Anthropogenic effects on site use and temporal interactions of terrestrial mammals in Harenna Forest, Ethiopia.

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Abstract (Academic)

There has been little research comprehensively documenting wildlife species in Harenna Forest within the Bale Mountains National Park of Ethiopia. This area is one of the few remaining afro-alpine biodiversity hotspots and is home to numerous endemic plants and animals and offers socio-economic benefits to the neighboring communities. Human population pressure, weak land protection policies, and uncertain land tenure rights have led to increases in farmland for subsistence and coffee farming, livestock grazing, and reduction of afro-alpine, shrubland and grassland habitats. Given these challenges, I used 48 camera trap stations to produce an inventory of wildlife species and to determine factors influencing occupancy (i.e., habitat use), detection, and temporal activity and overlap. I recorded 26 terrestrial and arboreal mammalian species and I had sufficient data to model occupancy for 13 species and temporal activity for 14 species. Occupancy and detection were generally higher for herbivores and omnivores (occupancy: 0.28-0.97; detection: 0.1-0.54) than carnivores (occupancy: 0.31-0.80; detection: 0.04-0.18). I found more evidence of positive anthropogenic impacts on herbivore and omnivore occupancy than negative, while detection was influenced by habitat or landscape features, rather than by humans. Carnivore occupancy was largely unaffected by anthropogenic or habitat variables, but detection was strongly, and mostly positively, influenced by anthropogenic impacts.

Temporal activity analyses revealed that, for herbivores and omnivores, only tree hyraxes (*Dendrohyrax arboreus*) and crested porcupines (*Hystrix cristata*) were nocturnal, Menelik

bushbucks (*Tragelaphus scriptus meneliki*) were crepuscular, and the remaining species ranged from diurnal to cathemeral. Neither similar body size nor similar diet affected overlap between species pairs. However, overlap with human temporal activity was low for Menelik bushbucks (Δ=0.45) and common duikers (*Sylvicapra grimmia*) appeared to become less active at stations with high human use. For carnivores, leopards (*Panthera pardus*) and honey badgers (*Mellivora capensis)* were crepuscular, and the remaining species were nocturnal. I found evidence that carnivores overlapped less when they were more similar in body size to other carnivores (average Δ=0.67-0.71) compared to species more dissimilar in body size (average Δ=0.75), although there was variation across species. In general, carnivores overlapped much less with humans (average Δ=0.20) than did herbivores (average Δ=0.52) and omnivores (average Δ=0.43). Spotted hyenas (*Crocuta crocuta*), in particular, appeared to alter activity to reduce overlap with humans.

This study provides baseline information on presence, distribution, and activity of large- and medium-sized terrestrial and arboreal mammals in an understudied biodiversity hotspot. My findings are concerning for biodiversity conservation as rare and endangered species (e.g., mountain nyalas (*Tragelaphus buxtoni*), Ethiopian wolves (*Canis simensis*)) were rarely or never photographed, and larger carnivores (e.g., lions (*Panthera leo*), leopards, jackals), generally had low capture rates. The species with higher capture rates, occupancy, and activity tended to be those that can tolerate or take advantage of human activity and disturbance. Species sensitive to human disturbance eventually may be lost unless measures can be put in place to reduce human impacts. This baseline knowledge is important for future studies examining trends in mammalian wildlife populations, such as site extinction and colonization, or changes in overlap with humans, in a landscape that is continuing to experience human-caused, landscape change.

Anthropogenic effects on site use and temporal interactions of terrestrial mammals in Harenna Forest, Ethiopia.

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General Audience Abstract

Harenna forest, which is located in Bale Mountains National Park, Ethiopia is an important habitat to both wildlife and people. However, it faces a number of challenges as a result of population growth leading to increased coffee farming and livestock grazing resulting in reduced habitat for wildlife species. I used 48 cameras located across the forest to record presence of terrestrial mammals and document their distribution and daily activity across the landscape. I also used data such as vegetation indices, elevation, and distances to human-disturbed areas to determine what influenced wildlife species. Cameras recorded 26 species of mammals. I had enough data to determine distribution for 13 species and daily activity for 14 species. I found that presence across the landscape and activity of herbivores and omnivores was generally higher than that of carnivores. Additionally, I found that human activity or disturbance often had a positive influence on herbivore and omnivore distribution, but my ability to detect species in camera traps was primarily influenced by habitat or landscape features. Carnivore distribution on the landscape was not influenced much by humans or habitat, but their detectability was often positively influenced by presence of humans.

In addition to daily activity, I also analyzed overlap in activity between species pairs and between species and humans, to determine whether wildlife changed their temporal activity to overlap less with similar sized competitors or in response to high human use. For herbivores and omnivores, I found that tree hyraxes and crested porcupines were active at night, Menelik's

bushbucks were active at sunrise and sunset, and cape bushbucks, common duiker, olive baboon, bushpig, and giant forest hogs were active either during the day or throughout the day and night. I found little evidence that the herbivores or omnivores avoided each other temporally and only the Menelik bushbuck and duiker appeared to avoid humans. For carnivores, I found that leopards and honey badgers were active early morning and evening, and the common genet, African civet, white-tailed mongoose, and spotted hyenas were all active at night only. Carnivores generally overlapped less with humans than herbivores and omnivores. I found some evidence that carnivores more similar in body size had lower temporal overlap with each other and that spotted hyaenas appeared to avoid activity during times of day when humans were active.

My study not only provides baseline information on terrestrial and arboreal mammals present in Harenna forest, Ethiopia, but is also necessary for understanding how wildlife species use the landscape and particularly how presence of humans influences wild animal behavior. My findings are concerning for biodiversity conservation because I had few to no photographs, respectively, of the endangered mountain nyala and Ethiopian wolf. In fact, most of the species with a wide distribution on the landscape, or with high activity, were common or smaller species that are tolerant of, or could take advantage of, human disturbance. Without concerted effort to curtail the current landscape change caused by humans, the area is likely to lose species less tolerant of humans, and biodiversity will ultimately decline.

Dedication

To Fafa, Gracie and Kiptoo

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Chapter 1 : Introduction

Bale Mountains National Park (BMNP) was established in 1971 to protect endangered mountain nyalas (*Tragelaphus buxtoni*) and Simien wolves (*Canis simensis*; also known as Ethiopian wolves), and it covers an area of 2200 km^2 (Figure 1; Hillman, 1986). The park is located 450 kilometers south-east of Addis Ababa (the capital city), Ethiopia in the Oromia regional state (Figure 1; Hillman, 1986; Kidane et al., 2012; Mamo et al., 2015; Umer et al., 2007). BMNP lies between 06°29' N, 39°03' E and 07°10' N, 40°00' E (Mezgebu & Workineh, 2017a). The park was also established to protect the Afro-alpine habitat, which serves as the water catchment area for five of the largest rivers in Ethiopia: Wabi Shebele, Welmel, Dumal, Web, and Ganale (Hillman, 1986; Mezgebu & Workineh, 2017a). These rivers, alongside the over 40 streams and springs, are critical for the 12 million people downstream in Ethiopia, Northern Kenya, and Somalia, who rely on these water resources (OFWE, Farm Africa, 2016).

BMNP was proposed as a UNESCO 200 bioregion as a potential (legal status and gazettement pending) world heritage site to protect biodiversity and endemic species (UNESCO 2008). Bale eco-region (BER), where BMNP is located, is the largest, most contiguous mountain massif in Africa and the last remaining relatively pristine afro-alpine biodiversity hotspot (Evangelista et al., 2017; Kidane et al., 2012; Reber et al., 2018; Wakjira et al., 2015; Tessema, 2017). BMNP is home to at least 77 mammal and 170 bird species, with 160 mammal and bird species endemic to Ethiopia (Demeke & Lemma, 2017). In addition to the endangered mountain nyala (Atickem et al., 2011, 2013; Evangelista et al., 2008, 2012, 2017: Mamo et al., 2015) and the Ethiopian wolf (Stephens et al., 2001), BMNP is also home to the giant mole rat (*Tachyoryctes macrocephalus*) (Stephens et al., 2001; Siebert, 2004). There also are a number of primates such as the Bale monkey (*Chlorocebus djamdjamensis*), the vervet (*Chlorocebus pygerythrus*) and the

grivet (*Chlorocebus aethiops*) (Mekonneh,1999; Kingdon, 2015). Additionally, there are at least 23 plant species endemic to BER out of 163 that are endemic to Ethiopia from 1321 known plant species in the area (Kidane et al., 2012; Siebert & Ramdhani, 2004; Tessema, 2017).

1.1 Challenges

Despite the uniqueness and importance of this area as a potential world heritage site due to high biodiversity and endemism and water conservation significance, there are no recent comprehensive data on the terrestrial mammal populations in the area (Lavrenchenko, 2000), especially from Harenna forest, the study site, apart from a few records of endangered Ethiopian wolves and mountain nyalas (Asefa, 2016; Atickem et al., 2011, 2013; Evangelista et al., 2008, 2017, 2012; Hillman, 1986; Mamo et al., 2015; Refera & Bekele, 2004; Stephens et al., 2001). In addition, the locals rely heavily on BMNP resources for their livelihoods by growing coffee, livestock grazing, subsistence crop farming, or for sources of water (Wakjira et al., 2013). BMNP also faces conservation challenges related to human pressures associated with forest use and increasing human settlement (Wakjira et al., 2013; Watson, 2013). Loss of biodiversity and agricultural expansion have stemmed from weak to non-existent park management policies, population growth, food insecurity, unemployment, unclear land tenure rights, socio-political factors, and drought. (Bewket, 2002; Mezgebu & Workineh, 2017a). Agricultural encroachment has been linked to overgrazing, settlements, and conversion of forest lands to forest coffee plantations, fires, timber extraction, and unsustainable collection of wood for fuel.

Change detection matrices reveal that over the last 40 years, the area has changed from a largely natural (forest, shrubland and grassland) to a more developed landscape (farmland) (Hailemariam et al., 2016). In tropical regions, anthropogenic changes like habitat conversion are mostly responsible for biodiversity loss and terrestrial land transformation. This stems mostly from

human population growth (Demeke & Lemma, 2017; Hailemariam et al., 2016; Kidane et al., 2012; Mezgebu & Workineh, 2017b; Siraj et al., 2018; Wakjira et al., 2015; Tessema, 2017). Ethiopia is made up of 43% mountainous regions with endemic species richness monotonic in the mountainous regions (Kidane et al., 2019). Additionally, 85% of human, and over 75% of livestock, populations are found in these areas. Hailemariam et al. (2016) and Mezgebu & Workineh (2017a) showed that forest cover from 1985 to 2015 has been reduced significantly from 21% to 18%, while farmlands increased from 15% to 23%. Additionally, in Afroalpine and Erica-dominated areas, farmlands and urban settlements have increased between years 1985 to 2015 (Hailemariam et al., 2016; Kidane et al., 2012). Forests and shrubland lost most of their land between 1995 and 2005 (Hailemariam et al., 2016), while most of the grasslands were lost between 2005 to 2015. For Afroalpine, Ericaceous-dominated woodlands, land use and land cover (LULC) data showed moderate losses of these habitat types as well (Hailemariam et al., 2016). During this time, most of the land was converted to agriculture, specifically for the growth of coffee, since coffee prices began to increase, boosting international value for Ethiopian coffee, and farmers now have better access to the market (Wakjira et al., 2013). Farmlands gained 50,271 ha between 1985 to 1995, gained 138,703 ha between 1995-2005, and gained 103,320 ha between 2005 and 2015 (Hailemariam et al., 2016). Forests were the major contributor to farmlands as forest loss was 123,751 ha between 1985 and 2015. Shrubland ranked second in losses at 93,078 ha lost, and grasslands ranked third in loss at 83,158 ha between 1985 and 2015 (Hailemariam et al., 2016).

1.1.1 Population Growth-Human and Livestock

Population growth in Bale region, within and outside of the park, is at a steady rate of 2.3% annually and since population size reached 85 million in 2013, population pressure around protected areas has risen (Demeke & Lemma, 2017). Population size increased from 8,500 people

to about 79,000 people within the Bale region (Hailemariam et al., 2016) from 1985 to 2015. In addition, livestock in the area is estimated at 3,124,305 and consists of cattle, goats, and sheep (Hailemariam et al., 2016; OFWE, Farm Africa, 2016). This has resulted in high demand for food and land to support people and their livestock, leading to more forest land being converted to cropland. This expansion reduces natural resources that support wildlife and contributes to habitat fragmentation leading to local extinction of wildlife species (Demeke & Lemma, 2017; Stephens et al., 2001). Hailemariam et al. (2016) and Wakjira et al. (2013) show that the major driver of LULC change is cropland farming, which accounts for 96% of deforestation. This has been linked to underlying socio-economic factors such as poverty and legal and illegal logging (wood extraction) (Geist and Lambin 2001) and weak law enforcement (OFWE, Farm Africa, 2016).

1.1.2 Growth of Coffee

Bale region, since before the 1900s, has been used to grow coffee, which is an understory, shade-tolerant plant (Wakjira et al., 2013). Bale Mountains and Harenna Forest are conducive for coffee because of tree shade as well as temperature and rainfall (Wakjira et al., 2013). Before and during the 1900s, coffee was grown and used for traditional medicine as well as for rituals (Wakjira et al., 2013). Towards the end of the 19th century, Islamic teachers introduced consumption of coffee as a beverage (Wakjira et al., 2013). As a result, regulation was introduced regarding coffee picking and coffee protection (Evangelista et al., 2017; Mezgebu & Workineh, 2017b, 2017a; OFWE, Farm Africa, 2016; Shiferaw & Suryabhagavan, 2019; Siebert, 2004; Siebert & Ramdhani, 2004; Wakjira et al., 2013). In the mid-nineteenth century, coffee was introduced as barter trade commodity, which led to an increase in demand for coffee (Wakjira et al., 2013). Coffee tending practices and policies surrounding the crop have evolved through over time (Wakjira et al., 2013). In 1996, after a weakened military regime in the Oromo area, the coffee market was stimulated

leading local people to sell coffee at the central market in Addis Ababa (Wakjira et al., 2013). This enabled integration of the trade into international markets, leading to increases in coffee prices and investment of resources into coffee growing and production. This led to intensification of farming of coffee in the Bale area to the detriment of the natural habitat. Migration into the area also increased in the mid-1990s due to enhanced coffee production (Kidane et al., 2012; Mezgebu & Workineh, 2017a; Tadesse Wakjira et al., 2015; Wakjira et al., 2013).

1.2 Ecoregion and Study Area

1.2.1 Land cover types of the Bale Ecological Region (BER)

BER experiences 2 seasons, a dry season from November to February and a bimodal rainy season, one with a peak from April to May and the second in September to October (Hailemariam et al., 2016; Siebert & Ramdhani, 2004). BMNP experiences varied amount of rainfall and the variability in altitude result in variable habitats (Siebert & Ramdhani, 2004). BER is made up of three main zones- the Southern Harenna Forest, which is found 1600-3500 m above sea level (m.a.s.l), the central Sanetti plateau and peak area between 3500 and 4400 m.a.s.l, and the northern Gaysay/Adeley Forest and a grassland area, which is at 3000 and 3500m asl (Hillman, 1986) (Figure 1). Tullu Deemtu, the second highest peak in Ethiopia (4377 m.a.s.l), is also found in BMNP (Hillman, 1986) (Figure 2). I am describing all habitat types found in BMNP, but cameras were only set in the Afromontane region.

1.2.1.1 Lowlands

As the Weyib river channeled through the limestone foothills of the park it formed an extensive cave system (Siebert, 2004). The vegetation in the area is dry, thorny, savanna with grasslands. Succulent forbs are also common (Siebert & Ramdhani, 2004). Teff (*Eragrostis tef*), a cereal used to make Ethiopia's staple food, injera, is also found at this altitude (Mezgebu &

Workineh, 2017a; OFWE, Farm Africa, 2016; Siebert, 2004; Siebert & Ramdhani, 2004; Siraj et al., 2018). This habitat is the most utilized for agricultural practices such as tef farming and livestock grazing during rainy seasons (Kidane et al., 2012).

1.2.1.2 Afromontane Region - The region where cameras were set.

Above the plains is an Afromontane Forest belt that rises to about 3200 m.a.s.l and is known as the escarpment (Siebert, 2004; Umer et al., 2007) (Forest-Figure 2). The escarpment divides the area into a Northeast and Southwest region. This Afromontane region is where coffee farming takes place (Kidane et al., 2012; Kuzmicheva et al., 2018) and the southwest region is where Harenna Forest is found (Figures 1 and 2) (Siebert, 2004). The landscape in the north is characterized by patches of former extensive forests where junipers and East African rosewood (*Hagenia abyssinica*) grow (Siebert, 2004; Umer et al., 2007). In the open forests, white Abyssinian rose (*Rosa abyssinica*), and Simian beech (*Rapanea simensis*) grow, while endemic Solanecio gigas, a member of the sunflower family, grows in damp areas (Siebert, 2004). In the south, the escarpment is characterized by typically denser forests of yellowwood with mountain bamboos interspersed (Siebert, 2004; Umer et al., 2007). The trees are usually covered by epiphytes, lianas, and creepers and they reach ~30 m in height. Grasslands develop in areas where drainage between forests is impeded due to human activities and marshy conditions occurring along the streams (Siebert, 2004). Endemic flowering plants have developed at higher altitudes and in areas near human developments, resulting in gardens due to the growth of torch lilies (Siebert, 2004; Umer et al., 2007).

1.2.1.3 Subalpine Zone

Reaching 3500 m.a.s.l and above the tree line is the subalpine region (Erica Forest/shrub-Figure 2). This region is characterized by ericaceous heathland (Siebert, 2004; Umer et al., 2007)

that experiences mist that causes growth of lichens, wildflowers, moss, and grass. Pastoralists, in attempting to have more grass, burn the heather giving rise to stunted, re-growing trees (Siebert, 2004; Umer et al., 2007). The transition zone to the Afroalpine region contains heather (*Erica trimera*) and dwarf shrub (*Helichrysum citrispinum*) (Siebert, 2004; Umer et al., 2007). There are a few endemic species in this region such as giant globe thistle (*Echinops longisetus*) and *Rubus erlangeri*, a member of the blackberry family (Siebert, 2004; Umer et al., 2007).

1.2.1.4 Afroalpine Region – Central Sanetti Plateau Zone

At above 4000 m.a.s.l, is the Afroalpine region where the Sanetti Plateau is found. The area has rock formations resulting from lava flows (Siebert, 2004) (Figure 2). At the highest peaks, there are rocks and exposed soils with little vegetation (Reber et al., 2018; Siebert, 2004). Slope, drainage, and rodent activity determine the plant communities in this region (Reber et al., 2018; Siebert, 2004). Giant mole rats are responsible for continuously moving the soils (Demeke & Lemma, 2017; Siebert, 2004; Wakjira et al., 2015; Watson, 2013). Lichens and mosses also grow in this region with plants growing along the drainage lines and bogs. Erica-Helichrysum grows in this area in the basaltic geology between 2900 and 3500 m.a.s.l. (Siebert & Ramdhani, 2004). Lobelias such as *Lobelia rhynchopetalum* (giant lobelia) and *Lobelia gibberoa* make this habitat unique (Kidane et al., 2012; Mezgebu & Workineh, 2017a, 2017b Siebert & Ramdhani, 2004; Watson, 2013; Demeke & Lemma, 2017; Kidane et al., 2012; Siebert, 2004; Watson, 2013). The Afroalpine ecosystem is also considered one of the 34 Conservation International Biodiversity Hotspots and is listed as an important area for birds (Kidane et al., 2012).

1.3 Background on camera study, target species, and *a priori* hypotheses for occupancy and detection.

The camera trapping study occurred in Harenna Forest, southeast Ethiopia (Figure 1) which is located in Bale Mountains National Park (BMNP). Harenna forest covers 3,000 km^2 and ranges in altitude from 1,300-3,500 m.a.s.l (Figure 1). Photographic camera trap data were collected from December 2015 to September 2016; cameras were placed 0.5-2 kms apart in three different surveys: December 2015 - April 2016, April 2016, and September 2016 in an effort to photograph a melanistic leopard that was rumored to be in the area as well as a lion that was living on heavily forested, the human-dominated landscape. Data from the study were used to provide baseline information on medium and large sized terrestrial mammals in Harenna, which is useful in examining mammalian population trends on the rapidly changing landscape. The objectives of this study are as follows:

1. Determine presence and distribution of terrestrial species and habitat and biotic factors influencing habitat use (including humans) using single season occupancy modeling for 13 target species from camera trap data.

2. Examine species interactions by investigating the relative influence of other wildlife species, humans, and domestic animals using 2-species, co-occurrence modeling, while including important habitat variables that influence distribution and detection.

3. Examine temporal activity patterns of 14 target species and overlap between species pairs including humans and domestic animals (cows, dogs, donkeys, horses).

Of the 26 terrestrial mammal species photographed, we obtained enough data to model occupancy and co-occurrence of 13 species: Menelik bushbuck (*Tragelaphus sylvaticus*), cape bushbuck

(*Tragelaphus sylvaticus*), common duiker (*Sylvicapra grimmia*), giant forest hog (*Hylochoerus meinertzhageni*), bush pig (*Potamochoerus larvatus*), olive baboons (*Papio anubis*), crested porcupine (*Hystrix cristata*), African civet (*Civettictis civetta*), honey badger (*Mellivora capensis*), common genet (*Genetta genetta*), white-tailed mongoose (*Ichneumia albicauda),* spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*). Representative photographs of each of these target species are shown in Appendix 1.1 (herbivores and omnivores) and Appendix 1.2 (carnivores).

I first used a single-species occupancy modeling approach for these target species to determine their distribution across the landscape, while incorporating imperfect detection (MacKenzie et al, 2017). To build such occupancy models, I researched the biology and ecology of these target species to determine factors that I thought might influence occupancy and detection. I briefly outline these factors below.

1.4 Herbivores and Omnivores

We photographed 14 species of herbivores and omnivores (see Chapter 2 for details). Of these, only 7 species had enough detections to model occupancy (Appendix 1.1). For these 7 target species, I created a set of *a priori* models that included landscape and biotic covariates that I thought would influence occupancy and detection based on the species' biology and ecology (Table 1.1). For example, Menelik's and cape bushbucks prefer temperatures less than 30° C, they prefer marshes more than open savannahs, and they prefer riparian areas and thickets where temperatures are lower (Dankwa-Wiredu & Euler, 2002). Vegetation height, slope, aspect, and land use activities generally have an influence on occupancy of ungulates (Mamo et al., 2015). Thus, I expected occupancy would be higher in grasslands, increase with closer proximity to water bodies, and detection probabilities will be higher in cooler seasons (Table 1.1).

Common duikers prefer areas with tall grass that allow sufficient cover from predators and provide escape routes (Wilson 2013, Baker and Brown 2014). They also are highly adaptable to populated areas, persisting in urban and semi-urban areas with much of their historic range remaining the same despite anthropogenic changes. They also persist near agricultural areas where natural vegetation is undisturbed. Therefore, I expected occupancy and detection to increase the closer they are to forest edges or human settlements (Table 1.1).

Giant forest hogs and bush pigs both prefer grasslands, green vegetation cover, and availability of water (Mekonnen et al., 2018). Therefore, I expected their occupancy and detection probabilities to increase in grasslands and forested areas as well as with a decrease in distance to rivers (Table 1.1). We also predicted that occupancy and detection would be influenced by large predator rates and occupancy (Guo et al.,2017).

Availability of food and water as well as predation risk seem to be the driving factors behind whether or not olive baboons would occupy a particular habitat (Barton et al., 1996). Olive baboons have been characterized as generalist species especially in the face of anthropogenic changes (Hill &Winder, 2019). However, studies have shown that seasonality is the most important factor that influences their habitat selection (Musyoki & Strum, 2016). Predation, especially from spotted hyenas, leopards (Bidner et al.,2018), and crown eagles (Paliencia et al., 2017) also influence their occurrence and behavior. Thus, I expected olive baboon occupancy and detection to decrease in the presence of spotted hyenas and leopards and to increase with increase in seasonal rainfall (Table 1.1).

Finally, crested porcupines have been categorized as generalist species and their responses to different habitat types are directly tied to food availability (Lovari et al., 2017; Mori et al., 2014). Studies show that typically they avoid agricultural areas especially during colder weather, but as

it becomes warmer, they select for agricultural lands more (Mori et al., 2014). Thus, I expected porcupine occupancy and detection probabilities to mainly vary according to seasons and with proximity to agriculture (Table 1.1).

1.5 Carnivores

We photographed 12 total species of carnivores (see Chapter 2 for details). Of these, only 6 species had enough detections to model occupancy (Appendix 1.2). For these 6 target species, I created a set of *a priori* models that included landscape and biotic covariates that I thought would influence occupancy and detection based on the species biology and ecology and (Table 1.1). For example, African civets are opportunistic feeders that thrive in riparian, natural, and degraded forests as well as in human landscapes (Table 1.1). They also select for lower elevation areas and avoid short grass and grasslands while preferring plains and shrubs (Durant et al., 2010). A study in Serengeti showed that probability of detection for civets decreases with an increase in distance to water (Durant et al., 2010) and increased when cameras are placed on trails (Admassu et al., 2010). In dry seasons, research shows that they consume coffee (Habtamu et al., 2017). Therefore, I expected that civet occupancy and detection would be higher closer to buildings, agricultural land, and water, and would decrease with increase in elevation.

Honey badgers have been shown to prefer areas close to water with a higher number of trees and can use anthropogenically modified habitats because they prefer eucalyptus areas (Kheswa et al., 2018). Therefore, I expected occupancy and detection probabilities of honey badgers to increase the closer they are to forest edges and agricultural areas (Table 1.1).

Common genets tend to prefer thickets and trees and select for areas near water (ravines) for availability of food and shelter from predators (Camps and Alldredge 2013; Virgos et al., 2001; Camps 2011). They tend to avoid areas with roads and trails and show preference for pine forest

and holm oak forests over crops, lowlands, and areas with human development (Camps and Alldredge, 2013). I hypothesized that common genet occupancy and detection will be higher in thicketed areas and increase with an increase in distance to roads, trails, and forest edges. They may also have higher occupancy/detection the closer they are to human settlements (Table 1.1).

White-tailed mongooses are found in a diverse range of habitats. Studies have shown that they prefer areas among rocks and empty buildings with surrounding bushes (Admasu et al., 2004; Foley et al., 2014). Given the option, they also prefer woodlands and bushes compared to farmlands, grasslands, and their least preferred habitat is dense forests (Admasu et al., 2004; Foley et al., 2014. Therefore, I predicted that mongoose occupancy and detection would be higher closer to agricultural land and buildings (Table 1.1).

Studies show that distance to water, human settlements, and roads alongside agricultural practices, type of soil, terrain, presence of other carnivores, and forest cover influence occupancy and detection of spotted hyenas (Ramesh, et al. 2017). Thus, I expected hyena occupancy and detection to increase as distance to forest edge, human settlements, and water decline (Table 1.1). I expected trap rates of large predators (lions and leopards) will cause a decrease in detection of spotted hyenas (Ramesh et al., 2017). I expected that their occurrence and detection will increase in presence of humans and domestic animals due to presence of anthropogenic food sources (Gade 2006; Abay et al., 2011).

