity centers followed an inhomogeneous Poisson distribution dependent on habitat and we found species' activity centers, with the exception of aardwolf, were concentrated in non-mopane areas. These results highlight the importance of floodplains, grasslands, and acacia woodlands to the carnivore community in northern Botswana. For the large carnivore species, 95% confidence intervals were much larger in mopane than in non-mopane areas reflecting the uncertainty associated with these estimates due to a limited number of individuals photographed and limited number of spatial recaptures in mopane-dominated habitats. If we had assumed a homogeneous distribution of activity centers, our estimates of density would have been biased and we would not have gained valuable insights into species' differential habitat use.

Our research framework capitalizes on the wealth of information collected by camera traps, the robustness of spatial models in regards to study design, and on recent advances in density estimation. Our multispecies approach provides a repeatable methodology for simultaneously estimating the densities of multiple sympatric carnivore species. We demonstrate the utility of our camera trap study design for collecting spatial capture-recapture information on a diversity of carnivore species and how this data can be assessed using SECR models both with (Efford *in press*) and without unresolved sightings (Borchers and Efford 2008) to estimate species' densities in multiple habitat types. Despite the flexibility afforded by this approach, we only identified one study that used a single camera trapping array to estimate the densities of multiple carnivores but it was restricted to individually identifiable species and assumed

carnivore densities were uniform across the study area (O'Brien and Kinnaird 2011). We utilized recent advances in statistical modeling (Chandler and Royle 2013, Efford *in press*) to estimate the densities of both uniquely identifiable species and species where only a subset of individuals were marked. Our approach is applicable not only to camera trap surveys, but any type of survey (e.g., hair snares, scat transects, physical capture and marking) that can produce encounter history data with corresponding spatial information about the location of capture (Royle et al. 2009). Field surveys require large financial and logistical efforts in order to obtain adequate data for reliable inference (Sollmann et al. 2011). In a field where money, time, and personnel are generally limited, our multispecies study design will result in considerable savings when compared to multiple field surveys each targeting a single species (O'Brien and Kinnaird 2011). Additionally, application of our approach to the increasing number of camera trap studies would result in a more efficient use of available data and a more comprehensive understanding of wildlife populations.

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Table 4.1. Number of photographic detections (Det.), number of individuals (Indiv.), median number (range) of recaptures of individuals, and number of unresolved sightings (i.e., photos only identifiable to the species-level) for the focal carnivore species of a camera trap survey in Ngamiland District, Botswana, 2015.

Common name	Scientific name		Det.	Indiv.	Recaptures	Unresolved
Spotted hyena	*Crocuta crocuta*		783	234	2 (1 − 16)	164
Leopard	*Panthera pardus*	F	101	37	2 (1 − 10)	27
		M	218	30	5 (1 − 33)	14
Wild dogs	*Lycaon pictus*		280	50	5 (1 − 15)	22
Serval	*Leptailurus serval*		38	23	1 (1 − 6)	8
African civet	*Civettictis civetta*		207	91	1 (1 − 18)	126
Aardwolf	*Proteles cristatus*		27	16	1 (1 − 5)	0
Lion	*Panthera leo*		89	23	4 (1 − 8)	59

Table 4.2. Summary statistics (estimated parameter values and 95% confidence intervals) from spatially explicit capture-recapture models based on photographic captures of carnivores in Ngamiland District, Botswana, 2015, including maximum-likelihood density estimates (D) in mopane (*Colophospermum mopane*) and non-mopane habitat, buffer widths and the resulting state space areas, and estimates of baseline encounter rate $g0$ and scale parameter σ.

