# USE OF BAITED CAMERA TRAPS TO SAMPLE CARNIVORE COMMUNITIES IN EASTERN BOTSWANA

by

LAUREN CLAIRE SATTERFIELD

(Under the Direction of John P. Carroll and Clinton T. Moore)

## ABSTRACT

Human-wildlife conflict and habitat loss are threatening carnivore populations in southern Africa, where the bulk of carnivore research focuses on large, charismatic predators. However, scant research exists on basic aspects of medium and small carnivore ecology in southern Africa. The Mashatu Game Reserve is a 25,000 ha, unfenced private reserve in eastern Botswana. I investigated occupancy, detection, and habitat use of the carnivore community in the Mashatu Game Reserve using baited camera traps during winter of 2012 and 2013. Three main bait types were assessed: impala meat, cheesecloth soaked in spent cooking fat, and non-baited controls. Further, I assessed carnivore and prey activity patterns by using data gathered from camera traps as part of the occupancy study. Results demonstrated differences in bait preference and habitat type by species. Further, I found heterogeneity of temporal activity among carnivores of similar prey bases.

INDEX WORDS: Africa; Bayesian analysis; Botswana; camera trapping; carnivore; competition; detection; mesopredator; occupancy; predator; prey; temporal partitioning

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B.A., Mount Holyoke College, 2009

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May 2014

# DEDICATION

I dedicate this thesis to wild carnivores across the globe. May continued research and conservation efforts show strength as they defend your place in the ecosystem.

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African bushveld with more skill, enthusiasm, and excitement than I ever could have anticipated. I do believe my days in southern Africa are far from over.

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# CHAPTER 1

# INTRODUCTION AND LITERATURE REVIEW

Carnivores worldwide are threatened by an increasing human population, and resulting habitat fragmentation and habitat loss (Treves and Karanth 2003, Cardillo et al. 2004, Crooks et al. 2011). Drivers of human-carnivore conflicts for the world's approximately 250 terrestrial mammalian carnivores can be classified into two major categories: habitat fragmentation and degradation, and livestock predation (Treves and Karanth 2003, Thirgood et al. 2005, Crooks et al. 2011). One study found that, on average, only 54.3% of a species' geographic range consists of high-quality habitat, and only 5.2% consisted of high-quality habitat within protected areas (Crooks et al. 2011).

Livestock predation by carnivores has been cited as perhaps the most common source of conflict between humans and carnivore species (Thirgood et al. 2005), particularly in the case of large predators (Treves and Karanth 2003). Examples include grey wolves (*Canis lupus*) killing poultry (chickens, turkeys, and ducks) and beef cattle, goats, and sheep in the United States (Treves et al. 2004), jaguars (*Panthera onca*) preying upon cattle in Brazil (Quigley and Crawshaw Jr 1992), snow leopards (*Unica uncia*) attacking domestic yak and goats in Nepal (Oli et al. 1994), brown bears (*Ursus arctos*) killing sheep in Norway (Zimmermann et al. 2003), and lions (*Panthera leo*) attacking cattle and donkeys in Tanzania (Kissui 2008). Threat of attacks on humans and disease transmission are among other common sources of conflict (Thirgood et al. 2005). Legal and illegal killing of problem animals, sanctioned hunts, relocation, and fencing of habitat areas have been employed as responses to human-carnivore conflicts. Thus, habitat becomes further divided and carnivore numbers continue to decline (Treves and Karanth 2003).

The carnivore species guilds on the African continent, while not isolated from these conflicts, does remain largely intact with limited extinctions and fewer threatened species as compared to Europe, Asia, and the Americas (Dalerum et al. 2009). Further, cases of large transfrontier conservation efforts in Africa and a shift towards ecotourism have further mitigated conflicts on the continent compared to other regions (Weber and Rabinowitz 1996, Dalerum et al. 2008, Selier et al. 2014).

Botswana in particular boasts several large national parks and conservation areas, including Chobe National Park, Kgalagadi Transfrontier National Park, Makgadikgadi Pans National Park, Gemsbok National Park, Moremi Wildlife Reserve, and Nxai Pan National Park, and the country operates under a model of community-based conservation where wildlife is considered a public resource (Campbell 1973, Twyman 2000). Traditionally, communities could harvest wildlife through hunting. However, as of 2014, the country officially banned all hunting (Donovan 2013). The implications of this decision on conservation efforts in Botswana are yet to be seen. The restriction is beneficial in attracting tourists opposed to hunting. However, it also prevents hunters from spending what are often substantial amounts of money to pursue hunts within the country, and limits the financial ability of previous hunting concession managers to retain these areas as undeveloped parcels of land (Donovan 2013).

In addition to public areas, Botswana also contains privately-owned game reserves. Mashatu Game Reserve is an approximately 25,000 ha unfenced patchwork of private land holdings in eastern Botswana (-22°10' S, 29°3' E) (Mashatu Game Reserve 2013). Mashatu Game Reserve lies within the Northern Tuli Game Reserve (Notugre), a 75,000 ha property bordered on three sides by the Matloutse, Limpopo, and Shashe Rivers. Notugre is a portion of the proposed 490,000 ha Greater Mapungubwe Transfrontier Conservation Area (GMTFCA), which would span across Botswana, Zimbabwe, and South Africa (Figure 1.1).

I investigated the use of camera traps to study carnivores on the Mashatu Game Reserve, Botswana. In particular, this study is motivated by the paucity of information on smaller guilds of carnivores, particularly in southern Africa (Blaum et al. 2009, Holmern and Røskaft 2013). I believe this lack of information on smaller African carnivores is due to several factors, including fewer species at risk of extinction (Ray et al. 2005), less conflict with livestock herders (Ogada et al. 2003), and less funding as compared to larger carnivores (Wilkie and Carpenter 1999, Scholfield and Brockington 2009). However, it is important to study these species before they face potential declines characteristic of their larger counterparts (Redford et al. 2011). Further, some mesopredator species in the region are understudied and population trends are unknown (Caro and Stoner 2003, IUCN 2013).

As noted, habitat fragmentation is a universal problem among families of Carnivora (Crooks et al. 2011). White a study by Crooks et al. did not find a relationship between habitat fragmentation and body size, it was reported that species in areas with less fragmentation had larger geographic ranges (Crooks et al. 2011). In general, a direct relationship exists between carnivore body size and home range size, with smaller species using smaller areas than larger species (Kelt and Van Vuren 1999). Thus, smaller carnivores may be at increased risk of negative effect of habitat fragmentation (Crooks et al. 2011). Further, lack of correlation between fragmentation and carnivore body size may be due to limited available data on smaller carnivore species, especially in southern Africa, rather than due to a true trend within these smaller guilds.

In Chapter 2, I investigated occupancy and detection of carnivores on the Mashatu Game Reserve using baited camera traps. The effect of habitat on occupancy was also assessed. In particular, I explore the effectiveness of cooking fat as an alternative to meat bait, and I compare baited sites to unbaited control sites in both riverine and upland areas. Many data collection methods used for larger carnivores are impractical for smaller carnivores due to body size differences. Further, the use of meat as bait in carnivore study often poses complications, as is the case in Botswana due to the new ban on hunting (Donovan 2013) and where harvesting of wild animals as bait was difficult nonetheless due to the establishment of numerous protected parks in the country (Campbell 1973). Developing effective sampling methods for smaller carnivore guilds, especially methods that are reasonable given the remote field conditions of southern Africa, will help inform future studies.

In Chapter 3, I examined factors affecting daily activity patterns of these carnivores and their prey. Associations between activity and lunar phase, habitat, and minimum nighttime temperature are explored. Temporal shifts play a role in avoidance of interspecific killing among carnivores, which is generally influenced by species body size (Polis et al. 1989, Palomares and Caro 1999), allowing a diversity of species to survive despite competition. Studies in competition theory assert that predator-predator interactions, in combination with resource needs and prey activity, can affect both activity peaks and activity pattern shifts within species (Carothers and Jaksić 1984, Caro and Stoner 2003, Hayward and Slotow 2009, Cozzi et al. 2012).

As the composition of large, dominant carnivore communities changes, the mesopredator release hypothesis theorizes that shifts will then occur in lower guilds of carnivores, restructuring both prey and predator community composition (Crooks and Soulé 1999). Understanding which predators will outcompete others, or which prey species are most at risk due to high temporal overlap with mesopredators, will allow managers to focus monitoring efforts on these conditionally imperiled species. In the event of declines, understanding interspecies interactions and predicting community composition changes will allow managers to focus conservation and research efforts on species most at risk. Managers might, for example, predict that one carnivore species will be outcompeted by another for access to a critical prey item, and respond by improving and increasing critical habit for this vital prey species. Thus, researching and understanding relationships among smaller guilds of carnivores will allow conservation organizations to better predict changes to this group in light of declines in larger carnivores.

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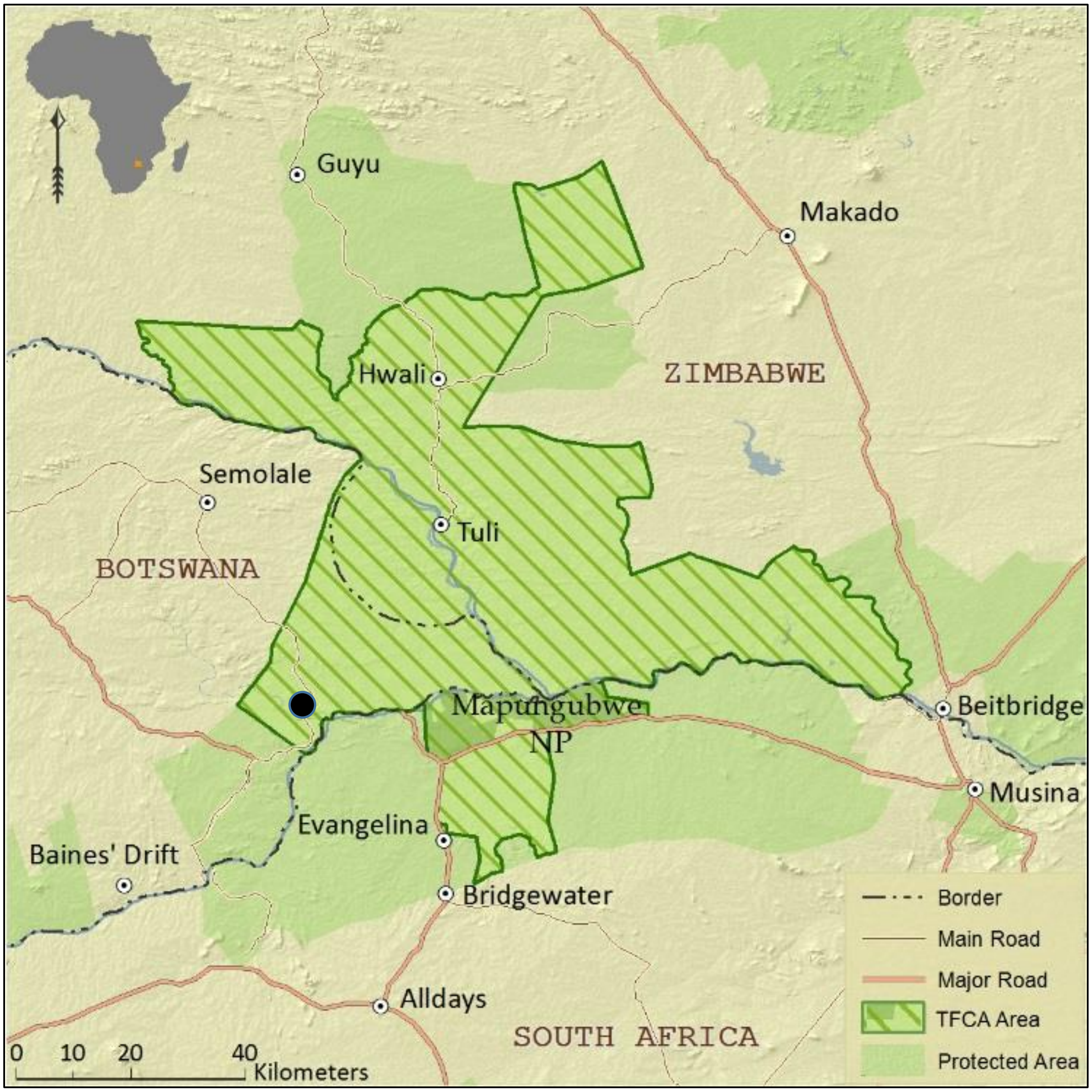

**Figure 1.1.** Map of the proposed Greater Mapungubwe Transfrontier Conservation Area (GMTCFA). The goal of this transfrontier park is to link existing conservation areas (in light green) to create a continuous conservation landscape. The black dot represents the study site along the Motloutse River within the Northern Tuli Game Reserve (Notugre), a portion of the proposed GMTCFA

# CHAPTER 2

# OCCUPANCY AND DETECTION OF THE CARNIVORE COMMUNITY IN EASTERN BOTSWANA USING BAITED CAMERA TRAPS[1]

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[1] Satterfield, L.C., Thompson, C.T., Snyman, A., Candelario, L. and Carroll, J.P. To be submitted to *Oryx*.

## ABSTRACT

Human-wildlife conflict and habitat loss are threatening carnivore populations worldwide. This is especially true in southern Africa, where the bulk of carnivore research focuses on large, charismatic predators. However, scant research exists on basic aspects of medium and small carnivore ecology in southern Africa, including information on population size, distribution, diet, habitat preferences, and interspecies interactions. Further, innovative data collection methods are needed as most reserves occur in remote areas with strict guidelines regarding what research activities can be conducted on-site. Mashatu Game Reserve is a 25,000 ha, unfenced private reserve in eastern Botswana bordered by farms, villages, and other game reserves, allowing a unique opportunity to study an open system in this region. We investigated occupancy, detection, and habitat use of the carnivore community at Mashatu using baited camera traps during winter of 2012 and 2013. Three main bait types were assessed: impala meat, cheesecloth soaked in spent cooking fat (fat rags), and non-baited controls. Fourteen of 17 carnivore species known to inhabit the area (82%) were remotely captured among the approximately 17,000 photos taken during the study. We constructed hierarchical community models, with and without sampling and habitat covariates, for a multi-species analysis of the carnivore community inhabiting the study area. Our results demonstrated variation in bait preference and habitat type by species, and among meso-mammal predators as compared to larger carnivores. We found that large carnivores were detected at higher rates at sites baited with meat, while smaller carnivores either responded equally to meat and fat rags, suggesting that fat rags may be substituted for meat baits for these species, or demonstrated no difference among visitation of baited sites as compared to control sites. Large-spotted genet (*Genetta tigrina*) detection rates were highest at fat rag sites, supporting the use of this method as a

preferred sampling technique for this species. We found support for use of riverine habitat by many species, in particular African civet (*Civettictis civetta*), brown hyena (*Hyaena brunnea*), and large-spotted genet.

## INTRODUCTION

Human-wildlife conflict and habitat loss are a universal threat to wild species and natural systems (Fahrig 1997, Mateo-Tomás et al. 2012), including carnivores communities. It is estimated that of the world's 25 biodiversity "hotspots," none has more than one-third of their original habitat remaining (Brooks et al. 2002). Annual deforestation rates among these areas range from 0.5% to 4.05% (Brooks et al. 2002). Crooks et. al. studied 246 terrestrial mammalian carnivores and found that high-quality habitat averaged only 54.3% of species' range and only 5.2% of a species' range was both in high-quality habitat and located in protected areas (Crooks et al. 2011). Further, they found that global hotspots for carnivore habitat are experiencing the highest rates of habitat fragmentation and deforestation, meaning that critical regions are most at risk (Crooks et al. 2011). To protect and properly manage carnivores and other species native to a region, background information and baseline data are critical in deciphering trends in each species and monitoring the health and viability of any particular population.

The decline of large carnivores and the need for further research dedicated to the order Carnivora extends to southern Africa (Ray et al. 2005, Ripple et al. 2014). While large carnivores in the region continue to be studied extensively (Caro and Stoner 2003, Ogada et al. 2003, Ray et al. 2005, Dalerum et al. 2008), focused research on medium and small carnivores is needed to inform conservation organizations about the role this guild plays in the southern African ecosystem (Martinoli et al. 2006). Further, innovative and efficient data collection methods focused on specific guilds are needed as a) most reserves occur in remote areas with strict guidelines regarding what research activities can be conducted on-site, b) funding sources that would allow for detailed methods commonly used on larger carnivores (e.g. GPS collars, etc.) are comparatively harder to obtain for medium and small carnivores, c) methods practical for larger carnivores may be impractical for smaller-bodied species, and d) most field sites in southern Africa operate on scant resources and thus methods that reduce the need to import materials are preferred.

In recent years, advancement in digital photography and camera trapping technology have allowed unprecedented opportunities for such minimally invasive, low-cost, low-manpower, highly informative data collection (Rowcliffe and Carbone 2008), making this an ideal tool for the community in question. In order to increase the effectiveness of camera traps and reduce the length of required sampling periods, species- or guild-specific baits are used to draw species of interest to camera trap stations. A literature review of baits used to lure carnivores during camera trapping or track station studies yielded the following options: peanut butter, eggs, fruit, fish, meat, offal, blood, live animals, pet food, Calvin Klein Obsession aftershave, synthetic fatty acid lures, and carnivore urine (Gil-Sánchez et al. 2011, Thorn et al. 2009, Barea-Azcón et al. 2006, Wilson and Delahay 2001). The latter four lures are hard to come by in remote areas of southern Africa. Of the remaining options, most are impractical or unsafe to keep in a remote field camp setting where refrigeration is scarce or nonexistent and stored bait has the potential to draw large predators such as lions, leopards, and hyenas into bush camps, posing a risk to researcher safety.

For carnivores, meat is an obvious bait choice that could theoretically be harvested on-site or acquired from a local village and disbursed the same day, eliminating the need for import or storage. However, procurement of meat for research presents its own issues. Some studies have asserted that carnivore attacks on domestic prey is, in many cases, a learned response (Graham et al. 2005, Woodroffe et al. 2005) not to be encouraged. Gray wolf (*Canis lupus*) advocates in the United States, for example, have advised against the use of livestock meat to bait carnivores, especially when those carnivores have the potential to depredate livestock, as it may train a behavioral response to livestock in previously non-problematic individuals (Greater Yellowstone Coalition 2012). Finally, many domestic livestock species carry diseases that could be easily transmitted to wild ungulates (e.g., Henderson and Brooksby 1948, Alexandersen et al. 2003), further evidencing that domestic livestock meat is not a responsible choice for bait. However the alternative, use of local game meat, also poses difficulties. For example, as of 2014 Botswana no longer allows any game or trophy hunting (Donovan 2013). Some collection is still allowed for research purposes in Botswana, but such permits are increasingly hard to procure, as was the case on the study site (Snyman 2013, *pers. comm.*).

This study aimed to evaluate the effectiveness of cooking fat as a bait alternative for sampling carnivores in eastern Botswana, with consideration given to detection rates and accessibility in a bush camp. We investigated the use of meat and used cooking fat as bait for all predator groups. We studied the effectiveness of cheese cloth soaked in spent cooking fat (fat rags), the latter being a plentiful waste product produced in most bush camp kitchens, as compared to locally harvested impala meat and unbaited control cameras, in estimating occupancy and detection rates among carnivores. We hypothesized that detection rates associated with cooking fat baits were greater than or not different from detection rates associated with impala meat baits, and that detection rates associated with either bait type would be higher than those for control sites for all species. Further, we investigated the effect of habitat type as an occupancy covariate in the analysis to determine the use and importance of this habitat for species in the region, especially in light of declines in riverine habitat. It is our goal that future studies of carnivores, and particularly mesopredators, in the region will benefit from the species-specific sampling methods and habitat preferences outlined here.

## METHODS

### *Study area*

Research was conducted within the Mashatu Game Reserve (henceforth “Mashatu”), an approximately 25,000 ha unfenced patchwork of private land holdings in eastern Botswana (-22°10' S, 29°3' E) (Mashatu Game Reserve 2013), allowing a unique opportunity to study an open system in this region (Figure 2.1). The 3,300 ha study area lies in a western land holding within Mashatu (22°13' S, 28°58' E) (Figure 2.1), leased by EcoTraining, a wilderness guide training and education company. Mashatu lies within the Northern Tuli Game Reserve (Notugre), a 75,000 ha property bordered on three sides by the Matloutse, Limpopo, and Shashe Rivers. Notugre is a portion of the proposed 490,000 ha Greater Mapungubwe Transfrontier Conservation Area (GMTFCA), which would span across Botswana, Zimbabwe, and South Africa. Thus, while connected to vast expanses of conservation land, the site is in close proximity to farms, villages, and other game reserves.