Leopards are thought to have strong affinity to water, prefer grasslands and lower altitude areas, as well as abundant rainfall, and select forest edges because of prey availability (Abade et al., 2014: Balme et al., 2009). Thus, I expected leopard occupancy and detection to increase in grasslands and with river density or with proximity to rivers, and to decrease with distance away from water and at higher elevation. I expected that they would avoid areas with increased human

presence. I also expected that detection will increase in areas where trap rates of prey are higher (Table 1.1).

1.6 Spatial and temporal co-occurrence

In addition to occupancy, the ability of species to co-exist is influenced by either direct factors such as intraguild predation or interference competition, or indirectly by trophic cascades or exploitative competition (MacArthur & Levins, 1967; Davis et al., 2011; Hernández-SaintMartín et al., 2013). Managers and scientists need such information to inform conservation and management of ecological communities (Hillerislambers et al., 2012). This is important for understanding the potential for interactions among species such as interspecific competition and resource partitioning on both spatial and temporal scales.

Spatial co-occurrence models use single species occupancy modelling to estimate what sites are occupied based on habitat/biotic covariates from single season models and additionally incorporate the occupancy/detection of other potentially competing species (Mackenzie et al., 2004). Flexibility in this method allows for the estimation of probabilities of potential interaction between species using likelihood-based methods and addresses aspects of community structure such as competition and predator-prey relationships (Mackenzie et al., 2004).

Co-occurrence modelling incorporates detection/ non-detection of both species as well as habitat covariates in the modelling process and does not require equal sampling efforts for all the sites (Mackenzie et al., 2004). I built on my single season occupancy model results from the first objective to determine important habitat variables for each target species to include in modelling co-occurrence. This way, I was able to parse out whether habitat, interacting species, or both, are important predictors of species occurrence across the landscape.

In addition to spatial segregation that could be driving community structure, species could also segregate temporally to mitigate interspecific competition or foster coexistence (Davis et al., 2011; Hernández-SaintMartín et al., 2013). For carnivores, evidence shows that the temporal niche axis is fundamental for co-existence where a subordinate competitor may adjust their activity to avoid overlap less with a dominant competitor (Lutherini et al., 2009; Gerber et al., 2012; Carothers et al.,1984; Harmen et al., 2011). This segregation has been shown to occur along body size gradient, with more similar species showing more temporal avoidance (Sunarto et al., 2015). Thus, I expected the more similar in body size, especially for carnivores, the lower temporal overlaps there would be.

I used Kernel density estimate (KDE), a non-parametric method of determining the probability density function (PDF) of a continuous, circular, random variable (Ridout & Linkie, 2009) to assess temporal overlap between species pairs. In this case, time of capture is the continuous, circular random variable. It is non-parametric because it does not assume any underlying distribution for the variable (Ridout & Linkie, 2009). Essentially, at every datum (time interval), a kernel density function is created with the datum at its center to ensure that the kernel is symmetrical. The PDF is then estimated by adding all of these kernel functions and dividing by the number of data points (Ridout & Linkie, 2009). High density estimates come from having more observations that are close to the point of observation (i.e., more observations around the same time period in this case) as opposed to the areas that have fewer observations (Ridout & Linkie, 2009). Thus, more photographic records at certain times of the day will lead to higher KDE estimates for those time periods. The confidence intervals were estimated using a bootstrapping technique (Ridout & Linkie, 2009).

To examine overlap between species pairs, I estimated the coefficient of overlap of the probability density functions between all species pairings. If the coefficient of overlap Δ_1 between a species pairs are low, it indicates temporal avoidance (Ridout & Linkie, 2009). A Δ_1 =1.0 indicates complete overlap whereas a Δ_1= 0 is no overlap in time of activity. The target species considered for this analysis were the carnivore species (African civet, honey badger, common genet, white-tailed mongoose, spotted hyena, and leopard), the ungulates species (Menelik bushbuck, cape bushbuck and common duiker) and humans and domestic animals (humans, cows, goats, dogs, and donkeys)

I expected that carnivore species of the same size (e.g., spotted hyenas and leopards) will avoid each other temporally with leopards being nocturnal. I expected that domestic animals and humans will be diurnal with high overlap while native wild ungulates will be more crepuscular to nocturnal to potentially avoid domestic species during the day. I expected that native ungulates (Menelik's bushbuck, common duiker, and cape bushbucks) will still overlap temporally as dictated by resource availability, but those that are more closely related, or more similar in body size, may have slightly less temporal overlap to potentially reduce competition. I also expected that small carnivores, white-tailed mongooses (Do Linh et al., 2016), African civets (Ray, 2013), and common genets (Pesaresi, 2020) will overlap temporally because they are nocturnal, although mongooses can be diurnal on some occasions (Stuart, 1981).

This study provides vital baseline information on the presence and distribution of the medium- to large- sized terrestrial mammal community in a biodiversity hotspot and potential UNESCO World heritage site, where little information currently exists on the status of wildlife species. It also explores spatial and temporal ecology of the mammalian community, highlighting the relative influences of anthropogenic versus other natural biotic and abiotic features influencing

time of activity, occurrence, distribution across the landscape and show importance of human activities on the landscape.

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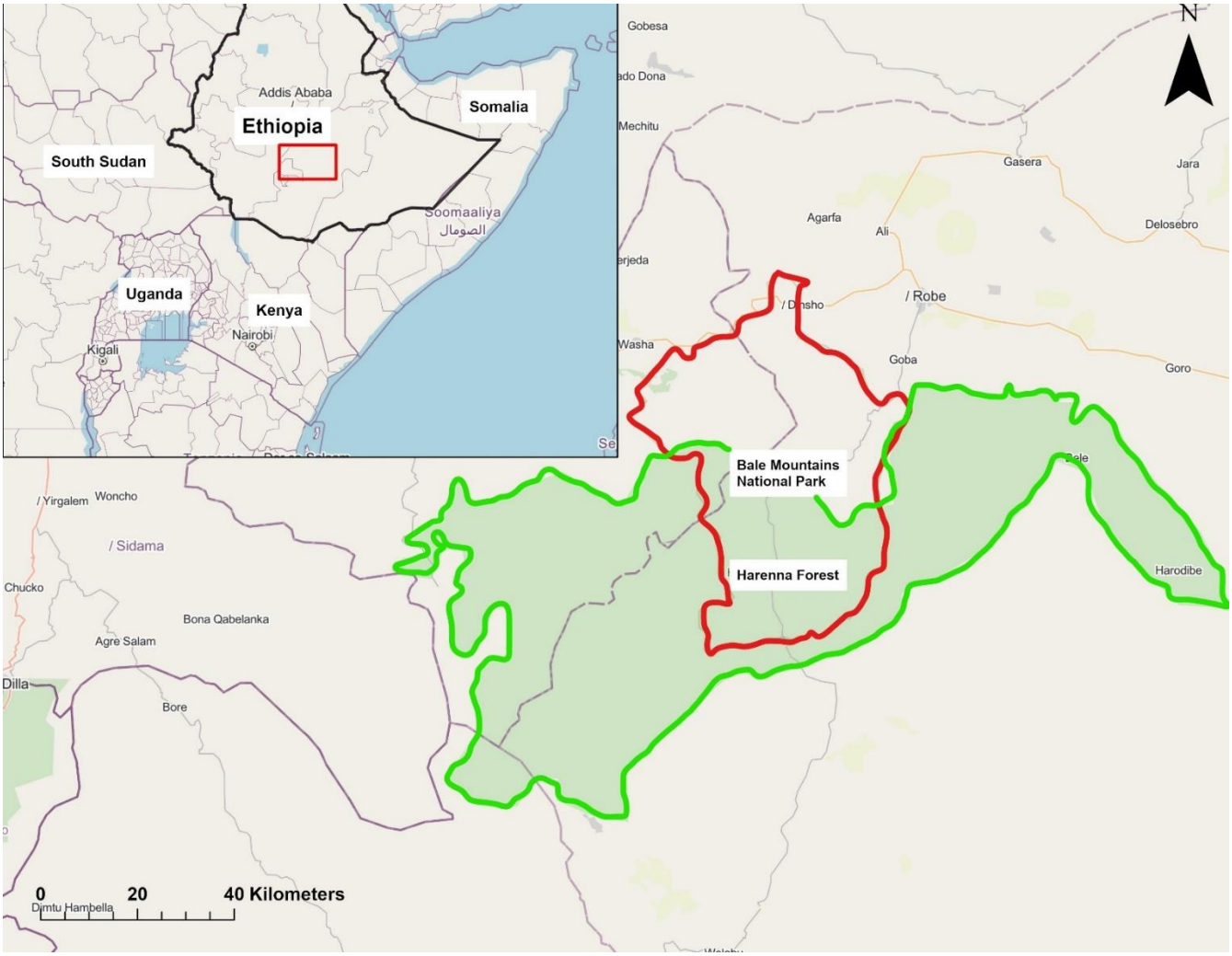


Figure 1.1 Map showing the location of Ethiopia (inset, red square highlights the location of the camera surveys), Harenna forest (green outline) and Bale Mountains National Park (red outline), Ethiopia, where the camera trap study took place in 2015-2016.

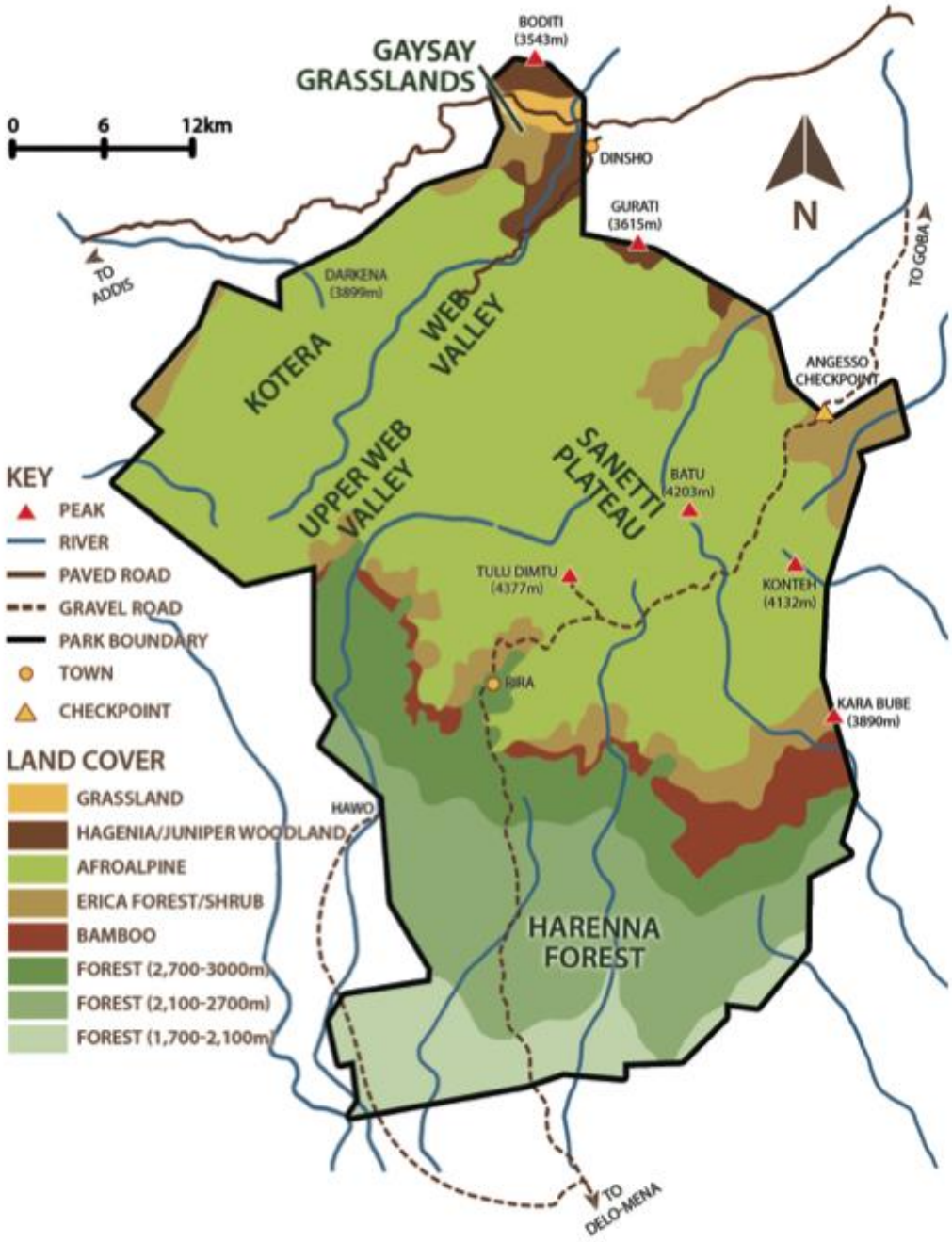


Figure 1.2. Map showing habitat types found in Bale Mountains National Park in Ethiopia from Bale Travel Guidebook-Frankfurt Zoological Society (2013). Camera traps for this study were placed in the Harenna

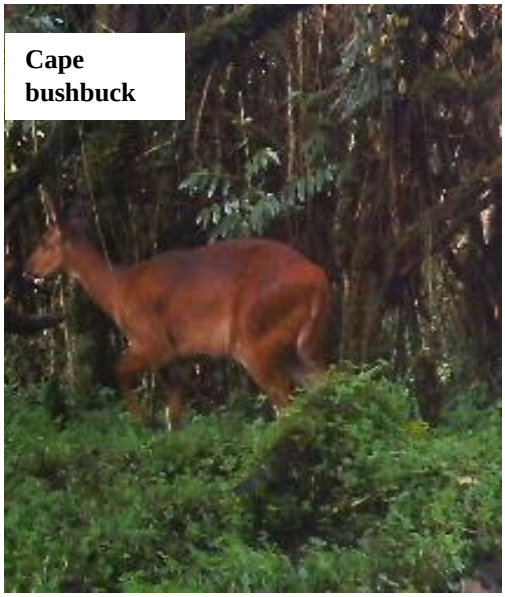
Table 1-1 Table showing landscape variables hypothesized to influence occupancy (psi or Ψ), detection probabilities (p) and both occupancy and detection, of the target species that had enough data to model. A plus sign indicates a positive relationship, and a negative sign indicates a negative relationship, between the covariate and occupancy and detection of the target species. Note, however, that with distance measures below, a plus sign indicates that occupancy increases with distance away from the feature. If there is no sign in a cell, I did not expect any influence of the habitat or landscape feature.

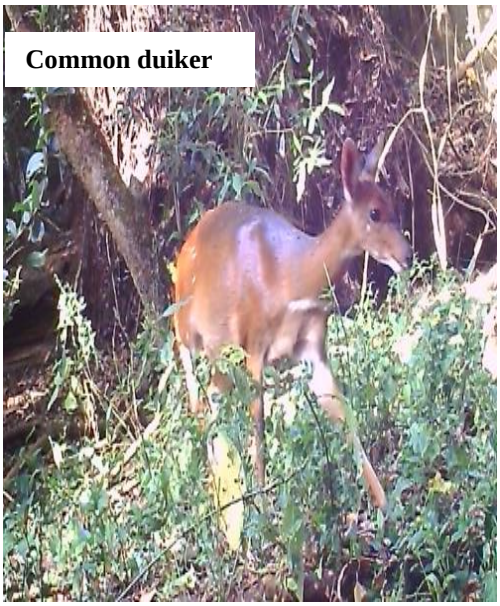
Variable	**Menelik bushbuck**	**Cape bushbuck**	**Common Duiker**	**Giant forest hog**	**Bush pig**	**Olive Baboon**	**Crested porcupine**	**African civet**	**Honey badger**	**Common genet**	**White-tailed mongoose**	**Spotted hyena**	**Leopard**
Landscape covariates hypothesized to influence both occupancy (Ψ) and detection (p) probabilities													
Land cover type (listed habitat types indicates a positive association with that type)	Thickets, marsh	Thicket, marsh	Tall grass, savannah woodland habitat	Grass			Deciduous woodland, shrub wood		Eucalyptus trees	Forest with tree and dense underbrush vegetation cover			
Elevation	+	+							-	-			
Distance to river -note positive (+) means species found farther from river	+		+					-	-	+		-	-
Distance to park boundary (+ is farther away)			+				-			-		-	-
Distance to settlement (+ is farther away)			+				-			+		-	+
Distance to agricultural land			+			+	-	+	+	+	+		
Activity rate of prey species	+	+	+		+		+	+	+	+	+	+	+
Activity rate of human/domestic animals			+				-					+	+

Trapping rates of other large predators (lions, hyenas, leopards)	+	+	+	+	+	+	+	+	+	+	+	+
Covariates hypothesized influence detection (p) probability only												
Temperature	< 30 °C			+								+
Amount of rainfall									+			+

1.8 Appendix

Herbivores and Omnivores with enough data to conduct occupancy.






Bush pig


Olive baboon


Crested porcupine

Carnivores with enough data to conduct occupancy modelling.

Chapter 2 : Site-use analyses reveal mammalian wildlife community predominately comprised of species tolerant to human impacts in Harenna Forest, Ethiopia.

2.1 Abstract

There has been little research documenting terrestrial mammals in Harenna Forest within the Bale Mountains National Park of Ethiopia. As human populations increase, Harenna is affected by land clearing to grow coffee, livestock grazing, which we caught on camera, bee keeping, and growing human settlements. I used 48 camera trap stations to non-invasively monitor wildlife to conduct the first inventory of terrestrial wildlife species in this understudied area. In addition to a species inventory, I also calculated traps rates and conducted occupancy analyses to determine species activity and distribution. To determine factors influencing species occurrence and detection, I used landscape covariates such as vegetation indices; normalized difference of vegetation index (NDVI) and enhanced vegetation index (EVI), elevation, distances to forest edge, agriculture, roads, water, buildings, and the park boundary, as well as biotic factors such as trap rates of humans and domestic animals, prey, carnivores, and large predators. I recorded a total of 26 terrestrial mammalian species and there were sufficient data to model occupancy for 13 species. Occupancy and detection were generally higher for herbivores and omnivores compared to carnivores. For herbivores and omnivores, responses were mixed depending on species, but I found more evidence of positive effects on anthropogenic impacts on species occupancy than negative, while detection was largely not affected by humans and was instead affected by habitat or landscape features. Carnivore occupancy was only affected by one anthropogenic variable, distance to buildings, which was positive, and one habitat variable, elevation which was negative. Carnivore detection, however, was strongly influenced by anthropogenic impacts and almost always in the positive direction. Although human and domestic trap rates were the highest, they

only affected detection of spotted hyena (*Crocuta crocuta*). This could mean that human effect was everywhere, so effect was negligible. The mammalian species of Harenna forest appear to be composed primarily of species that are widely distributed, mostly smaller for the carnivores such as white-tailed mongoose (*Ichneumia albicauda*), African civet (*Civettictis civetta*), and common genets (*Genetta genetta*), and shown in other studies to be tolerant of human activities. These findings are concerning for biodiversity conservation as rare and endangered species (e.g., mountain nyalas (*Tragelaphus buxtoni*), Ethiopian wolves (*Canis simensis))* or larger carnivores (e.g., lions (*Panthera leo*), leopards (*Panthera pardus*), jackals (*Canis aureus* and *Canis adustus*)) were rarely or never photographed in these surveys and human use was high. This study provides baseline information on presence and distribution of large- and medium-sized terrestrial mammals in an understudied biodiversity hotspot. This information is useful for future studies examining trends in mammalian populations such as site extinction and colonization, in a rapidly changing landscape and can aid in management decisions regarding habitat preservation or restoration.

Key Words: anthropogenic, detection, camera-traps, Ethiopia, Harenna Forest, occupancy.

2.2 Introduction

Bale Mountains National Park (BMNP) covers an area of 2200 km^2 and was established in 1971 to protect endangered mountain nyalas (*Tragelaphus buxtoni*) and Simien wolves (*Canis simensis*; also known as Ethiopian wolves), (Hillman, 1986). The Park is located 450 kilometers southeast of Addis Ababa (the capital city), Ethiopia in the Oromia regional state (Hillman, 1986; Kidane *et al*., 2012; Mamo *et al*., 2015; Umer *et al*., 2007). BMNP lies between 06°29' N, 39°03' E and 07°10' N, 40°00' E (Mezgebu & Workineh, 2017a) (Figure 1.1). The Park was established to protect the Afro-alpine habitat, which serves as the water catchment area for five of the largest rivers in Ethiopia: Wabi Shebele, Welmel, Dumal, Web, and Ganale (Hillman, 1986; Mezgebu & Workineh, 2017a). These rivers, alongside the over 40 streams and springs, are critical for the 12 million people downstream in Ethiopia, Northern Kenya, and Somalia, who rely on these water resources (OFWE, Farm Africa, 2016).

BMNP was declared a UNESCO 200 bioregion as a potential world heritage site to protect biodiversity and endemic species (UNESCO 2008). Bale eco-region (BER), where BMNP is located, is the largest, most contiguous mountain massif in Africa and the last remaining pristine afro-alpine biodiversity hotspot (Evangelista *et al*., 2017; Kidane *et al*., 2012; Reber *et al*., 2018; Tadesse *et al*., 2015; Tessema, 2017). The area hosts an array of endemic plant and animal species. BMNP is home to at least 77 mammalian and 170 bird species, with 160 mammals and birds endemic to Ethiopia (Demeke & Lemma, 2017). In addition to the endangered mountain nyala (Atickem *et al*., 2011, 2013; Evangelista *et al*., 2008; 2012; 2017; Mamo *et al*., 2015) and the Ethiopian wolf (Stephens *et al*., 2001), BMNP is also home to the giant mole rat (*Tachyoryctes macrocephalus*) (Stephens *et al*., 2001; Siebert 2004). There are also a number of primates such as the Bale monkey (*Chlorocebus djamdjamensis*), the vervet (*Chlorocebus pygerythrus*), and the

grivet (*Chlorocebus aethiops*) (Mekonneh,1999; Kingdon, 2015). Additionally, there are at least 23 plant species endemic to BER out of 163 that are endemic to Ethiopia, out of 1321 known plant species in the area (Kidane *et al*., 2012; Siebert & Ramdhani, 2004; Tessema, 2017).

Despite the uniqueness and importance of this area as a potential world heritage site due to its high biodiversity, endemism, and water conservation significance, there are no recent comprehensive data on the terrestrial mammalian populations in the area, especially from Harenna forest, the study site, apart from a few records of endangered Ethiopian wolves and mountain nyalas (Asefa, 2016; Atickem *et al*., 2011, 2013; Evangelista *et al*., 2008; 2017; 2012; Hillman, 1986; Mamo *et al*., 2015; Refera & Bekele, 2004; Stephens *et al*., 2001). In addition, the local people rely heavily on BMNP resources for their livelihoods by growing coffee, livestock grazing, subsistence crop farming, or sources of water (Wakjira *et al*. 2013). BMNP also faces conservation challenges related to human pressures associated with forest use and increasing human settlement (Wakjira *et al*., 2013; Watson, 2013). Loss of biodiversity and agricultural expansion have stemmed from weak to non-existent park management policies, population growth, food insecurity, unemployment, unclear land tenure rights, socio-political factors, and drought (Bewket, 2002; Mezgebu & Workineh, 2017a). Agricultural encroachment has been linked to overgrazing, settlements, and conversion of forest lands to forest coffee plantations, fires, timber extraction, and unsustainable collection of wood for fuel.

Change detection matrices reveal that over the last 40 years, the area has changed from a largely natural to a more developed landscape (Hailemariam *et al*., 2016). This stems mostly from human population growth (Demeke & Lemma, 2017; Hailemariam *et al*., 2016; Kidane *et al*., 2012; Mezgebu & Workineh, 2017b; Siraj *et al*., 2018; Wakjira *et al*., 2015; Tessema, 2017). Hailemariam *et al*. (2016) and Mezgebu & Workineh (2017a) showed that forest cover from 1985

to 2015 has been reduced significantly from 21% to 18%, while farmlands increased from 15% to 23%. Additionally, in Afroalpine and Erica-dominated areas, farmlands and urban settlements have increased between years 1985 to 2015 (Hailemariam *et al*., 2016; Kidane *et al*., 2012). Forests and shrubland lost most of their land between 1995 and 2005 (Hailemariam *et al*., 2016), while most of the grasslands were lost between 2005 to 2015. For Afroalpine, Erica-dominated woodlands, Land Use and Land Cover (LULC) data showed moderate losses as well (Hailemariam *et al*., 2016). During this time, most of the land was converted to agriculture, specifically for the growth of coffee since coffee prices began to increase, boosting international value for Ethiopian coffee, and farmers now have better access to the market (Wakjira *et al*., 2013).

Because so little is available in the literature about the wildlife of the Harenna Forest, the goal of this study was to use camera trap surveys of the terrestrial mammal community to conduct an inventory to document species presence in the region. In addition to species presence, my objective was also to determine trapping rates and distribution of terrestrial species and to examine the habitat and biotic factors influencing habitat use (including humans) using single season occupancy modeling from camera trap records for those species with sufficient data. I was particularly interested in anthropogenic impacts on species occupancy and distribution considering the recent human-induced landscape changes. I grouped the species into two categories: herbivores, omnivores, and carnivores. I developed *a priori* models predicting the impacts of landscape features and biotic factors based on the species' ecology (Appendix 2.1). The species inventory and occupancy analyses provide baseline information on species presence and distribution, which are essential in developing wildlife management plans for biodiversity conservation in this understudied ecosystem.

2.3 Materials and Methods

2.3.1 Study area

The Harenna forest is located on the southern part of BMNP in the Oromia state and spans 3,000 km^2 with altitude ranging from 1,300-3,500 meters above sea level (m.a.s.l) (Figure. 1.1). Vegetation is montane rainforest and serves as a source of small rivers for irrigation (Wakjira *et al*., 2012). The Oromo people, the local community that heavily relies on the forest, are semi-pastoralists (Wakjira *et al*., 2012). Apart from pastoralists relying on the forest for livestock, the forest is important for coffee growth of Arabica coffee by locals and immigrants (Ascrizzi & Flamini, 2019; Wakjira *et al*., 2012). Wild coffee accounts for 20% of the total coffee produced in Ethiopia (Ascrizzi & Flamini, 2019). The forest provides the right temperature, humidity, soil, and pollinators that are optimal for coffee growth (Ascrizzi & Flamini, 2019). Part of Harenna forest is protected as part of BMNP and some of it falls under controlled hunting (Atickem *et al*., 2011).

2.3.2 Camera trap records and trap rates

Camera trap data were collected from December 2015 to September 2016 in the Harenna Forest of BMNP, Ethiopia. Bushnell cameras, located in the Afromontane region of BMNP, were placed 0.5-2 km apart in 3 separate surveys: December 2015-April 2016, April 2016, and September 2016 (Table 1.1, Figure 1.2). The field team placed a total of 85 single camera stations on trails, in clusters, or in a grid-like pattern that, when combined, covered approximately 268 km^2. This survey area was estimated by creating a 250 m buffer around all the cameras, given the cameras were placed 0.5-2 kms apart and to avoid any spatial correlation, and estimating area covered using a minimum convex polygon in ArcGIS. Cameras were placed 40-50 cm off the ground and operated for 24 hours a day. No bait or lure was used. Data from all cameras and time periods were combined and I summarized total captures and calculated trap rates of all species

recorded including humans and domestic animals. Trap rate was calculated by dividing the number of capture events by the total number of trap nights (i.e., capture events per 100 trap nights [Kelly & Holub, 2008]). A trap night refers to a 24-hour period that the camera is functioning (Murphy *et al*., 2018). A capture event was defined as the number of capture events of distinctly different individuals of a particular species within a 30-minute time period (Di Bitetti *et al*., 2006).