Common	D (no./100 km^2)			Buffer	State space	$g0$	σ (km)
name	Mopane	Non-mopane	Overall	width (km)	(km^2)		
Spotted	10.9	14.4	12.7	25	6,337	0.06	4.1
hyena	(5.46 – 21.68)	(11.31 – 18.29)	(8.84 – 19.03)			(0.058 – 0.073)	(3.91 – 4.34)
Leopard-	1.2	4.9	3.1	15	3,738	0.1	2.3
female	(0.20 – 7.20)	(3.19 – 7.45)	(1.76 – 7.33)			(0.07 – 0.14)	(2.02 – 2.62)
Leopard-	1.2	2.1	1.7	20	4,969	0.2	3.2
male	(0.24 – 5.59)	(1.27 – 3.55)	(0.78 – 4.53)			(0.15 – 0.22)	(2.93 – 3.51)
Wild	1.1	3.6	2.4	25	6,337	0.07	4.8
dogs	(0.24 – 5.30)	(2.44 – 5.35)	(1.38 – 5.33)			(0.054 – 0.079)	(4.40 – 5.23)
Serval	0.0	10.2	5.3	5	1,666	0.06	1.2
		(5.65 – 18.24)	(2.94 – 9.48)			(0.027 – 0.147)	(0.85 – 1.55)

African civet	9.5 (7.21 – 12.56)	16.8 (14.46 – 19.63)	13.3 (10.98 – 16.24)	6	1,867	0.2 (0.17 – 0.26)	1.3 (1.18 – 1.44)
Aardwolf	3.7 (2.00 – 6.68)	0.0	1.8 (0.96 – 3.21)	5	1,666	0.06 (0.026 – 0.130)	2.2 (1.64 – 3.03)
Lion	1.2 (0.6 – 2.77)	2.5 (2.05 – 3.09)	1.9 (1.3 – 2.94)	25	6,337	0.07 (0.044 – 0.110)	3.9 (3.26 – 4.56)

Figure Captions

Figure 4.1. Layout of our camera trap survey in northern Botswana, 2015.

Figure 4.2. The range of distances separating 221 camera stations during a camera trap survey in Ngamiland District, Botswana, 2015. We spaced cameras at a range of distances to adequately reflect movements of small and wide-ranging carnivore species.