The area is part of the Zambezian and Mopane woodland ecoregion within the larger Southern African Bushveld biome containing tropical and subtropical grasslands, savannas, and shrublands (WWF 2014*a*). Average temperature extremes are -4°C and 46°C (WWF 2014*b*). Average annual total rainfall varies between 450mm and 710mm, with most precipitation falling during the wet, summer months spanning from November to April (WWF 2014*a*). The area is mostly flat with a few rocky outcrops (kopjes) and an average elevation of approximately 550m (Mashatu Game Reserve 2013). Dominant flora include stunted mopane (*Colophospermum* *mopane*) woodland, mixed flats of umbrella thorn (*Acacia tortilis*) and mustardbush (*Salvadora australis*), with bands of large fever berry (*Croton megalobotrys*) thickets along riverbanks. Recorded temperatures during the dry winter months of the study ranged from -1°C to 40°C. Annual total rainfall for Mashatu itself averages 400mm. Drought hit the reserve in 2012 with water sources beginning to dry up in April - several months early. Annual rainfall was 101.5mm for the year (Mashatu Game Reserve 2014). In contrast, 2013 was unseasonably wet with widespread flooding and 300mm of rain falling in January alone (IFRC 2013, Mashatu Game Reserve 2014).

The nearby Solomon's Wall, a natural feature which at one time dammed the Matloutse River and caused widespread flooding, rendered the study area's soils rich in nutrients. Thus, the site supports abundant wildlife. The members of Carnivora known to inhabit the area include the lion, leopard, cheetah, spotted hyena, brown hyena (*Hyaena brunnea*), aardwolf (*Proteles cristata*), black-backed jackal, bat-eared fox (*Otocyon megalotis*), African wildcat (*Felis silvestris lybica*), African civet, honey badger, large-spotted genet (*Genetta tigrina*), small-spotted genet (*G. genetta*), banded mongoose, Selous' mongoose, slender mongoose (*Galerella sanguinea*), dwarf mongoose (*Helogale parvula*), and white-tailed mongoose (*Ichneumia albicauda*). Besides lion and leopard, the only other "big five" game on-site is the African elephant (*Loxodonta africana*). Of the remaining two species listed as "big five" game, rhinoceroses (*Diceros bicornis*, *Ceratotherium simum*) do not inhabit the area, and until late 2013, Cape buffalo (*Syncerus caffer*) were shot on site if they managed to cross into Notugre due to concerns over transmission of hoof-and-mouth disease (*Aphthae epizooticae*) to livestock (Snyman 2013, *pers. comm.*).

African wild dogs historically occupied the area but were extirpated. In 2008, 18 individuals were reintroduced to Mashatu as part of the Northern Tuli Predator Project. In July 2012, just before the current study began, the pack was found poisoned by the pesticide Temik®, rendering wild dogs once again locally extinct (NTPP 2014). This event was indicative of the more widespread human-carnivore conflict that exists in the region. Thus, it is unlikely that African wild dogs were resident on the site at the time of the study.

All research was conducted under Institutional Animal Care and Use Committee (IACUC) approval under Animal Use Protocol (AUP) number A2013 04-002-Y1-A0 and Ministry of Environment, Wildlife, and Tourism Research Permit EWT 8/36/4 XXV (37).

### *Field methods and study design*

This study consisted of camera trapping using Moultrie M80 Game Spy infra-red-triggered game cameras housed in a metal box and locked to a tree or shrub to prevent theft by people and damage by animals, especially elephants. Cameras operated 24 hr $day^{-1}$ during sampling periods in July and August of 2012 and June, July, and August of 2013 (Table 2.1). Trapping in 2012 served as a pilot study for trapping in 2013. Three bait types were assessed: control sites, impala meat sites, and fat rag sites. All cameras were placed at approximately 0.5m high in order to target the full size range of the carnivore community. Extra branches and high grasses were cut away from the camera lens to reduce the frequency of accidental triggers.

In 2012, impala meat baits were placed along roads at intervals of approximately ~1 km or greater apart. Placement along roads was implemented both for researcher safety, and to increase the change of encountering carnivores. Similarly, fat rag and control sites were placed along roads and alternated every ~0.5 km. Thus, sites of the same bait type were ~1km or greater from one another.

Once again in 2013, systematic random site placement was used such that fat rag and control sites were alternated every ~0.5 km. Impala meat sites were then selected within 100m or less of previous control sites, preserving ~1km distance between sites of the same bait type. Fat rag sites remained in the same locations throughout the study. Baits were refreshed on all sites on the same day each week. Cameras were also checked for functionality and battery life at all sites at least once between bait refreshments.

To assess effect of habitat, half of the sites within each bait type each year were placed along the Matloutse River in large fever berry thickets (river sites), while the other half were placed away from the river in mopane, mustardbush, and umbrella thorn flats (upland sites). Thus, n=5 sites were sampled for each habitat type within each bait type for all periods, except control sites in 2013, where n=4 for river sites and n=5 for upland sites due to a camera malfunction (Table 2.1). All river sites were >1km from any upland site throughout the study (Figure 2.2).

### *Bait collection and site set-up*

Control sites required only a single tree or shrub on or near a road or game trail. Impala meat and fat rag sites were also chosen on or near roads and game trails to standardize the probability that an animal would encounter a sampling site by chance.

Two male impala were harvested off the property on the first day of the impala meat study each year. Each impala was field dressed and divided into five parts consisting of the combined head and ribcage plus four body quarters. Thus, 2 impala yielded all 10 baits needed for each year’s study. Impala sites required one tree with a low, overhanging branch plus a second tree or shrub located 8-10m away. One piece of impala meat was tied securely to the overhanging branch, while the camera was attached to the other plant. Branches were selected so as to make access by leopards or other tree-climbing carnivores difficult or impossible. However, one impala site had to be moved during the first week of the study in 2013 as the branch selected was found to be easily accessible to leopards, compromising the bait. Entrails were distributed evenly among the impala meat sites. A portion of the rumen contents were distributed at each site to further attract predators. During the subsequent two bait refreshment periods, approximately 0.5L of a 50/50 mixture of the remaining rumen contents and water (added to keep the substance moist) was poured over the original piece of meat to enhance scent. No meat was replaced during the study period either year due to the difficulty in securing harvest permits.

Each week the camp cooked meals of vegetables, eggs, chicken, beef, and pork using sunflower oil, olive oil, and butter. Liquid fat left over after cooking was stored throughout the week. Further, fat was collected and stored each week after cleaning the kitchen's fat trap. The camp has not reported any issues with carnivores attempting to enter the kitchen to access food or stored fat. A fat trap separates fat and food particles out of wash water so that only graywater drains into a septic system, preventing clogs. Squares of cheese cloth were cut to 30cm x 30cm and fully submerged in this mixture so as to allow the fat to soak through. The resulting squares were used as bait for the fat rag sites. These sites required two trees or shrubs located approximately 3-6m apart. One plant served as the camera post, while the other was cut at 0.5m as a bait post. A single fat rag was strapped to the top of each bait post using cable ties.

If fat rags were found to be completely removed from posts during battery checks between bait refreshments, a small piece of cheesecloth approximately 5cm x 15cm was cable tied to the post and drizzled with approximately 0.25oz of fat mixture. This was not intended to be a bait refreshment. Rather, it served to distract visiting individuals from simply chewing on the bait post itself until the next scheduled bait refreshment, thus preserving the posts for the duration of the study.

*Bayesian community analysis*

To test the effectiveness of fat rag baits as a potential substitute for impala meat, we began by calculating the probability of occupancy $(\psi_{ij})$ and detection $(p_{ij})$ of species $i\ (=1,\ldots,N)$ at site $j\ (=1,\ldots,J)$ for control, fat rag, and impala meat baits separately for each year. Occupancy is a measure of true species presence or absence at a site; therefore, a site was known to be occupied $(\psi_{ij}=1)$ if a species was detected at least once at that site during the sampling period. Detection is a measure of how likely it is that a species will be observed at the site given that it occupies the site.

We define a "site" as the point at which a camera is placed, plus a circle of radius 0.5 km or less (area of ~0.79 km$^2$) around that point. Because sites of the same bait type were placed approximately 1 km apart, if a species traveled more than 0.5 km away from a bait, it would no longer be within the associated site. Instead, it would have crossed over the midway point between baits, and thus be in closer proximity to and within the defined site of another bait, or otherwise outside the study area entirely. For species that would be attracted to both fat rags and impala baits, the site area would be even smaller. That is, the camera and bait location, plus a circle of radius 0.25 km or less (area of ~0.20 km$^2$) around that point. This is because all sites were approximately 0.5 km apart. Thus, once an individual is more than 0.25 km away from one bait, the individual would again have crossed over the midway point between baits, and thus be in closer proximity to and within the defined site of another bait, or otherwise outside the study area entirely.

We do acknowledge the confounding effect of these indeterminate plot sizes, as discussed by Efford and Dawson 2012. Further, we acknowledge the undefined distance from which an individual could be drawn in from outside the study area due to acute sense of smell, making an estimate of maximum site area problematic for sites at the edge of the study area. For example, brown hyenas can smell scents of even old carcasses from at least 2 km away (Mills and Hofer 1998). Due to these concerns, combined with the fact that this study is more concerned with the detection process than with the occupancy itself, we will not place great emphasis on interpretation of species spatial use resulting from the occupancy portion of this analysis.

We assumed a closed model whereby a site, either occupied or unoccupied, remained in that status throughout the course of the study each year. Four possible true conditions may result from each sampling occasion: a species is present and observed (detection), a species is present and not observed (imperfect detection), a species is not present and not observed (true absence), or a species is not present but observed (error in data collection). We disregard the latter possibility here as we isolated photographs in which an animal was present but species was uncertain. If we were unsure of a species identification, we sought confirmation by a second researcher familiar with the study area in a blind trial. If the species could still not be confirmed, or if no identification could be made (e.g., a blurred photo of a tail tip), then we excluded the data from analysis. Thus, we assumed that estimates of occupancy were confounded only by imperfect detection $(p_{ij} < 1)$. By estimating how often a species is present but undetected over repeated sampling among sites known to be occupied $(p_{ij} > 0$ for at least one sampling occasion $(k = 1, \ldots, K)$ implies that $\psi_{ij} = 1$ for all sampling occasions), we can improve occupancy estimates by inferring the number of sites at which no detections occurred (and thus naïve occupancy $= 0)$ but at which the species may have been present.

We built hierarchical community models following Dorazio and Royle (2005) and Zipkin et al. (2010) to assess individual species occupancy and detection resulting from each bait type each year. The community model approach allows individual species estimates as described above to be improved by combining data from all species of the community in question (Dorazio and Royle 2005, Dorazio et al. 2006). The basic assumption is that $\psi_{ij}$ is influenced by a species-level effect independent of site $(u_i)$ *and* by a site-level effect on occurrence independent of species $(\alpha_j)$. Similarly, it is assumed that detection, $p_{ij}$, is influenced by a species-level effect $(v_i)$ *and* by a site-level effect $(\beta_j)$. In other words, characteristics of each site have some constant effect on the occupancy and detection of all species in the community. The following logit-scale linear combinations result (Dorazio and Royle 2005):

$$\begin{aligned} \text{logit}\,\psi_{ij} &= u_i + \alpha_j, \\ \text{logit}\ p_{ij} &= v_i + \beta_j. \end{aligned} \tag{1}$$

We modeled $\alpha_j$ as $\beta_j$ with linear combinations of parameters representing site-level covariates. We incorporated habitat (river or upland) as a covariate on occupancy, and bait type (control, fat rag, or impala) as a covariate on detection. This resulted in the following models:

$$\begin{aligned} \text{logit}\,\psi_{ij} &= u_i + \alpha_i \bullet IndR_j, \\ \text{logit}\ p_{ij} &= v_i + \beta_{1i} \bullet IndI_j + \beta_{2i} \bullet IndF_j, \end{aligned}$$

where $\alpha_i$ is the effect of river on $\text{logit}\,\psi_{ij}$, $\beta_{1i}$ and $\beta_{2i}$ are effects of bait type on $\text{logit}\ p_{ij}$, and $IndR_j$ , $IndI_j$ , and $IndF_j$ are binary indictor vectors for river habitat sites, impala bait sites, and fat rag bait sites, respectively. We defined a sampling occasion as a 24-hour period beginning and ending at sunrise each day. Days that cameras did not collect data (e.g., battery died, elephants redirected the camera field of view, etc.) were censored in the analysis. The resulting conditional likelihoods for occupancy within each habitat type each year, and detection of individual species within each bait type each year, along with 95% Bayesian credibility intervals, were calculated using Program R version 3.0.2 and WinBUGS version 1.4.3 under a Bayesian framework (n=3 chains, n=30,000 iterations/chain, n=5,000 burn-in, n=5 thinning) (Figure 3) (Lunn et al. 2000, R Core Team 2013).

To further investigate the species-level effects of habitat on occupancy and bait on detection, we computed the probability that a parameter was greater than zero as a test of significance (Table 3). For bait parameters, impala and fat rags sites were each compared to the unbaited control sites. For the habitat parameter, river sites were compared to upland (reference) sites. When the estimate value is equal to 0, it shows no difference from the control or reference. Thus, a p-value of 0.5 would coincide with estimates centered at 0, and show no trend towards or away from a factor level. Alternatively, values above or below 0.5 indicate trend toward the chosen factor or toward the reference, respectively. The magnitude of each effect was also reported as the mean parameter estimate along with the upper and lower 95% Bayesian credibility intervals (BCI).

## RESULTS

Thirteen of the eighteen carnivore species believed to inhabit the study area (72%) were detected. Dwarf mongoose, and Selous' mongoose were not observed during the study in 2012 or 2013. White-tailed mongoose was detected in 2013 only. Also 2013, a single detection of aardwolf likely occurred, but the species identity was not conclusive due to poor photo resolution, and thus this detection was not included in the analysis.

The community analysis with habitat as a covariate yielded no significant differences among occupancy values for any species in 2012 (Figure 2.3), but in 2013 differences were found for African civets and brown hyenas, with increased occupancy in river areas for both species (Figure 2.5). In 2012, no significant differences in detection rates were observed among the three bait types (Figure 2.4). This was likely due to low sample sizes during this pilot year (Table 2.3). In 2013 differences in detection rates among bait types were found for five species (Figure 2.6).

In 2013, detection rates for brown hyenas were significantly different among all bait types, with impala meat sites yielding a higher detection rate than fat rag sites, and fat rag sites yielding a higher detection rate than controls. Similarly, a significant difference was found for spotted hyenas, with impala meat yielding a higher detection rate than either fat rag or control sites. Impala meat and fat rag sites yielded similar detection rates for both jackals and civets, with these bait types yielding a significantly higher rate than the control in both cases. Finally, the fat rag detection rate for large-spotted genets was significantly higher than either control or impala sites, which were not significantly different from each other (Figure 2.6).

The analysis of the parameter estimates supported and informed results from the occupancy and detection analysis (Table 2.3). P-values indicated the probability of the specified hypothesis. For bait covariates, p-values represented the probability that the indicated bait increased detections as compared to control sites. Support existed for one or both bait types for almost all species both years. The only exceptions were spotted hyena and leopard, which exhibited a p-value of 0.31 and 0.22, respectively, for fat rag baits in 2013. The magnitude of these effects was given by the mean value and 95% Bayesian confidence interval. The impala meat effect was significant and positive for African wildcat in 2012 and for African civet, black-backed jackal, brown hyena, honey badger, leopard, small-spotted genet, and spotted hyena in 2013. The fat rag effect was significant and positive for large-spotted genet in 2012 and for African civet, African wildcat, black-backed jackal, brown hyena, and large-spotted genet in 2013. For the habitat covariate, p-values represented the probability that river sites has increased occupancy as compared to upland sites. Support was found for African civet, African wildcat, black-backed jackal, banded mongoose, honey badger, and large-spotted genet in 2012, and for all species except bat-eared fox, small-spotted genet, and spotted hyena in 2013. This indicates that the occupancy probability was higher in riverine areas for these species. The river effect was significant and positive for large-spotted genet in 2012 and for African civet, African wildcat, banded mongoose, brown hyena, honey badger, large-spotted genet, and leopard in 2013.

## DISCUSSION

Large carnivores are often the focus of research efforts, and are frequently used as biodiversity indicators (Ray et al. 2005, Dalerum et al. 2008, Ripple et al. 2014). This is especially true in southern Africa, where conservation areas are increasingly divided and fenced off, leading to increased conflict with villagers over land use and access (Hayward and Kerley 2009). In contrast to studies on resident large predators such as the African lion (*Panthera leo*), leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) and spotted hyena (*Crocuta crocuta*) (e.g., Ripple et al. 2014, Woodroffe et al. 2007, Hayward et al. 2007), scant research exists on basic aspects of medium and small carnivore ecology in southern Africa, particularly information on distribution and preferred sampling methods (Blaum et al. 2009, Holmern and Røskaft 2013).

This lack of attention may be due to the fact that, with the exception of black-backed jackals (*Canis mesomelas*) (Gusset et al. 2009), a mid-sized canid, larger predators are most likely to come into conflict with livestock herders (Ogada et al. 2003) and that research dollars are often more available for large, charismatic megafauna (Wilkie and Carpenter 1999, Scholfield and Brockington 2009). Ray et. al. suggest that this lesser focus on smaller carnivores also may be due to a reduced risk of extinction among the group as compared to larger carnivores (Ray et al. 2005). However, even where this is true, Redford et. al. strongly caution against the "crisis-oriented" approach that prevails in conservation, that is, measuring conservation need by risk of extinction rather than true health and viability of a population (Redford et al. 2011). Further, some obscure mesopredator species, such as Selous' mongoose (*Paracynictis selousi*), have been studied in few published papers at all (Caro and Stoner 2003). When they are studied, research of medium and small carnivores is frequently motivated by linkages to zoonoses (e.g. banded mongoose (*Mungos mungo*) as carriers of leptospirosis), human use (e.g. civet (*Civettictis civetta*) musk and civet coffee), or crop predation (e.g. honey badgers (*Mellivora capensis*) raiding chicken coops) (Jobbins et al. 2013, Marcone 2004, Holmern and Røskaft 2013), with less attention paid to empirical exercises in ecology or species biology.

To fill this gap in knowledge, we assessed habitat use and bait preferences of the carnivore community in eastern Botswana using baited camera traps during the winter of 2012 and 2013. Results suggest that fat rags may be substituted for impala meat when sampling the mesopredator community in eastern Botswana, whereas studies on large carnivores may not benefit from this method. Of the large carnivores, lions were not detected at all, either due to ineffectiveness of bait, or as a result of the low lion density on the study site and generally large home range sizes of lions as compared to the sampling area (Snyman 2010). Results suggest that meat is preferred to fat rags when sampling both brown and spotted hyenas. These results were supported by significant effect sizes for impala sites for both species in 2013. However, brown hyenas did display higher detections at fat rag sites than at control sites, a result supported by the 2013 estimated effect, suggesting that this method might be used for this species in some cases. Similar detection rates were observed for leopards among all bait types according to the analysis of detection rate. However, the Bayesian confidence interval for fat rags and impala detection rates overlapped at the extremes of these intervals, and the effect size for impala bait was significant compared to control sites. Further, photographs themselves revealed that leopards spent time attempting to eat impala baits while no such effort was made at fat rag stations, suggesting that fat rag detections may have been chance encounters rather than deliberate visits to a bait site. Thus, meat baits are likely an excellent bait for these larger carnivores. However, logistical constraints limit application.

Fat rag baits did yield similar detection rates to impala meat for all medium and small carnivores except for large-spotted genets, where fat rag baits significantly increased the detection rate. The estimates of this effect was consistent across both years. This result is particularly notable due to the fact that insufficient data exists on population trends of the large-spotted genet (Table 2.2). Methods for increasing detection of this species would be useful in future surveys. Bait (impala or fat rag) increased detection rates for civets and jackals as well, suggesting that use of bait for these species may be beneficial. The estimated effects further suggested that fat rag baits increase African wildcat detections, and that impala baits increase honey badger and small-spotted genet detections. Bat-eared fox were only detected at control and fat rags sites, supporting the use of fat rags as bait for the species, however due to low detection rates these results might be due to chance.

Future research requiring camera trapping or live capture of large carnivores and meso-mammal predators in southern Africa will benefit from the findings presented here. Investigators can use the habitat preferences noted to select trapping sites appropriate for their target species. Studies on the meso-mammal predator complex in southern Africa that use fat rags as lure will likely benefit from similar or increased species detections with lower costs and far fewer logistical and permit requirements as compared to those that employ meat as bait. The fat rag method eliminates the need for harvesting meat on-site, storing meat in camp, or shipping meat in from an external source. Further, it provides a use for a waste product found in most bush camps. Finally, and perhaps most importantly, fat rags may also help in studying meso-mammal predators in areas where large predators are common, by specifically targeting and attracting these subordinate carnivores. Use of a universal bait preferred by large and small carnivores alike, such as impala meat, when attempting to trap a specific, and perhaps uncommon carnivore species, can logically result in a situation whereby the target species avoids the bait site due to the presence of dominant, interspecific competitors. Use of fat rag baits for meso-mammal predator studies may reduce the effects of interspecific competition from larger carnivores at bait sites, target this smaller guild, make use of a readily available waste product, and potentially alleviate some of the logistical issues inherent in the use of meat baits. Further, the results of this study support the use of cameras or trapping sites baited with fat rags as a suitable option for future monitoring programs in southern Africa focused on meso-mammal predators.