2.3.3 Single season occupancy

For those species with enough data, I used an occupancy modeling framework to assess abiotic and biotic factors affecting species distribution and detection across the landscape. Occupancy modelling provides an estimate of species occurrence across a study area using detection/non-detection data while accounting for spatial variation and variation in detection probabilities (MacKenzie *et al*., 2002). I used data from remotely triggered cameras as my detectors across the landscape. I created detection histories for each target species at each camera station resulting in a matrix of detections (1s) and non-detections (0s) over a given survey, which I used to estimate two population parameters: occupancy and detection probabilities, both of which are bounded by 0 and 1, with 0 indicating never detected and never occupied and 1.0 indicating 100% detection and 100% occupancy at a site or across the landscape (MacKenzie *et al*., 2002; Murphy *et al*., 2018; Murphy *et al*., 2019). I collapsed capture histories for all species except Menelik bushbucks (which was not collapsed because data converged and did not need to be collapsed) into two-day occasions to improve model convergence. For this study, occupancy refers to probability of site use rather than true occupancy since multiple cameras might be located within a single animal's home range.

2.3.3.1 Landscape and anthropogenic covariates

Since station-level covariates such as trail type, understory density, and forest types were not available or collected manually at each site, I only used landscape and anthropogenic covariates for analysis that I extracted from remotely sensed and shapefile data (GIS). The landscape covariates thought to influence occupancy and detection of target species, based on what is known about their natural history were: vegetation indices (described below), elevation, distance to forest edge, distance to agriculture, distance to roads, distance to water, distance to buildings, distance to park boundary, and percentage cover type of trees, shrubs, grasslands, and croplands within 250 m of each camera station. I used this buffer size for all species to characterize the general habitat surrounding the cameras and because any larger buffer size would lead to overlap in buffers at neighboring stations, introducing autocorrelation.

Using the camera locations, I used ArcGIS Pro 2.8.3 to extract land use and land cover data, elevation data (2015 and 2016) from multiple websites such as Opens Street Maps, USGS, World Database on Protected areas, European State Agency, and Sentinel 2A for Landsat images as well as shapefiles. These images and layers were used to estimate landscape covariates such as distances from each camera to the nearest water, road, park boundary, forest edge, agricultural areas, and buildings. Elevation of each camera trap station was extracted from a digital elevation map (DEM) from Space Shuttle Radar Topography Mission (SRTM). I also extracted habitat types from land cover data obtained from European Satellite Agency (http://2016africalandcover20m.esrin.esa.int/). I used two vegetation indices downloaded from MODIS (https://lpdaac.usgs.gov/product_search/): NDVI and EVI, which I used as a measure of resource availability. NDVI (Normalized Difference Vegetation Index) is a coarse estimate of vegetation health that allows vegetation monitoring over time. EVI (enhanced vegetation index) is

also used to quantify amount of chlorophyl in vegetation but also accounts for atmospheric conditions and background noise. EVI is more sensitive to dense vegetation than NDVI. All remotely sensed data was from 2015 or 2016 or both. I also used number of days the cameras were active, as proxy for trapping effort, as one of the covariates.

Trap success describes the level of activity of each species at each camera location, which could influence detection or occupancy of the target species. Therefore, I included trap success of humans and domestic animals combined because they occurred together, and other carnivores and prey as biotic covariates for large carnivores (lions, spotted hyenas, and leopards) for the target species; Menelik bushbuck, cape bushbuck, common duiker, olive baboon, giant forest hogs and bushpig (Mackenzie *et al*., 2002; Murphy *et al*., 2018, 2019).

For my generated a list of covariates in my a *priori* models (Appendix 2.1), I tested for correlation using a Pearson correlation matrix, and any highly correlated variables ($r = |0.7|$) were not included in the same model (Appendix 2.2). I also z-scored the continuous variables to normalize and standardize them so that they were centered on zero, to improve maximum likelihood convergence for models (Ragazzini and Zadeh, 1952) and so that the beta (β) coefficients would be comparable. I modelled occupancy in Program PRESENCE and used Akaike Information Criterion (AIC) to rank models and perform model selection to determine the top-ranking models with delta AIC < 2.0 denoting competing models (Burnham and Anderson 2002). I considered a covariate supported when the 95% confidence intervals (95% CIs) did not overlap zero for continuous variables and if the 95% CIs do not overlap each other for categorical variables.

2.4 Results

Out of the original 83 cameras deployed, 34 cameras were destroyed by cattle or stolen, and 1 camera station malfunctioned, leaving 48 single camera-stations from which I obtained data.

Between December 2015 and September 2016, we collected 42,241 photos of wild animals, humans, and domestic animals across 12,951 photographic events (photos of distinct number of animals within 30-minute intervals) in 2,378 trap nights, photographing 26 wild mammal species (Table 2.1). Omnivores were the most photographed (3,032), followed by herbivores (826) and lastly carnivores (513). Humans (2,185), cows (5,618), dogs (2), donkeys (261), and goats (312) combined were the most photographed (8,378). Mountain nyalas and wild dogs were also captured, but no Ethiopian wolves were photographed (Table 2.1). We also obtained 340 photos of birds including the Abyssinian ground thrush, Hadeda ibis, lemon dove, Ruppell's robin, and 235 unidentified songbirds (Table 2.1).

I had enough photographed captures to model occupancy and detection for 13 of the 26 terrestrial wildlife species. The herbivores and omnivores included the Menelik bushbuck (*Tragelaphus sylvaticus*), cape bushbuck (*Tragelaphus sylvaticus*), common duiker (*Sylvicapra grimmia*), giant forest hog (*Hylochoerus meinertzhageni*), bush pig (*Potamochoerus larvatus*), olive baboon (*Papio anubis*), and crested porcupine (*Hystrix cristata*). The carnivores included African civet (*Civettictis civetta*), honey badger (*Mellivora capensis*), common genet (*Genetta genetta*), white-tailed mongoose (*Ichneumia albicauda),* spotted hyena (*Crocuta crocuta*), and leopard (*Panthera pardus*).

We found that elevation was correlated with distances to water, buildings, and park boundary, and that distance to agriculture was correlated with distances to park boundary, road, water, and to buildings, while distance to buildings was correlated to distance to park boundary (Appendix 2.1). Correlated covariates were not included within the same models.

2.4.1 Occupancy/site use and detection

Across all species, herbivores and omnivores tended to have higher naïve occupancy than carnivores, with the highest obtained for olive baboons (0.85) and the lowest for honey badgers (0.17) (Figure 2.2A and 2.2B). Estimated average occupancy (i.e., after incorporating detection) across sites was 0.70 or above for all herbivores and omnivores except the Menelik bushbuck, which had the lowest occupancy of all modeled species at 0.28. Olive baboons had the highest occupancy at 0.97. For carnivores, only 3 species were above 0.7 estimated occupancy (African civets, common genets and spotted hyaenas) while the remaining were below 0.45 (honey badger, white-tailed mongoose, and common leopard). Detection also was generally higher for herbivores and omnivores than for carnivores (Figure 2.3A and 2.3B). We estimated lowest average detection across sites in honey badgers (0.04) and the highest in cape bushbucks (0.54).

2.4.1.1 Herbivores and Omnivores

For the herbivore and omnivore species, average occupancy ranged from 0.28 (SE=0.15) (Menelik bushbuck) to 0.97 (SE=0.07) (olive baboon) (Figure 2.2A) and detection ranged from 0.10 (SE=0.05) (common duiker) to 0.54 (SE=0.09) (cape bushbuck) (Figure 2.3A). For the following analyses, we present results in figures only for covariates exerting strong effects on occupancy and detection, although we describe all effects below.

For Menelik bushbucks, there were three competing models (Table 2.2) indicating that occupancy decreased with increase in elevation and with distance away from park boundary, and increased with distance away from roads, however, only the latter two effects were strong and supported (Figure 2.4). For detection, there was strong evidence to support the positive effect of trap rate of large predators (lions, leopards, and spotted hyenas) and negative effect of EVI on detection of Menelik bushbucks (Figure 2.5).

For cape bushbucks, three competing models showed that distance to buildings (inside and outside the park) only weakly affected occupancy of cape bushbucks, increasing with distance away from buildings (Table 2.2). Distance to road, however, showed strong effects with cape bushbuck occupancy decreasing with distance from roads (Figure 2.4). Beta estimates on detection also showed strong effects indicating higher detection of cape bushbucks farther away from buildings (Figure 2.5).

For common duikers, there were 7 competing models (Table 2.2), but all indicated only weak effects on occupancy. These weak effects included negative influences of NDVI and trap rates of domestic animals and humans on duiker occupancy. Duiker occupancy also decreased with distance away from water and increased with distance from buildings, but again, these effects were weak. For detection however, we found strong but opposing effects of NDVI and percentage of trees and shrubs within 250 m buffer around camera stations. NDVI was negatively related to duiker detection while percentages of trees and shrubs were positively associated with duiker detection (Figure 2.5).

I found a weak negative effect of NDVI and a strong positive effect of trap rates of large predators (Figure 2.4) on occupancy of giant forest hogs in only one top model (Table 2.2). Shrub cover had a positive, but weak effect on detection of giant forest hogs, but trap rate of large predators strongly and negatively influenced detection of forest hogs (Figure 2.5).

Beta estimates from 5 competing models (Table 2.2) showed strong negative effect of elevation and strong positive effect of distance to water on bush pigs with occupancy increasing with distance away from water (Figure 2.4). Percentage of both trees and shrubs also had only weak effects on detection of bush pigs with detection increasing with shrub cover and decreasing with tree cover.

For olive baboons, there were three competing models (Table 2.2), but all effects were weak. These weak effects indicated that baboon occupancy was higher further away from the park boundary and from buildings and was negatively related to trap rates of large predators (lions, leopards, and spotted hyenas). For detection, I found a strong influence of distance to water such that baboon detection increased the farther away from water (Figure 2.5).

Effects of distance to water, distance to road, and distance to park boundary on occupancy of crested porcupines were all weak in the 3 competing models (Table 2.2). Occupancy of porcupines increased with distance from park boundary and decreased with distance away from roads and water. I found a strong negative effect of percentage of trees on porcupine detection (Figure 2.5).

2.4.1.2 Carnivores

For carnivore species, average occupancy varied from a low of 0.31 (SE=0.39) for leopards to a high of 0.80 (SE=0.22) for common genets (Figure 2.2B), while detection ranged from a low of 0.04 (SE=0.04) for honey badgers to a high of 0.18 (SE=0.07) for white-tailed mongooses (Figures 2.3B). For the following analyses, I present results in figures only for covariates exerting strong effects on occupancy and detection, although I describe all effects below.

For African civets, I found only weak effects in three competing models (Table 2.3) including positive effects of detection of large predators, elevation, and humans and domestic animals on civet occupancy. For detection, distances to water and forest edge found strong effects with civet detection decreasing with distance from both forest edge and water (Figure 2.7) and increasing with increase in trap rates of large predators whose effect was weak.

I found a weak positive effect of the number of active days cameras on honey badger occupancy in only one top model (Table 2.3). For detection, I also found only weak effects such that badger detection increased with trap rate of large predators and it decreased with distance away from road.

Increase in detection of large predators led to an increase in occupancy of common genets although these effects were weak across 2 competing models (Table 2.3). However, distance to agriculture exhibited strong effects on detection of common genets with detection increasing with distance away from agriculture (Figure 2.7).

Although effects were weak in 5 competing models (Table 2.3), trap rate of humans and domestic animals was positively associated with occupancy of white-tailed mongoose, and mongoose occupancy increased with distance away from water. I did, however, find a strong negative effect of elevation on mongoose occupancy (Figure 2.6) and occupancy strongly decreased further away from buildings. For detection, models with distance to roads and distance to agriculture performed best and showed strong effects. Mongoose detection declined with distance away from the road and increased with distance away from agricultural areas (Figure 2.7).

I found only weak effects of covariates on occupancy of spotted hyenas in five competing models (Table 2.3). These effects indicated that hyena occupancy was higher closer to park boundaries and buildings, positively influenced by trap rates of large predators, and was lower at higher elevations. For detection, I found strong positive effects of trap rate of humans and domestic animals and distance to roads with hyena detection lower further away from the road (Figure 2.7).

For leopards, I had 13 competing models (Table 2.3), and none had any strong effects on occupancy or detection. Apart from the null models, covariates in these 13 competing models on

occupancy were distances to agriculture, park boundary and roads, as well as prey and carnivore trap rates and vegetation indices. Covariates that emerged as important but weak on detection were vegetation indices, carnivore, and human and domestic animal trap rates as well as distances to park boundary and agriculture.

2.4.1.3 Humans and domestic animals

We obtained 1,505 photo events of humans (without researchers) and domestic animals 484 of which were cows, 1 dog, 144 donkeys, 20 goats, 8 horses, 7 mules, and 849 of humans. The human activity recorded was either walking by or grazing livestock.

2.5 Discussion

In the camera trap surveys, I documented 26 species of medium to large terrestrial mammals and multiple bird species providing a baseline inventory on which to base future research. It should be noted however, that humans and their domestic animals dominated the captures and the high levels of camera theft and damage indicate that this important protected area is likely highly impacted by anthropogenic factors. Nonetheless, 6 of our 7 herbivore and omnivore species with enough data to model, had high occupancy rates of over 0.70 across the site, indicating that some species, even large ones like cape bushbucks and giant forest hogs, can exist at such levels of human impact. However, I only obtained 4 photo-events of the endangered mountain nyala, which we expected to see, indicating that this species is rare across the site, which is cause for concern. Carnivores tended to have lower occupancy and detection than herbivores and omnivores, but 3 species were widespread with occupancy over 0.7 (African civet, common genets, and spotted hyaenas). The remaining 3 species (honey badger, white-tailed mongoose, and common leopard) occurred across less than half of the study area (occupancy below 0.45) and other medium and large species like golden jackals, side-striped jackals, and lions had only 1-3

photo-events across the entire survey, perhaps indicating the levels of human use are hindering these species' distributions.

2.5.1 Factors Influencing Herbivores and Omnivores

For herbivores and omnivores, 3 of our 5 strong and supported effects on occupancy were related to anthropogenic influences, but these effects were not always in the same direction for the different species. For example, occupancy increased for Menelik bushbucks with distance away from the road, while the opposite occurred for cape bushbucks, which occupied areas closer to the road. Menelik and cape bushbucks both prefer dense vegetation where food and cover are available, but cape bushbucks have been shown to select for areas along roads (Girma *et al.*, 2018; Yazezew *et al.*, 2011), potentially because these areas could have high quality food sources (e.g., secondary growth vegetation) and cover near road edges (Keken *et al.*, 2019). Menelik bushbucks have been shown to prefer forest habitats (Yazezew *et al*., 2011; Yalden *et al*., 1984; Girma *et al*., 2012; Zehirun *et al*., 2012), which is consistent with finding them farther from the road, since our study site has forested areas distributed farther from the road.

Menelik bushbuck was also influenced by distance to the park boundary with occupancy increasing closer to the boundary. This could be explained by a number of factors including their selection for mixed plantation in drier months (Girma *et al*., 2015; Yalden *et al*., 1985) which is found at park boundaries in Bale Mountains National Park (Mamo & Bekele, 2011; Pittiglio *et al*., 2012; Stephens *et al*., 2001).

The other two strong effects were not related to human impacts and influenced only the omnivores, the giant forest hog and bush pig. Interestingly, giant forest hog occupancy increased with large predator trap rate, but it should be noted that forest hog occupancy was high over the entire study area, and thus the increase was small in magnitude. It is unlikely that forest hogs are

seeking places with large predator activity, but rather they all may be selecting for features that were not measured in this study. While predators are known to take giant forest hogs in other habitats (Thomas, 1904), it also may be that they are not preyed on much by carnivores in our study considering the low detection or occupancy of lions and leopards in our site. Bush pig occupancy was influenced only by elevation such that it was near 1.0 at below 1500 m and occupancy dropped rapidly at 2000 m elevation and higher. Research shows that bush pig distribution is vast and influenced majorly by availability of food and water and cover (Amills *et al*., 2017). This could be the major reason driving their occupancy at lower elevations since there is less cover at higher elevations since the habitat changes from forest to bamboo (Kidane *et al*., 2012; Kuzmicheva *et al*., 2018; Siebert, 2004; Umer *et al*., 2007)

In contrast to occupancy, for detection I found that most of our strong effects (8 out of 9 total) on herbivores and omnivores were related to biotic or habitat features with only one related to anthropogenic effects. Of the 8 non-anthropogenic influences, 2 were biotic and 5 were related to habitat. The biotic influences were the same (large predator trap rate) but in different directions for different species: Menelik bushbuck and giant forest hog detection was positively and negatively (respectively) related to large predator trap rate. Since Menelik bushbuck are a prey of large predators, this finding is likely due to both types of species increasing activity in similar areas due to some habitat or climate feature I was unable to account for. Since we previously found that forest hogs were in the same areas with large predators (i.e., occupancy positively related), our results for detection suggest they may change their behavior in such areas to become less detectable when large predators are highly active.

Of the five habitat-related, strong effects on detection, four were related to cover and one to water. For example, EVI and NDVI both had negative influences on Menelik bushbuck and

common duiker detection, respectively. For duikers, this finding is with Estes (2012) who found that common duikers are more abundant in savannahs and dry woodlands and these areas have low vegetation indices (NDVI and EVI). For Menelik bushbucks, however, which are known to select for high cover (Girma, 2015), this result is more likely explained by detection bias. Cameras may be less likely to detect these species when vegetation cover was very high. This is because cameras trap were not always set on road and trails, but many times were off trail in thick habitat.

We also found that percentage of trees within a 250 m radius of camera traps positively influenced common duiker detection and negatively influenced crested porcupine detection. For duikers, detection was very low until percentage of trees reached about 97% and then detection rapidly increased. Studies show that when common duikers are disturbed by humans and livestock, they are adaptable and select for woodland areas with low secondary growth and with natural vegetation (Birss *et al*., 2016), which is consistent with the vegetation structure in this area, and thus may increase their detection is such areas. Porcupines are known to select for areas closer to agriculture and can be higher in grassland as opposed to shrubby areas (Ramesh *et al.*, 2015). Thus, while I did not find any strong effects on porcupine occupancy, our results indicate crested porcupines had higher detection in more open habitat.

Olive baboon detection increased with distance away from water. Olive baboons are known to travel to find water, and they are opportunistic omnivores whose behavior is heavily influenced by availability of food (Hill, 2000; Kifle 2021; Strum 1991), which may be far from water in this case.

The only anthropogenic effect we found was that cape bushbuck detection increased the farther away from buildings. Cape bushbucks have been shown to prefer dense woody areas with dense vegetation for concealment and cover to avoid predation (Kingdon 2015; Atkins *et al*. 2019).

This is consistent with buildings in our study site, which occur in more open areas, thus bushbucks could be less active in such areas to avoid detection.

2.5.2 Factors Influencing Carnivores

For the carnivores, there was only a single anthropogenic, a single habitat, and no biotic influence on species occupancy. The two strong effects were both on white-tailed mongoose indicating that mongoose occupancy declined with elevation and with distance away from buildings. Other studies (Asmasu *et al*., 2004; Estes 1991) found that white-tailed mongooses were found at elevations lower than 2,500 m, which in our study would be associated with agricultural areas in Harenna. Previous studies had mixed results for habitat selection with some showing that mongooses are more likely to use forested areas (Martinoli *et al.*, 2006) and others that they would avoid forested areas and select for savannahs and dense bushes (Smith *et al.*, 2017). White-tailed mongooses are also known to adapt to human-modified landscape (Admasu *et al*., 2004), which would be consistent with our findings here of lower elevation and proximity to buildings positively influencing mongoose occupancy.

In contrast to our few effects on occupancy, we found that carnivore detectability was influenced by many factors, and 6 out of 7 of these were related to the anthropogenic features of distances to road, agriculture, forest edge, and human and domestic animal trap rates. For example, African civet detection decreased further away from forest edge. African civets are known to be habitat-generalist that thrive in human-modified landscapes (Mills *et al.*, 2019; Easter *et al.*, 2020), or in forest and riverine habitats with high prey availability, which could explain why more detections were closer to forest edges, which likely exemplifies both of these preferences in our study site.

Both common genets and white-tailed mongoose detection increased with distance from agricultural areas. While it is known that white-tailed mongoose readily uses human-dominated and agricultural areas (Admasu *et al*., 2004), this result indicates that they may change their behavior to become more difficult to detect in such areas due to human persecution (Bouley and Carter, 2020; Easter *et al.*, 2020). Common genets are known to be present in areas with high shrub cover since vegetation cover influences their behaviors (Camps, 2011; 2013; Virgós *et al*., 2001). These factors could make it harder to target them with remote cameras in open areas, thus detection is biased low near agriculture.

We found that white-tailed mongooses and spotted hyenas were both detected closer to roads and detection declined with distance away from roads. This is perhaps not surprising for mongooses, since our findings and previous research highlight their affinity for anthropogenic features. Additionally, other studies found they were more likely to be detected at camera stations set on roads (Larrucea et al., 2007). Similarly, research on hyenas shows that they have adapted well to human-dominated landscapes and that they use roads for movement rather than areas with dense understory (Schuette *et al*, 2013, Boydston *et al*., 2003; Bearder and Randall, 1978; Vitale *et al.*, 2020). Additionally, we found that hyena detection increased with trap rate of human and domestic animals, which is not surprising considering they exhibit behavioral plasticity that makes them highly adaptable to human-dominated landscapes (Boydston *et al*.,2003; Kissui, 2008). Thus, hyena detection appears positively influenced by human features.

The only non-anthropogenic influence we found was that African civet detection increased with proximity to water. Civets are known to prefer area with permanent water (Estes 2012; Caro & Stoner 2003) especially in drier habitats (Rautenbach and Nel, 1975).

2.6 Conclusion and management implications

Of the four strong anthropogenic effects we found for herbivores and omnivores, two showed positive influences (distance to park boundary and distance to road) and one a negative influence on occupancy (distance to road), while the remaining was negative on detection (distance to buildings). While there were some human effects (including the positive ones) on occupancy, detectability was largely unaffected by human influence compared to the effects of biotic (large predator trap rate) and especially, habitat features in our study (EVI, NDVI, percentage of trees and shrub within 250m radius). Thus, herbivores and omnivores did not appear to change their behavior (i.e., become more cryptic) as a response to human footprint, but instead other factors, or camera bias, drove detection. The species displaying the most sensitivity to human impacts was Menelik bushbucks, which also displayed the lowest occupancy. Previous studies show that livestock encroachment reduces forage quality and understory species (Stephens *et al*., 2001; Atickem *et al*., 2011; Evangelista *et al*., 2007), affecting Menelik's bushbuck populations (Girma *et al*., 2015; Stephens *et al*., 2001).

For carnivores, of the 7 strong anthropogenic effects on occupancy and detection, 5 of them (1 on occupancy and 4 on detection) showed positive relationships to human impacts. The species displaying positive influences were African civets, white-tailed mongoose, and spotted hyena, all species that have been shown in other studies to tolerate human activity. These species, in addition to genets, all had with high occupancy in our study.

Our findings indicate that the species that were most widespread in our study area were mostly those that could tolerate human activity or were relatively small carnivores (with the exception of hyenas), and this is concerning for biodiversity conservation in Harenna forest (Delibes & Gaubert, 2007; Gaubert et al., 2011; Estes 1991; Admassu et al., 2004; Chatterjee et al.,2020). Species

known to be sensitive to human impacts (Menelik's bushbuck) were found farther into the forest, had low occupancy (leopards), or had low photo-captures (mountain nyalas).

Human disturbances are known to alter ecosystem performance by altering animal spatial and temporal patterns as well as increasing human-wildlife conflicts and wildlife extirpation (Carter *et al*, 2015; Niedballa *et al*., 2019; Ogutu *et al*., 2010). Locals agree that weak policies, deforestation leading to habitat fragmentation, degradation, and loss, and agricultural expansion causing immigration in to Harenna, are impacting available natural resources, increasing fires and human wildlife conflict, and are responsible for threats to wildlife (Mekonen *et al*., 2017, Amare 2015a). Of the 10 villages (kebele) sampled in the Bale eco-regions, at least 85% of the interviewees agreed that wildlife populations are declining (Mekonnon *et al*., 2017).

Moving forward, we suggest resurveying this area and collecting supplemental data at the station level on habitat/trail features or other human impacts such as signs of poaching, which would enable deeper understanding of factors influencing site use by multiple species in the face of anthropogenic changes. This could be compared to the baseline information provided here, to examine changes in occupancy through time such as site-level extinction and colonization in the rapidly changing landscape.

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Table 2-1 Species (common and scientific names), number of photographs, number of events (i.e., distinctly different individuals photographed within 30-minutee periods), trap rate (number of events divided by total trap nights times 100) for all species caught on 48 cameras from the 3 surveys combined (December 2015-September 2016) in Harenna Forest, Bale Mountains National Park, Ethiopia. Bold indicates species for which there were enough data to model occupancy.

Common Name (Local Name)	Scientific name	Number of photos	Number of events	Trap rate
Herbivores and Omnivores				
Menelik's Bushbuck	*Tragelaphus scriptus meneliki*	2254	242	18.223
Cape Bushbuck (Imbabala)	*Tragelaphus sylvaticus*	2543	295	22.214
Common Duiker	*Sylvicapra grimmia*	237	49	3.69
Giant Forest Hog	*Hylochoerus meinertzhageni*	1571	139	10.467
Bush Pig	*Potamochoerus larvatus*	2631	237	17.846
Olive baboon	*Papio anubis*	5224	288	21.687
Crested Porcupine	*Hystrix cristata*	298	52	3.916
Mantled Guereza	*Colobus guereza*	7	3	0.226
Mountain Nyala (Balbok)	*Tragelaphus buxtoni*	94	4	0.301
Tree Hyrax	*Dendrohyrax arboreus*	521	48	3.614
Natal Multimammate Mouse	*Mastomys natalensis*	8	3	0.226
Vervet Monkey (Grivet)	*Chlorocebus pygerythrus*	18	4	0.301
Warthog	*Phacochoerus africanus*	119	11	0.828
Aardvark	*Orycteropus afer*	70	11	0.828
Carnivores				
African Civet	*Civettictis civetta*	241	68	5.12
Honey badger	*Mellivora capensis*	93	22	1.657
Common Genet	*Genetta genetta*	853	246	18.524
White-tailed Mongoose	*Ichneumia albicauda*	408	117	8.81
Spotted Hyena	*Crocuta crocuta*	233	63	4.744
Leopard	*Panthera pardus*	140	33	2.485
Common Dwarf Mongoose	*Helogale parvula*	35	12	0.904
Golden Jackal	*Canis aureus*	12	1	0.075
Lion	*Panthera leo*	9	3	0.226
Marsh Mongoose	*Atilax paludinosus*	3	2	0.151
Side-striped Jackal	*Canis adustus*	9	1	0.075
Slender Mongoose	*Galerella sanguinea*	10	3	0.226
Birds				
Abyssinian ground thrush	*Geokichla piaggiae*	66	27	2.033
Hadeda Ibis	*Bostrychia hagedash*	6	1	0.075

Lemon Dove	*Columba larvata*	30	10	0.753
Ruppell's Robin	*Cossypha semirufa*	3	1	0.075
Unknown Songbirds		235	71	5.346
Humans and domestic animals				
Human	*Homo sapiens*	8727	849	0.639
Cows	*Bos taurus*	10191	484	0.364
Dog	*Canis lupus familiaris*	6	1	0.001
Goats	*Capra aegagrus hircus*	119	20	0.015
Donkey	*Equus asinus*	468	144	0.108
Mule	*Equus asinus* × *Equus caballus*	43	7	0.005
Total		61,529	5,189	156.78

Table 2-2 Top-ranking, single season occupancy models (ΔAIC < 2.0), Delta AIC, AIC weights (AIC wt), model likelihood, number if parameters (No. par) for herbivores and omnivores in Harenna Forest, Bale Mountains National Forest, Ethiopia from camera surveys conducted in December 2015-September 2016. Bold and italicized covariates are the supported effects with bold denoting positive relationship and italicized denoting negative relationship. Negative effect for distance means occupancy increases as you get farther away.