Figure 4.3. Maximum-likelihood density estimates for a species residing at low densities, African wild dog (*Lycaon pictus*), and a species residing at high densities, spotted hyena (*Crocuta crocuta*), based on a camera trap survey (dots represent camera stations) in northern Botswana, 2015. To define the state space (i.e., an area large enough to include the activity centers of all individuals exposed to trapping) for both species, we surrounded our study area with a 25km buffer.
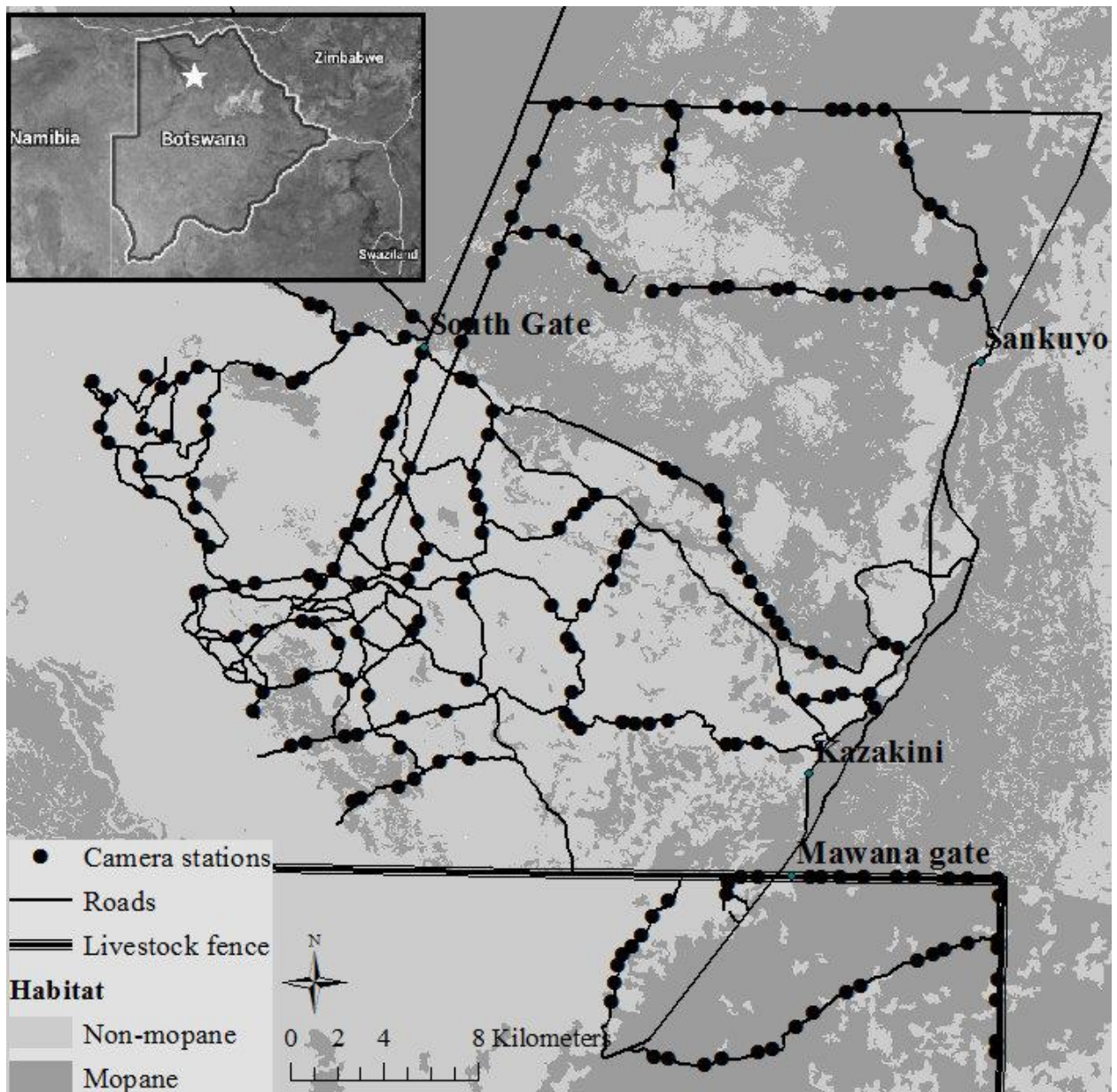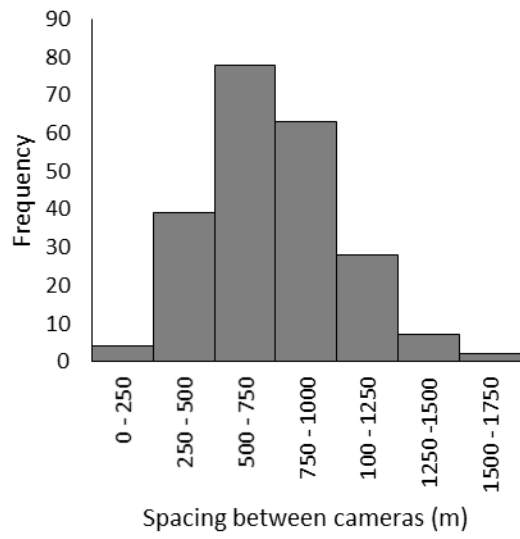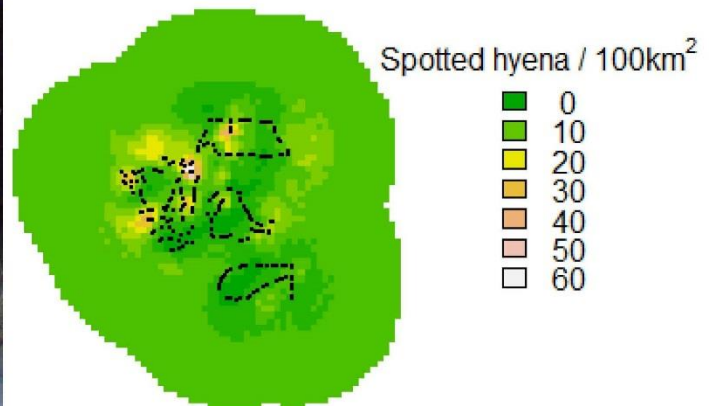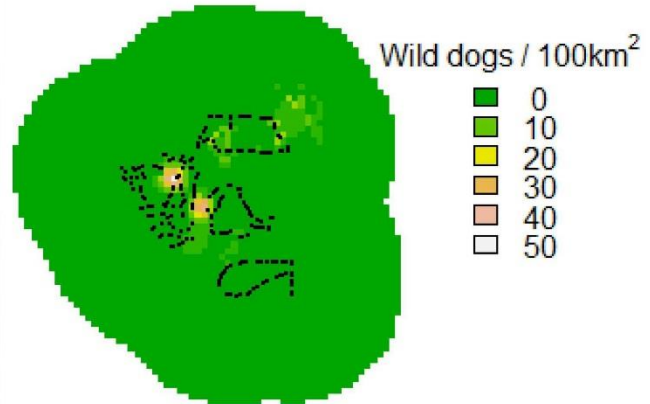
Figure 4.1.