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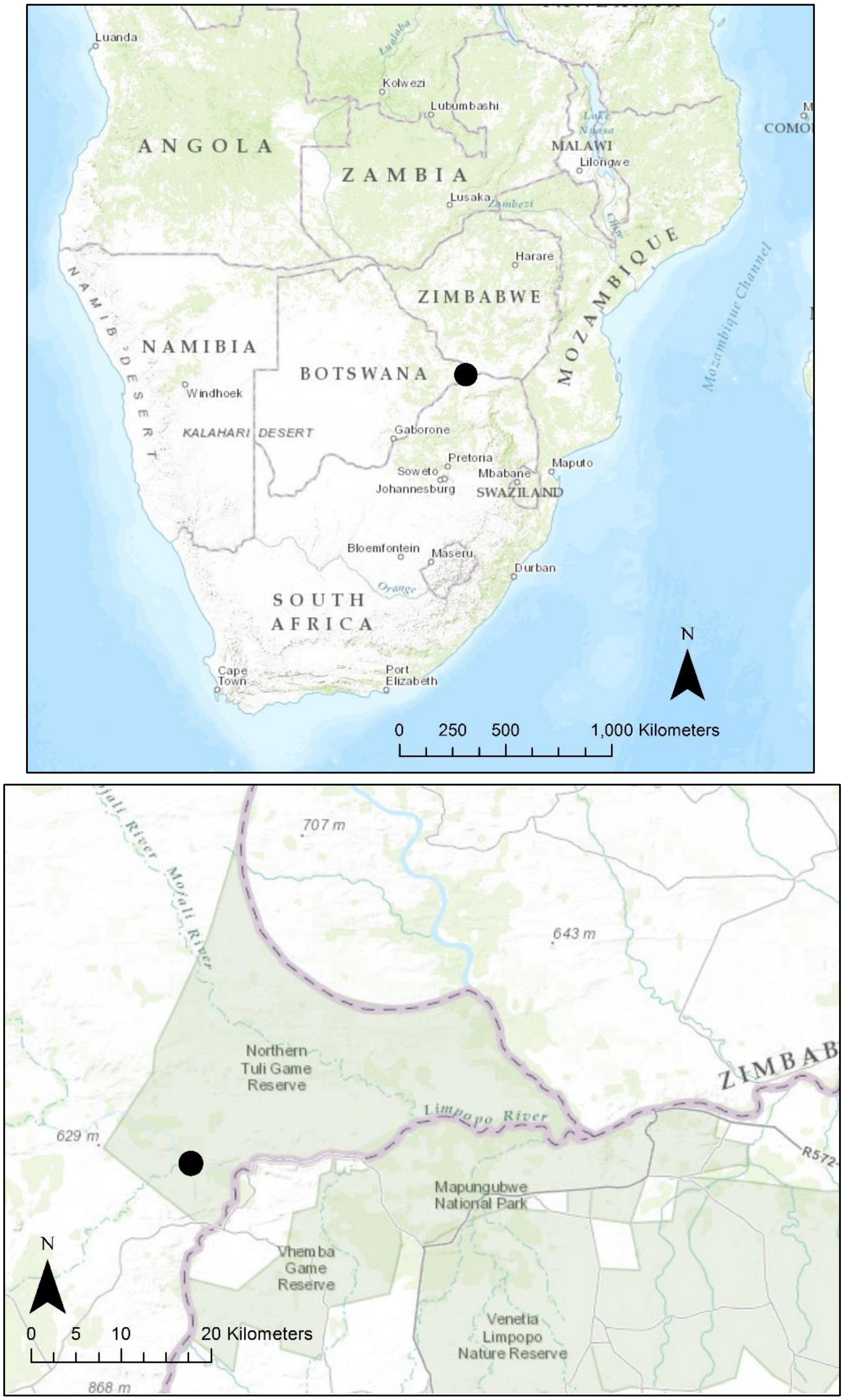

**Figure 2.1:** Map of southern Africa (top) and location of the study area within the Northern Tuli Game Reserve, Botswana (bottom). Study site is indicated by a black dot, and is situated near the intersection of the borders of Botswana, Zimbabwe, and South Africa. The site itself lies along the Motloutse River. Game reserves, private farms, and villages blanket the surrounding area.

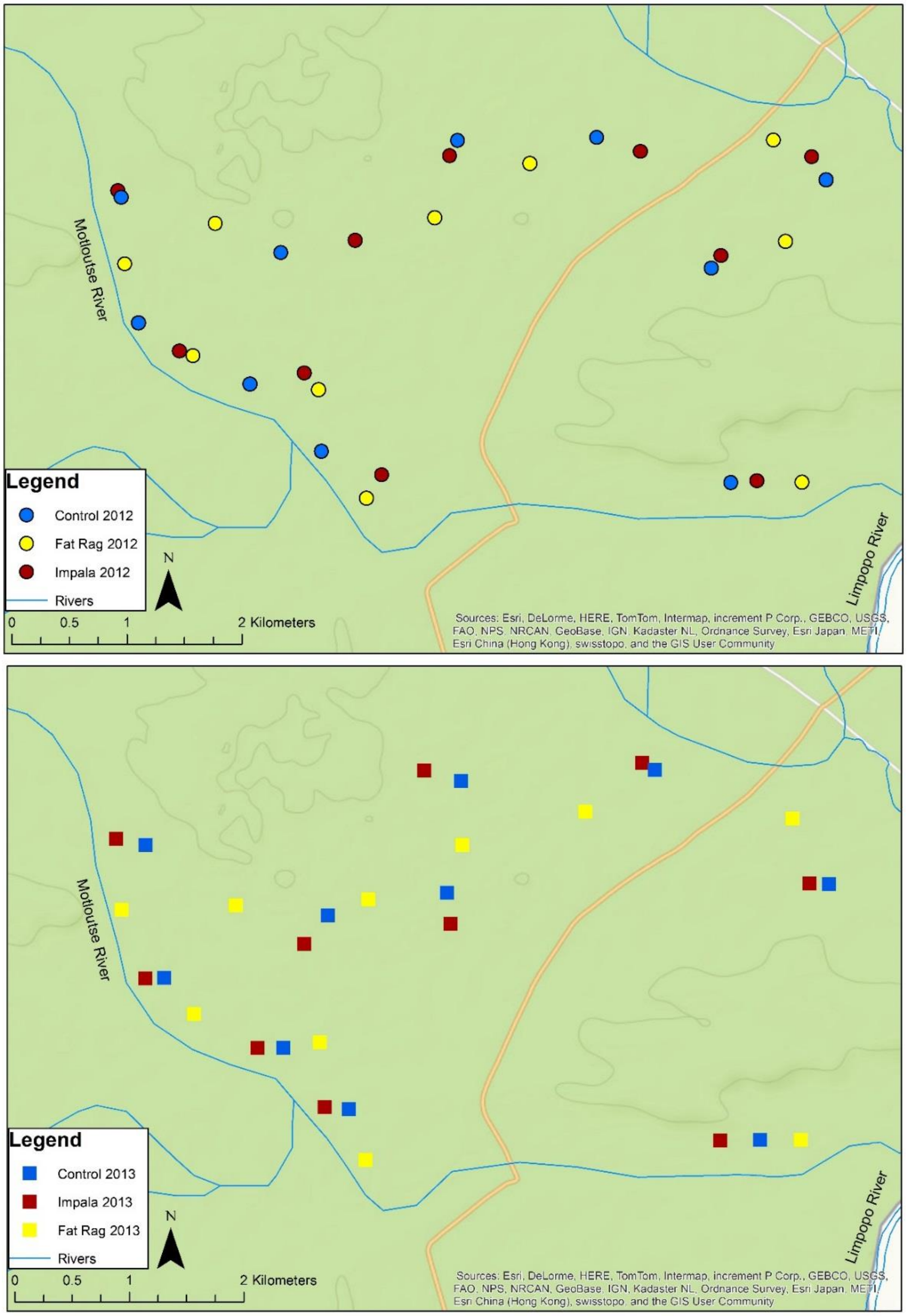

**Figure 2.2:** Map of camera locations by bait type on the study site for 2012 (top) and 2013 (bottom) on the Mashatu Game Reserve, Botswana. In 2012, fat rag and control sites were sampled concurrently, while impala meat sites were set at a different time. Similarly, in 2013, control and fat rag sites were sampled concurrently, and then fat rag and impala sites were sampled concurrently.

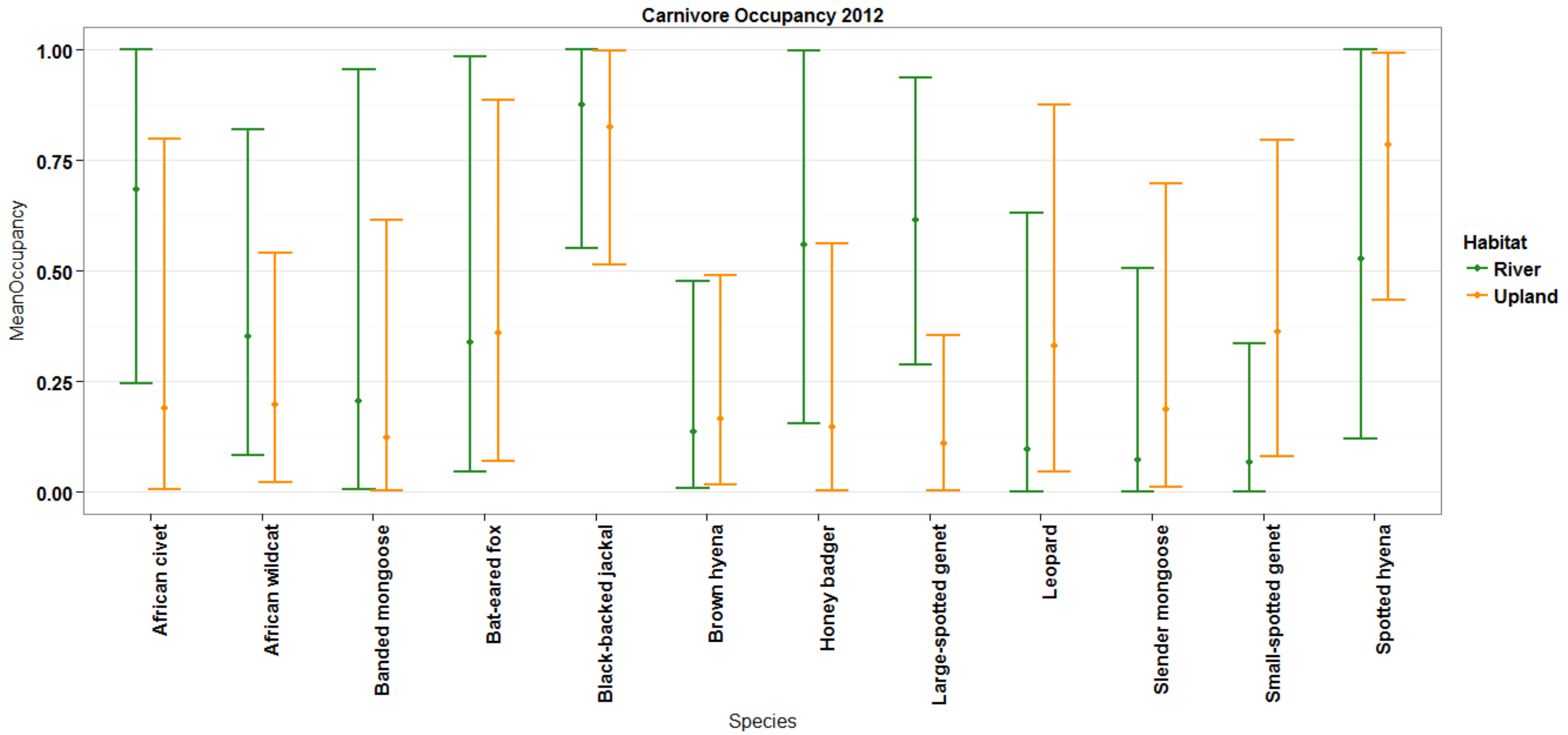

**Figure 2.3.** Mean occupancy of carnivore species on the Mashatu Game Reserve, Botswana in 2012. Mean occupancy estimates and 95% Bayesian credibility intervals are shown for each habitat by species. No significant differences in habitat preference within species were found in 2012.

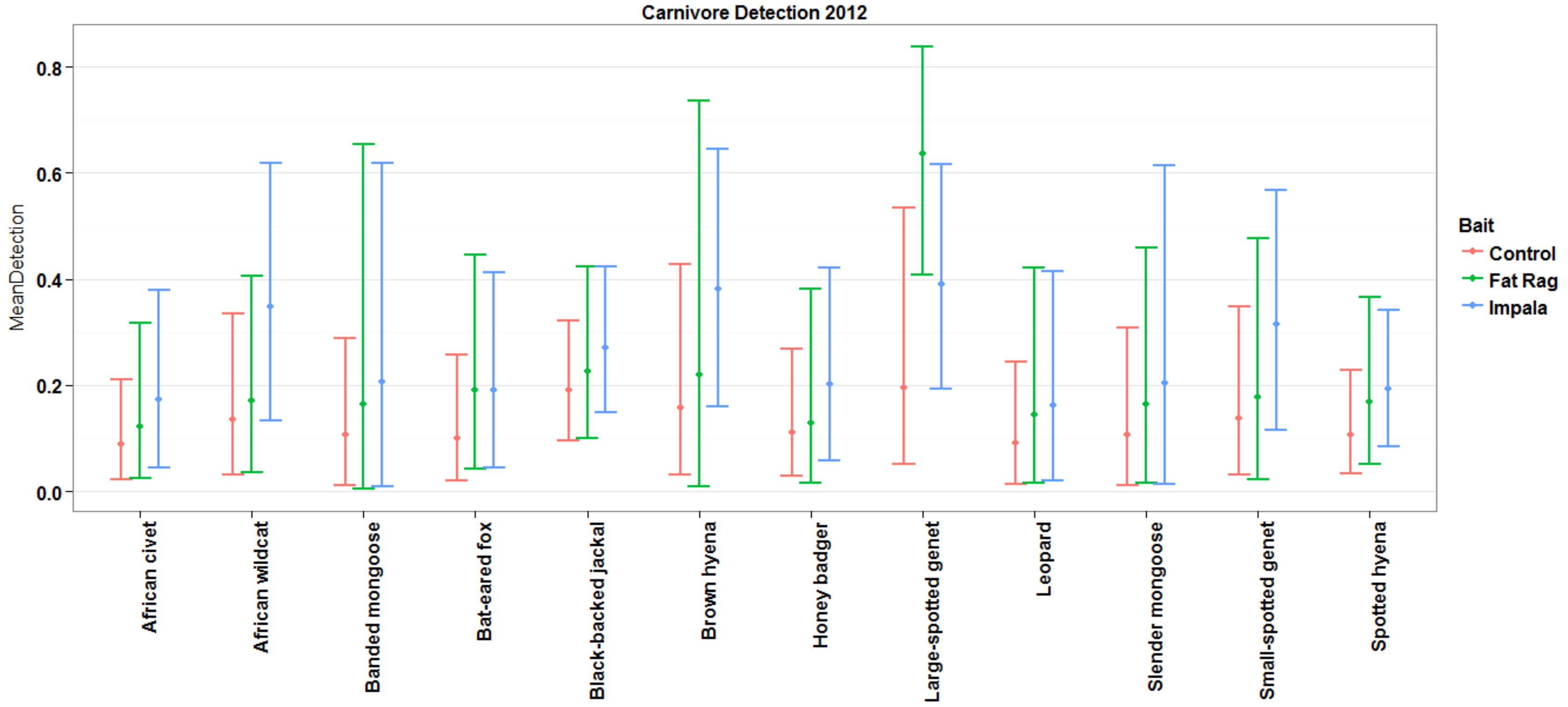

**Figure 2.4.** Mean detection of carnivore species on the Mashatu Game Reserve, Botswana in 2012. Mean detection estimates and 95% Bayesian credibility intervals are shown for each bait type by species. No significant differences in detection by bait type was found for any species in 2012. Note that while detection estimates span from 0 to 1, the y-axis is truncated at the highest detection value.

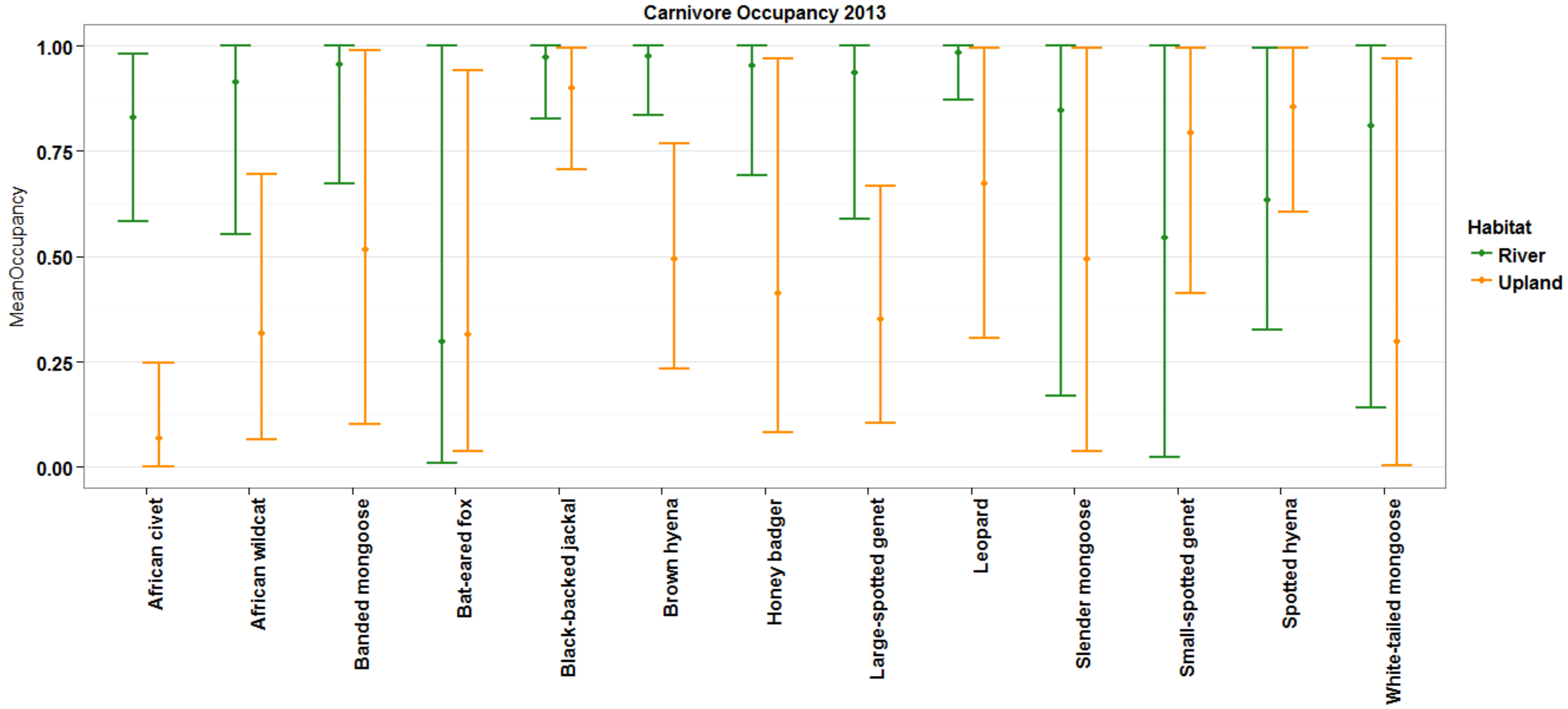

**Figure 2.5.** Mean occupancy of carnivore species on the Mashatu Game Reserve, Botswana in 2013. Mean occupancy estimates and 95% Bayesian credibility intervals are shown for each habitat by species. In 2013, African civet and brown hyena showed a significant difference in habitat preference, with higher occupancy at river sites.