Common name	Model *	AIC	Delta AIC	AIC wt	Model Likelihood	No. par	-2 loglikelihood
Menelik bushbuck	psi(elevation+**distance to roads**), p(carnivores+*EVI*)	919.11	0	0.47	1	6	916.8
	psi(**distance to roads**), p(**carnivores**+*EVI*)	920.15	1.04	0.28	0.59	5	910.15
	psi(*distance to park boundary*), p(**carnivores**+*EVI*)	920.37	1.26	0.25	0.53	5	910.37
Cape bushbuck	psi(*distance to roads*+buildings), p(**distance to buildings**)	276.11	0	0.34	1	5	266.11
	psi(*distance to roads*+distance to agriculture), p(**distance to buildings**)	276.24	0.13	0.32	0.94	5	266.24
	psi(*distance to roads*), p(**distance to buildings**)	276.67	0.56	0.26	0.76	4	268.67
Common duiker	psi(distance to water), p(**trees+***NDVI*)	288.8	0	0.12	1	5	278.8
	psi(.), p(**shrub+***NDVI*)	289.89	1.09	0.07	0.58	4	281.89
	psi(.), p(**trees+***NDVI*)	289.96	1.16	0.07	0.56	4	281.96
	psi(distance to water), p(**shrub+***NDVI*)	289.98	1.18	0.06	0.55	5	279.98
	psi(NDVI), p(**trees+***NDVI*)	290.07	1.27	0.06	0.53	5	280.07
	psi(humans), p(**trees+***NDVI*)	290.38	1.58	0.05	0.45	5	280.38
	psi(buildings), p(**trees+***NDVI*)	290.44	1.64	0.05	0.44	5	280.44

Giant forest hog	psi(NDVI+*carnivores*), p(shrub+*carnivores*)	515.32	0	0.87	1	6	503.32
Bush pig	psi(*elevation*), p(shrub)	747.58	0	0.18	1	4	7.39
	psi(distance to water), p(trees)	748.17	0.59	0.13	0.74	4	740.17
	psi(*elevation*), p(trees)	748.74	1.16	0.1	0.56	4	740.74
	psi(distance to water), p(trees)	749.3	1.72	0.08	0.42	4	741.3
	psi(.), p(shrub)	749.54	1.96	0.07	0.38	3	743.54
Olive baboon	psi(carnivores+distance to park boundary), p(**distance to water**)	851.01	0	0.2	1	5	841.01
	psi(carnivores), p(**distance to water**)	851.43	0.42	0.16	0.81	4	843.43
	psi(distance to buildings), p(**distance to water**)	851.9	0.89	0.13	0.64	4	843.9
Crested porcupine	psi(distance to water), p(*trees*)	322.5	0	0.39	1	4	314.5
	psi(distance to roads), p(*trees*)	323.22	0.72	0.27	0.7	4	315.22
	psi(distance to park boundary), p(*trees*)	324.02	1.52	0.18	0.47	4	316.02

* = model description

psi = occupancy

p = detection

carnivores = trap rate of carnivores

humans = trap rate of humans and domestic animals

NDVI = normalized difference vegetation index

EVI = enhanced vegetation index

shrub = percent shrub within 250m buffer of the camera

trees = percent trees within 250m buffer of the camera

Table 2-3 Top-ranking, single season occupancy models (ΔAIC < 2.0), Delta AIC, AIC weights (AIC wt), model likelihood, number of parameters (No. par) for carnivores in Harenna Forest, Bale Mountains National Forest, Ethiopia from camera trap surveys in December 2015-September 2016. **Bold** and italicized covariates are the supported effects with bold denoting positive relationship and italicized denoting negative relationship. Negative effect for distance means occupancy increases as you get farther away.

Common name	Model *	AIC	Delta AIC	AIC wt	Model Likelihood	No. par	-2 loglikelihood
African civet	psi(elevation+humans), p(*distance to water*+carnivores)	371.73	0	0.20	1	6	359.73
	psi(elevation+humans), p(*distance to forest edge*+carnivores)	372.50	0.77	0.14	0.68	6	360.50
	psi(carnivores+elevation), p(*distance to water+distance to forest edge*)	373.11	1.38	0.10	0.50	6	361.11
Honey badger	psi(camera days), p(carnivores+distance to roads)	129.94	0	0.42	1	5	119.94
Common genet	psi(carnivores), p(**distance to agriculture**)	686.01	0	0.33	1	4	678.01
	psi(.), p(**distance to agriculture**)	687.70	1.69	0.14	0.43	3	681.70
White-tailed mongoose	psi(distance to water+humans), p(*distance to roads*+**distance to agriculture**)	311.22	0	0.18	1	6	299.22
	psi(elevation+humans), p(*distance to roads*+**distance to agriculture**)	311.36	0.14	0.18	0.93	6	299.36
	psi(humans+*distance to buildings*), p(*distance to roads*+**distance to agriculture**)	311.96	0.74	0.13	0.69	6	299.96
	psi(*distance to buildings*), p(*distance to roads*+**distance to agriculture**)	312.50	1.28	0.10	0.52	5	302.50
	psi(*elevation*), p(*distance to roads*+**distance to agriculture)**	33.18	1.96	0.07	0.38	5	303.18
Spotted hyena	psi(distance to buildings), p(*distance to roads*+**humans**)	331.64	0	0.15	1	5	321.64
	psi(distance to park boundary), p(*distance to roads*+**humans**)	331.65	0.01	0.15	0.99	5	321.65

	psi(elevation), p(*distance to roads*+**humans**)	332.02	0.38	0.13	0.83	5	322.02
	psi(distance to water), p(*distance to roads*+**humans**)	332.48	0.84	0.10	0.66	5	322.48
	psi(carnivores), p(*distance to roads*+**humans**)	332.87	1.23	0.08	0.54	5	322.87
Leopard	psi(.), p(carnivores+EVI)	256.84	0.00	0.07	1.00	4	248.84
	psi(.), p(carnivores)	25.64	0.80	0.04	0.67	3	251.64
	psi(.), p(EVI)	257.81	0.97	0.04	0.61	3	251.81
	psi(distance to agriculture), p(carnivores+EVI)	258.17	1.33	0.03	0.51	5	248.17
	psi(.), p(.)	258.20	1.36	0.03	0.50	2	254.20
	psi(.), p(NDVI)	258.35	1.51	0.03	0.47	3	252.35
	psi(distance to park boundary), p(.)	258.40	1.56	0.03	0.45	3	252.40
	psi(prey), p(carnivores)	258.41	1.57	0.03	0.45	4	250.41
	psi(.), p(carnivores+humans)	258.47	1.63	0.03	0.45	4	250.47
	psi(NDVI+carnivores), p(carnivores)	258.50	1.66	0.03	0.44	5	248.50
	psi(.), p(distance to agriculture)	258.53	1.69	0.03	0.43	3	252.53
	psi(.), p(carnivores+distance to water)	258.60	1.76	0.02	0.42	4	250.60
	psi(road), p(.)	258.77	1.93	0.02	0.41	3	252.77

* = model description

psi = occupancy

p = detection

camera days = number of days cameras were operational

carnivores = trap rate of carnivores

humans = trap rate of humans and domestic animals

NDVI = normalized difference vegetation index

EVI = enhanced vegetation index

shrub = percent shrub within 250m buffer of the camera

trees = percent trees within 250m buffer of the camera

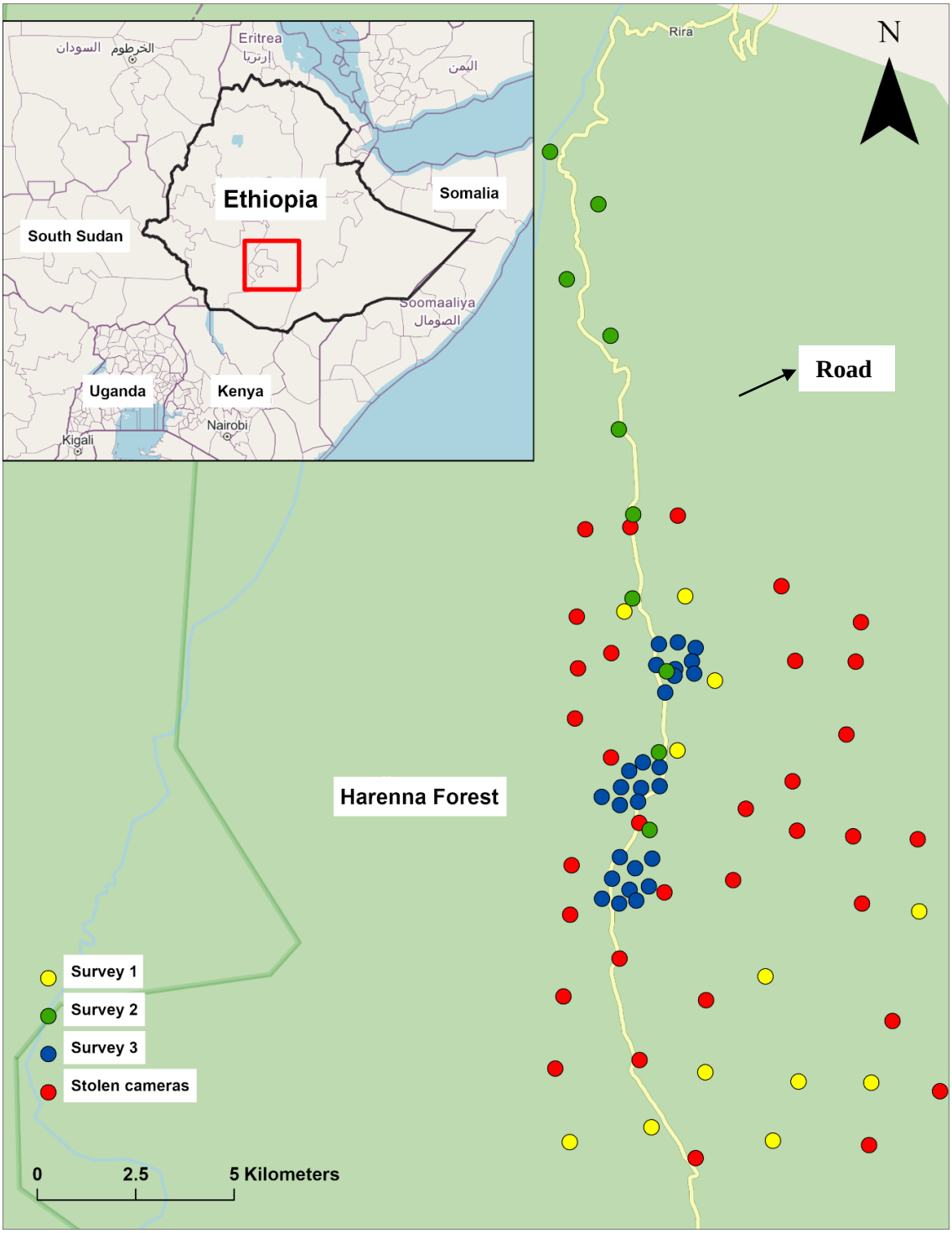


Figure 2.1. Inset shows the location of Bale Mountains National Park (BMNP) within Ethiopia with red square highlighting the location of the camera surveys. Camera locations in Harenna Forest, BMNP, are denoted as: yellow depicting survey 1 (December 2015-April 2016) green depicting survey 2 (April 2016), blue depicting survey 3 (September 2016), and red showing stolen/destroyed cameras.

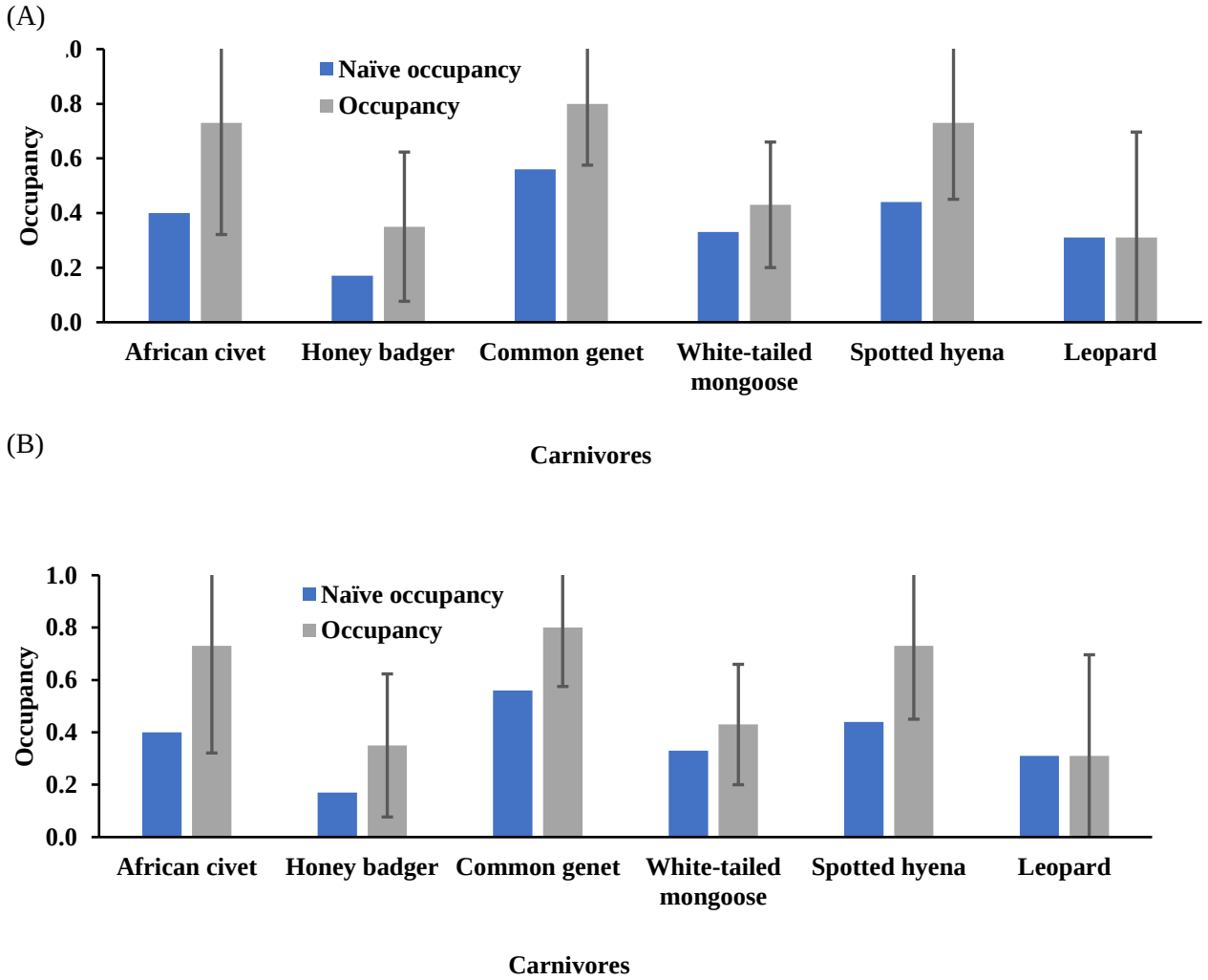


Figure 2.2. Differences in naïve occupancy (total % of stations with the species present) and average estimated occupancy (after incorporating detectability) across all cameras for seven herbivores and omnivores (A) and for six carnivores (B) in Bale Mountain National Park, Ethiopia surveyed by camera traps in 2015-2016. Error bars indicate 95% confidence intervals.

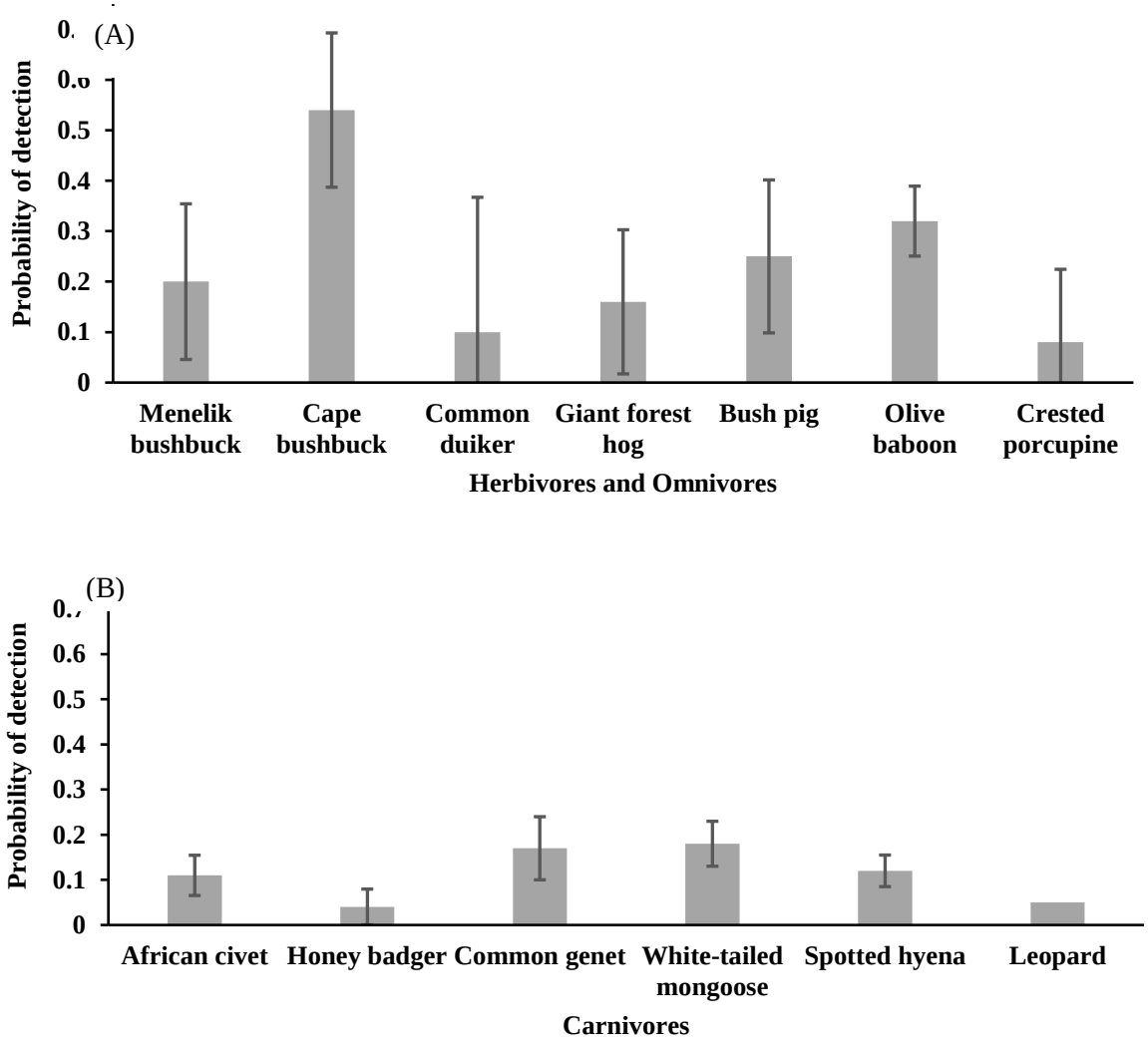


Figure 2.3. Detection probabilities for seven herbivore and omnivore species (A) and for six carnivore species (B) in Bale Mountain National Park, Ethiopia surveyed by camera traps in 2015-2016. Error bars indicate 95% confidence intervals. Detection probabilities for seven herbivore and omnivore species (A) and for six carnivore species (B) in Bale Mountain National Park, Ethiopia surveyed by camera traps in 2015-2016. Error bars indicate 95% confidence intervals.

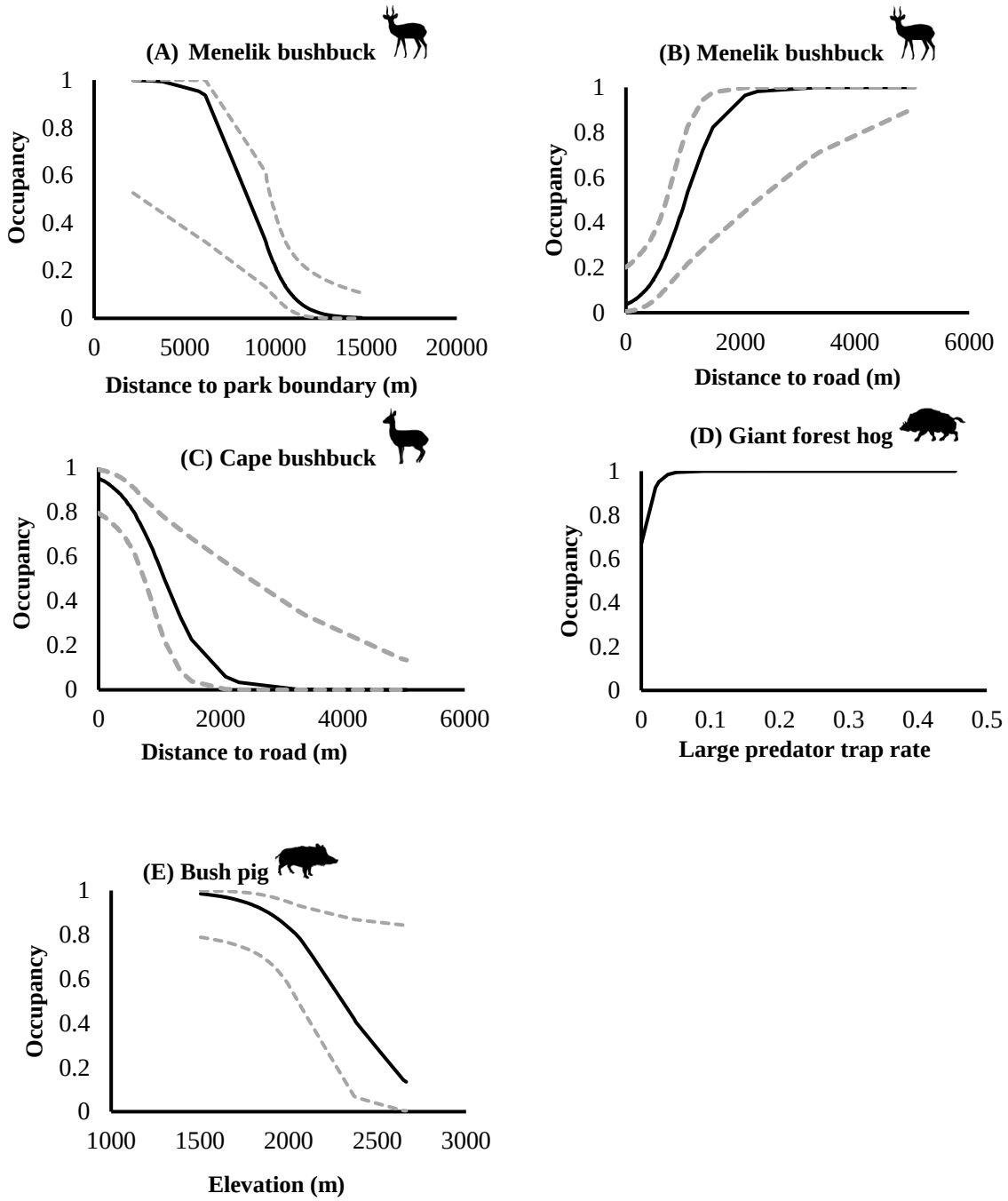
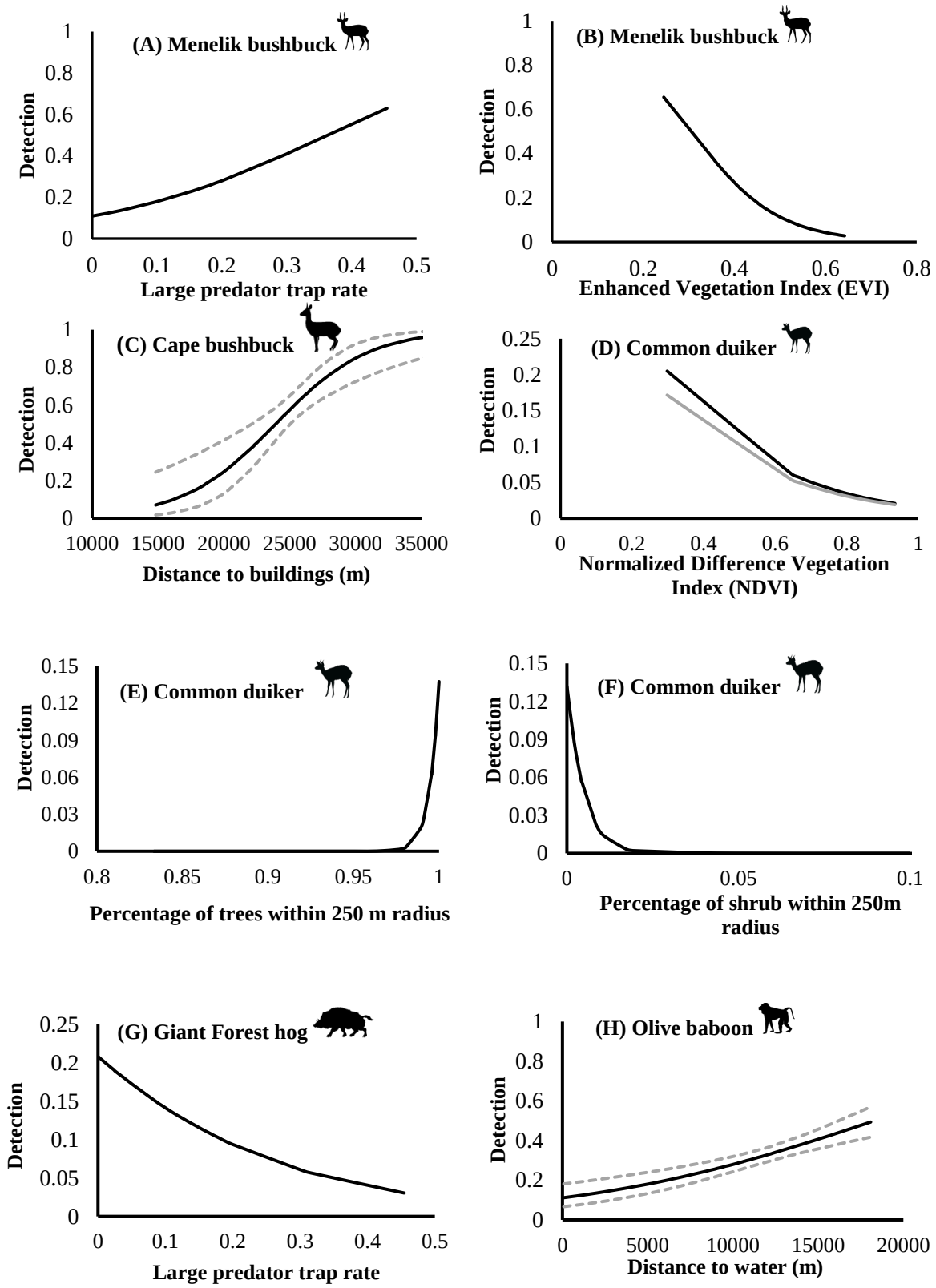


Figure 2.4. Single season occupancy estimates for herbivores and omnivores in Harenna forest, Ethiopia from camera trap surveys in 2015-2016. Probability of occupancy for Menelik bushbuck as a function of distances to park boundary (A) and road (B), cape bushbucks as a function of distance to road (C), giant forest hog as a function of large predator trap rate (D), and bush pigs as a function of elevation (E). Results presented are from covariates displaying strong effects in top or competing occupancy models.