Figure 4.2.

Figure 4.3.

V. CONCLUSION

Ensuring the future well-being of our planet is dependent on reducing the rate of biodiversity

loss (Hooper et al. 2012). Accomplishing this formidable task in the face of human pressures

requires an understanding of species' ecology and population dynamics (Kelling et al. 2009,

Feeley and Silman 2011). Consistent and comparable information on the status and ecology of

many wildlife populations, however, is lacking (Ahumada et al. 2011). Camera traps offer a

potentially feasible method for amassing this type of information as they collect standardized

metadata that can be integrated across species and observers and compared across sites and years

(Burton et al. 2015, Schmeller et al. 2015). Accordingly, camera traps have recently been

highlighted as a potential tool for addressing broad-scale ecological inquiries and for monitoring

global biodiversity (O'Brien et al. 2010, Ahumada et al. 2013; Steenweg et al. 2016). To date,

however, few studies employing camera trap surveys have capitalized on the wealth of

community information collected by cameras as attention is typically focused on an individual

species (Karanth and Nichols 1998, Silver et al. 2004). My research advances camera trap

analyses from single to multi-species assessments by providing standardized, repeatable metrics

for assessing entire wildlife communities or a specific guild of species (e.g., carnivores). These

metrics are applicable to camera trap studies worldwide and their application would likely result

in a better understanding of the spatial ecology of terrestrial wildlife communities as well as the

composition and densities of elusive carnivore communities.

At a more local scale, my dissertation research provides information on the distributions,

densities, and ecology of the terrestrial wildlife community in northern Botswana, with a focus

on mammalian carnivore species. To provide this information, I assessed data from a multi-year

camera trap survey using advanced analytical techniques, which accounted for imperfect

detection, a limitation of many wildlife studies (Burton et al. 2015). I focused on the carnivore community, specifically, because 1) many African carnivores (e.g., lions- *Panthera leo* and African wild dogs- *Lycaon pictus*) are experiencing population declines and range contractions, 2) carnivores can exert strong, regulatory effects on ecosystems, and 3) carnivores are among the species most highly valued by the wildlife-based tourism industry, a large contributor to the Botswana's GDP (Ginsberg 2001, Lindsey et al. 2007, Estes et al. 2011, Ripple et al. 2014). I was pleased to find that in my study area, large carnivore species did not appear to be in decline as has been suggested. My estimated distributions and densities are comparable to what the Botswana Predator Conservation Trust has been observing in the area since 1989 and for some species, I actually recorded higher densities than what was previously known (e.g., leopards- *Panthera pardus*). Additionally, I documented the presence of Cape fox (*Vulpes chama*), side-striped jackal (*Canis adustus*), Cape clawless otter (*Aonyx capensis*), and brown hyena (*Hyaena brunnea*), carnivore species which had previously not been known to occupy the area. This was welcome news and suggests that, in my study region, the diverse carnivore community is thriving.