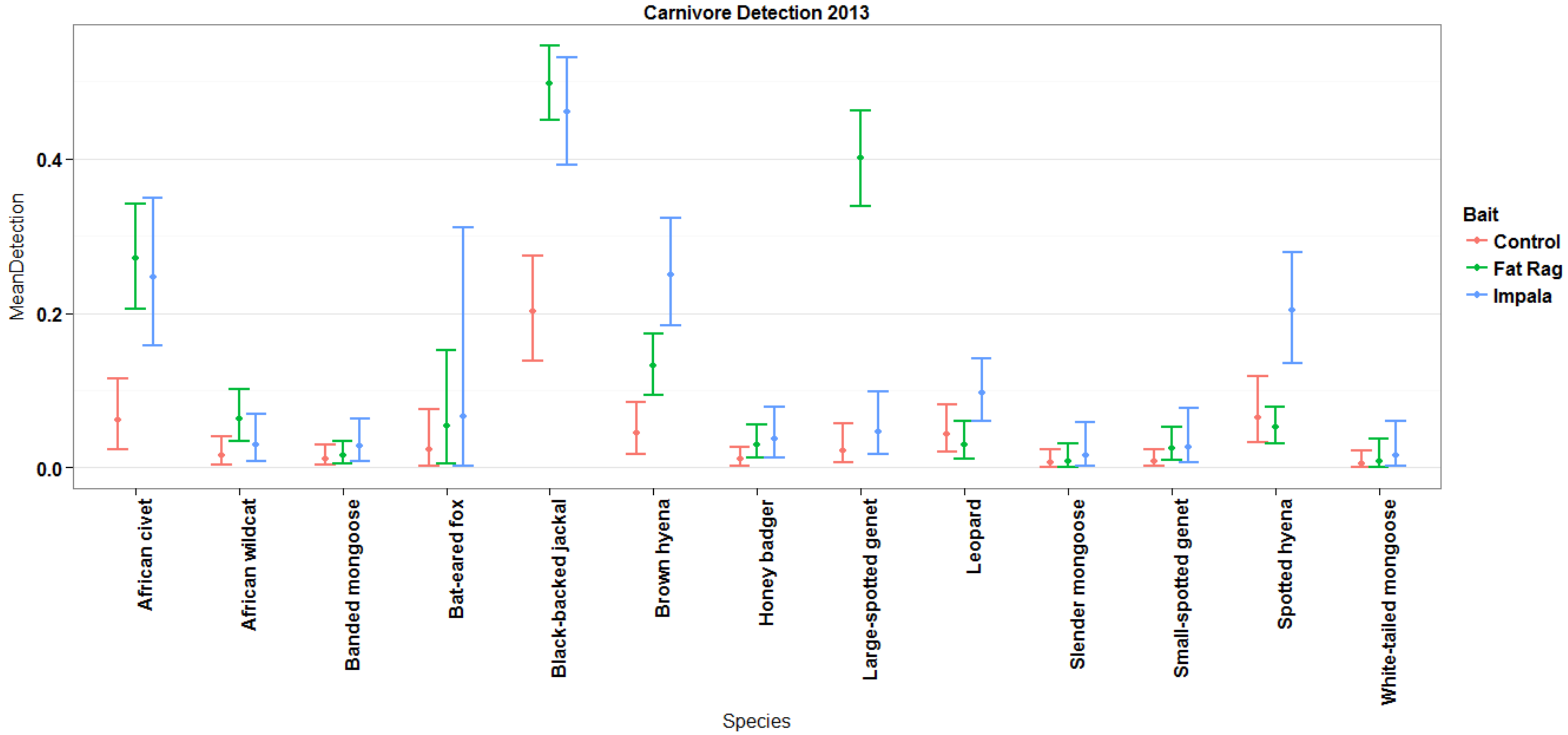

**Figure 2.6.** Mean detection of carnivore species on the Mashatu Game Reserve, Botswana in 2013. Mean detection estimates and 95% Bayesian credibility intervals are shown for each bait type by species. Significant differences in detection by bait by species were found in 2013. In general, large carnivores had higher detections at impala meat sites, while smaller carnivores had higher detections at baited sites as compared to unbaited sites, or otherwise no differences in detection were found. Small-spotted genets had highest detection at fat rag sites. Note that while detection estimates span from 0 to 1, the y-axis is truncated at the highest detection value.

**Table 2.1.** Characteristics of study design and camera sampling effort.

| Year | Dates | Bait type | n Sites | Paired | 24 hr Periods | Effort (days) |
|---|---|---|---|---|---|---|
| 2012 | 22 Jul – 28 Jul | Impala Meat | 10 | Yes[1] | 6 | 60 |
| | 31 Jul – 5 Aug | Control | 10 | No | 5 | 50 |
| | 31 Jul – 5 Aug | Fat Rag | 10 | No | 5 | 50 |
| 2013 | 12 Jun – 2 Jul | Control | 9[2] | No | 20 | 180 |
| | 12 Jun – 22 Jul | Fat Rag | 10 | No | 40 | 400 |
| | 3 Jul – 22 Jul | Impala Meat | 10[2] | No | 19 | 190 |

[1] For the impala meat study in 2012, ten sites were established with two cameras each. Data from both cameras were combined to generate site-specific data for analysis.

[2] One of the initial 10 cameras failed during the control study in 2013 and had to be removed from that analysis. It was replaced with a Bushnell brand camera for the subsequent impala meat study.

**Table 2.2.** Members of the order Carnivora known to inhabit Mashatu Game Reserve. X denotes the bait type (CT=control, IM=impala meat, FR=fat rag) at which each was observed each year. International Union for Conservation of Nature and Natural Resources (IUCN) Red List status (LC=Least Concern, VN=Vulnerable, NT=Near Threatened, EN=Endangered) and IUCN population trend are also listed (IUCN 2013).

| | | | | | ***2012*** | | | ***2013*** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Family** | **Species** | **Common Name** | **IUCN Status** | **IUCN Trend** | **CT** | **IM** | **FR** | **CT** | **IM** | **FR** |
| Canidae | *Canis mesomelas* | Black-backed jackal | LC | Stable | X | X | X | X | X | X |
| | *Lycaon pictus* | African wild dog[1] | EN C2a(i) | Decreasing | | | | | | |
| | *Otocyon megalotis* | Bat-eared fox | LC | Unknown | | X | X | X | | X |
| Felidae | *Felis silvestris lybica* | African wildcat | LC | Decreasing | | X | X | X | X | X |
| | *Panthera leo* | Lion | VN A2abcd | Decreasing | | | | | | |
| | *Panthera pardus* | Leopard | NT | Decreasing | | X | X | X | X | X |
| Herpestidae | *Helogale parvula* | Common dwarf mongoose | LC | Stable | | | | | | |
| | *Herpestes sanguineus* | Slender mongoose | LC | Stable | | | X | X | X | X |
| | *Ichneumia albicauda* | White-tailed mongoose | LC | Stable | | | | | X | X |
| | *Mungos mungo* | Banded mongoose | LC | Stable | X | | | X | X | X |
| | *Paracynictis selousi* | Selous' mongoose | LC | Unknown | | | | | | |
| Hyaenidae | *Crocuta crocuta* | Spotted hyena | LC | Decreasing | X | X | X | X | X | X |
| | *Hyaena brunnea* | Brown hyena | NT | Decreasing | | X | | X | X | X |
| | *Proteles cristata* | Aardwolf | LC | Stable | | | | ?[2] | | |
| Mustelidae | *Mellivora capensis* | Honey badger | LC | Decreasing | X | X | X | | X | X |
| Viverridae | *Civettictis civetta* | African civet | LC | Unknown | X | X | X | X | X | X |
| | *Genetta genetta* | Small-spotted genet/Common genet | LC | Stable | | X | X | | X | X |
| | *Genetta tigrina* | South African large-spotted genet | LC | Unknown | | X | X | X | X | X |

[1] Note that it is unlikely that *L. pictus* was resident on-site during any study period. A lethal poaching event killed all resident pack members on 6 July 2012.

[2] One photograph believed to be *P. cristata* was recorded. However, it could not be verified due to poor resolution, and thus it was excluded from analysis.

**Table 2.3.** Table of estimates for covariate effects. P-values assess the percent of times out of n=3000 iterations that the parameter on the covariate was greater than that of the control or reference. For baits, impala and fat rags sites are each compared to control sites. For habitat, river sites are compared to upland (reference) sites. Magnitude is given by the mean estimate and the upper and lower 95% Bayesian credibility intervals (BCI). Significant effects (where the BCI does not include 0) are bolded and italicized.

|  | Covariate |  | *Bait: Impala ( $\beta_{1i}$ )* |  |  |  | *Bait: Fat Rag ( $\beta_{2i}$ )* |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| Year | **Species** | **n** | **p-value** | **Mean** | **L_BCI** | **U_BCI** | **p-value** | **Mean** | **L_BCI** | **U_BCI** |
| *2012* | African civet | 6 | 0.90 | 0.79 | -0.49 | 2.03 | 0.67 | 0.31 | -1.24 | 1.79 |
|  | African wildcat | 8 | ***0.98*** | ***1.34*** | ***0.05*** | ***2.93*** | 0.64 | 0.27 | -1.35 | 1.82 |
|  | Banded mongoose | 1 | 0.81 | 0.67 | -1.30 | 2.33 | 0.59 | 0.19 | -2.45 | 2.56 |
|  | Bat-eared fox | 6 | 0.89 | 0.79 | -0.50 | 2.12 | 0.84 | 0.77 | -0.73 | 2.35 |
|  | Black-backed jackal | 28 | 0.84 | 0.47 | -0.52 | 1.40 | 0.64 | 0.20 | -0.91 | 1.29 |
|  | Brown hyena | 6 | 0.97 | 1.35 | -0.02 | 3.03 | 0.59 | 0.17 | -2.41 | 2.52 |
|  | Honey badger | 6 | 0.89 | 0.74 | -0.51 | 1.98 | 0.53 | 0.01 | -1.92 | 1.63 |
|  | Large-spotted genet | 23 | 0.95 | 1.10 | -0.28 | 2.54 | ***0.99*** | ***2.17*** | ***0.35*** | ***3.93*** |
|  | Leopard | 2 | 0.83 | 0.64 | -0.90 | 2.06 | 0.70 | 0.45 | -1.40 | 2.23 |
|  | Slender mongoose | 1 | 0.82 | 0.70 | -1.14 | 2.36 | 0.72 | 0.48 | -1.39 | 2.31 |
|  | Small-spotted genet | 6 | 0.96 | 1.16 | -0.12 | 2.64 | 0.63 | 0.24 | -1.68 | 1.93 |
|  | Spotted hyena | 13 | 0.91 | 0.74 | -0.31 | 1.83 | 0.78 | 0.52 | -0.81 | 1.87 |

**Table 2.3. (cont'd)**

| | Covariate | | *Bait: Impala ($\beta_{1i}$)* | | | | *Bait: Fat Rag ($\beta_{2i}$)* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Year | **Species** | **n** | **p-value** | **Mean** | **L_BCI** | **U_BCI** | **p-value** | **Mean** | **L_BCI** | **U_BCI** |
| *2013* | African civet | 67 | ***1*** | ***1.68*** | ***0.84*** | ***2.69*** | ***1*** | ***1.82*** | ***0.98*** | ***2.81*** |
| | African wildcat | 8 | 0.85 | 0.65 | -0.74 | 1.76 | ***1*** | ***1.55*** | ***0.36*** | ***2.84*** |
| | Banded mongoose | 9 | 0.94 | 0.91 | -0.31 | 1.98 | 0.70 | 0.35 | -1.10 | 1.62 |
| | Bat-eared fox | 5 | 0.84 | 0.78 | -1.17 | 2.29 | 0.85 | 0.87 | -0.80 | 2.54 |
| | Black-backed jackal | 316 | ***1*** | ***1.23*** | ***0.75*** | ***1.73*** | ***1*** | ***1.38*** | ***0.92*** | ***1.86*** |
| | Brown hyena | 79 | ***1*** | ***2.02*** | ***1.21*** | ***2.99*** | ***1*** | ***1.23*** | ***0.43*** | ***2.19*** |
| | Honey badger | 13 | ***0.99*** | ***1.33*** | ***0.28*** | ***2.49*** | 0.97 | 1.13 | -0.08 | 2.42 |
| | Large-spotted genet | 105 | 0.93 | 0.84 | -0.33 | 1.88 | ***1*** | ***3.54*** | ***2.38*** | ***4.64*** |
| | Leopard | 32 | ***0.98*** | ***0.89*** | ***0.05*** | ***1.70*** | *0.22* | -0.41 | -1.47 | 0.63 |
| | Slender mongoose | 3 | 0.91 | 0.90 | -0.62 | 2.11 | 0.55 | 0.06 | -1.96 | 1.81 |
| | Small-spotted genet | 10 | ***0.98*** | ***1.23*** | ***0.03*** | ***2.40*** | 0.97 | 1.27 | -0.03 | 2.57 |
| | Spotted hyena | 53 | ***1*** | ***1.33*** | ***0.58*** | ***2.08*** | *0.31* | -0.22 | -1.06 | 0.60 |

## Table 2.3. (cont'd)

| | Covariate | | *Habitat: River ($\alpha_i$)* | | | |
|---|---|---|---|---|---|---|
| Year | **Species** | **n** | **p-value** | **Mean** | **L_BCI** | **U_BCI** |
| *2012* | African civet | 6 | 0.97 | 3.42 | -0.16 | 10.89 |
| | African wildcat | 8 | 0.78 | 0.98 | -1.30 | 3.69 |
| | Banded mongoose | 1 | 0.66 | 0.85 | -2.58 | 5.42 |
| | Bat-eared fox | 6 | *0.45* | -0.01 | -2.87 | 3.72 |
| | Black-backed jackal | 28 | 0.67 | 1.18 | -2.67 | 7.82 |
| | Brown hyena | 6 | *0.41* | -0.36 | -3.33 | 2.41 |
| | Honey badger | 6 | 0.96 | 2.96 | -0.21 | 8.54 |
| | Large-spotted genet | 23 | 1 | *3.16* | 0.56 | 6.81 |
| | Leopard | 2 | *0.10* | -2.99 | -10.99 | 1.09 |
| | Slender mongoose | 1 | *0.16* | -2.46 | -9.72 | 1.68 |
| | Small-spotted genet | 6 | *0.04* | -3.51 | -10.71 | 0.34 |
| | Spotted hyena | 13 | *0.21* | -1.09 | -4.79 | 5.25 |
| | *Total* | *106* | | | | |
| *2013* | African civet | 67 | ***1*** | ***5.03*** | ***2.40*** | ***8.83*** |
| | African wildcat | 8 | ***1*** | ***5.79*** | ***0.87*** | ***15.46*** |
| | Banded mongoose | 9 | ***0.98*** | ***6.25*** | ***0.00*** | ***19.58*** |
| | Bat-eared fox | 5 | *0.42* | 0.32 | -3.67 | 9.18 |
| | Black-backed jackal | 316 | 0.88 | 3.87 | -1.35 | 13.44 |
| | Brown hyena | 79 | ***1*** | ***7.24*** | ***1.49*** | ***22.16*** |
| | Honey badger | 13 | ***0.99*** | ***6.78*** | ***0.68*** | ***20.89*** |
| | Large-spotted genet | 105 | ***1*** | ***6.80*** | ***1.04*** | ***21.41*** |
| | Leopard | 32 | ***0.99*** | ***6.70*** | ***0.72*** | ***20.54*** |
| | Slender mongoose | 3 | 0.91 | 5.21 | -1.39 | 18.93 |
| | Small-spotted genet | 10 | *0.39* | 0.82 | -6.35 | 18.69 |
| | Spotted hyena | 53 | *0.13* | -1.34 | -4.59 | 3.39 |
| | White-tailed mongoose | 8 | 0.96 | 6.37 | -0.44 | 24.02 |
| | *Total* | *713* | | | | |

# CHAPTER 3

# TEMPORAL PARTITIONING OF THE 24-HOUR DAY AMONG MEMBERS OF THE CARNIVORE COMMUNITY IN EASTERN BOTSWANA[1]

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[1] Satterfield, L.C., Snyman, A., Candelario, L. and Carroll, J.P. To be submitted to *Oryx*.

## ABSTRACT

Temporal partitioning allows species to reduce competition for food and resources, or avoid predators or other aggressive species, by adapting activity times that optimize survival. Temporal partitioning has been studied in large African carnivores, but few studies exist exploring this strategy in medium and small carnivores (Waser 1980, Mills et al. 1984, Zielinski 1988). We used camera trapping data collected from June and July 2013 to investigate predator and prey activity on a portion of the 25,000 ha Mashatu Game Reserve, Botswana. All sizes of carnivore and prey were assessed. We classified photos into 15 minute intervals, only retaining one entry or "data event" per species per site per day for each interval on a 24-hour clock. We used circular-linear regression and a von Mises transformation to model carnivore activity against the covariates lunar phase, habitat, and minimum nighttime temperature. We generated density relationships for each covariate by species and circular time density plots by species for both predator and prey. Carnivore-prey associations and carnivore-carnivore competition was also assessed for species retained in this study. High variation existed in activity patterns among both predator and prey species. All covariates were correlated with effects on activity time for at least one carnivore species. Temporal activity of African wildcat (*Felis silvestris lybica*) and small-spotted genet (*Genetta genetta*) was most influenced by lunar phase, while activity of banded mongoose (*Mungos mungo*) and black-backed jackal (*Canis mesomelas*) was most influenced by minimum nighttime temperature. Leopard (*Panthera pardus*) activity was most influence by habitat, while all other species in this study responded temporally to both lunar phase and habitat. In particular, this study highlights the need for more numerous and more detailed studies on medium and small carnivore communities in southern Africa.

# INTRODUCTION

Numerous factors have been shown to affect the temporal distribution of daily carnivore activity, including time of year, temperature, lunar phase, habitat, body size, sex, reproductive status, and activity patterns of prey (Zielinski 1988, Palomares and Caro 1999, Di Bitetti et al. 2006, Chen et al. 2009, Hayward and Slotow 2009, Schmidt et al. 2009). Studies have also investigated how activity patterns of a species' competitors and its rank in ecological hierarchy affect its activity (e.g., Palomares and Caro 1999, Zielinski 2000, Hayward and Slotow 2009). Thus, the degree to which activity of two species coincides plays a role in avoidance of interspecific killing among carnivores. Risk of altercations between species is generally influenced by species body size, tendency to unite into groups, age, and sex (Polis et al. 1989, Palomares and Caro 1999), allowing a diversity of species to survive despite competition. Several papers (Caro and Stoner 2003, Hayward and Slotow 2009, Lucherini et al. 2009, Cozzi et al. 2012, Ramesh et al. 2012) have investigated this theory of temporal partitioning, or temporal avoidance, of competitors or predators to increase access to resources and avoid risk.

Carothers and Jaksić (1984) theorized that temporal partitioning, rather than some other coexistence strategy, is most likely to result from interference competition. That is, species that are prevented from accessing available needed resources, such as prey, via interference competition from a dominant or competitor species are more likely to enact or evolve a temporal avoidance of their competitors. Such a relationship was found, for example, among Andean (*Leopardus jacobita*) and Pampas cats (*Leopardus colocolo*) in the Andes Mountains. The two species shared similar prey preferences, and the study found that the former exhibited mostly diurnal activity and latter mostly nocturnal activity (Lucherini et al. 2009).

Alternatively, shifts in habitat or diet are more logically the result of exploitation competition, where one species reduces availability of a shared resource, typically via occupation or consumption (Carothers and Jaksić 1984). This model was partially supported by Karanth and Sunquist (2000), who found distinct primary prey bases among tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*) in India, but little evidence for temporal or spatial avoidance, suggesting that where interference competition is not present, division of prey targets may drive activity patterns and reduce competition. Numerous studies have supported the theory that carnivore activity patterns are at least partially influenced by the activity patterns of their primary prey (e.g., Lode 1995, Ramesh et al. 2012, Zielinski 1988), however Hayward and Slotow (2009) did not find any evidence for a prey-driven shift in activity pattern among large African carnivores.

Temporal activity information is needed for conservationists to understand the resource needs and availability of their subject species, and to develop informed conservation and management protocols (Cozzi et al. 2012). Carnivores are increasingly at risk from human encroachment and persecution, habitat augmentation and fragmentation, and decline of prey species due to these factors as well as human use and competition with livestock (Oehler and Litvaitis 1996, Treves and Karanth 2003, Karanth and Chellam 2009). Consequently, if the activity pattern of a species is influenced by competition with other carnivores, changes in carnivore dynamics would also likely have an influence on changes in prey abundance and temporal activity. As top carnivores decline, it is theorized through the mesopredator release hypothesis that the influence of medium and small carnivores on their ecological systems will increase as a result of reduced top-down pressure and reduced competition from dominant carnivores (Litvaitis and Villafuerte 1996, Crooks and Soulé 1999). The mesopredator release hypothesis combined with realized threats to top carnivores worldwide and general lack of data advises an increased need for information regarding the life history of lower-guild carnivores.