(A) Menelik bushbuck
Detection
Large predator trap rate
(B) Menelik bushbuck
Detection
Enhanced Vegetation Index (EVI)
(C) Cape bushbuck
Detection
Distance to buildings (m)
(D) Common duiker
Detection
Normalized Difference Vegetation Index (NDVI)
(E) Common duiker
Detection
Percentage of trees within 250 m radius
(F) Common duiker
Detection
Percentage of shrub within 250m radius
(G) Giant Forest hog
Detection
Large predator trap rate
(H) Olive baboon
Detection
Distance to water (m)

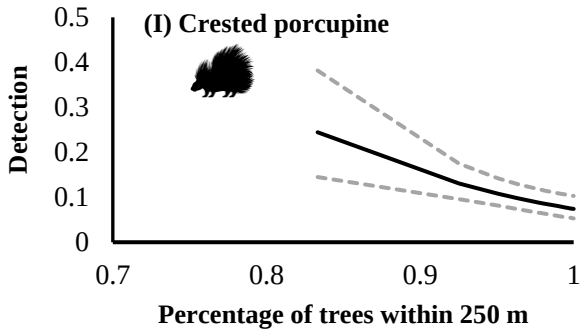


Figure 2.5. Single season probability of detection estimates for herbivores and omnivores in Harenna forest, Ethiopia from camera trap surveys in 2015-2016. Probability of detection for Menelik bushbucks as a function of large predator trap rate (A) and EVI (B), cape bushbuck as a function of distance to buildings(C), common duiker as a function for NDVI (D), and as a function of percentage of trees and percentage of shrubs within 250m radius of camera stations (E&F), giant forest hog as a function of large predators (lions, spotted hyenas and leopards) (G), olive baboons as a function of distance to water (H), and crested porcupine as a function of percentage of trees within 250m radius of camera stations (I). Results presented are from covariates displaying strong effects in top or competing occupancy models.

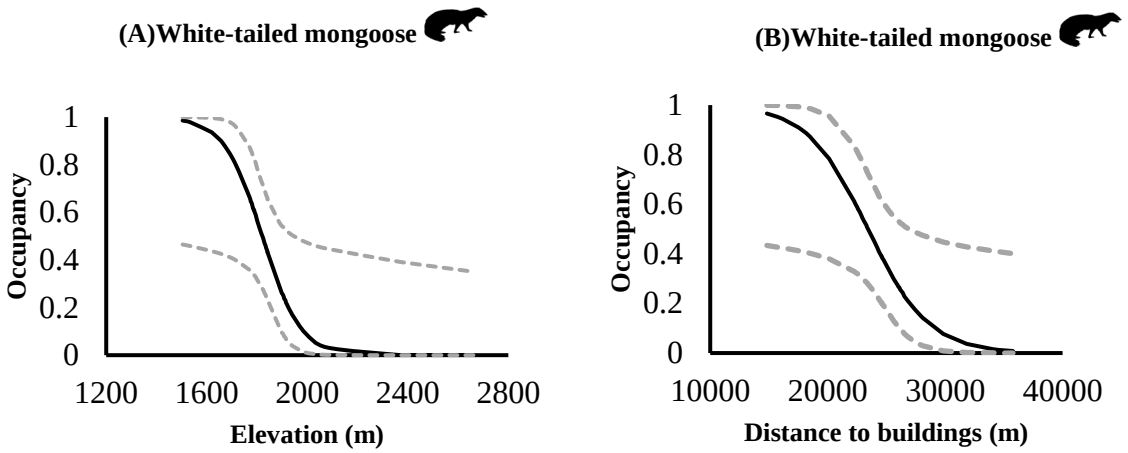


Figure 2.6. Single season occupancy estimates for carnivores in Harenna forest, Ethiopia from camera trap surveys in 2015-2016. Probability of occupancy for white-tailed mongoose declines with elevation (A) and increase in distance to buildings (B). Results presented are from the covariates displaying strong effects in top or competing occupancy models for carnivores.

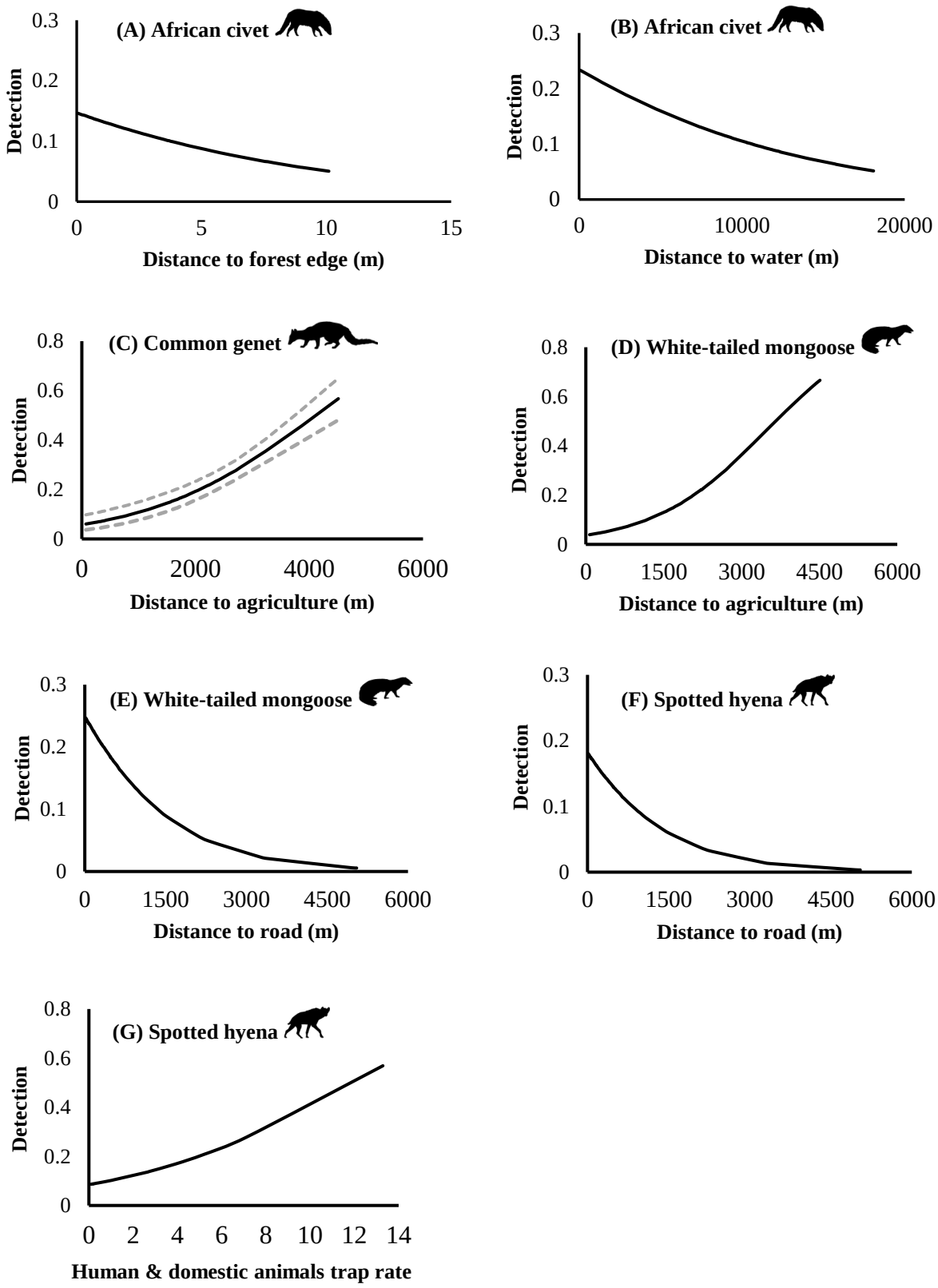

(A) African civet
Detection
0.3
0.2
0.1
0
0
5
10
15
Distance to forest edge (m)
(B) African civet
Detection
0.3
0.2
0.1
0
0
10000
20000
Distance to water (m)
(C) Common genet
Detection
0.8
0.6
0.4
0.2
0
0
2000
4000
6000
Distance to agriculture (m)
(D) White-tailed mongoose
Detection
0.8
0.6
0.4
0.2
0
0
1500
3000
4500
6000
Distance to agriculture (m)
(E) White-tailed mongoose
Detection
0.3
0.2
0.1
0
0
1500
3000
4500
6000
Distance to road (m)
(F) Spotted hyena
Detection
0.3
0.2
0.1
0
0
1500
3000
4500
6000
Distance to road (m)
(G) Spotted hyena
Detection
0.8
0.6
0.4
0.2
0
0
2
4
6
8
10
12
14
Human & domestic animals trap rate

Figure 2.7. Single season probability of detection estimates for carnivores in Harenna forest, Ethiopia from camera trap surveys in 2015-2016. Probability of detection for African civets as a function of distances to forest edge (A) and water (B), common genet as a function of distance to agriculture (C), white-tailed mongoose as a function of distances to agriculture and road (D&E), spotted hyena as a function of distance to road (F) and trap rate of humans and domestic animals(G). Results presented are from covariates displaying strong effects in top or competing occupancy models.

2.9 Appendix

Table showing landscape variables hypothesized to influence occupancy (psi or Ψ), detection probabilities (p) and both occupancy and detection, of the target species that had enough data to model. A plus sign indicates a positive relationship, and a negative sign indicates a negative relationship, between the covariate and occupancy and detection of the target species. Note, however, that with distance measures below, a plus sign indicates that occupancy increases with distance away from the feature. If there is no sign in a cell, I did not expect any influence of the habitat or landscape feature.

Landscape covariates hypothesized to influence both occupancy (Ψ) and detection (p) probabilities													
Habitat type (listed habitat types indicates a positive association with that type)	Thickets, marsh	Thicket, marsh	Tall grass, savannah woodland habitat	Grass			Deciduous woodland, shrub wood		Eucalyptus trees	Forest with tree and dense underbrush vegetation cover			
Elevation	+	+							-	-			
Distance to river - note positive (+) means species found farther from river	+		+					-	-	+		-	-
Distance to park boundary (+ is farther away)			+				-			-		-	-
Distance to settlement (+ is farther away)			+				-			+		-	+
Distance to agricultural land			+			+	-	+	+	+	+		
Activity rate of prey species	+	+	+		+		+	+	+	+	+	+	+
Activity rate of human/domestic animals			+				-					+	+
Trapping rates of other large predators (lions, hyenas, leopards)	+	+	+	+	+		+	+	+	+	+	+	+
Covariates hypothesized influence detection (p) probability only													

Temperature	< 30 °C	+		+
Amount of rainfall			+	+

Table showing Pearson's correlation matrix between continuous variables used in occupancy models of camera trap data obtained from Harenna Forest, Bale Mountains National Park, Ethiopia. Bolded numbers indicate highly correlated covariates, and these were not used together in the same model.

	NDVI	**EVI data**	**Number of active camera days**	**Elevation**	**Distance to forest edge**	**Distance to agriculture**	**Distance to roads**	**Distance to water**	**Distance to buildings**	**Distance to park boundary**
NDVI	1.00									
EVI data	0.21	1.00								
Number of active camera days	0.14	0.01	1.00							
Elevation	-0.18	0.13	-0.24	1.00						
Distance to forest edge	0.13	0.07	0.22	-0.04	1.00					
Distance to agriculture	0.17	-0.03	0.49	-0.54	0.12	1.00				
Distance to roads	0.13	0.08	0.64	-0.36	0.19	0.55	1.00			
Distance to water	0.23	-0.06	0.34	**-0.90**	0.13	0.61	0.58	1.00		
Distance to buildings	-0.24	0.04	-0.35	**0.91**	-0.13	-0.66	-0.60	**-0.96**	1.00	
Distance to park boundary	-0.18	-0.03	-0.53	**0.74**	-0.17	**-0.72**	**-0.83**	**-0.84**	**0.91**	1.00

NDVI: Normalized Difference Vegetation Index
EVI: Enhanced Vegetation Index

Chapter 3 : Differential influences of humans and competitors on temporal activity and overlap in herbivores, omnivores, and carnivores of Bale Mountain National Park, Ethiopia

3.1 Abstract

Harenna forest, in Bale Mountain National Park, Ethiopia (BMNP), is an Afromontane biodiversity hotspot that is home to numerous endemic plants and animals and is important to the local Oromo tribe. Recent population growth has led to clearing of forest, shrub, and grassland to make way for subsistence crops, coffee growing, human settlements, and livestock grazing. To document species presence and analyze spatial and temporal activity of wildlife in this understudied ecosystem, the field team set 48 camera stations in Harenna forest, BMNP from December 2015 to September 2016. I used Kernel Density Estimation to assess temporal activity and overlap in 14 terrestrial mammals. I estimated the coefficient of overlap (Δ) of the probability density functions between species pairings. I divided species by diet type (herbivores, omnivores, and carnivores) and size to assess whether temporal overlap was lower for species of similar diet and size, to potentially avoid competition. I also examined human impacts on wildlife by determining overlap between humans and native species and by sub-setting the data and calculating overlap for camera stations with high human use ($\geq$15 observations) compared to those with no human use. In herbivores and omnivores, only tree hyraxes (*Dendrohyrax arboreus*) and crested porcupines (*Hystrix cristata*) were nocturnal, Menelik bushbucks (*Tragelaphus scriptus meneliki*) were crepuscular, and the remaining species ranged from diurnal to cathemeral. Neither body size nor diet affected overlap between species pairs. Overlap with human temporal activity was low for nocturnal species (0.04-0.08) and for Menelik bushbuck (0.45), while common duikers (*Sylvicapra grimmia*) appeared to become less active, especially in the morning, at stations with

high human use. For carnivores, leopards (*Panthera pardus*) and honey badgers (*Mellivora capensis*) were crepuscular, and the remaining species were nocturnal. We found that some evidence that carnivores overlapped less (average 0.67-0.71) when they were more similar in body size (average 0.75), although there was variation across species. In general, carnivores overlapped much less (average 0.20) with humans than herbivores (average 0.52) and omnivores (average 0.43). Spotted hyenas (*Crocuta crocuta*), in particular, appeared to alter activity to reduce overlap with humans. This study provides baseline information on activity patterns and overlap in terrestrial mammals from a little-known forest ecosystem, highlighting how humans alter activity in multiple target species.

Keywords

Activity, anthropogenic, carnivores, Kernel Density Estimation (KDE), overlap, ungulates.

3.2 Introduction

Anthropogenic changes are known to alter wildlife foraging behavior and community interactions resulting in reduced animal fitness and changes in evolutionary behavior due to fear (Gaynor et al, 2019; Suraci et al., 2019), and risk avoidance that impacts trophic cascades (Hebblewhite et al., 2005; Schmitz et al., 1997). With the growing human footprint on the landscape, there is a reduction in natural resources available for wild animals. Wildlife may respond to these changes, especially in areas where they co-occur with humans, by shifting their temporal activity rather than shifting spatially (Kronfeld-Schor & Dayan, 2003). For example, Monette et al. (2020) found that jaguars were generally cathemeral but exhibited more nocturnal activity as human use increased. In fact, Gaynor et al. (2018) showed that in human dominated landscapes, mammals can partition their time to be more active at night by an average factor of 1.36. In addition to avoiding humans on the landscape, species may segregate temporally to

mitigate interspecific competition and foster coexistence with similar species (Hernández-Saint Martín et al., 2013). For example, in carnivores, evidence shows that the temporal niche axis is fundamental for co-existence where a subordinate competitor may be nocturnal but adjust its activity to avoid overlap with the dominant competitor (Lucherini et al., 2009; Gerber et al., 2012; Carothers et al.,1984; Harmsen et al., 2011). This segregation mostly appears to occur along the body size niche axis, with species more similar in body size (that use similar resources), showing more temporal avoidance (Sunarto et al., 2015).

Harenna forest is located in the southwestern escarpment of Bale Mountains National Park (BMNP), Ethiopia, in the largest, most contiguous mountain massif in Africa and contains the last remaining relatively pristine afro-alpine biodiversity hotspot (Evangelista *et al*., 2017; Kidane *et al*., 2012; Reber *et al*., 2018; Wakjira *et al*., 2015; Tessema, 2017). It is home to at least 170 bird species and 77 mammalian species, and numerous endemic plant and animal species (Demeke & Lemma, 2017). Within the area, there are two endangered species, the mountain nyala, *Tragelaphus buxtoni*, (Atickem *et al*., 2011, 2013; Evangelista *et al*., 2008; 2012; 2017; Mamo *et al*., 2015) and the Ethiopian wolf, *Canis simensis*, (Stephens *et al*., 2001), as well as the giant mole rat (*Tachyoryctes macrocephalus*) (Stephens *et al*., 2001, Siebert 2004), Bale monkey (*Chlorocebus djamdjamensis*), vervet (*Chlorocebus pygerythrus*) and grivet (*Chlorocebus aethiops*) (Mekonnen,1999; Kingdon, 2015). The Bale region, and the Harenna forest within it, face a number of challenges. Local people rely heavily on BMNP resources for their livelihoods by growing coffee, livestock grazing, subsistence crop farming, or for sources of water (Wakjira *et al*., 2013). BMNP also faces anthropogenic changes in regard to forest use and increasing human settlement (Wakjira *et al*., 2013; Watson, 2013). Lack of strong park management policies, food insecurity, socio-political challenges, and population growth have resulted in loss of biodiversity

(Bewket, 2002; Mezgebu & Workineh, 2017a). Increasing agricultural use has led to overgrazing, increase in settlements, and conversion of forest lands to forest coffee plantations, increased fires and timber extraction, and unsustainable collection of wood for fuel. Studies show that forest cover in Bale has reduced from 21% to 18% and farmlands from 15%-23% from 1985-2015 (Hailemariam *et al*., 2016; Mezgebu & Workineh 2017a).

My objective was to examine temporal activity patterns and overlap of 8 herbivore and omnivore species, and 6 carnivore species from a camera trapping study conducted in 2015 and 2016 in Harenna forest, BMNP. The herbivores and omnivores included, from smallest to largest: tree hyrax (*Dendrohyrax arboreus*), crested porcupine (*Hystrix cristata*), common duiker (*Sylvicapra grimmia*), olive baboon (*Papio anubis*), cape bushbuck (*Tragelaphus sylvaticus*), Menelik's bushbuck (*Tragelaphus sylvaticus*), bush pig (*Potamochoerus larvatus*), and giant forest hog (*Hylochoerus meinertzhageni*). The carnivores included, from smallest to largest: common genet (*Genetta genetta*), white-tailed mongoose (*Ichneumia albicauda*), honey badger (*Mellivora capensis*), African civet (*Civettictis civetta*), spotted hyena (*Crocuta crocuta*), and leopard (*Panthera pardus*). I also aimed to determine whether human use impacted overlap between species pairs and therefore I included temporal activity of humans and domestic animals (cows, dogs, donkeys, and horses) combined.

I hypothesized that native herbivores (common duikers, cape bushbucks, Menelik bushbucks), arboreal omnivores (tree hyraxes, crested porcupines, olive baboons) and larger grazing omnivores (olive baboons, bush pigs, giant forest hogs) would overlap temporally as dictated by high resource availability, but those with similar diet that are more similar in body size, may have less temporal overlap to potentially reduce competition. I expected that domestic animals and humans will be diurnal, and in areas with high human use, native wild herbivores would be

more crepuscular to nocturnal to avoid domestic species during the day. For carnivores, I expected that carnivore species closer in body size (e.g., spotted hyenas and leopards), which are more likely to prey on limited similar food sources, would avoid each other temporally compared to species more different in body size, which likely prey on different diet items. I also anticipated that small carnivores, white-tailed mongooses (Do Linh *et al*., 2016), African civets (Ray, 2013), and common genets (Ruedi & Pesaresi, 2020) would overlap temporally since they are known to be nocturnal, but they would shift peaks of nighttime activity to avoid each other. I also expected that most carnivores, would be more crepuscular to nocturnal to avoid encounters with humans and domestic animals, which are mostly diurnal.

Considering that there have not been any studies in Harenna forest, Ethiopia examining the terrestrial mammalian community, this study will provide a comprehensive overview of temporal activity and potential for interactions due to temporal overlap of the mammalian species in an understudied biodiversity hotspot. Baseline information on wildlife temporal activity patterns is important considering the BMNP area was declared a UNESCO 200 bioregion and potential world heritage site to protect biodiversity and endemic species (UNESCO 2008).

3.3 Materials and Methods

3.3.1 Study area and camera-trapping surveys

Harenna forest is part of Bale Mountains National Park (BMNP), Ethiopia, and is approximately 3,000 km^2 with elevation ranging from 1300 to 3500 m (Figure 3.1). It experiences two seasons, a rainy season from March to October, and a dry season is from November to February (Hillman 1988). The Harenna forest is found in the southwest escarpment of BMNP and is composed of Erica Forest, tall rainforest, and subtropical savanna habitats afforded by its large altitudinal range (see Chapter 2, Figure 3.1). At 1450 m, it is an open montane forest that is

relatively dry and is bordered by denser habitat composed of *Filicium decipiens*, *Celtis gompho phylla* and *Trema orientalis* and forms the upper limits of this stratum. The patchy and woody understory allows for the growth of wild coffee in this region (Chiodi & Pinard 2011, Uhlig & Uhlig, 1991). From 1600 m to 1900 m, it consists of mixed broad-leaf forest with the number of plant species present significantly reduced. At 2000 m, there is a more humid, Erica dominated forest, which transitions into 1-3 m tall Ericaceous scrub open habitat. The uppermost montane forest belt is the Hagenia-Hypericum zone mainly characterized by *Hagenia abyssinica*, *Hypericum revolutum*, *Rapanea melanophloeos*, and *Pittosporum viridiflorum* from 2300 m to 3100 m. This area also has mountain bamboo as undergrowth in the wetter slopes (Uhlig and Uhlig, 1991). At 4000 m to 4100 m, it becomes shrub, grassland and pastureland with Helichrysum dwarf-scrub, standing at 30-50 cm, being the most dominant plant in the Afro-alpine belt in the Bale Mountains. Giant lobelia (*Lobelia rhyncho- petalum*), a plant species endemic to Ethiopia, is found in this region (Miehe and Miehe 1994).

Detection/non-detection data for the terrestrial mammalian community were collected using camera traps from December 2015 to September 2016 in Harenna forest. The field team placed 85 camera stations approximately 0.5-2 km apart across multiple vegetation zones, at elevations ranging from 1600 m to 2600 m, covering an area of approximately 268 km^2 based on the minimum convex polygon resulting from a 250 m buffer placed around the whole grid in ArcGIS, after dissolving internal buffers. Due to theft and destruction by cattle, I obtained data from only 48 of the original 85 camera stations (Figure 3.1). The original objectives of the project was to get inventory of animal species present in Harenna and to capture photos of a melanistic leopard and a lion that had been observed to be close to the village and forest with thick understory.

3.3.2 Temporal co-occurrence

Kernel density estimation (KDE) is a non-parametric method of determining the probability density function (PDF) of a continuous, circular, random variable (Ridout & Linkie, 2009). In this case, time of capture is the continuous, circular random variable. It is non-parametric because it does not assume any underlying distribution for the variable (Ridout & Linkie, 2009). Essentially, at every datum (time interval), a kernel density function is created with the datum at its center to ensure that the kernel is symmetrical. The PDF is then estimated by adding all of these kernel functions and dividing by the total number of data points (Ridout & Linkie, 2009). High density estimates come from having more observations that are close to the point of observation (i.e., more observations around the same time period in this case) as opposed to the areas that have fewer observations (Ridout & Linkie, 2009). Thus, more photographic records at certain times of the day will lead to higher KDE estimates for those time periods.

I defined an independent capture event as distinct photo of a given mammalian species every 30 minutes. I defined the 'dawn' and 'dusk' based on sunrise and sunset data. Species primarily active an hour before and after dawn and an hour before and after dusk are referred to as crepuscular (Foster et al., 2013; Lucherini et al., 2009). I defined 'day' time period (denoted diurnal) as between dawn and dusk, whereas 'night' time period (denoted nocturnal) as between dusk and dawn. Species that are active at all times are categorized as cathemeral. I examined species activity continuously throughout the diel cycle, and based on their dominant activity pattern, they were categorized as diurnal, nocturnal, crepuscular, or cathemeral based on density of photographs for a particular period. I conducted this analysis on the 8 herbivores and omnivores, and the 6 carnivores, with enough captures (>20) to complete it.

To examine overlap between species pairs, I estimated the coefficient of overlap (Δ) of the probability density functions between species pairings. I used Δ_1 for sample sizes less than 50 and Δ_4 for sample sizes greater than 50 following Rowcliffe (2021). A Δ =1.0 indicates complete overlap whereas a Δ= 0 is no overlap in time of activity. I expected more competition between similar species (diet and size), and therefore I separated omnivores from herbivores and arboreal from terrestrial (although baboons exhibit both arboreal and terrestrial behavior, Druelle et al., 2021). For some species like tree hyraxes and crested porcupines, which are arboreal (Milner and Harris, 1999a) and nocturnal, I did not expect them to compete with the larger terrestrial omnivores (hogs and pigs), which are terrestrial and diurnal. Thus, I did not compare overlap for such species that were unlikely to interact. I estimated temporal activity overlap patterns between herbivores (Menelik-duiker, Menelik-cape, duiker-cape) and arboreal omnivores (baboon-hyrax, baboon-porcupine, hyrax-porcupine) and terrestrial grazing omnivores (baboon-hog, baboon-pig, hog-pig). I did the same pair-wise overlap analysis for all six carnivores (e.g., leopard-hyena, mongoose-civet, mongoose-genet, mongoose-honey badger, etc.), to determine if species more similar in size had lower temporal overlap. If the coefficient of overlap between a species pairs is low, it may indicate temporal avoidance (Ridout & Linkie, 2009).