The information resulting from my dissertation can be used by the Ministry of Environment, Wildlife, and Tourism to help inform effective conservation and management actions and to predict species- and community-level responses to land use and environmental changes. As an example, I found support for a negative relationship between human disturbance, and the occupancy and richness of terrestrial mammals. Specifically, I found the occupancy probabilities and richness of 44 mammal species increased with increasing distance from the livestock fence (i.e., in areas located further into protected areas). These results are consistent with trends of land-use change and fragmentation being some of the greatest threats to

biodiversity worldwide (Alkemade et al. 2009, Butchart et al. 2010). Additionally, this edge effect suggests the negative impacts of land use and human-wildlife conflict (e.g., poaching and retaliatory killing) are radiating from the livestock areas into the protected wildlife areas. Thus, in addition to maintaining and effectively managing protected areas in Botswana, I recommend increased patrolling along the protected area borders in an effort to minimize edge effects. If the threat of human persecution was minimized along protected area borders, it is likely that wildlife would expand their distributions into these areas essentially resulting in an increase in the size of protected areas and available wildlife habitat. Larger protected areas would not only aid in the conservation of biodiversity, but also in the safeguarding of landscapes and protection of essential ecosystem services (Bertzky et al. 2012, Watson et al. 2014).

I also found vegetation cover had a large influence on the distributions and densities of wildlife populations in northern Botswana. The dominant vegetation covers in my study area included floodplains/grasslands (i.e., open habitat) and mopane shrub and woodlands (i.e., closed habitat). Percent coverage of grasslands and floodplains had a large, positive influence on the occupancy and richness of terrestrial mammals at both the community- and species-level. I also found, more specifically, that vegetation cover played a notable role in shaping carnivore communities. Overall, there were more individual carnivores and more carnivore species in open habitats than in closed. Estimated carnivore densities, for example, were greater in open habitat for every species (n = 6) but the aardwolf.   It should be noted, however, that mopane-dominated habitats have been found to be important to wildlife populations elsewhere in Botswana. Additionally, my survey did not encompass the heart of the wet season (i.e., December-January) when mopane shrub and woodlands may have had a larger, positive influence on wildlife distributions and densities.

The generally positive associations between carnivore occupancy and carnivore density, and grasslands/floodplains is likely why I also found carnivores to be positively associated with each other (i.e., intraguild species). These results differed from other systems in which dominant carnivores have been shown to locally exclude subdominant carnivores from prey-rich areas (Durant 1998, Creel and Creel 1996). The positive associations among intraguild species in my study area suggests competitor/predator avoidance did not play a large role in shaping the carnivore community and rather, carnivore distributions were driven by resource availability. My findings, which underscore the importance of open habitats and the resources they provide, support regional conservation initiatives focused on grasslands as this biome is vulnerable to future land-use pressures such as conversion to farmlands and livestock grazing areas (Biggs et al. 2008) and benefits a broad diversity of species, including both carnivores and their prey (e.g., impala and zebra). Additionally, over a quarter of the world's grasslands have already been lost to agricultural expansion (DeFries et al. 2004) and the remaining grasslands are threatened by woody encroachment (Ratajczak et al. 2012).

My research framework capitalized on both the community information collected by cameras and recent advancements in statistical modelling. The community information collected by cameras, for example, facilitated my comprehensive assessment of how intraguild competitors and predators, prey populations, and landscape features impacted the seasonal distributions of carnivores. This analysis, as well as my other multi-species assessments, resulted in a more comprehensive and efficient use of available data when compared to single species approaches, where the majority of photos are discarded and potentially valuable data unused. Multi-species assessments are now possible due to recent advances in analytical techniques, such as multi-species hierarchical occupancy models, which I used to assess the

spatial ecology of 44 terrestrial mammals. Unlike traditional community analyses, these multi-species models allowed me to retain species identity while properly accounting for multiple sources of uncertainty (Kéry and Royle 2008, Zipkin et al. 2010). Additionally, by integrating data across species using a community- and group-level hyper-parameter, I was able to estimate occupancy probabilities and community, group, and species-specific responses to environmental and anthropogenic features, including for species that were rarely observed (Dorazio and Royle 2005; Kéry and Royle 2008, Zipkin et al. 2010). My study is the first to employ this approach to evaluate the distributions of an entire terrestrial mammal community (>0.5 kg).