A study of the status of the 55 species of small carnivores in southern Africa found that while no species were listed as endangered or extinct on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species, population trends are decreasing for 27% and unknown for another 46% (Do Linh San et al. 2013). Gaps in knowledge must be filled in order to properly protect and manage these carnivores. In southern Africa, many studies have been conducted looking at temporal partitioning among larger African carnivores, namely lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*), and hyenas (*Crocuta crocuta*, *Hyaena brunnea*) (e.g., Kolowski and Holekamp 2006, Hayward and Slotow 2009, Cozzi et al. 2012). However, few studies in southern Africa or elsewhere have been conducted looking at temporal partitioning among the medium and small carnivore complex, and existing studies are dated (e.g., Waser 1980, Mills et al. 1984, Zielinski 1986, 1988).

Further, temporal analyses of small African carnivores discuss broad categories of temporal distribution, describing species as nocturnal, diurnal, or crepuscular (Mills et al. 1984, Zielinski 1986). However, circular analysis, which allows evaluation of time on a continuous, 24-hour scale, is more informative, giving insight into activity peaks throughout a day (Brunsdon and Corcoran 2006).

We investigated, for the first time in southern Africa, temporal use among large, medium, and small carnivores and their prey, and the first to do so using circular analysis of time data. We examine temporal partitioning of this community as it relates to activity of large carnivores, activity of prey species, changes in lunar cycle, and variation in minimum nighttime temperature. We test the hypotheses that lunar phase, habitat, minimum nighttime temperature, or the combination of all three factors, influence carnivore activity. We also investigate temporal distribution of prey species.

## METHODS

### *Study Site*

This study was conducted on approximately 3,300 ha of the EcoTraining, Inc. concession of the Mashatu Game Reserve (Figure 3.1), an approximately 25,000 ha unfenced patchwork of private land holdings in eastern Botswana (-22°10' S, 29°3' E) (Mashatu Game Reserve 2013). It is part of the Southern African Bushveld biome (WWF 2014*b*), which is characterized by major vegetation of stunted mopane (*Colophospermum mopane*) woodland, mixed flats of umbrella thorn (*Vachellia tortilis*, formerly *Acacia tortilis*) and mustardbush (*Salvadora australis*), with bands of large fever berry (*Croton megalobotrys*) along rivers. The study area experiences two distinct seasons: a wet summer season from November to April, and a dry winter season from May to October (WWF 2014*a*). Recorded temperatures during the dry winter months of the study ranged between -1°C and 40°C. Annual rainfall for Mashatu itself averages 400mm (Mashatu Game Reserve 2014). Carnivore species known to inhabit the site include four members of the family Felidae, two members of Canidae, three members of Hyaenidae, one member of Mustelidae, and eight members of Viverridae. These are, respectively, lion, leopard, cheetah, African wildcat (*Felis silvestris lybica*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristata*), spotted hyena, brown hyena, honey badger (*Mellivora capensis*), African civet (*Civettictis civetta*), large-spotted genet (*Genetta tigrina*), small-spotted genet (*Genetta genetta*), banded mongoose (*Mungos mungo*), Selous' mongoose (*Paracynictis selousi*), slender mongoose (*Galerella sanguinea*), dwarf mongoose (*Helogale parvula*), and white-tailed mongoose (*Ichneumia albicauda*) (Mashatu Game Reserve 2013).

Potential prey species recorded on the site include nine members of Bovidae, two members of Cercopithecidae, one member of Equidae, one member of Giraffidae, one member of Hystricidae, one member of Pedetidae, one member of Sciuridae, two members of Suidae, one member of Orycteropodidae, one member of Elephantidae, two members of Procaviidae, and two members of Leporidae, plus various members of the class Aves (Mashatu Game Reserve 2013).

All research was conducted under Institutional Animal Care and Use Committee (IACUC) approval under Animal Use Protocol (AUP) number A2013 04-002-Y1-A0 and Ministry of Environment, Wildlife, and Tourism Research Permit EWT 8/36/4 XXV (37).

### *Field methods*

Camera trap data were recorded during June and July 2013. Cameras were initially established as part of an occupancy study investigating the effectiveness of baits and habitat type on species-specific detection and occurrence rates (Chapter 2). Visitation rates differed by bait type as found in Chapter 2. However, we assumed that bait type would not drive activity time, but rather that an individual would already need to be active (moving across the landscape) in order to encounter a bait or camera. Thus for this study, data were merged across bait sites.

We established 20 trapping sites each fitted with one Moultrie M80 Game Spy infrared-triggered camera set to take at least 2 shots per trigger event followed by a 15-second delay. Half of these sites were placed within a large fever berry belt along the Motloutse River, while the other half were placed ≥ 1 km away in upland areas consisting of stunted mopane, umbrella thorn, and/or mustardbush vegetation. Within each habitat area, cameras were placed systematically at ~0.5 km intervals in close proximity to roads. All cameras were angled down a road or game trail and set at ~0.5 m high to increase the chances of encountering mammalian species. One camera failed during the first 3 weeks of the study and had to be removed from analysis, resulting in only 19 sites during this period instead of the initial 20 sites. It was replaced with a Bushnell camera for the remainder of the study. Data were collected over the course of 40 days, with a "day" including a full night and spanning from sunrise to sunrise, providing a total effort of 780 trap-days.

### *Data preparation*

We divided each day into time intervals in order to capture information on species activity times without confounding data by repeatedly counting activity from one active individual over a short time span. Many camera trap studies subset data using time intervals of ≥30 min between visits from members of the same species (e.g., Negrões et al. 2012, Roberts 2011, Rovero and Marshall 2009) as a standard method to ensure independent records during capture-recapture analysis, thus minimizing or eliminating re-counting of the same individual. We chose a finer-scale 15-minute interval as we were not concerned about recounting the same individual, but rather with recounting the same activity event. We determined that a time interval shorter than 15 minutes would not be more informative from a practical or ecological standpoint, but might bias density estimates during periods where an individual remained at a site to investigate a bait or camera.

Data were reduced such that only one occurrence of a species per site per day was recorded within each time bin. Thus, a species could not be recorded more than 96 times (24 hours/day x 4 events/hour) at a particular site on a particular day. However, a species could be recorded up to 20 times during a 15-minute interval by appearing at multiple sites during that interval, receiving one data event for each site. Thus, each day afforded the potential for a species to generate up to 1,920 site-events (96 events/day x 20 sites). All analyses used this reduced data.

All species of predator and prey were recorded separately. All bird species were combined into a single category for the purposes of analysis except for helmeted guineafowl (*Numida meleagris*), which were recorded separately because they were of particular interest as a prey item for medium and small members of the carnivore complex.

Also recorded for each photographic event were lunar phase and minimum nighttime temperature, and each site was recorded in one of two habitat categories: river or upland. Lunar phase was divided into three categories by increasing light intensity: new moon or waxing/waning crescent (0), first or last quarter (1), and waxing/waning gibbous or full moon (2). Habitat type was within one of two categories: river or upland. No reliable weather station existed in adequate proximity to the study area. Thus, minimum nighttime temperature was a continuous variable recorded for each photograph by an internal thermometer built into each camera trap. Minimum nighttime temperature was determined by comparing temperatures recorded among all photographs during each 24-hour period, selecting the lowest among these (which always occurred during night hours), and assigning this as the minimum nighttime temperature for all photos taken during that 24-hour period.

### *Circular-linear regression analysis*

All analyses for this study were conducted using Program R, Version 3.0.2 (R Core Team 2013). We began by developing species-specific histograms of density for both predator and prey species of events recorded within each covariate: lunar phase, habitat, and minimum nighttime temperature. Density plots allow direct comparison of information from one species relative to others which may have different frequencies of photo capture events. Overlaid on each plot, in the form of a trend line, was the overall frequency of each level of covariate represented over the observation period. These trend lines represent the density of lunar phase, habitat, and minimum nighttime temperature, respectively, across all sites during the study. Species-specific frequency trends that follow these trend lines do not exhibit preference for or avoidance of activity with respect to that particular covariate. These plots provide information on which covariates are associated with increased or decreased activity events.

To investigate activity distribution throughout a day, we generated circular plots with activity events plotted on a 24-hour clock using the R package ‘circular’ (Lund and Agostinelli 2013). A density analysis line was graphed to show activity “peaks” or pulses throughout a day based on event data. Rose diagrams were plotted at the center of each clock diagram, with sector lengths proportional to the relative frequencies of events within program-defined time bins, again giving information about relative distribution of activity throughout a day. Circular plots convey information both on location of temporal peaks, as well as sample variation around peaks. These circular diagrams were generated for both predator and prey species.

We developed circular-linear regression models to evaluate the relationship between event times and covariates. Circular-linear regression allows linear independent variables (e.g., temperature, wind speed, etc.) to be related via a specialized link function to a circular dependent variable (e.g., time of day, months of year, compass bearing, etc.). The model tests the effect of covariates on the circular mean. This model yields coherent results that ordinary linear regression on the same data cannot. By transforming our daily time data onto a circular distribution, we preserve the relationship between 11:59pm and 12:00am (23:59 and 00:00 on a 24-hour clock), and these time values are interpreted at sequential minutes in the model. In linear models, this relationship would not be preserved, as 0 and 23 are not next to each other on a linear scale.

Event times were expressed as circular objects of radian values using the ‘circular’ function of the ‘circular’ package in R. Time values were first converted to decimal hours. Then, decimal hours were converted to radian values via the following equation:

$$\theta = \frac{2\pi\,(\mathrm{h})}{d},$$

where h represents the decimal hour to be converted, *d* represents the number of divisions (e.g., hours, months, etc.) in the circular object (d=24 for our data), and $\theta$ represents the resulting radian equivalent of the event time.

Circular time objects were regressed on the covariates using the ‘lm.circular’ function, which assumes that the circular object (conditional on the regressors) follows a von Mises distribution (Lund and Agostinelli 2013). The program employs Green’s iteratively reweighed least-squares algorithm to perform maximum likelihood regression on the model parameters (Green 1984, Fisher and Lee 1992). The probability density function of the von Mises distribution for random variable $\lambda$ and mean $\mu$ is represented by the equation

$$f(\lambda) = \frac{1}{2\pi I_0(\kappa)} e^{\kappa\cos(\lambda-\mu)} \text{ where } 0 \le \lambda, \mu \le 2\pi, \kappa > 0,$$

and where

$$I_0(\kappa) = \frac{1}{2\pi}\int_0^{2\pi} e^{\kappa\cos(\phi-\mu)}\, d\phi$$

is the zero-order modified Bessel function of the first kind, where $\kappa$ is a concentration parameter (Gill and Hangartner 2009). The ‘lm.circular’ package uses the relationship $\mu = \beta_0 + 2\bullet\tan^{-1}(\beta X)$ where $\mu$ is the unknown parameter estimating the mean, $\beta$ is either an individual parameter or a vector of parameters on the covariates, and $X$ is either a vector or matrix of independent linear covariates used to fit the model to the chosen circular dependent variable (Lund and Agostinelli 2013).

We developed four models to investigate the effects of lunar phase (0, 1, or 2; treated as a continuous predictor), habitat, and minimum nighttime temperature on species-specific carnivore activity. These consisted of three models testing each of the three covariates individually, and a fourth global model that incorporated all three covariates. Akaike's Information Criteria corrected for small sample sizes (AICc) was calculated from the maximum likelihood value that resulted from running each model (Burnham and Anderson 2004), allowing model selection among the four models tested for each carnivore species. Because the main focus of this analysis was carnivore temporal partitioning and activity patterns, we did not assess these models for prey species nor did we consider prey activity statistics as a predictor of carnivore activity.

Within our four models, we define peak activity time as the average or mean on a 24-hour clock of all activity times observed by a species during the study. We individually tested the covariates lunar phase, habitat, and minimum nighttime temperature. In addition, we tested the combined effect of all three via a global model. The mean value estimate, along with covariate effects, given in each model is a radian value representing a shift in peak activity time associated with the respective covariate. Then, we could interpret positive estimates as shifting peak activity to a time later in the day, or clockwise on the 24-hour clock, and negative estimates as shifting peak activity to a time earlier in the day, or counter-clockwise on the 24-hour clock.

In practice, however, many species had multiple activity peaks throughout a 24-hour period, as shown in the circular event density plots (Figure 3.8). Thus, it is not always informative to interpret a mean peak activity time estimate for this multimodal data. This is because, for example, data that demonstrates two peaks, one at approximately 4:00 and another at approximately 8:00, will yield a mean peak activity time value that falls in the trough between peaks, at approximately 6:00. Any covariate effect on this mean time would not actually correlate to a time when the species is highly active. However, significance of these mean estimates (as determined by p-values and confidence intervals that do not encompass zero) is informative as it demonstrates that a variable is associated with some shift in carnivore activity pattern over a 24-hour period, and thus might be important to the biology of that species.

Finally, in order to better assess potential predator-predator and predator-prey interactions, literature reviews were conducted to investigate the major prey categories of carnivores in this study, and separately the major carnivore competitors of carnivores in this study.

## RESULTS

We collected 5,759 camera trigger events recorded over 780 trap-nights across all species. However, some of these photos represented cases where an individual stayed at a camera site for an extended period of time, triggering a camera repeatedly. After reducing data into 15-min time bins and removing unknown cases (where an animal was observed, but species could not be determined), 2,680 photographic events remained across all species, consisting of 1,491 carnivore photos and 1,189 prey species photos.

We excluded from analysis species with less than 10 recorded events over the course of the study as sample sizes were too low to get even marginally reliable estimates of activity time. The following carnivores were excluded: bat-eared fox (n=5), slender mongoose (n=3), and white-tailed mongoose (n=2). Lion, cheetah, Selous' mongoose, dwarf mongoose, and aardwolf were known to be present on the study site but were not recorded at all during the study. The following prey species were excluded: aardvark (n=3), bushbuck (n=6), common duiker (n=6), giraffe (n=9), ostrich (n=4), springhare (n=2), tree squirrel (n=4), and waterbuck (n=7). Klipspringer, rock dassie, and yellow-spotted dassie were also known to be present, but were not recorded during the study.

After exclusion, ten carnivore species remained in the analysis: African civet (n=99), African wildcat (n=21), banded mongoose (n=16), black-backed jackal (n=811), brown hyena (n=120), honey badger (n=19), large-spotted genet (n=242), leopard (n=49), small-spotted genet (n=12), and spotted hyena (n=83). Fifteen prey species remained in the analysis: blue wildebeest (n=28), eland (n=12), elephant (n=229), impala (n=266), kudu (n=69), Burchell's zebra (n=22), bushpig (n=35), Cape porcupine (n=20), chacma baboon (n=142), common warthog (n=110), steenbok (n=68), helmeted guineafowl (n=13), scrub hare (n=13), vervet monkey (n=12), and various bird species (n=110).

### *Covariate density plots*

Carnivore species detections negatively correlated with moon phase via observation of event density as compared to lunar category (decreased activity event density with increasing light) were African wildcat, honey badger, spotted hyena, and possibly brown hyena. However, brown hyena activity may have simply followed the common lunar trend (Figure 3.2). Small-spotted genet exhibited some positive correlation between activity and moon phase. However, the pattern was also consistent with the common lunar trend, with small sample size making the distinction difficult. Of the prey species groups, blue wildebeest, Burchell's zebra, bushpig, and possibly kudu were positively correlated with moon phase (Figure 3.3). However, the latter may have been following the common trend line and all but bushpig are primarily diurnal.

Carnivore species with >50% of events in upland habitat include black-backed jackal, small-spotted genet, and spotted hyena. Meanwhile, African civet, African wildcat, banded mongoose, brown hyena, honey badger, large-spotted genet, and leopard had >50% of events in river habitat (Figure 2.4). No carnivore species had values identical to or nearly identical to the common trend line, which suggests a habitat influence on activity. For prey, species with >50% of events in upland habitat include blue wildebeest, eland, scrub hare, vervet monkey, and possibly warthog and steenbok. However, warthog, steenbok, and vervet monkey may simply approximate the common trend line. Prey species with >50% of events in river habitat include kudu, Burchell's zebra, bushpig, Cape porcupine, chacma baboon, helmeted guineafowl, and various birds (Figure 3.5). Elephant and impala may also exhibit more activity in river areas, or may simply follow the common trend line.

For most predatory species, event density data for minimum nighttime temperature follows the common trend line. Data suggest that activity decreases with increasing minimum temperature, if a trend exists at all (Figure 3.6, Figure 3.7). For prey, zebra and Cape porcupine appeared to diverge from the common trend, with more activity on warmer nights than was expected (Figure 3.7). However, most predator and prey species generally follow the common trend line, indicating that minimum nighttime temperature may not be a primary driver of activity for many, or any, species in this analysis.

### *Circular event density plots*

Circular activity plots of events (suggesting activity) for carnivores showed the majority of density during nocturnal hours (almost no daytime events) for African civet, African wildcat, brown hyena, honey badger, large-spotted genet, leopard, small-spotted genet, and spotted hyena. Of these, African civet, brown hyena, and large-spotted genet showed skewedness towards nighttime hours prior to midnight, while spotted hyena and honey badger events were skewed towards hours after midnight. African wildcat and leopard demonstrated crepuscular trends. Black-backed jackal were more nocturnal than diurnal, but had locations distributed throughout the 24-hour period. Banded mongoose was primarily diurnal with the majority of event density after noon (Figure 3.8).

Circular activity plots of events for prey showed the majority of density during nocturnal hours for bushpig, Cape porcupine, and scrubhare. Bushpig density was centered around midnight while scrubhare and Cape porcupine density patterns suggested some crepuscular activity. Steenbok were also active during early morning and late evening hours, and throughout the night. Impala, kudu, chacma baboon, helmeted guineafowl, and various bird species were primarily diurnal, with activity density skewed towards afternoon hours, and the first two demonstrating some activity throughout the night. The combined bird species showed event density skewed towards the morning but did not demonstrate any noteworthy activity during nighttime hours (Figure 3.9).

*Circular-linear regression analysis*

Model selection with AICc on analysis of the four circular-linear regression models yielded a top model for each species. The lunar phase-only model (k=3) resulted as the top model for African wildcat, large-spotted genet, and small-spotted genet. This was also the top model for brown hyena and spotted hyena. However, the $\Delta$AIC value between this and the next two best models was less than 2 in the case of both hyena species, suggesting similar weight among the top three models for these species. Those models were lunar, habitat, and global for brown hyena and lunar, habitat, and minimum nighttime temperature for spotted hyena. The habitat-only model (k=3) resulted as the top model for leopard. The model assessing minimum nighttime temperature as the only covariate (k=3) resulted as the top model for banded mongoose, black-backed jackal, and honey badger. However, similar to the results for both hyenas, the top three models (minimum nighttime temperature, habitat, and lunar phase) were within 2 units of other another for honey badger, suggesting similar weight among them for this species. African civet was the only species yielding the most support for the global model (k=5) (Table 3.1).

Within the lunar phase-only model, African civet (p=0.001, mean=-0.09, SE=0.03), African wildcat (p=0.005, mean=-0.5, SE=0.19), black-backed jackal (p=0.013, mean=0.05, SE=0.02), brown hyena (p=0.020, mean=0.08, SE=0.04), large-spotted genet (p<0.000, mean=-0.09, SE=0.03), and small-spotted genet (p<0.000, mean=-0.41, SE=0.11) had significant p-values and 95% confidence intervals that excluded 0, suggesting that these species may be active earlier or later with increasing lunar light intensity (Table 3.3).

For the habitat-only model, African civet (p<0.000, mean=1.00, SE=0.07), brown hyena (p<0.000, mean=-0.16, SE=0.04), large-spotted genet (p<0.000, mean=0.13, SE=0.04), and leopard (p<0.000, mean=-0.60, SE=0.15) had significant p-values and 95% confidence intervals that excluded 0. Because events at river sites were modeled as 1 and events at upland sites were modeled as 0, estimates can be interpreted as indicating that species may be active earlier or later in river habitats as compared to upland areas (Table 3.4).

Within the minimum nighttime temperature-only model, black-backed jackal (p=0.003, mean=-0.02, SE=0.01) had a significant p-value and 95% confidence interval the excluded zero, suggesting that this species might be active earlier or later with increasing minimum nighttime temperature (Table 3.5).

For the lunar variable within the global model, species with significant p-values and 95% confidence intervals that excluded 0 on the lunar variable were large-spotted genet (p=0.018, mean=-0.10, SE=0.05), small-spotted genet (p<0.000, mean=-0.43, SE=0.10), and spotted hyena (p=0.009, mean=-0.11, SE=0.04). For the habitat variable, species with significant p-values and 95% confidence intervals that excluded 0 were brown hyena (p=0.007, mean=-0.16, SE=0.07), honey badger (p=0.021, mean=0.90, SE=0.44), large-spotted genet (p=0.002, mean=0.22, SE=0.08), leopard (p=0.002, mean=-0.63, SE=0.22), and small-spotted genet (p=0.006, mean=0.80, SE=0.32). For the minimum nighttime temperature variable, only black-backed jackal (p=0.012, mean=-0.02, SE=0.01) had a significant p-value and 95% confidence interval that excluded 0. Note that African civet and African wildcat had noticeably large estimates and standard errors. This was likely due in part to the lack of any events at upland sites in the case of the former, and a small sample size (n=21) in the case of the latter (Table 3.2).