To categorize species diel activity and the temporal overlap between species pairs, I used activity and overlap packages in R (Rowcliffe, 2021; Linkie and Rideout, 2009). For each detection event, I converted clock times to radians while accounting for sunrise and sunset times within activity package in R (Vazquez *et al*., 2019; Rowcliffe, 2021). For each species, I used overlap package in R to estimate overlap coefficient for each species pair. To obtain 95% confidence intervals (CIs), I used 10,000 bootstraps and compareCkern function in activity (Rowcliffe, 2021).

3.3.3 Human effects

Since humans presence is likely to influence mammalian species' temporal behavior, I conducted KDE analysis on human activity and estimated overlap between humans and herbivores (i.e., human-Menelik, human-duiker, human-cape), humans and arboreal omnivores (human-crested porcupine, human-tree hyrax, human-olive baboon), humans and terrestrial omnivores (human-hog, human-pig) and humans and carnivores (human-common genet, human-white-tailed mongoose, human-honey badger, etc.). I also subset the data into camera stations that had high levels of human use (≥15 observations of humans and domestics) compared to those where I did not have any humans or domestic animals detected. I then compared overlap at the high human use stations to those with no human use for the herbivores, omnivores, and carnivores. I removed all human observations that were classified as researchers. The high versus no human use analysis was only possible for 6 species with enough captures at both types of stations including: common duiker, cape bushbuck, olive baboon, bush pig, giant forest hog, and common genet.

3.4 Results

Across the 48 camera stations, I obtained 40,422 photos across 3,426 photographic events in 2,378 trap nights and photographed a total of 26 mammalian species (see list in Table 3.1 of Chapter 2), in addition to humans and domestic animals. For my 14 species of interest, honey badgers had the lowest number of capture events (22) while cape bushbucks had the highest (295), excluding humans and domestic animals, which surpassed all wildlife at 1,512 events (Table 3.1).

3.4.1 Temporal activity

Based on kernel density analysis for the omnivores and herbivores, I found that olive baboons were diurnal and tree hyraxes and crested porcupines were nocturnal (Figure 3.2). I also found that Menelik bushbucks exhibited crepuscular temporal activity and bush pigs, giant forest

hogs, cape bushbucks, and common duikers were cathemeral in this habitat (Figure 3.2). For carnivores, I found that leopards and honey badgers were crepuscular while spotted hyenas, African civets, common genets, and white-tailed mongoose were nocturnal (Figure 3.3).

3.4.2 Species overlap

3.4.2.1 Herbivores

Among the herbivores, I generally found high overlap between Menelik bushbucks, cape bushbucks, and common duikers (Table 3.2, Figure 3.4). The average overlap for herbivores was 0.81, the highest overlap was between common duikers and cape bushbucks (0.83), and the lowest was between Menelik's bushbucks and common duikers (0.79) (Figure 3.4). Thus, there was little evidence to support that similar body size led to lower overlap among the ungulate herbivores (Figure 3.4).

3.4.2.2 Arboreal and terrestrial omnivores

For arboreal omnivores, I found a wide range of overlap between species primarily because baboons were diurnal while the tree hyraxes and crested porcupines were nocturnal (Table 3.2, Figure 3.5). Therefore, baboons overlapped only 0.04 and 0.03 with porcupines and hyraxes, respectively, while overlap between the two nocturnal species was high at 0.71. For terrestrial omnivores, which all exhibited diurnal to crepuscular activity, average overlap was 0.61 and the highest overlap was between giant forest hogs and bush pigs (0.76), while the lowest was between olive baboons and bush pigs (0.45) (Table 3.2, Figure 3.5). As with the herbivores, there was little evidence of body size or diet similarity causing lower temporal to overlap for omnivores.

3.4.2.3 Carnivores

All carnivores were nocturnal or crepuscular with carnivore overlap ranging from a low of 0.55 for African civets and honey badgers to a high of 0.90 for white-tailed mongooses and

common genets (Table 3.2, Figure 3.6). However, it should be noted that the low end in overlap is caused by African civet being exclusively nocturnal, while the honey badger was crepuscular. Interestingly, I did find evidence that the more similar in body size, the lower the temporal overlap. Overlap between the species most similar in size, denoted by those on the outer diagonal in Figure 3.6, averaged 0.71, and next most similar (the next diagonal) averaged 0.67, while overlap for the remaining species with larger differences in body size averaged 0.75.

3.4.3 Temporal overlap between humans and domestic animals and species

3.4.3.1 Humans and domestic animals and herbivores and omnivores

Assessing temporal overlap between herbivores and humans and domestic animals revealed that duikers had the highest overlap with humans at 0.57, while cape bushbucks and humans were intermediate at 0.53 and Menelik's bushbucks and humans overlapped the least at 0.45, with an average overlap of 0.52 for herbivores (Figure 3.7). For overlap between arboreal omnivores (baboons, hyraxes, porcupines) and humans and domestic animals, the lowest overlap was between humans and tree hyraxes (0.04) and the highest was between humans and olive baboons (0.85) (Table 3.2, Figure 3.7). For terrestrial omnivores (baboons, hogs, and pigs), lowest overlap was 0.51 for humans-pigs and highest was again for humans-baboons (0.85).

3.4.3.2 Humans and domestic animals and carnivores

For humans/domestic animals and carnivores, the lowest overlap was between humans and common genets (0.07) and the highest between humans and honey badger (0.47) (Table 3.2, Figure 3.8). The average overlap between the carnivores and humans (0.21) was much lower than for the herbivores (0.52) and omnivores (0.35) because most carnivores were not diurnal, as human were.

3.4.4 High vs low human activity stations

For the 6 species with enough data to separate high human versus no human use camera stations, I found that olive baboons did not alter their activity due to high human use, but instead had similar activity (overlap of 0.93) at both types of stations (Figure 3.9). The common duiker, on the other hand, appeared to be the most impacted by human use exhibiting the lowest amount of overlap (0.60) at high versus no human use stations, and, when humans were absent, they demonstrated less cathemeral activity and more diurnal activity, especially between 06:00 and noon (Figure 3.9). The range in overlap between human use types for the remaining species was between 0.77 and 0.85 and the changes due to human activity were more subtle. For example, Cape bushbucks had similar activity with and without humans, with one exception of becoming more nocturnal between 22:00 and 24:00 at stations with high human activity. Bush pigs appeared to shift their activity peaks to midday and to dusk hours when humans were absent. The giant forest hog shifted to more crepuscular activity, especially in the morning, and had higher crepuscular peaks when humans were absent, while the opposite was true for common genets, which became more crepuscular at stations with high human use, although in general, they were mostly nocturnal.

3.5 Discussion

3.5.1 Activity patterns and temporal overlap with other wildlife

3.5.1.1 Herbivores and Omnivores

Common duikers, cathemeral in this study, have been shown to exhibit crepuscular activity depending on season (Houngbégnon et al., 2020). Houngbégnon et al. (2020) suggest that activity time of duikers could be extended during periods of lower food availability, however, I do not have data on foraging resources in the area. The cathemeral behavior I found for cape bushbucks

is consistent with other findings (Verheyen 1955; Jacobsen 1974). It is interesting, however, that other studies have shown that predation avoidance (Epperly 2021) causes cape bushbucks to be nocturnal, which I did not find. Perhaps low levels of occupancy and detection I found for large carnivores (Chapter 2) indicate there is not enough predation pressure on cape bushbucks to alter their activity times. My findings regarding crepuscular activity of Menelik bushbucks is consistent with earlier studies as they have been shown to spend the day resting to avoid heat and are active at daybreak and twilight (Castelló 2016; Kingdon 1982).

Past studies have shown that olive baboons spend most of their diurnal activity grooming, resting, foraging, moving, and vocalizing (Eley 1989; Maurice & Lameed, 2018), but I could find no studies documenting diel activity with KDE analysis. I found olive baboons to be strongly diurnal with activity beginning around 6:00 and reaching a high peak at 14:00 and then declining to no activity just past 18:00. This is important baseline information considering that most studies of olive baboons are from more open savannahs (Rowell, 1966; 1969; Okecha & Newton-Fisher, 2006; Paterson, 2006; Ross *et al*., 2011) rather than forested habitats (but see Johnson *et al*., 2012, for forest baboon food habitats).

Tree hyrax activity patterns have been shown to vary geographically (Freeman 2018) with observations in the wild showing nocturnality, while those in captive populations were diurnal (Rudnai 1984, Milner & Harris, 1999a). Change to nocturnality in tree hyraxes has been attributed to avoiding predation and to foraging activities, but since all the predators in this habitat were nocturnal as well, nocturnality could be instead attributed to human disturbance (see below). In crested porcupines, temporal activity also has been shown to vary between nocturnal and crepuscular (Corsini *et al.*, 1995) to diurnal depending on season, and they are known to avoid moonlight (Felicioli, 1994; Felicioli & Santini, 1991). Crepuscular behavior is mostly attributed

to foraging while diurnal behavior is observed around burrows (Corsini *et al*, 1995), therefore, nocturnal activity I found might also result from avoiding humans (see below).

For the terrestrial omnivores, giant forest hogs have been shown to be adaptable to many habitat types, both closed and open (Estes, 1991; Treves *et al*, 2010). During wet seasons, forest hogs have been observed feeding during the day and sleeping at night (Klingel & Klingel, 1999), whereas in the Aberdares in Kenya, a similar habitat as Harenna, forest hogs tended to forage during the night due to high temperatures (Kingdon 1979; Klingel & Klingel 2004b). Therefore, my finding of cathemeral activity could indicate that forest hogs have high plasticity in activity times, although it should be noted that I was not able to incorporate seasonality in my analysis. In bush pigs, diurnal behavior has been attributed to movement and feeding especially in habitats with dense cover (Ghiglieri *et al*., 1982), although other studies have observed them to be nocturnal (Dorst & Dandelot, 1970; Kingdon 1979). Change in activity times could be caused by seasonality, which I could not test for, which could explain their cathemeral activity (Venter *et al*., 2016) in my study.

For the herbivores pairs I generally found high overlap (0.79-0.83) in activity regardless of body size. For omnivores, I found moderate to high overlap (0.45-0.76) regardless of body size, except between the two species that were nocturnal (tree hyrax and crested porcupine) and the remaining species that were not. The nocturnal species, which were very similar in body size to each other, had high overlap (0.71). Therefore, even though most of the species have been reported to exhibit plasticity in timing of diel activity, they did not appear to alter activity to avoid competition with species of similar diet and body size.

3.5.1.2 Carnivores

My results concur with other studies showing that both common genets and African civets are nocturnal (Pesaresi & Ruedi, 2020; Kingdon, 1977; Estes, 1991), but previous studies were from acacia woodlands of Serengeti in Tanzania (Waser 1980), mosaic habitat in Uganda (Mills *et al*. 2019), farmlands outside of BMNP, Ethiopia (Adamsu *et al*., 2004a), and patchy forest interspersed with coffee in western Ethiopia (Mertens *et al*., 2020). Thus, we provide information on nocturnal activity for these species in a more contiguous forested landscape, especially given that Mertens *et al*. (2020) showed that civets preferred natural forest. I also found that civets and genets had high nocturnal activity overlap (0.89) as has been shown in other studies (Mertens *et al.*, 2020).

Although white-tailed mongooses are widespread, they have only been studied in detail in east Africa in the savannah habitat of Serengeti (Waser, 1980; 1981; Waser & Waser, 1985) and in the mosaic of farmland and grassland adjacent to BMNP (Admasu *et al*. 2004b). These studies and others (Ikeda *et al*. 1982) have shown that white-tailed mongooses are almost exclusively nocturnal, in concordance with my findings in BMNP. However, there is no information from other studies on overlap with other small carnivores. I found high overlap with the other nocturnal carnivores ranging from 0.83 (African civet) to 0.87 (common genet).

In BMNP, I found spotted hyenas to exhibit primarily nocturnal activity. However, other studies found that spotted hyena activity varies considerably with some reporting diurnal (Rainy & Rainy 1989) and others reporting crepuscular to nocturnal activity (Kolowski *et al*., 2007; Hayward and Slotow 2009; Sogbohossou *et al*. 2017; Kruuk 1972). Hyenas are usually dominated by lions through food stealing and direct killing (Watts and Holekamp 2009), yet despite this have significant overlap in activity patterns (Hayward and Slowtow 2009). However, in this study site

I had very few lion capture events and thus, competition with lions is not likely to be the reason for nocturnality. Spotted hyenas had moderate overlap with leopards (0.66), indicating they may modify activity to avoid them, or their nocturnal activity may result from avoidance of human activity (see below) or a combination of both.

In arid South Africa, honey badgers were more diurnal in the cold-dry season, while they were more nocturnal in the hot season, likely to avoid high temperatures (Begg *et al*. 2016). In tropical dry deciduous forest of India, however, honey badgers were nocturnal (Chatterjee *et al*., 2020). Yet in other studies honey badgers were shown to change their activity patterns in the presence of other carnivores likely to reduce antagonistic interactions (Nigam *et al*., 2018, Gubbi *et al*., 2014). Similar to a study in Serengeti (Allen *et al*. 2018), I also found little to no evidence of temporal avoidance of other predators by honey badgers, but rather overlap between honey badgers and all other carnivores was similar (0.55-0.64) regardless of species or size. Given that honey badgers are widely distributed but poorly understood, this study adds ecological knowledge of honey badger crepuscular activity in a forested environment.

Like honey badgers, it appears that leopards can also alter their timing of activity. For example, leopards were found to be more diurnal in rainforests of Gabon (Henschel & Ray 2003) and Thailand (Ngoprasert *et al*. 2007) than in African savannah landscapes (Hayward and Slowtow 2009) or in Afrotropical rainforest and open Miombo woodlands (Havmøller *et al*. 2020), where they exhibited cathemeral activity. However, Havmøller *et al*. (2020) also noted that male leopards were much more nocturnal than females. A possible explanation for differences in activity times, is to minimize competition with lions and spotted hyenas, which are absent in rainforests (Hayward and Kerley 2008; Balme *et al.* 2017). However, in our study, where lions were largely absent, and

we found moderate temporal overlap with spotted hyenas (0.66), providing some evidence of temporal avoidance to prevent niche overlap in the two largest carnivores analyzed in this study.

For the carnivore guild as a whole, it appears that three largest of my target species (honey badgers, hyenas, and leopards) can change their timing of activity in response to other species, habitat, or weather, effects which we did not test for in this study. But, for the three other small species (civets, mongooses, and genets) all past studies, including mine, have found them to be almost entirely nocturnal. Given that some species appear unable to vary much in temporal activity, it is perhaps surprising that I still found evidence of lower overlap (0.67-0.71) for species that were closer in body size, than for those species more dissimilar in body size (0.75), indicating that temporal shifts may be subtle, especially for the small nocturnal species. For example, genets had slightly later peaks in nocturnal activity than white-tailed mongooses. This type of partitioning likely enables carnivores to coexist by reducing risks of negative contact between species of similar size and diet (Schoener 1974; Holt & Polis, 1997). Temporal partitioning among carnivores more similar in body size, also has been observed in a camera trapping study of five felid species in Madagascar (Sunarto *et al*., 2015).

3.5.2 Temporal overlap with humans

3.5.2.1 Herbivores and Omnivores and humans

Of the three herbivores species, Menelik bushbucks, which were shown to have generally low occupancy and were found farther from roads (Chapter 2), also had the lowest temporal overlap with humans (0.45, this study). Considering they had high overlap with the other herbivores, this indicates Menelik bushbucks may be particularly sensitive to human activity, changing time of activity to avoid humans, consistent with activity studies from other populations (Waser, 1975). For cape bushbucks, other studies show them to be more nocturnal in response to human presence

(Jacobsen 1974), but we found moderate overlap with humans (0.53) and high overlap in activity at stations with and without humans (0.85). Duikers have been shown to be affected by human activities, especially hunting, which impacts their activity patterns (Croes *et al*. 2007). We found moderate overlap between duikers and human (0.57), but unlike bushbucks, at stations with high human activity, duikers substantially lowered their morning activity. Therefore, herbivores activity is largely not affected by the other herbivores, but they appear affected differentially by humans with Menelik bushbucks being potentially most sensitive, duikers intermediate, and bushbucks relatively less sensitive.

For the arboreal omnivores, olive baboons and human overlapped substantially, and they had almost identical activity patterns at station where humans were present or not (0.93), indicating they do not appear to change behavior as a result of human activity. Crested porcupines and tree hyraxes both overlapped little with humans and since tree hyraxes can be diurnal to avoid humans (Kingdon, 1977; Lovari *et al*., 2017; Pigozzi & Patterson, 1990) and porcupines can be crepuscular (Topp-Jørgensen *et al*., 2009), the strong nocturnality, high overlap with each other, and lowest overlap with humans, indicates that humans are likely causing their strong nocturnality in this study.

Bush pigs had moderate overlap with humans while giant forest hogs had the highest overlap with humans of all the herbivores and omnivores, except the olive baboon. Both species had lower overlap with humans in the morning hours compared to the late afternoon and early evening. Additionally, there was little difference in bush pig and forest hog activity patterns at stations with and without humans, indicating that these species' activity patterns do not appear to be influenced much by each other or by humans. Interestingly, a study in Uganda found a positive relationship between hogs and domestic animals in space use (Mugume *et al*., 2015). Additionally,

bushpigs are also known to raid crops and have been a source of human-wildlife conflict and are hunted in Madagascar (Rakotoarivony *et al*., 2022). Forest hogs and bush pigs, therefore, appear to use areas of human activity (Mugume *et al*., 2015; Smith *et al*., 2018) and may explain why we found little influence of humans on their temporal activity.

3.5.2.2 Carnivores and humans

As expected, the nocturnal species had very low overlap with humans (0.07-0.16), but this may result from some species potentially demonstrating obligate nocturnality (civets, mongooses, and genets), while humans and domestic animals were diurnal. Spotted hyenas, however, are known to shift temporal activity to become more nocturnal as a result of human activities or anthropogenic disturbance, as documented by several studies (Boydston *et al*., 2003; Kolowski & Holekamp, 2009; Pangle & Holekamp, 2010; Oriol-Cotterill *et al*., 2015, Schuette *et al*., 2013). Considering temporal overlap with leopards was moderate (0.66) but was extremely low with humans (0.15) it appears the spotted hyenas nocturnality may be driven more by humans in this study. Leopards, on the other hand, had almost double the overlap with humans (0.31) than hyenas, although it was still relatively low. Leopards have been shown to adapt fairly well to human-modified landscapes and prey on livestock (Abade *et al*., 2018; Athreya *et al*., 2013), which could explain their higher amounts of overlap with humans in this study.

Of the carnivores, honey badgers had the highest overlap with humans. In Iran, honey badgers did not entirely avoid human-dominated landscapes (Sharifi *et al*., 2020) as such landscapes can offer food availability food and movement corridors (Chiatante *et al*., 2017; Kheswa *et al*., 2018; Rosalino *et al*., 2014). Honey badgers are known to exhibit behavioral plasticity (Begg *et al*., 2003b; Widdows & Downs, 2015) and perhaps explaining their crepuscular activity with relatively high overlap with humans.

3.6 Conclusion

I used camera trap surveys to document activity times for 14 different mammalian species and quantify their temporal overlap with species of similar size and diet, and with humans. In general, herbivore and omnivore activity appeared unaffected by species of similar diet and body size, while human influences were variable. Menelik bushbucks and duikers appeared to avoid humans or high use human stations, whereas baboons, hogs, and pigs showed high overlap and lack of human temporal avoidance.

Carnivore temporal activity, on the other hand, appeared to be influenced by both interspecies interactions and human activity. There was some evidence of lower overlap for species more similar in body size and most species overlapped little with humans, except for honey badgers. Spotted hyenas and leopards, both known to alter activity based on human use, appeared to do the same in this study, but the response was stronger for hyenas.

Human photo-captures dominated our data set despite the fact that this area is a national park (Table 3.1). It also should be noted that I did not obtain enough photographs to model endangered species known (or assumed) to occur there (mountain nyala, Ethiopian wolves) or to model larger species (e.g., lions, jackals, aardvarks). It appears that BMNP is already highly impacted by human activities and better protection likely is needed, especially for species known to be sensitive to human disturbance or known to have high potential for human-wildlife conflict and low social tolerance. Nonetheless, I have provided baseline information on species whose activity is potentially affected by humans, which can inform the future study and management actions in an important area of high endemism and biodiversity.

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Table 3-1 Species, number of photos, number of evens and weight range in kilograms (kgs) for herbivore and omnivore species (from smallest to largest) and carnivores (from smallest to largest) that I analyzed caught on 48 cameras from the 3 surveys combined (December 2015-September 2016) in Harenna National Forest, Bale Mountains Park, Ethiopia

Common Species (Local name)	**Scientific Name**	**Number of photos**	**Number of events**	**Weight range for species (kgs)**	**Diet**
Herbivores and Omnivores					
Tree hyrax	*Dendrohyrax arboreus*	521	48	2 - 5	Bird eggs, forbs, leaves, fruit, insects, lizard (Gaylard & Kerley 1997)
Crested porcupine	*Hystrix cristata*	298	52	11 - 18	Tubers, bulbs, fruit (Bozzi & Laurenzi, 2016)
Common Duiker	*Sylvicapra grimmia*	237	49	12 - 25	Forbs, trees, bushes, fruits, seed, root, bark flowers, fungi, insects (Hoffman & Roth, 2003)
Olive baboon	*Papio anubis*	5224	288	22 - 37	Small mammals, invertebrates, and plants (Barton & Whiten 1994)
Cape Bushbuck (Imbabala)	*Tragelaphus sylvaticus*	2543	295	45 - 80	Invertebrates, small mammals, plants (Macleod *et al*., 1996)
Menelik's Bushbuck	*Tragelaphus scriptus meneliki*	2254	242	45 - 80	Leaves, shoots, buds, flowers, fruit (Girma, 2016)

Bush Pig	*Potamochoerus larvatus*	2631	237	54 - 115	Plant roots, rhizomes, tubers, fruits, insect larvae (Seydack, 2017)
Giant Forest Hog	*Hylochoerus meinertzhageni*	1571	139	100 - 225	Grass, leaves, forbs (IUCN, 2016)
Carnivores					
Common Genet	*Genetta genetta*	853	246	1 - 2	Birds. Bird eggs, frogs, insects, fruits (Amroun *et al*., 2014)
White-tailed mongoose	*Ichneumia albicauda*	408	117	1.8 - 5.2	Insects, bird, snakes (Martinoli, 2004)
Honey badger	*Mellivora capensis*	93	22	6.4 - 12	Honey, honeybee larvae, insects, amphibians, reptiles, mammals, birds, fruit, bulbs (Kruuk & Mills, 1983)
African Civet	*Civettictis civetta*	241	68	7 - 20	Fruit, small animals, insects (Habtamu *et al*., 2017)
Spotted Hyena	*Crocuta crocuta*	233	63	40 - 86	Medium to large sized mammals (Fester *et al*., 2021)
Leopard	*Panthera pardus*	140	33	50 - 90	Medium to large sized mammals (Kshettry *et al*., 2018)

Humans and domestic animals				
Human	8727	849	50-100	Meat, vegetable, fruit
Cows	10191	484	550-850	Grass
Dog	6	1	1.5-41	Meat
Goats	119	20	20-140	Grass, shrub
Donkey	468	144	100-500	Grass, shrub
Mule	43	7	275-700	Grass, shrub
Total	**40,422**	**3,426**		

Table 3-2 Temporal overlap (Δ) estimates and confidence intervals (lower CI and upper CI) between carnivore, herbivore, and omnivore species pairs (species 1 and Species 2) based on camera trap data obtained from December 2015 - September 2016 in Harenna Forest, Ethiopia.

Species 1	Species 2	Overlap (Δ)	Lower CI	Upper CI
Herbivores Pairings				
Common duiker	Cape bushbuck	0.83	0.73	0.92
Common duiker	Menelik bushbuck	0.79	0.68	0.89
Menelik bushbuck	Cape bushbuck	0.82	0.76	0.88
Omnivore Pairings				
Tree hyrax	Crested porcupine	0.71	0.56	0.85
Tree hyrax	Olive baboon	0.03	0.01	0.06
Olive baboon	Crested porcupine	0.04	0.00	0.09
Olive baboon	Bush pig	0.45	0.39	0.51
Olive baboon	Giant forest hog	0.63	0.55	0.71
Bush pig	Giant Forest hog	0.76	0.68	0.85
Carnivore Pairings				
Common genet	White-tailed mongoose	0.87	0.83	0.96
Common genet	Honey badger	0.57	0.39	0.72
Common genet	African civet	0.89	0.82	0.95
Common genet	Spotted hyena	0.85	0.82	0.96
Common genet	Leopard	0.64	0.50	0.76
White-tailed mongoose	Honey badger	0.61	0.48	0.79
White-tailed mongoose	African civet	0.83	0.76	0.94
White-tailed mongoose	Spotted hyena	0.84	0.76	0.95
White-tailed mongoose	Leopard	0.69	0.59	0.85
African civet	Honey badger	0.55	0.37	0.72
African civet	Spotted hyena	0.83	0.78	0.96
African civet	Leopard	0.64	0.51	0.79
Honey badger	Spotted hyena	0.64	0.48	0.82
Honey badger	Leopard	0.62	0.48	0.82
Spotted hyena	Leopard	0.66	0.51	0.81
Humans and Herbivores				
Humans and domestic animals	Common duiker	0.57	0.45	0.68
Humans and domestic animals	Cape bushbuck	0.53	0.48	0.59

Humans and domestic animals	Menelik bushbuck	0.45	0.40	0.5
Humans and Omnivores				
Humans and domestic animals	Crested porcupine	0.08	0.03	0.13
Humans and domestic animals	Tree hyrax	0.04	0.01	0.08
Humans and domestic	Olive baboon	0.45	0.40	0.51
Humans and domestic	Bush pig	0.51	0.45	0.57
Humans and domestic	Giant forest hog	0.68	0.61	0.75
Humans and Carnivores				
Humans and domestic animals	Common genet	0.07	0.06	0.09
Humans and domestic animals	White-tailed mongoose	0.16	0.06	0.15
Humans and domestic	Honey badger	0.47	0.31	0.62
Humans and domestic	African civet	0.09	0.04	0.14
Humans and domestic	Spotted hyena	0.15	0.08	0.22
Humans and domestic	Leopard	0.31	0.21	0.42

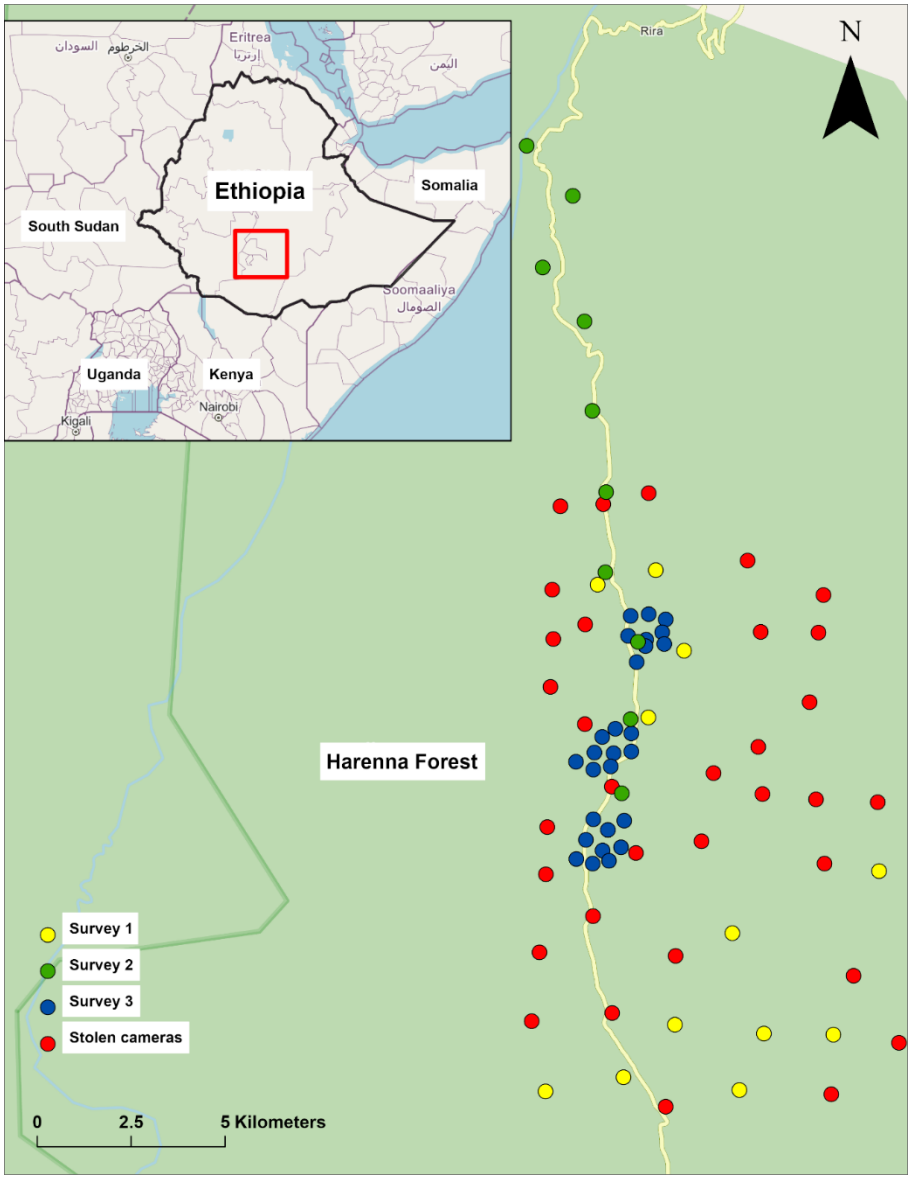


Figure 3.1. Inset shows the location of Bale Mountains National Park (BMNP) within Ethiopia with the red square highlighting the location of the camera surveys. Camera station locations in Harenna Forest, BMNP, are denoted as: yellow depicting survey 1 (December 2015-April 2016), green depicting survey 2 (April 2016), blue depicting survey 3 (September 2016), and red showing stolen/destroyed cameras.