My research is also the first to use a single camera trap survey and newly developed spatial models to estimate densities of both fully- and partially-marked species, while accounting for differential habitat use. The resulting density estimates for leopards, wild dogs, civets, servals, and aardwolves are the first published population density estimates for these species in Botswana. To simultaneously estimate the densities of multiple, sympatric species, I employed spatially explicit capture-recapture models without and with unresolved (i.e., photographs only identifiable to the species-level) sightings (Efford *in press*, Borchers and Efford 2008). These spatial density estimators are a new class of models that directly incorporate the locations of where animals were photographed, allowing them to account for differences among individuals in capture probability due to spatial location, to directly estimate density, and to perform well across a range of camera study designs and animal movement ranges (Borchers and Efford 2008, Sollmann et al. 2012, Sun et al. 2014).

To develop effective conservation planning and mitigate biodiversity loss, standardized metrics for monitoring and assessing biodiversity are needed (Jones et al. 2006, Ellison 2010, Schmeller et al. 2015). I addressed this need by developing approaches for leveraging data from

a single camera trapping grid to 1) assess the ecology and distributions of an entire wildlife community (n = 44 species), 2) test whether intraguild competitors/predators or resource availability had a larger influence on the seasonal distributions of carnivore species, and 3) estimate the densities of multiple, sympatric carnivore species. In southern Africa and Botswana specifically, this information will help inform land use policies and enable managers to better predict how anthropogenic and environmental changes may impact wildlife communities. For example, my models could be used to predict how the entire wildlife community, or a specific species of interest, may respond to the development of a safari lodge or the conversion of protected lands to livestock grazing lands. Furthermore, my models can be expanded to include climate-specific covariates that may become increasingly important as Botswana becomes hotter and drier and vegetation structure changes from tree and shrub savanna to more bush and shrub savanna (Ringrose et al. 2002). This would allow researchers and managers to project the impacts of the continually changing environment, including the influences of climate, vegetation, water availability, and interspecific interactions.

I also aim to develop a technical guide detailing how to carry out camera trap surveys (e.g., number of cameras, camera layout, entering camera data) and potentially, how to analyze camera trap data. In the future, wildlife guides or managers from the Department of Wildlife and National Parks can use this guide to implement camera trap surveys and then collaborate with the Okavango Research Institute or one of the many local non-governmental organizations to analyze the data. This would result in more systematic monitoring of wildlife across the country and help the Ministry of Environment, Wildlife, and Tourism to achieve their focal objective of increased monitoring.

At a broader scale, my research highlights the potential for camera traps, a field technique that has grown exponentially in popularity, to monitor global biodiversity in accordance with the Convention on Biological Diversity (O'Brien et al. 2010, Ahumada et al. 2013, Burton et al. 2015, Steenweg et al. 2016). I suggest broader application of my research framework would enable policy makers and managers to track, improve, and adapt policies and management actions aimed at addressing the loss of wildlife populations (Butchart et al. 2010, Schmeller et al. 2015). This information is particularly pertinent to the conservation of the many endangered, threatened, and declining carnivore species around the world (Ginsberg 2001, Schipper et al. 2008, Ripple et al. 2014). In conclusion, by employing camera traps and advanced, analytical approaches, my dissertation research provides information on the distributions, densities, and ecology of wildlife communities in northern Botswana as well as a research framework that will help progress camera trap analyses from single to multispecies assessments.

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