### *Predator-prey and predator-predator interactions*

We conducted a literature review to assess prey groups consumed by the 10 carnivore species in this analysis. Five groups were assessed: large game (adult), large game (young), medium game, small game, and birds (Table 3.6). Large game included the large ungulate species in this analysis, which were blue wildebeest, eland, elephant, impala, kudu, and Burchell's zebra and any other prey species of similar size and weight. Medium game includes bushpig, Cape porcupine, chacma baboon, common warthog and other game species of similar size and weight. Small game species include steenbok, scrub hare, vervet monkey, and other mammalian species of similar size and weight, or smaller. Birds included helmeted guineafowl and various other avian species. Information on prey and diet was often collected via scat analysis. Thus, this chart does not clearly distinguish species that were hunted as prey versus species that are scavenged, as this is beyond the scope of our study. Also, results only report the result of a literature review, and should not be interpreted as definitive information on diet.

All carnivores except African civet were reported to consume bird species, and all but African civet, banded mongoose, and large-spotted genet were reported to consume small game. All larger game classes were found only in the diets of black-backed jackal, brown hyena, leopard, and spotted hyena (Table 3.6).

To investigate competition among predators, a literature review was conducted to investigate occurrences of aggression (e.g., via kleptoparasitism, etc.), predation, or consumption (whether through hunting and killing or through scavenging carrion) of one carnivore species on another (Table 3.7). We refer to all such cases here as "aggression". Only species included in this analysis were assessed. For four species, African civet, African wildcat, large-spotted genet, and small-spotted genet, no instances of carnivore-carnivore aggression could be found. Banded mongoose was reported as an aggressor of other mongoose species (Waser et al. 1995). Black-backed jackal was reported as an aggressor of African wildcat, mongoose spp., honey badger, small-spotted genet, and other miscellaneous carnivores (Mills et al. 1984, Walton and Joly 2003). Brown hyena were reported to be aggressors of African wildcat, mongoose spp., black-backed jackal, honey badger, and miscellaneous carnivores (Mills and Mills 1978, Skinner and van Aarde 1981), and honey badgers of mongoose spp. and black-backed jackal (Kruuk and Mills 1983, Begg et al. 2003). Leopard and spotted hyena were reported aggressors of all other species (Mills 1984, Mills et al. 1984, Polis et al. 1989, Cooper et al. 1999, Di Silvestre et al. 2000, Henschel et al. 2005, Grimbeek 2006, Hayward et al. 2006, Kamler et al. 2009, Abay et al. 2011).

Also included was a summary table of a study comparing the potential for interspecific competition among 70 African carnivores (Caro and Stoner 2003). Competition was split into seven categories: >0% range overlap with the highest numbers of other carnivores; >33% range overlap with the highest number of other carnivores; >0% range overlap and common habitat shared with highest number of other carnivores; exploitive competition as evidenced by shared geographic range, habitat, and dietary habits with the highest number of other carnivores; risk of kleptoparasitism from the highest number of other carnivores; risk of interspecific killing from the highest number of other carnivores based on geographic and habitat overlap, and body size comparison; and high overall vulnerability. All species in this analysis ranked among the most at-risk species in one or more of these categories. This information is purely informative. It gives additional information regarding which species whose activity might be externally influenced by behavior of other carnivores. While such information would ideally be included in the model analysis, the complexity that would be involved was beyond the scope of this study.

## DISCUSSION

We found a wide range of temporal diversity among both predator and prey species, and within both diurnal and nocturnal periods. Lunar phase, habitat, and minimum nighttime temperature all had effects on peak activity for at least one carnivore species. Results suggest that species have varying responses to changes in these environmental factors, affording more opportunity for temporal partitioning. Large carnivores (leopards, spotted hyenas, brown hyenas, etc.) did exhibit some division of temporal use, suggesting a potential response to interference competition for prey. Peak carnivore activity was more difficult to associate with prey activity due to high overlap of prey species among carnivores, confounding interpretation of interference versus exploitation competition. However, results from this study could be combined with more detailed species-specific studies to investigate these effects.

The fact that all species assessed in this study ranked in one or more top categories for risk of interspecific competition (Table 3.7) (Caro and Stoner 2003) suggests that carnivore species on the Mashatu site could be prevailing due to their ability to survive despite extreme ecological pressures. In other words, despite the high biodiversity on the site (Mashatu Game Reserve 2013), the dominance of this particular composition of carnivore species may indicate stress on this system, reducing the ability for less hardy carnivores to survive in high numbers.

Gaps in knowledge of predator-predator interactions among medium and small carnivores, highlighted by Table 3.7, give further support of the need for more in-depth studies on mesopredators. For example, species most at risk of kleptoparasitism and present in our study included leopard, black-backed jackal, lion, cheetah, wild dog, spotted hyena, and brown hyena (Caro and Stoner 2003), suggesting that this form of exploitive competition is more prevalent among large carnivores. This interpretation may mirror reality, or may be a reflection of the level of detail at which large carnivores studies are conducted as compared to the more general nature of studies on the medium and small carnivore communities.

Beyond its conservation applications in southern Africa, knowledge of carnivore-specific peak activity times is helpful to safari lodges which seek to increase the chances that they will meet the expectations of their guests (Lindsey et al. 2007). Visitors often arrive with a list of specific species they desire to see during their brief trips to the region (*personal observation*). These guests even choose lodges based on past animal sightings data, and the real or perceived chance that they will see all the species on their list based on these data (*personal observation*). Certainly wildlife research should be driven first by a desire to benefit species health and viability, rather than by a need to satisfy the public. However, tourists' experiences are important in conservation due to their indirect effects, such as exposing the general public to lesser-known species and encouraging support (both legislatively and monetarily) of conservation and research (Ashley and Jones 2001, Lindsey et al. 2007). Thus, such dual-purpose research has compounding benefits to the communities investigated.

As with most studies, we encountered some limitations as we carried out this project. The use of carnivore-specific bait at camera sites may have limited our ability to gather larger sample sizes for prey species. We ignored bait type in this study due to the assumption that species encountering a camera would already be active (and thus that bait type would not drive activity), and the assumption that there would not be any interaction between bait type and covariates of interest. Therefore, although unlikely, unexpected trends may have existed. Non-detection of klipspringer, rock hyrax, and dwarf mongoose was likely due to the fact that no cameras were placed on kopjes (rock outcrops), the primary habitat of these species (Waser et al. 1995, Kotler et al. 1999, Norton 2011). Non-detection of the remaining species may have resulted from the fact that the study area was too small compared to the home range of lion and cheetah (Broomhall et al. 2003, Snyman 2010), and camera spacing too wide compared to the home range of Selous' mongoose, a species for which little data exists (Stuart et al. 2008, Schneider and Kappeler 2014).

Further, as this was a single-season study conducted during the dry, winter months in on a single site, results do not provide information on seasonal or geographic differences in activity patterns. Future studies on factors affecting activity patterns of large, medium, and small carnivores in the region could be conducted over larger areas, use higher camera density, include more habitat types, span multiple seasons and sites, and incorporate other factors such as level of human development, hunting or non-hunting areas, use for tourism, etc.

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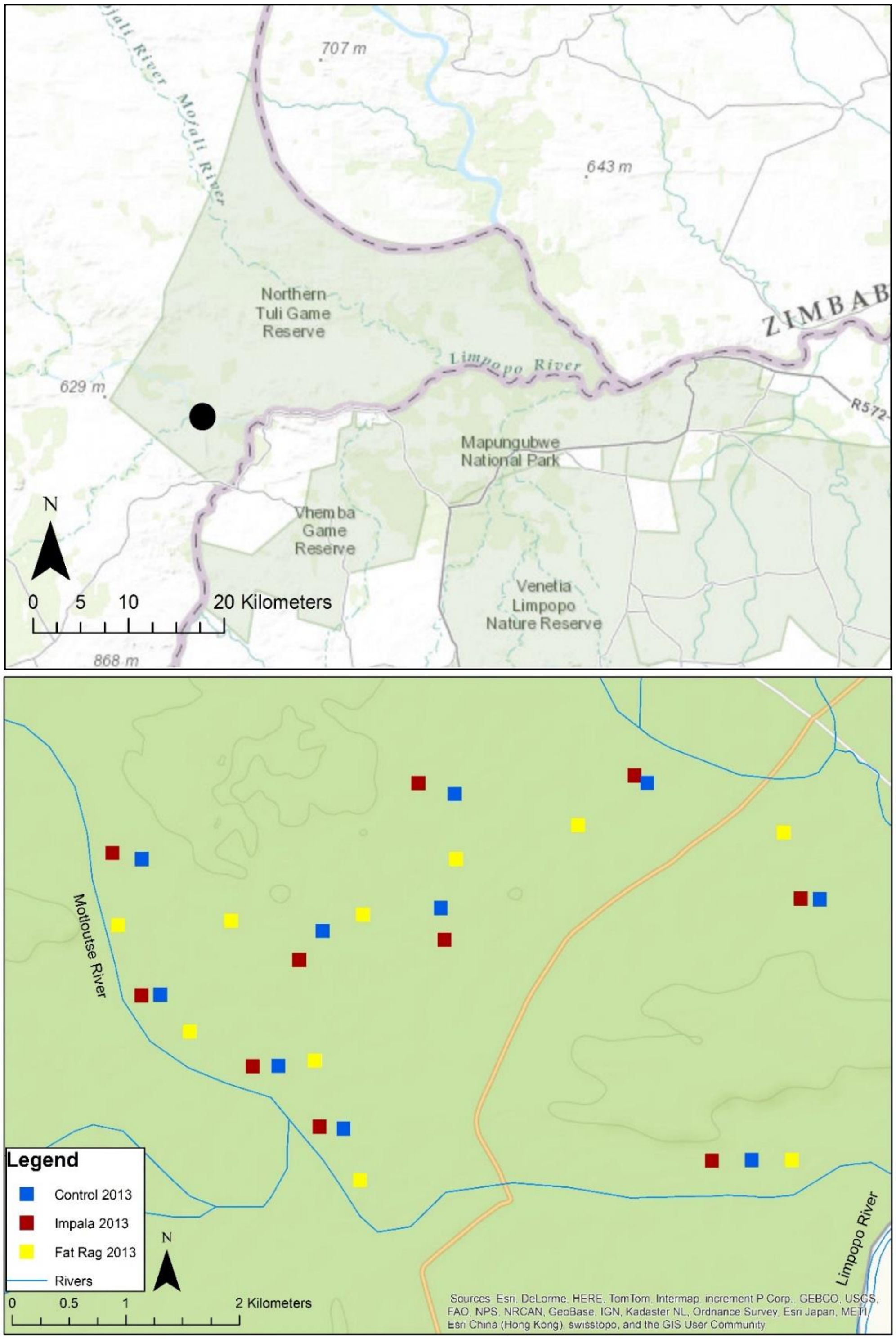


Sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, and the GIS User Community

**Figure 3.1**. Map of study area and camera sites on Mashatu Game Reserve, Botswana. Location of the study site within the Northern Tuli Game Reserve is shown (top). The black dot indicates the study area along the Motloutse River, near the intersection of the international borders of Botswana, South Africa, and Zimbabwe.

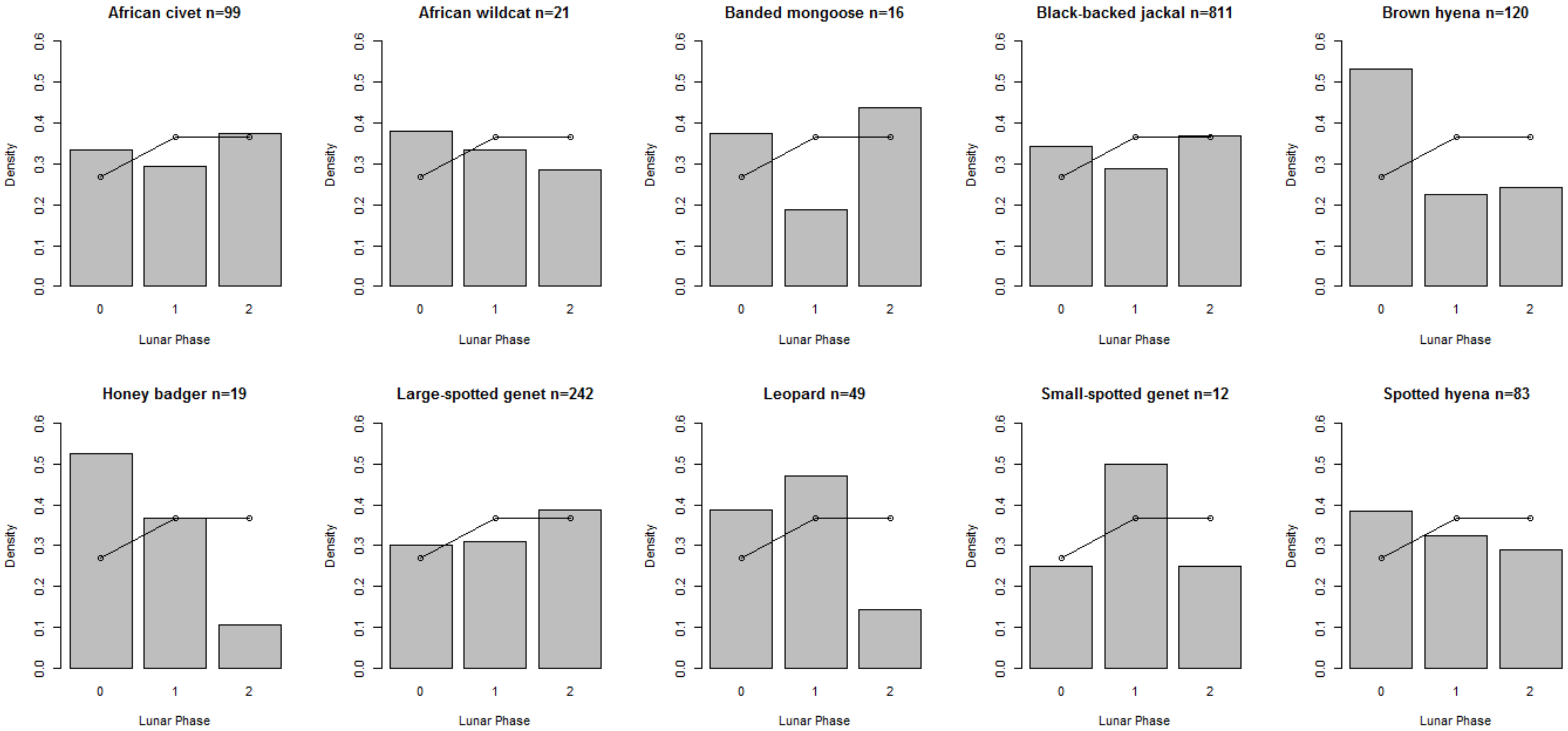


**Figure 3.2.** Density of carnivore species captures by lunar phase. Lunar phase was divided into three categories by increasing light intensity: new moon or waxing/waning crescent (0), first or last quarter (1), and waxing/waning gibbous or full moon (2). Overall lunar phase density experienced over the 40 days of the study is graphed on top of species-specific results.

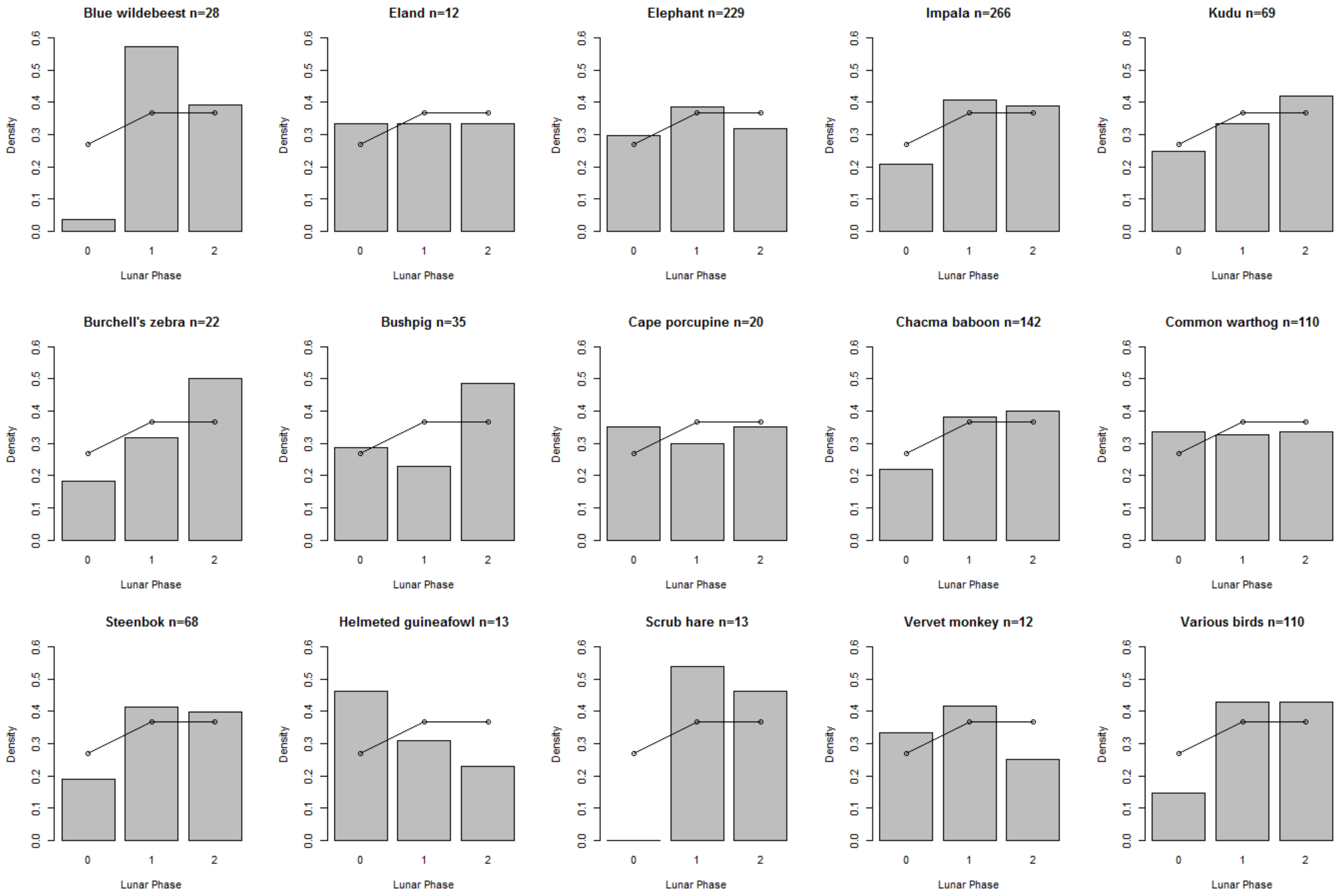


**Figure 3.3.** Density of prey species captures by lunar phase. Lunar phase was divided into three categories: new moon or waxing/ waning crescent (0), first or last quarter (1), and waxing/waning gibbous or full moon (2). Overall lunar phase density is overlaid.