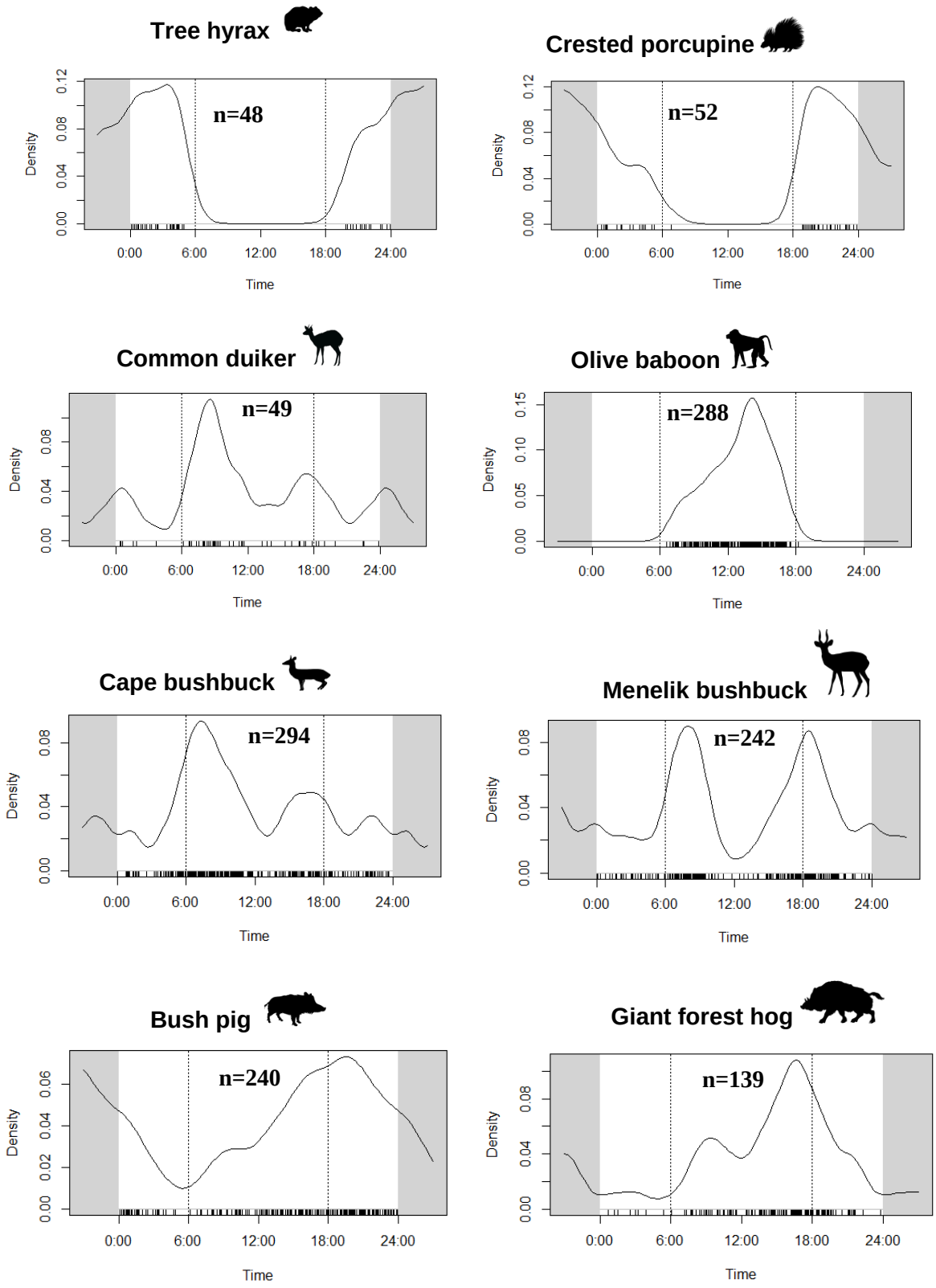

Tree hyrax
n=48
Crested porcupine
n=52
Common duiker
n=49
Olive baboon
n=288
Cape bushbuck
n=294
Menelik bushbuck
n=242
Bush pig
n=240
Giant forest hog
n=139
Density
Time
0:00
6:00
12:00
18:00
24:00

Figure 3.2. Herbivore and omnivore temporal activity plotted by Kernel density (y-axis) with number of photographic captures (black lines across bottom x-axis) across the diel cycle (24 hours) in Harenna forest from camera trap surveys in December 2015-September 2016. Dotted vertical lines indicate the times of sunrise and sunset.

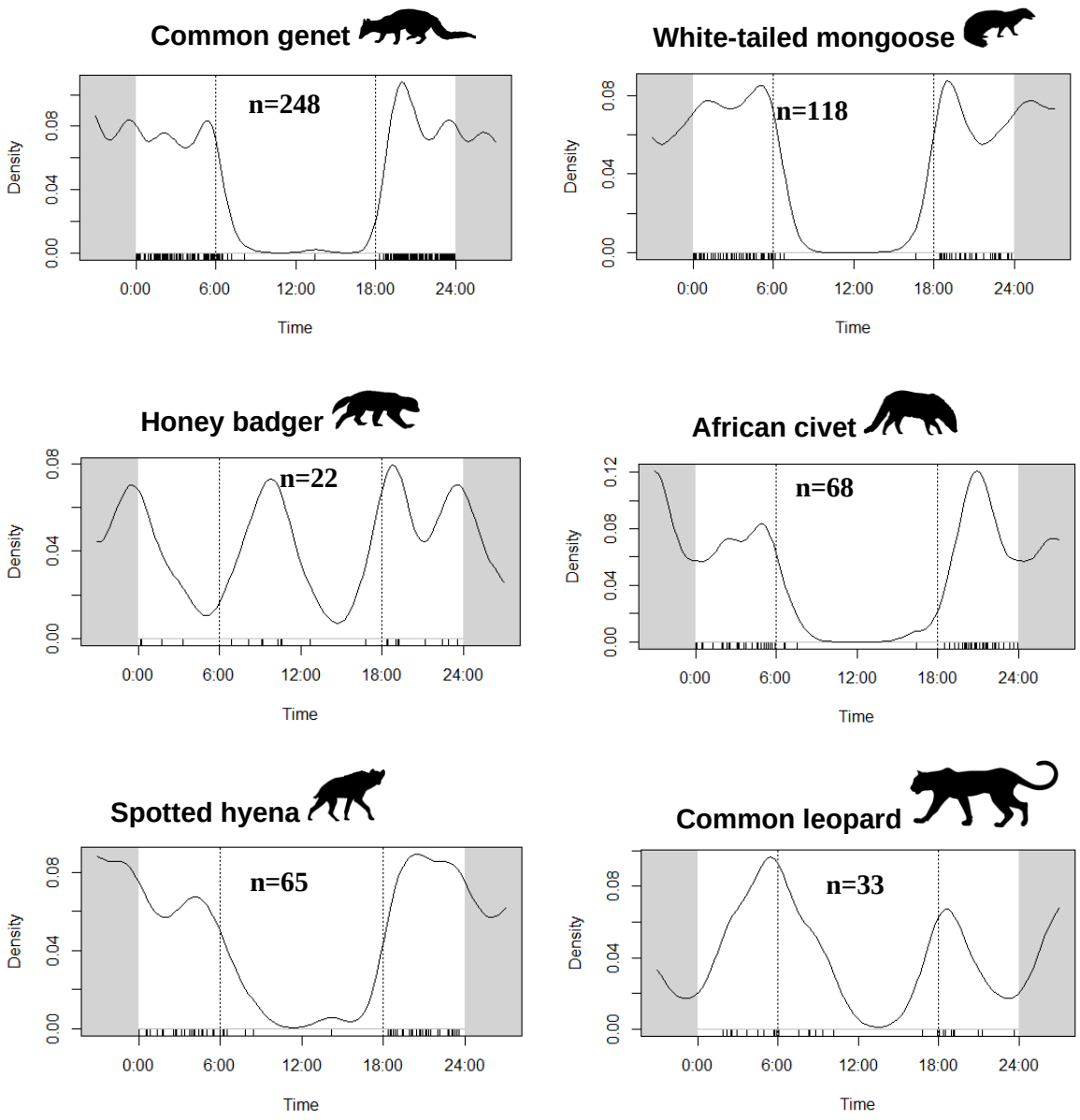


Figure 3.3. Carnivore temporal activity plotted by Kernel density (y-axis) with number of photographic captures (black lines on x-axis) across the diel cycle (24 hours) in Harenna forest from camera trap surveys in December 2015-September 2016. Dotted vertical lines indicate the times of sunrise and sunset.

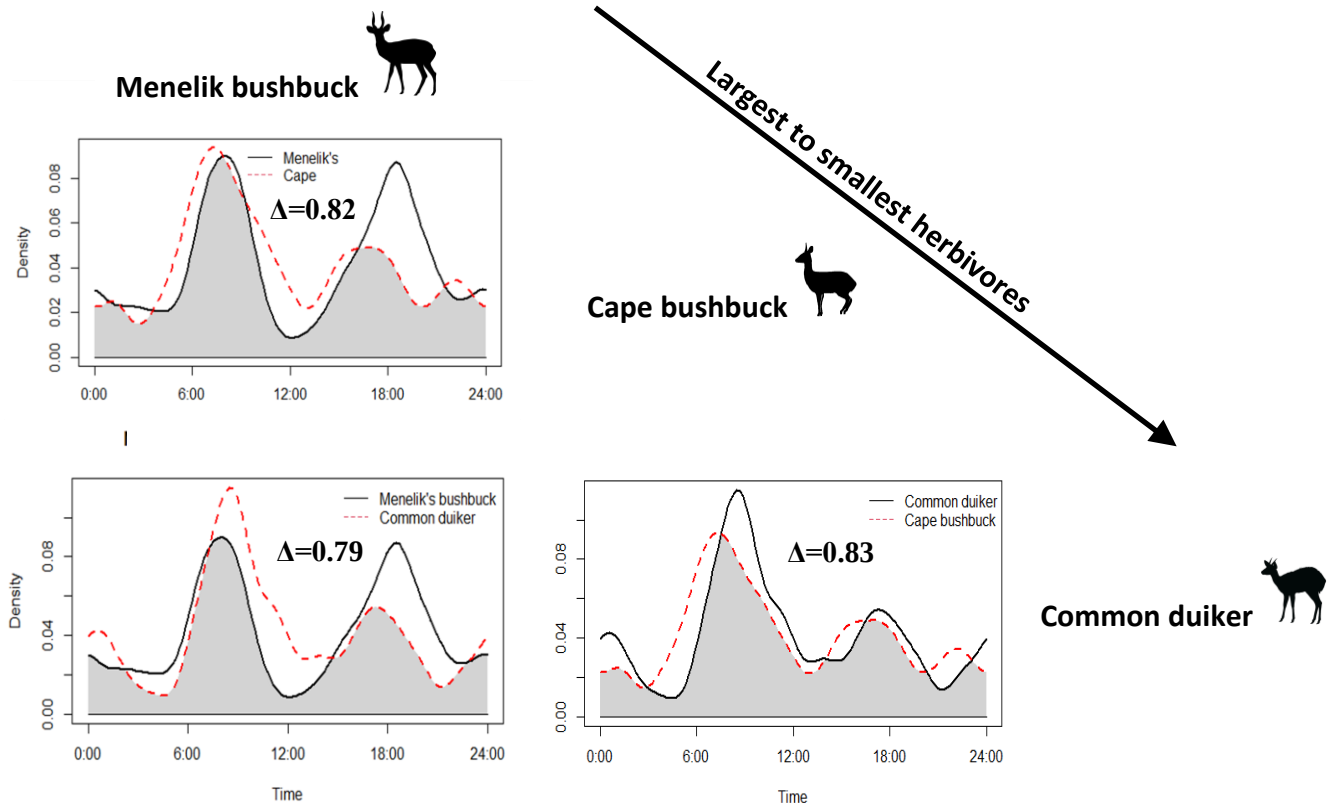


Figure 3.4. Overlap estimates (Δ) between herbivore species pairs resulting from photographic capture across diel cycle (x-axis) plotted against density of temporal activity (y-axis). Data from camera trap surveys in Harenna forest Ethiopia from camera trap surveys in December 2015-September 2016. Species are organized from largest at the top to smallest such that the outer diagonals represent species of more similar body sizes. Although it should be noted in this case the two bushbuck species are similar in size while the duiker is much smaller.

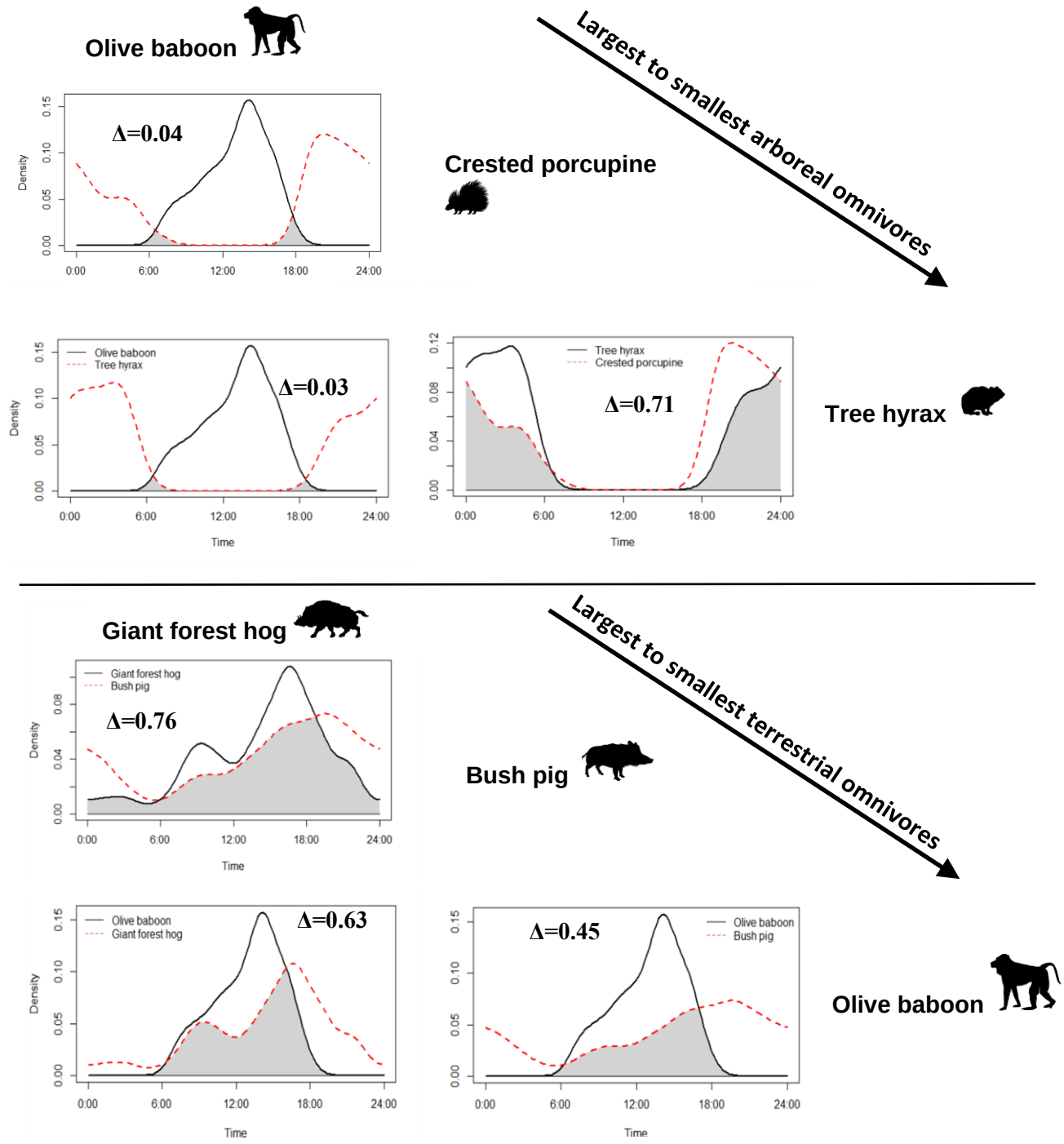


Figure 3.5. Overlap estimates (Δ) between omnivore species pairs resulting from photographic capture across diel cycle (x-axis) plotted against density of temporal activity (y-axis). In this case I only paired tree hyraxes with other species known to use trees such as crested porcupines and olive baboons (top panel). I did not include crested porcupines and tree hyraxes in the bottom panel because they were primarily nocturnal compared to the other diurnal omnivores. Data from camera trap surveys in Harenna forest, Ethiopia from survey in December 2015-September 2016.

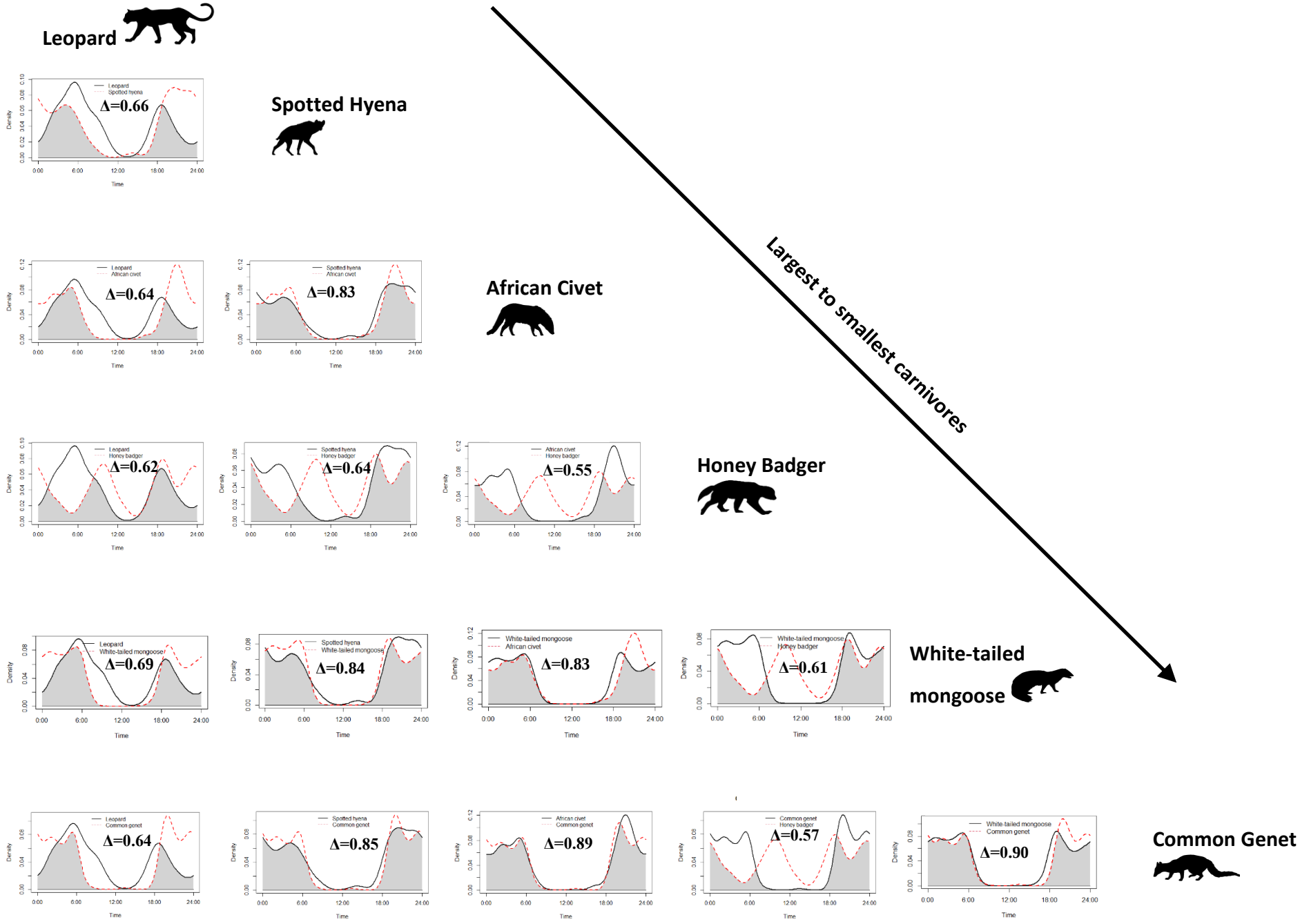
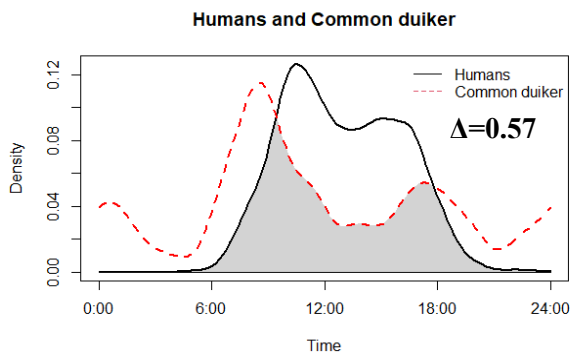
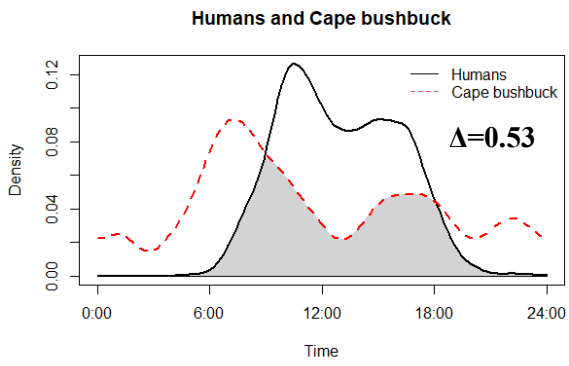
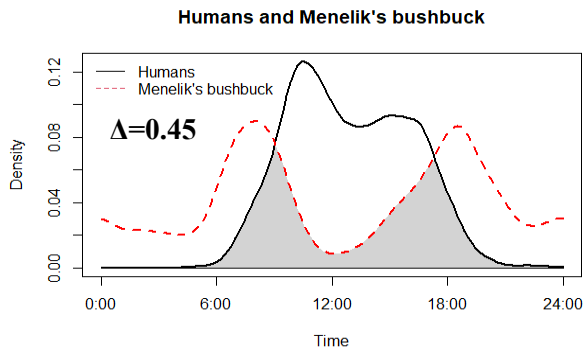
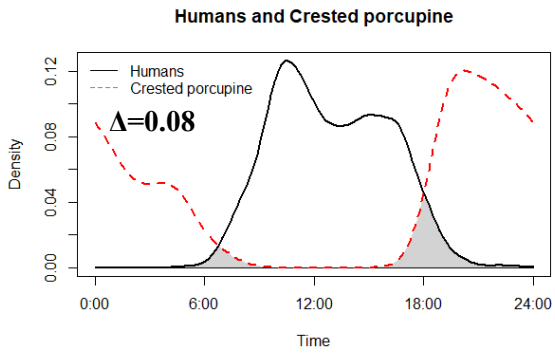

Leopard
Spotted Hyena
African Civet
Honey Badger
White-tailed mongoose
Common Genet
Largest to smallest carnivores
Leopard
Spotted hyena
Δ=0.66
Leopard
African civet
Δ=0.64
Spotted hyena
African civet
Δ=0.83
Leopard
Honey badger
Δ=0.62
Spotted hyena
Honey badger
Δ=0.64
African civet
Honey badger
Δ=0.55
Leopard
White-tailed mongoose
Δ=0.69
Spotted hyena
White-tailed mongoose
Δ=0.84
White-tailed mongoose
African civet
Δ=0.83
White-tailed mongoose
Honey badger
Δ=0.61
Leopard
Common genet
Δ=0.64
Spotted hyena
Common genet
Δ=0.85
African civet
Common genet
Δ=0.89
Common genet
Honey badger
Δ=0.57
White-tailed mongoose
Common genet
Δ=0.90
Density
Time
0:00
6:00
12:00
18:00
24:00

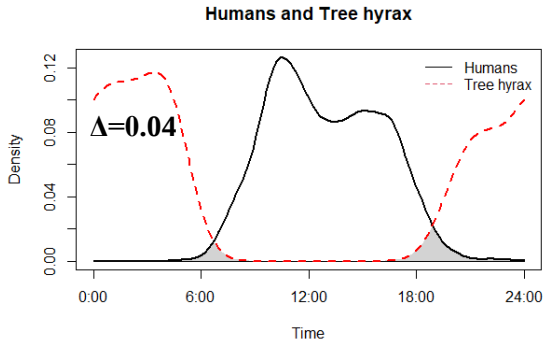
Figure 3.6. Overlap estimates (Δ) between carnivore species pairs resulting from photographic capture across diel cycle (x-axis) plotted against density of temporal activity (y-axis). Data from camera trap surveys in Harenna forest Ethiopia from camera trap surveys in December 2015-September 2016. Species are organized from largest at the top to smallest such that the outer diagonals represent species of more similar body sizes.