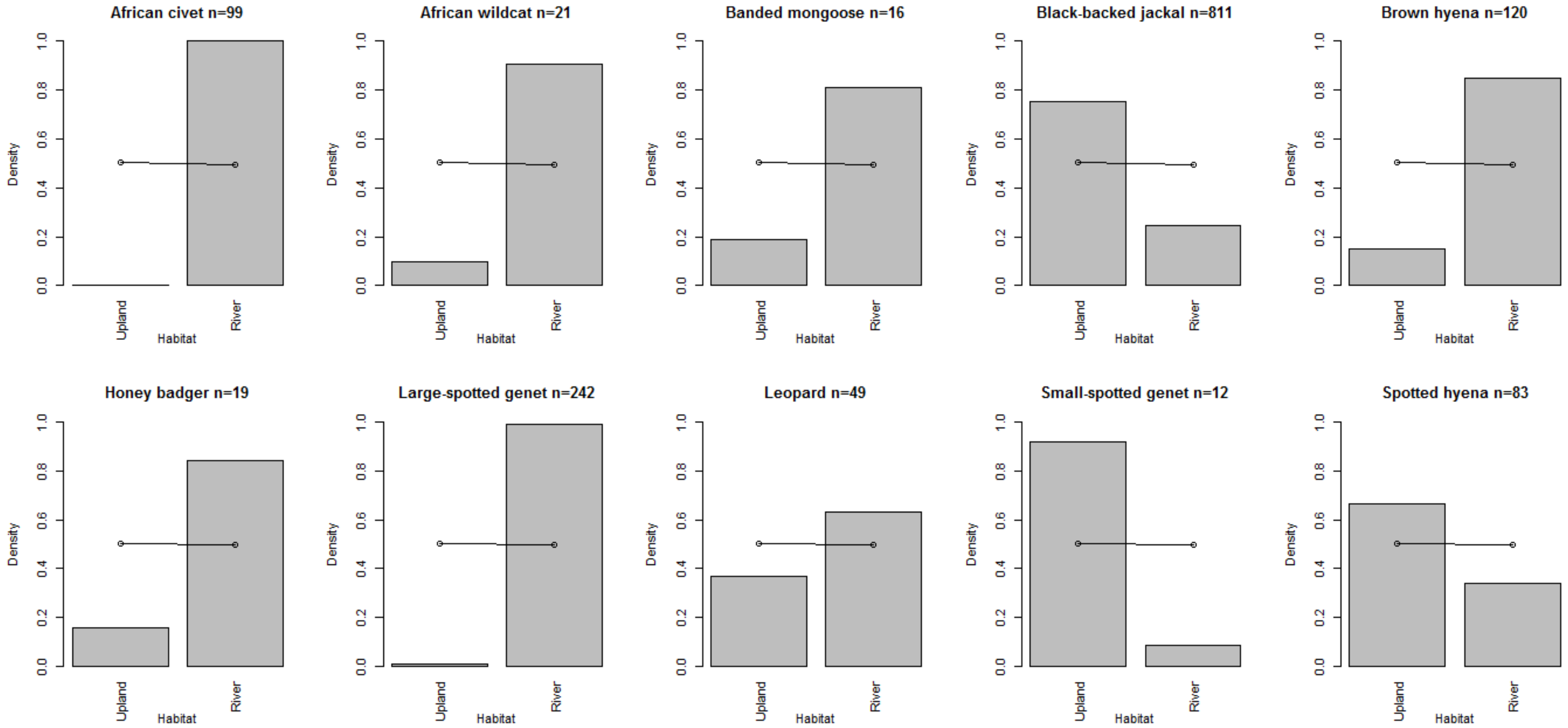


**Figure 3.4**. Density of carnivore species captures by habitat. Overall habitat density (river or upland) experienced over the study sites is overlaid.

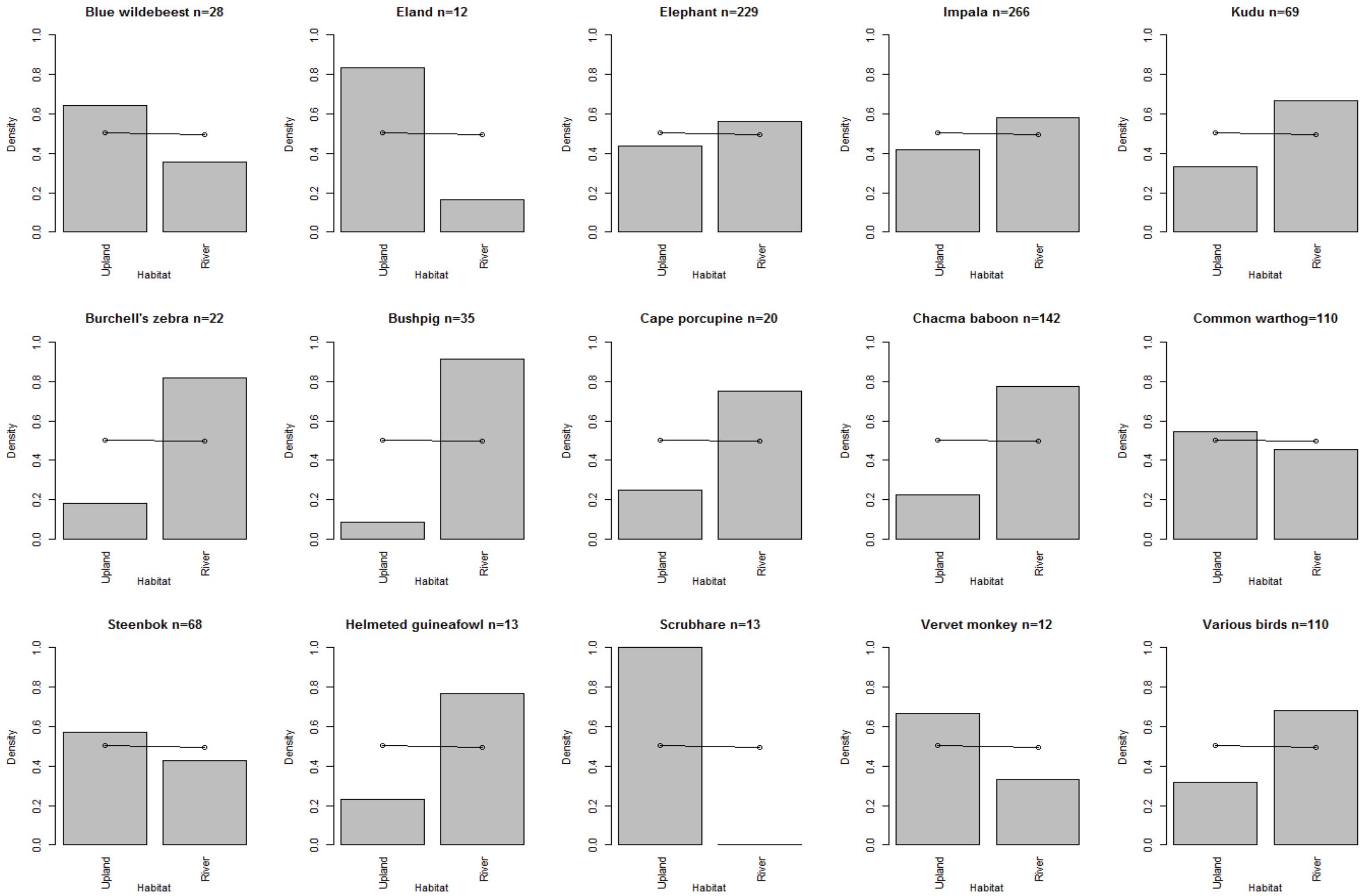


**Figure 3.5**. Density of prey species captures by habitat. Overall habitat density (river or upland) experienced over the study sites is overlaid.

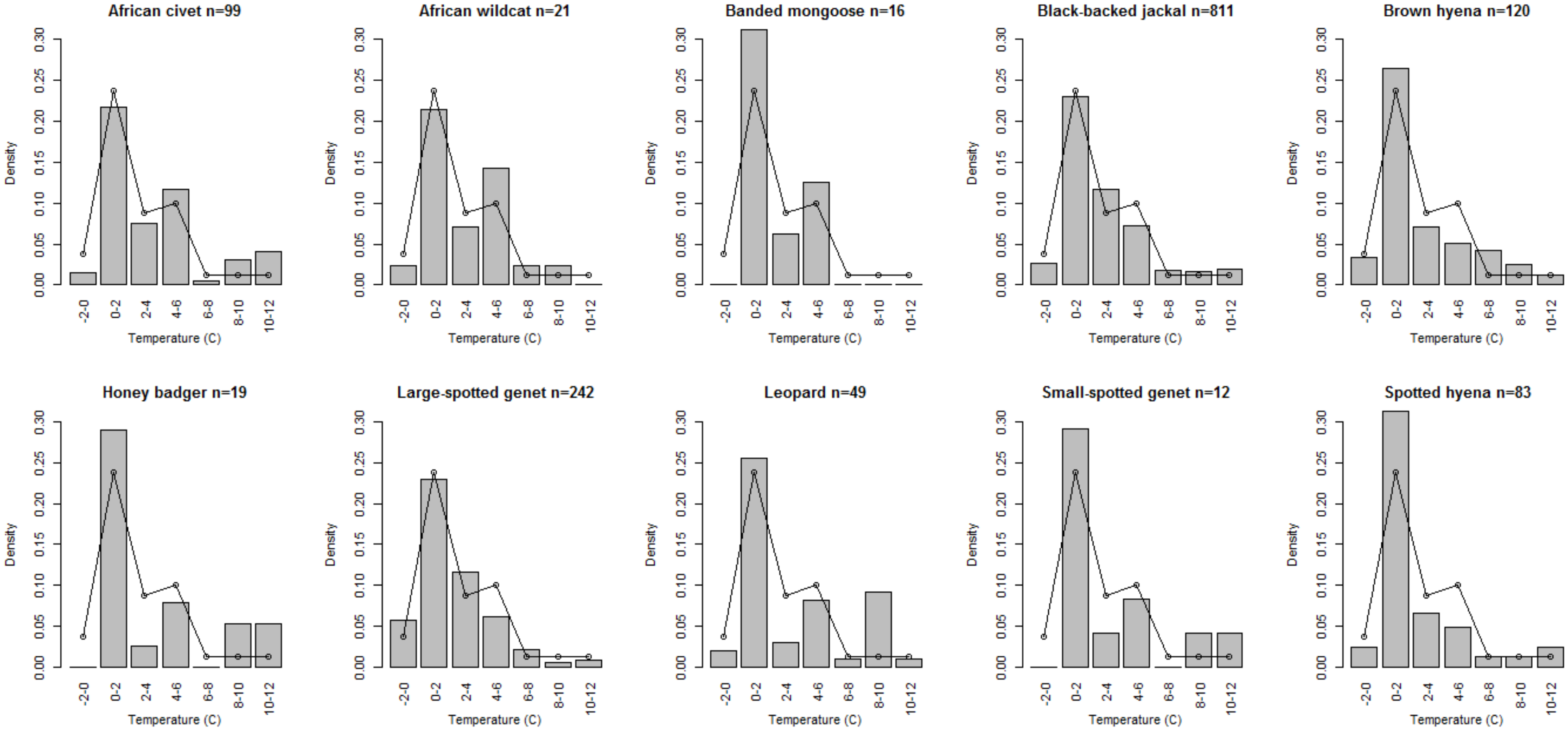


**Figure 3.6**. Density of carnivore species captures by minimum nighttime temperature. Overall minimum temperatures experienced over the 40 days of the study is overlaid.

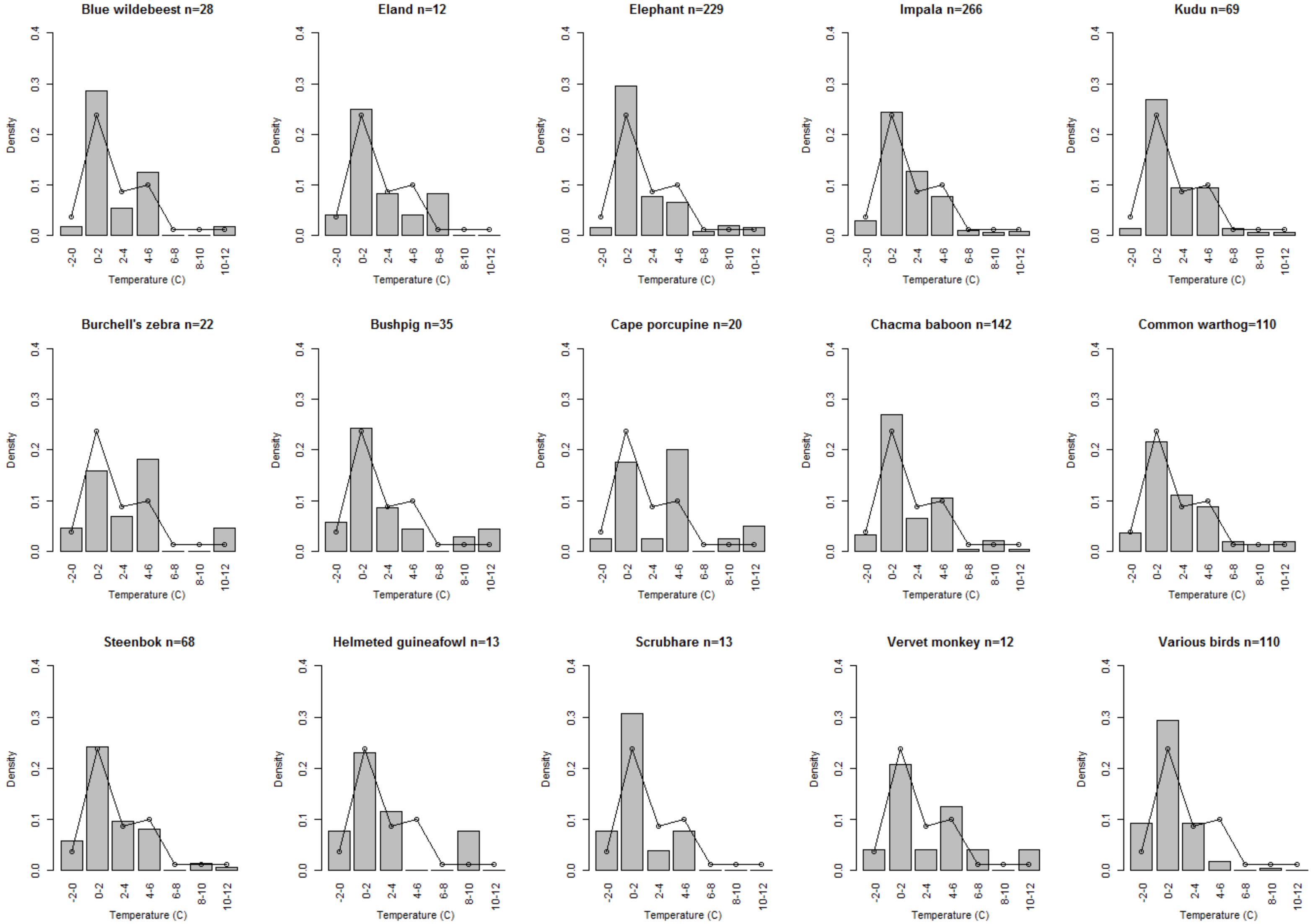
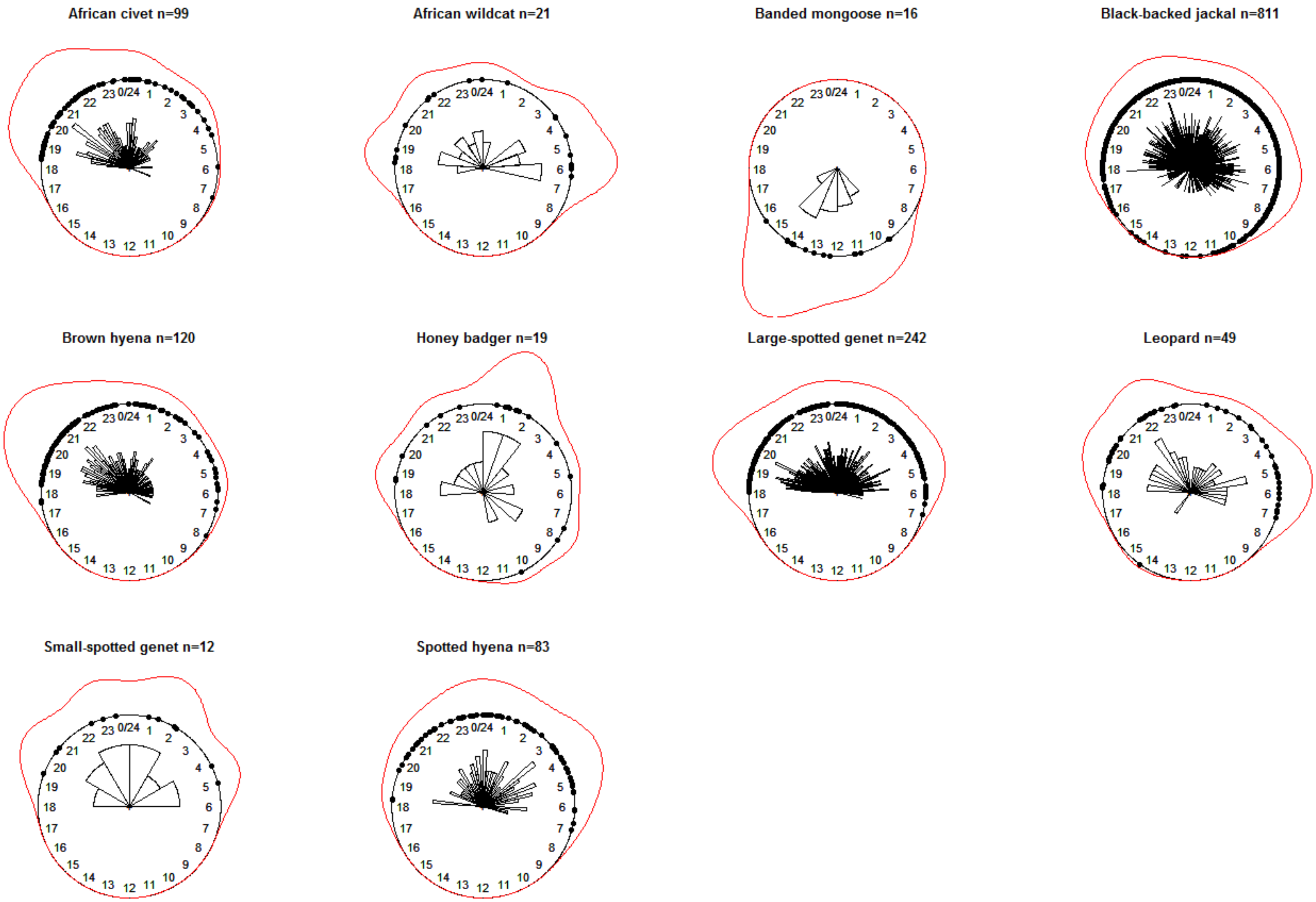


**Figure 3.7**. Density of prey species captures by minimum nighttime temperature. Overall minimum temperatures experienced over the 40 days of the study is overlaid.



African civet n=99

African wildcat n=21

Banded mongoose n=16

Black-backed jackal n=811

Brown hyena n=120

Honey badger n=19

Large-spotted genet n=242

Leopard n=49

Small-spotted genet n=12

Spotted hyena n=83

**Figure 3.8**. Circular distribution and density of events by predator species. Dots represent events and the red line models density of events (photographic captures) on a 24-hour clock. Sample sizes are shown next to each species.

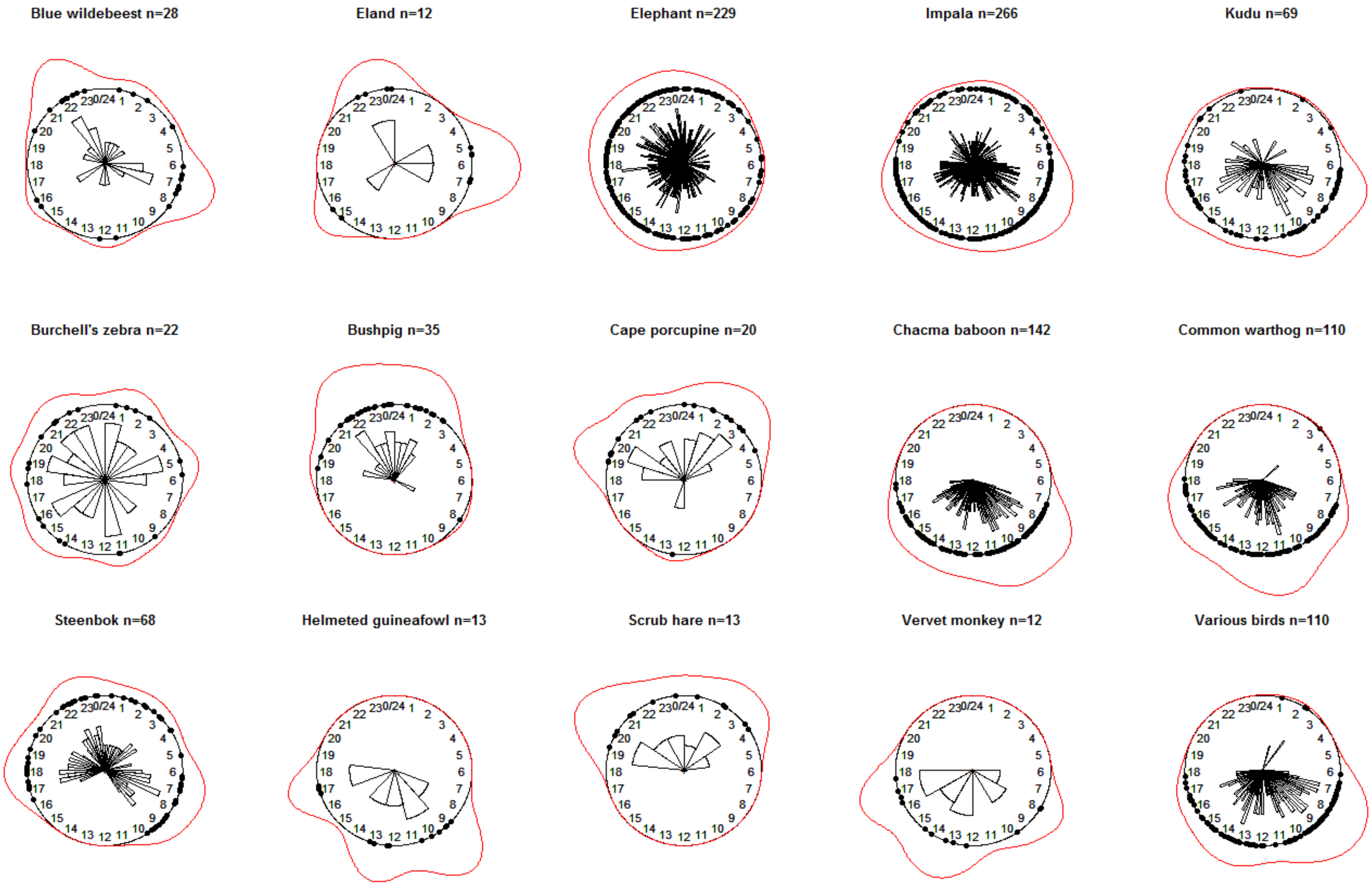


**Figure 3.9**. Circular distribution and density of events by prey species. . Dots represent events and the red line models density of events (photographic captures) on a 24-hour clock. Sample sizes are shown next to each species.