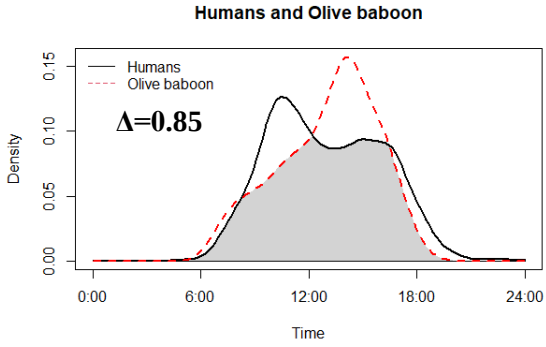

Humans and Common duiker
Humans
Common duiker
Δ=0.57
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time

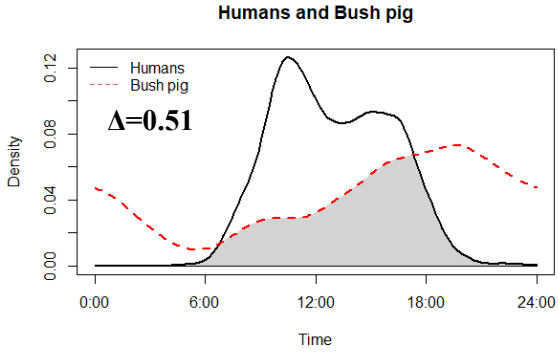

Humans and Cape bushbuck
Humans
Cape bushbuck
Δ=0.53
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time


Humans and Menelik's bushbuck
Humans
Menelik's bushbuck
Δ=0.45
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time


Humans and Crested porcupine
Humans
Crested porcupine
Δ=0.08
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time


Humans and Tree hyrax
Humans
Tree hyrax
Δ=0.04
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time


Humans and Olive baboon
Humans
Olive baboon
Δ=0.85
Density
0.00
0.05
0.10
0.15
0:00
6:00
12:00
18:00
24:00
Time


Humans and Bush pig
Humans
Bush pig
Δ=0.51
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time

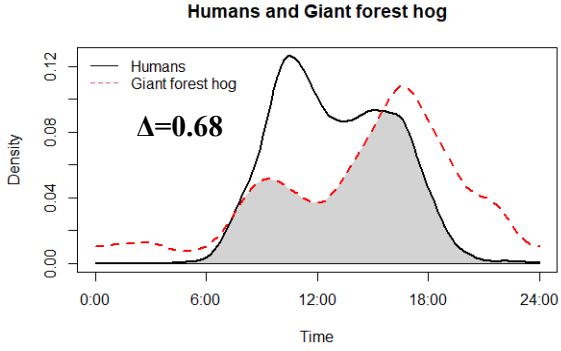

Humans and Giant forest hog
Humans
Giant forest hog
Δ=0.68
Density
0.00
0.04
0.08
0.12
0:00
6:00
12:00
18:00
24:00
Time

Figure 3.7. Overlap estimates (Δ) between humans and domestic animals and herbivore and omnivore species pairs across all camera stations from photographic capture across diel cycle (x-axis) plotted against density of temporal activity (y-axis). Data from camera trap surveys in Harenna forest Ethiopia from camera trap surveys in December 2015-September 2016.

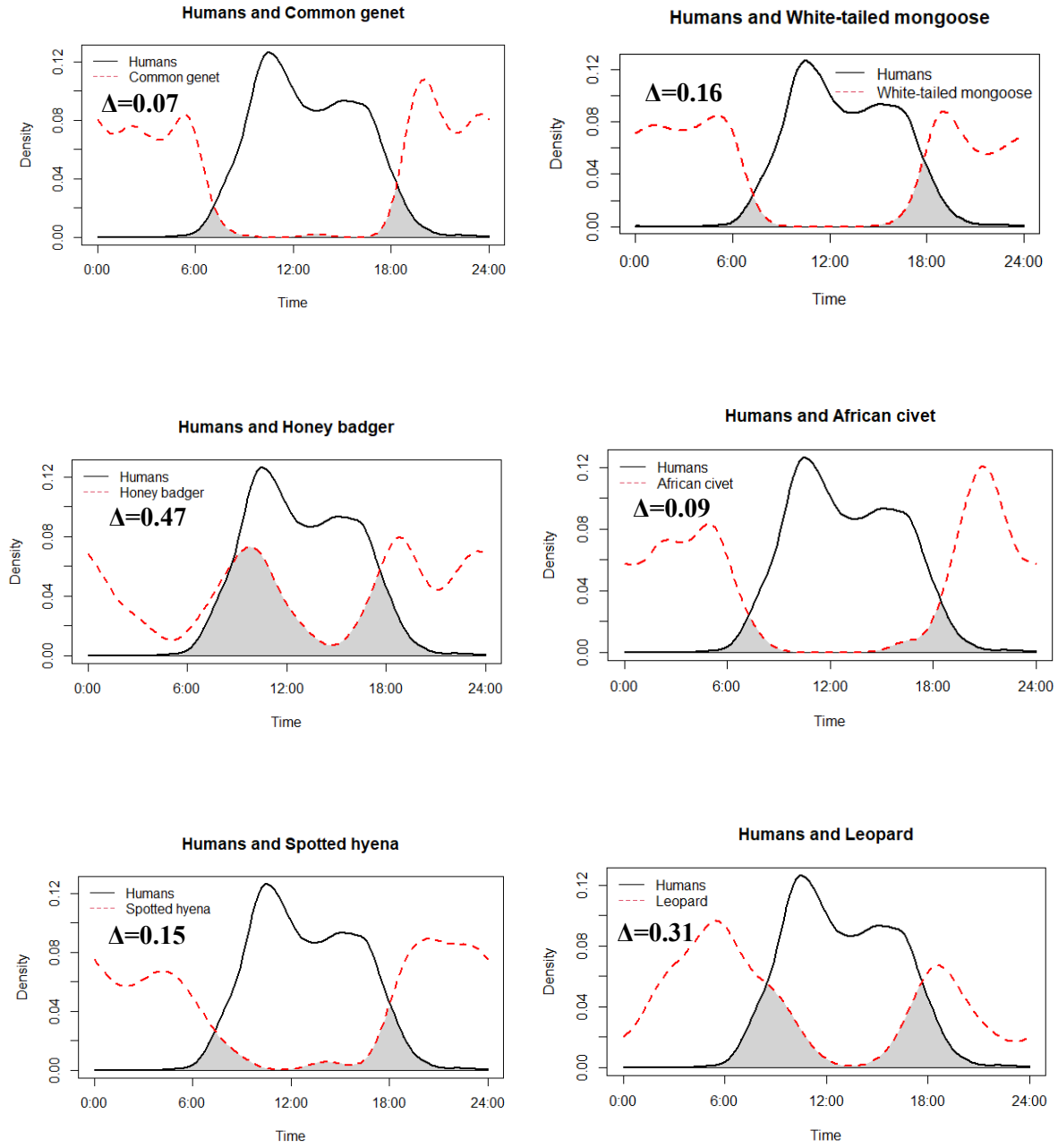


Figure 3.8. Overlap estimates (Δ) between humans and domestic animals and carnivore species pairs across all camera stations from photographic capture across diel cycle (x-axis) plotted against density of temporal activity (y-axis). Data from camera trap surveys in Harenna forest, Ethiopia from camera trap surveys in December 2015-September 2016.

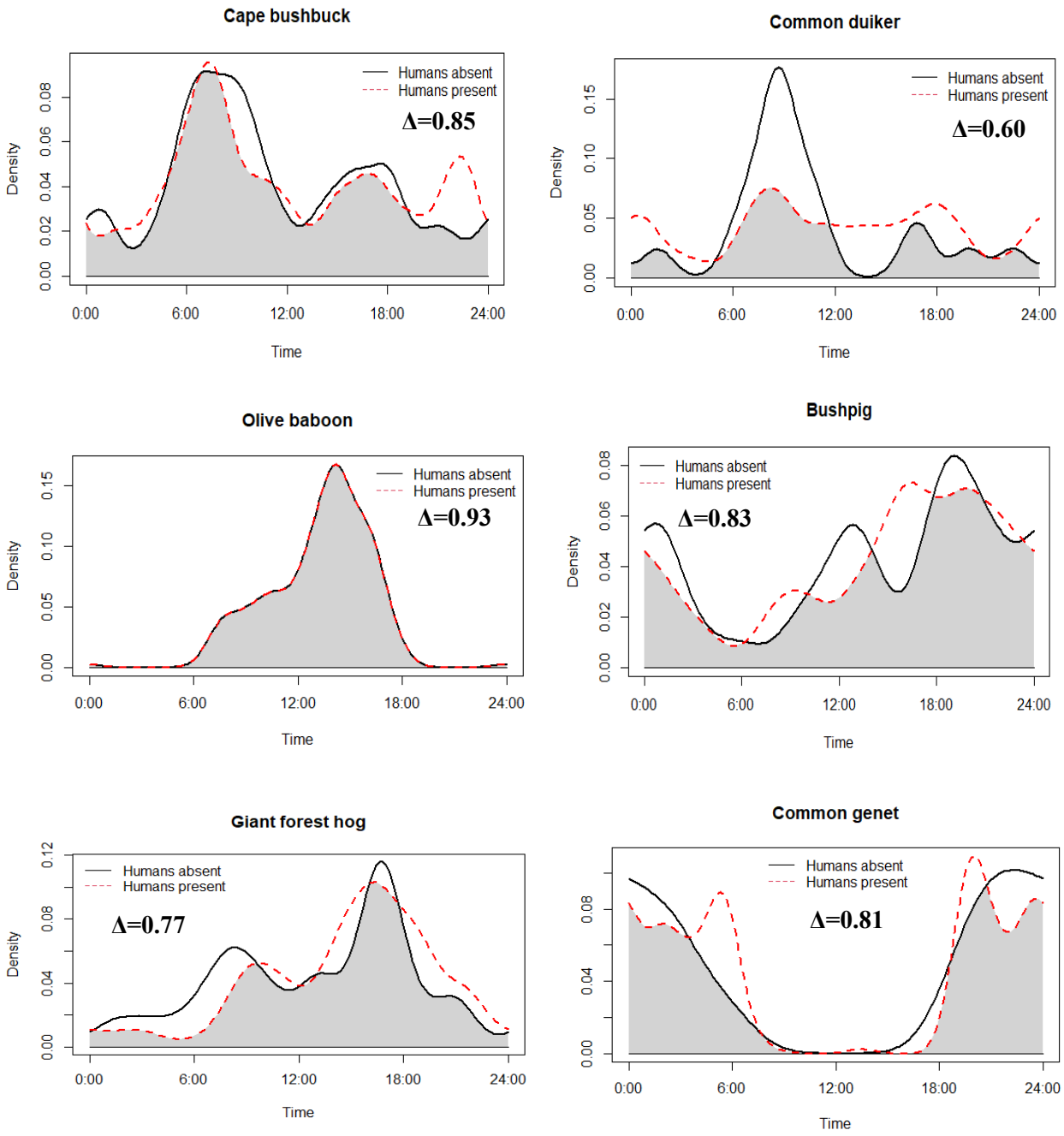


Figure 3.9. Overlap estimates (Δ) for all species with enough captures to compare activity at cameras where ≥15 humans were detected to those stations where no humans were detected in photographic captures across diel cycle (x-axis) plotted against Kernel density of temporal activity (y-axis). Data from camera trap surveys in Harenna forest Ethiopia from camera trap surveys in December 2015-September 2016.

Chapter 4 : Conclusion

There has been no comprehensive literature documenting wildlife species presence, distribution, and potential for interactions between mammals, and between mammals and humans, in Harenna forest, Ethiopia. To address this gap, my thesis focused on using data from a camera study in 2015-2016 to assess habitat use by mammals, influences of humans on habitat use and detection, and temporal overlap between species pairs within diet groups (herbivores, omnivores, and carnivores). I also assessed species overlap with humans and determined whether species changed their activity patterns when human presence was high versus low.

Chapter 2: "**Occupancy analyses reveal mammalian wildlife community predominately comprised of species tolerant to human impacts in Harenna Forest, Ethiopia."**

My objective was to determine trapping rates and distribution of terrestrial species and to examine habitat and biotic factors influencing habitat use (including humans) using single season occupancy modeling from camera trap records for those species with sufficient data. I was particularly interested in anthropogenic impacts on species occupancy and distribution considering the recent human-induced landscape changes. I grouped species into categories: herbivores and omnivores combined, and carnivores. Detection/non-detection data were collected from 48 cameras placed in Harenna forest, Ethiopia.

Chapter 3: **"Differential influences of humans and competitors on temporal activity and overlap in herbivores, omnivores, and carnivores of Bale Mountain National Park, Ethiopia."**

My objective was to examine temporal activity patterns and overlap of 8 herbivore and omnivore species, and 6 carnivore species. I used KDE analysis to examine overlap between

species pairs, by estimating coefficient of overlap (Δ) between species pairings. I expected more competition between similar species (diet and size), and therefore I separated out omnivores from herbivores and arboreal from terrestrial. I did the same pair-wise overlap analysis for all six carnivores and between all species and humans.

4.1 Findings for Herbivores and Omnivores

I found that 6 out of 7 herbivore and omnivore species had high occupancy (i.e., habitat use) of over 0.70, except for the Menelik bushbuck, which had low occupancy of only 0.45. I only obtained 4 photo-events of the endangered mountain nyala, which is concerning since it is expected to be found at this elevation range. I also found that 3 of 5 strong effects on habitat use were related to anthropogenic factors (2 positively-Menelik and cape bushbucks, 1 negative-Menelik bushbuck) rather than habitat.

Interestingly, for detection, I found that 8 out of 9 supported effects were related to biotic or habitat features with only one related to anthropogenic effects, and that was positive (Cape bushbuck and distance to road). Since humans largely had no (or positive) effects on herbivore and omnivore species detection, it did not appear that these species changed their behavior (i.e., became more cryptic and less detectable) due to impact of the human footprint.

Temporally, I found that species overlap was not affected by species of similar diet or body size, which might be expected if competition is driven by limited resource availability. Instead, I found temporal overlap was often higher for species closer in size or similar in diet, indicating that perhaps shared resources are not limited, and instead resource availability drives high overlap regardless of size, as found in other studies of herbivore and omnivores (Ritchie & Olff, 1999; Prins & Olff 1996).

In general, I found little impact of humans on herbivore and omnivore temporal activity, with some species (i.e., olive baboons) almost completely overlapping with humans even at stations with high human activity. Bush pigs and forest hogs may capitalize on humans, perhaps due to their crop raiding behavior. Tree hyraxes were nocturnal, possibly to avoid humans, although this species was only detected at one camera station. The two species potentially impacted by humans were Menelik bushbucks with the lowest overlap with humans, and duikers, which decreased activity (especially in the morning) at cameras with high human use. Besides these 2 species, 6 others had had relatively high overlap with humans, or did not change in response to human activity (Table 4.1).

In summary, with perhaps 2 exceptions (Menelik bushbuck and duiker), herbivores and omnivores were largely unaffected or were positively affected either spatially or temporally by each other, or by the human footprint (Table 4.1). This may reflect the fact that the species currently existing in Harenna forest are those already tolerant to humans and thus the community has been altered by humans to the advantage of such species. I found few captures of mantled guerezas, mountain nyalas, natal multimammate mice, Bale vervet monkeys, warthogs, and aardvarks (See Table 2.1, Chapter 2). However, mantled guerezas and Bale monkeys are typically found in the bamboo region, which is at higher elevation (2,300 to 3,200 m asl) than the area that was sampled (Mekonnen *et al*., 2012). Natal multimammate mice were probably not detected due to their small size. Research shows that in the presence of humans, mountain nyalas spend more energy on movement and vigilance as opposed to resting and foraging (Worku *et al*., 2021, Tadesse and Kotler, 2013). Low warthog detections could be attributed to their avoiding dense understory and forests (Deribe *et al*., 2008), which is where the cameras in our study were set up. I expected

to find more aardvark detections since there is currently no written evidence that shows they are affected or not by anthropogenic changes.

4.2 Findings for Carnivores

For carnivores, I found that 3 species were widespread with occupancy ≥ 0.7 (civet, genet, hyena), while 3 species showed low occupancy (honey badger, mongoose, leopard), but I obtained few photos of large carnivores (lions: 3 events; side-stripped jackal: 1 event; golden jackal: 1 event). Out of all species, I only found only 2 strong effects on occupancy (i.e. site-use), and both were for white-tailed mongoose (negative elevation and positive for anthropogenic). Thus, there was little evidence that humans or habitat influenced site-use for carnivores, for the covariates I included (Table 4.2). For detection, however, 6 of 7 strong effects were anthropogenic in nature and 5 were positively related to humans for civets, mongooses, and hyenas.

Interestingly, and unlike herbivores, temporal analyses revealed stronger effects of species on each other, such that species tended to have lower temporal overlap when they were more similar in body size (similar to Sunarto *et al*., 2015). In general, temporal overlap was lower between carnivores and humans than for herbivores and omnivores, but this could partly be driven by some species being obligately nocturnal (civets, genetic, mongooses). Although white-tailed mongoose are widespread in range, we present evidence on their overlap with other mammals, which has not been recorded in the past. Spotted hyenas appeared to have a strong response to humans, with very low overlap (0.15), and they are known to change temporal behavior in response to humans (Boydston *et al*., 2003; Kolowski & Holekamp, 2009; Pangle & Holekamp, 2010; Oriol-Cotterill *et al*., 2015, Schuette *et al*., 2013). Leopards also had low overlap with humans (0.31), but not as dramatic as hyenas. Honey badgers had highest overlap with humans and these species are known to use human landscapes (Table 4.2).

In summary, I found little influence of humans and domestic animal trap rate on occupancy, which could be an artefact of widespread presence of humans on the landscape making it harder to tease out human effects. I found more evidence of potential changes in temporal activity in response to both humans and each other, but many carnivores were not photographed indicating that they could be locally extirpated, or nearly so, due to inability to live with humans. The species that do survive in this landscape appear to be the ones that are more flexible in their ability to adjust temporally to avoid humans, or they do not have much overlap with humans to begin with due to their nocturnal nature. Surprisingly, we did not record any photographic events of domestic cats and only one event of a dog, which was with humans, suggesting little evidence of non-invasive species in the area sampled. That is perhaps a glimmer of good news for native mammalian species in Harenna.

4.3 Future directions

Co-occurrence models estimate what sites are occupied based on habitat/biotic covariates from single season models and additionally incorporate the occupancy/detection of other potentially competing species (Mackenzie *et al*., 2004). Flexibility in this method allows for estimation of probabilities of potential interaction between species using likelihood-based methods and addresses aspects of community structure such as competition and predator-prey relationships (Mackenzie *et al*., 2004). I have already begun co-occurrence modeling for carnivores to parse out competition versus habitat or human effects. In this way, I can gain better understanding of interspecific spatial co-occurrence (rather than just temporal) to assess the relative importance of competition versus habitat or human effects. I plan to investigate the relative influence of other wildlife species, humans, and domestic animals using 2-species, co-occurrence modeling, while

including important habitat variables that influence distribution and detection from my single species models in Chapter 2. The questions I intend to answer include:

- Do habitat covariates or interacting species or both, predict species co-occurrence across the landscape?
- Do herbivore and omnivore species co-occur?
- Do large carnivores (common leopards and spotted hyenas) co-occur with large herbivore and omnivore species?

This study offers baseline information and understanding of site-use and temporal patterns for some of the herbivore, omnivore, and carnivore species in Harenna forest, but is not exhaustive. For future analysis, I suggest resurveying the area and collecting camera station-level data such as soil type, fine scale land cover, types of trails, vegetation thickness, or human impacts such as poaching signs, type of human activity, type of agriculture nearest camera sites. I also suggest that cameras location consider home range of the animal being surveyed to space cameras based on a regime that could allow estimates of true occupancy rather that site-use. These will offer deeper understanding of factors influencing actual occupancy by multiple species in the face of anthropogenic changes, and if the data are collected at the same time each year, or if they are stratified by season, this can be used in a multi-season occupancy framework to estimate site extinction and colonization over time.

4.4 Challenges

Humans and domestic animals dominated the photo-captures, even within the national park, where technically, livestock are not allowed to be grazed. Additionally, the field team lost 37 out of the 85 camera stations due to theft and livestock damage, even though human and domestic animal trap rates did not appear to influence site use by mammals, except for detection of spotted

hyenas. This could be an artefact of widespread human distribution in the forest. Locals agree (85% of people surveyed) that wildlife populations are decreasing due to increased migration into the area, agriculture, and habitat fragmentation (Mekonen et al., 2017). Teasing out impacts of different human activities could aid future management by identifying those compatible with wildlife conservation. Low photographic captures of the mountain nyala and large carnivores (lions, leopards, jackals), could indicate that species of great ecological and cultural interest are being lost in an area they previously existed (Lavrenchenko, 2000; Hillman, 1986). I also provided evidence that some large carnivores were not captured (wild dog, Ethiopian wolf), or were potentially changing their temporal behavior (hyenas) to avoid humans. Some herbivores like Menelik bushbuck and duikers may be sensitive to humans but are currently still surviving in the study area.

Given the challenges facing Harenna, it is important to engage the government and local people to address weak park policies, deforestation leading to habitat fragmentation, degradation and loss, and agricultural expansion causing immigration in to Harenna. However, the locals have historically relied on this area, firstly through pastoralism and lately, through subsistence and growth of coffee. It will be important to engage the stakeholders in dialogue about the challenges of current practices, while developing alternative sustainable, viable livelihoods for the communities adjacent to the forests (Wakjira *et al*., 2015). Considering coffee farming is an important economic driver for this region, it would be important to assess its impact on conservation since it is grown in the southern region of Bale where Harenna forest is located. While coffee farming has been shown to be good for birds (Chang et al., 2018; Perfecto et al., 1996; Karanth et al., 2016), it should not be assumed to be good for herbivores, omnivores, or carnivores. Growing shade-tolerant coffee often comes at the expense of woody plants especially

in the Afromontane region since coffee needs some sunlight (Kewessa et al., 2019; Teketay, 1999; Gole & Senbeta, 2006). This is usually done by removing some canopy cover and some undergrowth vegetation (Gole & Senbeta, 2006; Teketay, 1999), which offers food and cover from predators for some species, especially Menelik and Cape bushbucks and bushpigs, that prefer dense vegetation (Girma *et al.*, 2018; Yazezew *et al.*, 2011; Amills *et al*., 2017). However, coffee is beneficial to some species such as African civets which eat coffee especially during the dry season (Habtamu et al., 2017). Therefore, in future assessments, it is important to include distance to, and area of, coffee farming as covariates on habitat use, occupancy, and detection, to determine impacts of coffee species distribution more directly.

Since Harenna is home to endangered and charismatic species and serves as the water supply to communities downstream, these factors can be a pivotal talking point in conservation education, to increase awareness of the importance of the area to locals and different stakeholders, to strengthen community-based conservation initiatives, and to address immigration problems in the area (Mekonen *et al*., 2017). Local organizations such as Ethiopian Wildlife Conservation Authority (EWCA), Ethiopian Wolf Conservation Program (EWCP), and Frankfurt Zoological Society (FZL), which have been working in Bale since 2004, and have been involved in conservation within Bale Mountains National Park (BMNP). EWCP is involved in monitoring Ethiopian wolves while FZL alongside EWCA, in monitoring mountain nyala populations and alpine lakes, as well as livestock and human settlement within the park. Other research has focused on land use and land cover changes (LULC) (Muhammed *et al*., 2021; Alemu *et al*., 2015, Kindu et al., 2013), wolves (Marino and Sillero-Zubiri, 2013), mountain nyalas and other species occurring in the park. In recent years, Ethiopia has faced political challenges that have led to the halting of conservation work and led to increased illegal settlement within the park. Since this

particular portion of the park is important for both animal species and local people, it is important to ensure its protection for biodiversity and the socio-economic benefits that it offers. Organizations supporting conservation have been forced to leave the area due to political unrest, thus moving forward, it will be important for the government to prioritize protecting this biodiversity area as an economic incentive for ecotourism and growth of shade-tolerant coffee in a way that appeases the locals, benefits local economy, and conserves wildlife by restricting illegal settlements, logging, clearing land for agriculture and managing human-wildlife conflict. Otherwise, BMNP will remain only a "paper park" supporting those wildlife species that can tolerate or capitalize on human use, while other important species may be lost.

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Table 4-1 Herbivore and omnivore species (common name), human, biotic, and habitat/landscape effects on occupancy and detection, degree of overlap with humans, and influence of high human use. A (-) indicates a negative effect of the covariate, a (+) indicates and positive effect, and a (o) indicates no discernable effect. NA is not applicable because we did not have enough data to test high versus low human use stations.

	Human effects			**Biotic effects**		**Habitat/landscape effects**						Temporal effects	
Species	Park boundary	Road	Buildings	Large predator trap rate	Large predator trap rate	Elevation	EVI	NDVI	% Trees within 250m radius	% Shrub within 250m radius	Water	Human overlap	Behavior change at high human use
Menelik bushbuck	$+^{occ}$	$-^{occ}$	o	o	$+^{det}$	o	$-^{det}$	o	o	o	o	Moderate	NA
Cape bushbuck	o	$+^{occ}$	$-^{det}$	o	o	o	o	o	o	o	o	Moderate	No
Common duiker	o	o	o	o	o	o	o	$-^{det}$	$+^{det}$	$-^{det}$	o	Moderate	Yes
Giant forest hog	o	o	o	$+^{occ}$	$-^{det}$	o	o	o	o	o	o	Moderate	No
Bush pig	o	o	o	o	o	$-^{occ}$	o	o	o	o	o	Moderate	Yes
Olive baboon	o	o	o	o	o	o	o	o	o	o	$-^{det}$	High	No
Tree hyrax	o	o	o	o	o	o	o	o	o	o	o	Low	NA
Crested porcupine	o	o	o	o	o	o	o	o	$-^{det}$	o	o	Low	NA

occ - Effect on occupancy

det - Effect on detection

Table 4-2 Carnivore species (common name), human and habitat/landscape effects on occupancy and detection and degree of overlap with humans and influence of high human use. Note there were no biotic effects on carnivores. A (-) indicates a negative effect of the covariate, a (+) indicates and positive effect, and a (o) indicates no discernable effect. NA is not applicable because we did not have enough data to test high versus low human use stations.

	Human Effects				**Habitat/landscape**			**Temporal overlap**	
	Buildings	Road	Agriculture	Humans & domestic animal trap rate	Elevation	Water	Forest edge	Human overlap	Behavioral change at high human use
Common genet	o	o	$-^{det}$	o	o	o	o	Low	Yes
White-tailed mongoose	$+^{occ}$	$+^{det}$	$-^{det}$	o	$-^{occ}$	o	o	Low	NA
Honey badger	o	o	o	o	o	o	o	Moderate	NA
African civet	o	o	o	o	o	$+^{det}$	$+^{det}$	Low	NA
Spotted hyena	o	$+^{det}$	o	$+^{det}$	o	o	o	Low	NA
Common leopard	o	o	o	o	o	o	o	Low	NA

occ - Effect on occupancy

det - Effect on detection