**Table 3.1**. Model selection results using AICc for circular-linear analysis of prey species. Lunar = lunar phase by increasing light intensity (0,1,2); Habiat = river habitat (modeled as 1) as compared to upland habitat (modeled as 0); MinTemp = minimum nighttime temperature in Celcius.

| Species | Model | k | AICc | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|
| African civet | | | | | |
| | Global | 5 | -142.495 | 0.000 | 0.875 |
| | Lunar | 3 | -138.027 | 4.467 | 0.094 |
| | MinTemp | 3 | -135.047 | 7.447 | 0.021 |
| | Habitat | 3 | -133.687 | 8.807 | 0.011 |
| African wildcat | | | | | |
| | Lunar | 3 | -5.254 | 0.000 | 0.683 |
| | MinTemp | 3 | -2.836 | 2.418 | 0.204 |
| | Habitat | 3 | -0.650 | 4.604 | 0.068 |
| | Global | 5 | 0.164 | 5.418 | 0.045 |
| Banded mongoose | | | | | |
| | MinTemp | 3 | -33.080 | 0.000 | 0.618 |
| | Lunar | 3 | -30.720 | 2.360 | 0.190 |
| | Habitat | 3 | -30.600 | 2.480 | 0.179 |
| | Global | 5 | -25.440 | 7.640 | 0.014 |
| Black-backed jackal | | | | | |
| | MinTemp | 3 | -304.770 | 0.000 | 0.696 |
| | Global | 5 | -301.525 | 3.245 | 0.137 |
| | Lunar | 3 | -300.970 | 3.800 | 0.104 |
| | Habitat | 3 | -299.970 | 4.800 | 0.063 |
| Brown hyena | | | | | |
| | Lunar | 3 | -131.193 | 0.000 | 0.386 |
| | Habitat | 3 | -130.853 | 0.340 | 0.326 |
| | Global | 5 | -129.434 | 1.759 | 0.160 |
| | MinTemp | 3 | -128.993 | 2.200 | 0.128 |
| Honey badger | | | | | |
| | MinTemp | 3 | -3.946 | 0.000 | 0.353 |
| | Habitat | 3 | -3.748 | 0.198 | 0.320 |
| | Lunar | 3 | -3.654 | 0.292 | 0.305 |
| | Global | 5 | 1.571 | 5.517 | 0.022 |
| Large-spotted genet | | | | | |
| | Lunar | 3 | -173.479 | 0.000 | 0.702 |
| | MinTemp | 3 | -169.739 | 3.740 | 0.108 |
| | Global | 5 | -169.566 | 3.913 | 0.099 |
| | Habitat | 3 | -169.399 | 4.080 | 0.091 |
| Leopard | | | | | |
| | Habitat | 3 | -23.607 | 0.000 | 0.881 |
| | Global | 5 | -18.885 | 4.722 | 0.083 |
| | MinTemp | 3 | -15.947 | 7.660 | 0.019 |
| | Lunar | 3 | -15.667 | 7.940 | 0.017 |
| Small-spotted genet | | | | | |
| | Lunar | 3 | -11.980 | 0.000 | 0.724 |
| | MinTemp | 3 | -9.134 | 2.846 | 0.175 |
| | Habitat | 3 | -6.998 | 4.982 | 0.060 |
| | Global | 5 | -6.240 | 5.740 | 0.041 |
| Spotted hyena | | | | | |
| | Lunar | 3 | -80.816 | 0.000 | 0.458 |
| | Habitat | 3 | -79.596 | 1.220 | 0.249 |
| | MinTemp | 3 | -79.336 | 1.480 | 0.219 |
| | Global | 5 | -77.181 | 3.635 | 0.074 |

**Table 3.2**. Model selection estimates and p-values from circular-linear analysis of prey species from the global model. Significant p-values and confidence intervals that do not include zero are bolded and italicized. Mean values and errors are given in radians and represent temporal shift.

| Species | | Global estimates | | | | |
|---|---|---|---|---|---|---|
| | | Lunar Phase | | | | |
| | n | p-value | Mean | SE | L_CI | U_CI |
| African civet | 99 | 0.052 | -12.87 | 7.93 | -28.40 | 2.67 |
| African wildcat | 21 | 0.403 | -22.05 | 90.06 | -198.56 | 154.47 |
| Banded mongoose | 16 | 0.460 | 0.00 | 0.05 | -0.09 | 0.10 |
| Black-backed jackal | 811 | 0.213 | 0.02 | 0.02 | -0.03 | 0.06 |
| Brown hyena | 120 | ***0.035*** | 0.09 | 0.05 | -0.01 | 0.18 |
| Honey badger | 19 | 0.054 | 1.06 | 0.66 | -0.23 | 2.36 |
| Large-spotted genet | 242 | ***0.018*** | ***-0.10*** | ***0.05*** | ***-0.19*** | ***-0.01*** |
| Leopard | 49 | 0.404 | -0.03 | 0.12 | -0.27 | 0.21 |
| Small-spotted genet | 12 | ***<0.000*** | ***-0.43*** | ***0.10*** | ***-0.62*** | ***-0.24*** |
| Spotted hyena | 83 | ***0.009*** | ***-0.11*** | ***0.04*** | ***-0.19*** | ***-0.02*** |

**Table 3.2 (cont'd)**

| Species | Global estimates (cont'd) | | | | | Global estimates (cont'd) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Habitat | | | | | Minimum Nighttime Temperature | | | | |
| | p-value | Mean | SE | L_CI | U_CI | p-value | Mean | SE | L_CI | U_CI |
| African civet | ***0.049*** | 44.65 | 26.92 | -8.11 | 97.42 | 0.062 | -3.46 | 2.24 | -7.85 | 0.94 |
| African wildcat | 0.284 | 1.89 | 3.30 | -4.59 | 8.36 | 0.191 | -0.81 | 0.92 | -2.62 | 1.00 |
| Banded mongoose | 0.115 | -0.09 | 0.07 | -0.23 | 0.05 | ***0.029*** | -0.05 | 0.03 | -0.10 | 0.00 |
| Black-backed jackal | 0.213 | -0.05 | 0.06 | -0.18 | 0.07 | ***0.012*** | ***-0.02*** | ***0.01*** | ***-0.03*** | ***0.00*** |
| Brown hyena | ***0.007*** | ***-0.16*** | ***0.07*** | ***-0.30*** | ***-0.03*** | 0.331 | 0.01 | 0.01 | -0.02 | 0.03 |
| Honey badger | ***0.021*** | ***0.90*** | ***0.44*** | ***0.03*** | ***1.77*** | 0.230 | 0.10 | 0.14 | -0.17 | 0.37 |
| Large-spotted genet | ***0.002*** | ***0.22*** | ***0.08*** | ***0.07*** | ***0.37*** | 0.396 | 0.00 | 0.02 | -0.03 | 0.03 |
| Leopard | ***0.002*** | ***-0.63*** | ***0.22*** | ***-1.06*** | ***-0.20*** | 0.407 | 0.01 | 0.03 | -0.06 | 0.07 |
| Small-spotted genet | ***0.006*** | ***0.80*** | ***0.32*** | ***0.18*** | ***1.43*** | 0.127 | 0.02 | 0.02 | -0.01 | 0.06 |
| Spotted hyena | 0.330 | -0.04 | 0.10 | -0.24 | 0.15 | 0.205 | -0.01 | 0.02 | -0.04 | 0.02 |

**Table 3.3**. Model selection estimates and p-values from circular-linear analysis of prey species from the lunar phase-only model. Significant p-values and confidence intervals that do not include zero are bolded and italicized. Mean values and errors are given in radians and represent temporal shift.

| Species | | Lunar Phase | | | | |
|---|---|---|---|---|---|---|
| | n | p-value | Mean | SE | L_CI | U_CI |
| African civet | 99 | ***0.001*** | ***-0.09*** | ***0.03*** | ***-0.15*** | ***-0.04*** |
| African wildcat | 21 | ***0.005*** | ***-0.50*** | ***0.19*** | ***-0.87*** | ***-0.12*** |
| Banded mongoose | 16 | 0.307 | 0.02 | 0.04 | -0.06 | 0.10 |
| Black-backed jackal | 811 | ***0.013*** | ***0.05*** | ***0.02*** | ***0.01*** | ***0.09*** |
| Brown hyena | 120 | ***0.020*** | ***0.08*** | ***0.04*** | ***0.00*** | ***0.15*** |
| Honey badger | 19 | 0.498 | 0.00 | 0.16 | -0.32 | 0.32 |
| Large-spotted genet | 242 | ***<0.000*** | ***-0.09*** | ***0.03*** | ***-0.14*** | ***-0.04*** |
| Leopard | 49 | 0.414 | -0.02 | 0.10 | -0.22 | 0.18 |
| Small-spotted genet | 12 | ***<0.000*** | ***-0.41*** | ***0.11*** | ***-0.61*** | ***-0.20*** |
| Spotted hyena | 83 | ***0.028*** | -0.08 | 0.04 | -0.16 | 0.00 |

**Table 3.4**. Model selection estimates and p-values from circular-linear analysis of prey species from the habitat-only model. Significant p-values and confidence intervals that do not include zero are bolded and italicized. Mean values and errors are given in radians and represent temporal shift.

| Species | | Habitat | | | | |
|---|---|---|---|---|---|---|
| | n | p-value | Mean | SE | L_CI | U_CI |
| African civet | 99 | ***<0.000*** | ***1.00*** | ***0.07*** | ***0.86*** | ***1.14*** |
| African wildcat | 21 | 0.402 | 0.05 | 0.18 | -0.31 | 0.40 |
| Banded mongoose | 16 | 0.464 | 0.01 | 0.06 | -0.12 | 0.13 |
| Black-backed jackal | 811 | 0.141 | -0.06 | 0.06 | -0.17 | 0.05 |
| Brown hyena | 120 | ***<0.000*** | ***-0.16*** | ***0.04*** | ***-0.24*** | ***-0.07*** |
| Honey badger | 19 | 0.273 | 0.10 | 0.16 | -0.21 | 0.40 |
| Large-spotted genet | 242 | ***<0.000*** | ***0.13*** | ***0.04*** | ***0.06*** | ***0.20*** |
| Leopard | 49 | ***<0.000*** | ***-0.60*** | ***0.15*** | ***-0.90*** | ***-0.31*** |
| Small-spotted genet | 12 | 0.273 | 0.25 | 0.41 | -0.55 | 1.04 |
| Spotted hyena | 83 | 0.258 | -0.06 | 0.09 | -0.22 | 0.11 |

**Table 3.5**. Model selection estimates and p-values from circular-linear analysis of prey species from the minimum nighttime temperature-only model. Significant p-values and confidence intervals that do not include zero are bolded and italicized. Mean values and errors are given in radians and represent temporal shift.

| Species | Minimum Nighttime Temperature | | | | | |
|---|---|---|---|---|---|---|
| | n | p-value | Mean | SE | L_CI | U_CI |
| African civet | 99 | 0.076 | -0.01 | 0.01 | -0.03 | 0.00 |
| African wildcat | 21 | ***0.037*** | 0.11 | 0.06 | -0.01 | 0.24 |
| Banded mongoose | 16 | ***0.029*** | -0.04 | 0.02 | -0.09 | 0.00 |
| Black-backed jackal | 811 | ***0.003*** | ***-0.02*** | ***0.01*** | ***-0.04*** | ***-0.01*** |
| Brown hyena | 120 | 0.222 | -0.01 | 0.01 | -0.03 | 0.01 |
| Honey badger | 19 | 0.283 | 0.02 | 0.03 | -0.04 | 0.07 |
| Large-spotted genet | 242 | 0.208 | 0.01 | 0.01 | -0.01 | 0.03 |
| Leopard | 49 | 0.253 | -0.02 | 0.02 | -0.06 | 0.03 |
| Small-spotted genet | 12 | ***0.047*** | 0.05 | 0.03 | -0.01 | 0.10 |
| Spotted hyena | 83 | 0.429 | 0.00 | 0.01 | -0.03 | 0.03 |

**Table 3.6**. Literature review summary of prey classes consumed by each carnivore species. An “X” indicates instances found in the literature whereby the species listed in a row consumed or was aggressive toward the prey class listed in each column. Blanks indicated cases where no such reference was found in the literature, and a “-“ represents cases where a species was not found to consume or be aggressive toward any of the prey classes listed in the columns.

| Common Name | Large Game – Adult | Large game – Young | Medium Game | Small Game | Birds | Source |
|---|---|---|---|---|---|---|
| African civet[2] | - | - | - | - | - | (Bekele et al. 2008) |
| African wildcat | | | | X | X | (Kok and Nel 2004, Herbst and Mills 2010) |
| Banded mongoose | | | | | X | (Rood 1975) |
| Black-backed jackal | X[1] | X | X | X | X | (Kaunda and Skinner 2003, Kok and Nel 2004, McKenzie 2007, Klare et al. 2010) |
| Brown hyena | X | X | X | X | X | (Mills and Mills 1978) |
| Honey badger | | | | X | X | (Begg et al. 2003) |
| Large-spotted genet | | | | | X | (Roberts et al. 2007) |
| Leopard | X | X | X | X | X | (Hayward et al. 2006) |
| Small-spotted genet | | | | X | X | (Larivière and Calzada 2001) |
| Spotted hyena | X | X | X | X | X | (Holekamp et al. 1997, Di Silvestre et al. 2000, Hayward 2006) |

[1] One authors notes that instances could be the result of scavenging while another observed jackals killing adult impala

[2] No prey in listed categories were reported

**Table 3.7**. Literature review summary of predator-predator competition. All documented cases of carnivore interspecies aggression are indicated with an "X". Areas of where the literature is deficient are indicated with a "-". General interspecific risk is also shown.

| Aggresse/Prey<br>Aggressor/Predator | African civet | African wildcat | Mongoose spp. | Black-backed jackal | Brown hyena | Honey badger | Large-spotted genet | Leopard | Small-spotted genet | Spotted hyena | Misc. carnivores | Source | Listed, by category, as having the highest potential for interspecific competition with other carnivores in a study of 70 African carnivore species (Caro and Stoner 2003) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | rs | rg | rh | ex | kp | ik | ov |
| African civet | - | - | - | - | - | - | - | - | - | - | - | *None found* | | x | x | | | | |
| African wildcat | - | - | - | - | - | - | - | - | - | - | - | *None found* | x | | | | | | |
| Banded mongoose | | | X | | | | | | | | | (Waser et al. 1995) | | x | | | | x | |
| Black-backed jackal | | X | X | | | X | | | X | | X | (Mills et al. 1984, Walton and Joly 2003) | | x | x | x | x | x | |
| Brown hyena | | X | X | X | | X | | | | | X | (Mills and Mills 1978, Skinner and van Aarde 1981) | | | | | x | | |
| Honey badger | | | X | X | | | | | | | | (Kruuk and Mills 1983, Begg et al. 2003) | x | | x | x | | | |
| Large-spotted genet | - | - | - | - | - | - | - | - | - | - | - | *None found* | | | x | x | | x | x |
| Leopard | X | X | X | X | X$^3$ | X$^3$ | X$^3$ | X$^1$ | X$^3$ | X | X | (Mills et al. 1984, Polis et al. 1989, Henschel et al. 2005, Grimbeek 2006, Hayward et al. 2006) | x | | x | x | x | | |
| Small-spotted genet | - | - | - | - | - | - | - | - | - | - | - | *None found* | | x | x | x | | x | x |
| Spotted hyena | X | X$^2$ | X | X | X | X | X | X | X | X$^1$ | X | (Mills 1984, Mills et al. 1984, Cooper et al. 1999, Di Silvestre et al. 2000, Kamler et al. 2009, Abay et al. 2011) | x | x | | | x | | |

[1] Potentially the result of self-grooming

[2] Listed only as "cat"

[3] Listed as a potential but unconfirmed prey item

rs = due to >0% range overlap with the highest numbers of other carnivores
rg = due to >33% range overlap with the highest number of other carnivores
rh = due to >0% range overlap *and* common habitat shared with highest number of other carnivores
ex = due to exploitive competition as evidenced by shared geographic range, habitat and dietary habits with the highest number of other carnivores
kp = due to risk of kleptoparasitism from the highest number of other carnivores
ik = due to risk of interspecific killing from the highest number of other carnivores based on geographic and habitat overlap, and body size comparison
ov = due to high overall vulnerability

# CHAPTER 4

# DISCUSSION AND CONCLUSIONS

The information presented here provides relevant data regarding the habitat preferences, preferred bait types, and peak activity times of predators common to southern Africa. A combination of these factors can be employed to determine the optimal trapping sites, times, and methods for each species. Further, temporal and habitat data is useful to safari guides seeking to increase the chances that they can show guests a particular predator in the wild. These data will allow guides to conduct tours at the appropriate time and in the best areas to maximize the chance of a sighting.

Results from Chapter 2 show that meat is preferred as a lure for larger carnivores, including leopard, spotted hyena, and brown hyena. However, cooking fat may be used effectively for meso-mammal predators. In particular, African civet and large-spotted genet, both members of the family Viverridae, along with black-backed jackals, showed increased detections with fat rag baits. In the case of large-spotted genets, cooking fat was the preferred bait, yielding a useful methodological result for future research on this understudied species (IUCN 2013). Future investigation on smaller guilds of southern African carnivores, such as the temporal analysis conducted in Chapter 3, may benefit from the effectiveness, reduced logistical complications, and accessibility of cooking fat as a lure. Further, monitoring programs in southern Africa, and particularly programs in remote areas that are also limited by financial resources and harvest regulations that might prevent procurement of meat baits, will benefit from these findings.

Further, we saw in Chapter 2 that large fever berry thickets along rivers provided important habitat for brown hyena and large-spotted genet. The conservation implications of this finding are wide-ranging. A portion of what is now Notugre was originally set aside as an elephant sanctuary in the 1940s (Spinage 1990). Today, African elephant are abundant on the Mashatu Game Reserve as the result of conservation initiatives and concentration of the species on the site due to hunting and habitat loss over the reserve's borders (Mashatu Game Reserve 2013, Snyman 2013 pers. comm.). Rising elephant numbers and the potential for overpopulation on the site mirror a general trend across Botswana, which holds the majority of the world's African elephant population in high concentration (Spinage 1990, Skarpe et al. 2004). Historical photographs of the region displayed in the Mashatu Main Camp natural history museum show that this vegetation band once extended 1-2 km away from the edge of the Motloutse River. During the time of this study, the band had been reduced to a width of just a few hundred meters. While no studies have demonstrated a direct link between the rise in elephant numbers and the extreme changes in vegetation on the site, it is widely known that elephants do alter their environments, and thus many studies consider the effects that high elephant density has on habitat (e.g., Ben-Shahar 1993, Trollope et al. 1998, de Beer et al. 2006). Future conservation efforts need to monitor the effects of concentrated elephant populations on habitat change, and the effect these changes may have on declining carnivore species and biodiversity in general.

Analysis of temporal distribution in Chapter 3 showed diversity in daily activity patterns among carnivores. Species of similar prey bases did exhibit some division of temporal use, suggesting a potential response to interference competition for prey. While peak activity times were investigated, longer-term assessments of activity over larger scales and in various seasons would be needed to make conclusive statements about species-specific activity patterns and temporal partitioning. However, results from this study could be combined with more detailed species-specific studies to investigate these effects. Further, I found evidence that lunar phase, habitat, and minimum nighttime temperature each affect activity in one or more of the species examined.

All carnivores species included in this study ranked in at least one top category for risk of interspecific competition in a study of 70 African carnivores (Table 3.7) (Caro and Stoner 2003). I theorize that this competition-adapted assemblage of carnivores at Mashatu might evidence external pressures and conflicts that could be excluding less robust species, making the site an important area to monitor as human conflict puts increasing pressure on predator populations.

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