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The Role of Apex Predators in Structuring the Spatial Behaviour of Mesopredators

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Award date:
2019

Awarding institution:
Bangor University

Link to publication

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Master of Science by Research

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The Role of Apex Predators in Structuring the Spatial Behaviour of Mesopredators

1.1 Abstract

Apex predators occupy the highest trophic level within an ecosystem, and can influence the behaviour of smaller mesopredators in several ways. Spatial behaviour describes the ways in which a species interacts with the physical environment around it. The presence of an apex predator can influence the spatial behaviour of a mesopredator; for example, by altering the habitat use of the mesopredator. This change in spatial behaviour can have wide-reaching and cascading effects, and may influence overall ecosystem biodiversity. It is hypothesized that when a track is present in a habitat, an apex predator will move along the track, whereas mesopredators will alter their spatial behaviour to avoid tracks, and minimize the likelihood of interacting with an apex predator. This research collected data from camera traps deployed in Zambezi National Park, Zimbabwe. Occupancy analysis was used to identify how the occupancy of apex predators along a track differed to the occupancy of mesopredators. Across 240 camera traps effort days, a total of 804 photographs of 21 species were captured. There were eleven target species in this research; eight of which were recorded during data collection. The data showed that species abundance was greatest along the track being sampled, compared to the adjacent off-track habitat. Occupancy analysis showed that species occupancy for most species was greatest along the track; indicating that the track is the preferred movement route for all species, regardless if they are an apex predator or mesopredator. The data did not provide clear and substantial evidence to support the hypothesis that mesopredators alter their spatial behaviour to avoid apex predators. Apex predators can be introduced into an ecosystem to be used as a conservation tool. This can be reliant on mesopredators altering their spatial behaviour in the presence of an apex predator. Further data collection and analysis is required to substantiate these claims. A manipulative experimental design, rather than observational, may also be useful for further research into this hypothesis.

In addition to data collection, this research has also provided photographic evidence of elusive species, which are not frequently witnessed within the Zambezi National Park, Zimbabwe. These images are crucial to highlight the importance of continued conservation efforts within the national park, and have educational value for conservation bodies and the local community.

1.2 Introduction

The continent of Africa contains some of the most diverse landscapes and ecosystems on the planet; from the lush rainforests in the Congo River basin, to the vast and expansive plains of the Serengeti (National Geographic, 2018). Africa is also home to some of the world's most iconic predators; most notably perhaps, the African lion. The African lion *(Panthera leo)* is an apex predator, meaning it occupies the highest trophic level of the ecosystem's food web, and is generally not predated upon by any other animal (Bauer *et al.*, 2016).

Apex predators are important ecosystem regulators, and can influence their ecosystem through top-down regulation (Bunnell *et al.*, 2013). Top-down regulation refers to the process whereby the top predator in an ecosystem influences the behaviour, community structure and/or density of species at lower trophic levels, and can ultimately influence entire ecosystem function (Bowyer *et al.*, 2005; Shen, 2011). There is typically only one apex predator within an ecosystem, but many mesopredators can occur within that ecosystem simultaneously (Wallach *et al.*, 2015a).

Mesopredators are predators that have an intermediate trophic ranking within the food web of the ecosystem in which they occur, relative to the apex predator (Ritchie *et al.*, 2012). There are no categorical size or body mass requirements for a species to be defined as a mesopredator, as this is context dependent; although they may be considered to have intermediate body size relative to the apex predator within the ecosystem. The role of a species as a mesopredator is context dependent (Chamberlain *et al.*, 2014; Haswell *et al.*, 2017), so classification should be based on the dynamics of individual food webs. Ritchie *et al.* (2012) argue that the functionality of a predator within an individual ecosystem should be emphasised, rather than other factors such as taxonomy or body mass, although these may be influential. It is widely accepted that mesopredators are therefore defined best through trophic dynamics, as a predator that occupies an intermediate trophic level of the food web in an ecosystem (Prugh *et al.*, 2009).

1.2.1 Landscape of Fear

The landscape of fear describes the impact that perceived predation risk from a predator has on the behaviour of a prey species, and subsequently, the surrounding environment (Laundré *et al.*, 2010; Wallach *et al.*, 2015b). Prey species can exhibit a behavioural response to the presence of predators, altering the way they use their environment to minimise the risk of

predation (Sönnichsen *et al.*, 2013; Lone *et al.*, 2014). This would be described as a spatial response, where prey species actively avoid areas that would increase their vulnerability to predation (Sih, 1984).

The reintroduction of grey wolves *(Canis lupus)* into Yellowstone National Park, is a well-documented example of this theory, showing the effects of perceived predation risk on the behaviour of a prey species, and the wider-reaching impacts on the environment (Laundré *et al.*, 2001; Fortin *et al.*, 2005). In the absence of grey wolves, following their extirpation from Yellowstone in the early 20th century, the population of elk *(Cervus canadensis)* increased significantly. With the reintroduction of wolves to the park in the 1990s, there was an immediate numerical response from the elk population, as they were predated upon by the wolves. However, a behavioural response was also observed, whereby the elk altered their habitat selection to reduce their predation risk (Mao *et al.*, 2005). This behavioural change initiated a trophic cascade, as ecological processes in Yellowstone changed (Fortin *et al.*, 2005). As the elk moved away from open areas of land where the risk of predation was highest, soil erosion began to decrease, allowing natural succession to occur, and influencing plant growth (Ripple and Beschta, 2003).

The landscape of fear theory does, however, focus on predator-prey relationships. There is less information in the literature regarding the interactions between apex predators and mesopredators, in the same context; for example, altering their habitat use to avoid predator interactions. Research from Yellowstone did show a behavioural response in coyotes *(Canis latrans)*, but this was not primarily a spatial response. Switalski (2003) showed that the reintroduction of wolves to Yellowstone National Park did have an impact on the behaviour of coyotes *(Canis latrans)*. Switalski (2003) documented coyotes being directly killed by wolves, but the reintroduction of wolves also altered the activity budgets of the coyotes. A wolf did not necessarily have to be present; if the coyote was in an area frequently used by wolves, this would elicit a behavioural response. The amount of vigilance behaviours increased, and resting time decreased. Switalski (2003) also commented that the behavioural changes exhibited by the coyotes in response to the reintroduction of the apex predator, could have cascading impacts on the ecosystem.

3.2.2 Apex Predator and Mesopredator Interactions

Interactions between apex predators and mesopredators can be costly; Switalski (2003) observed coyotes being killed by wolves following the reintroduction of the apex predator into

Yellowstone National Park. In Australia, dingoes *(Canis dingo)* have been observed killing introduced mesopredators such as the red fox *(Vulpes vulpes)* and the feral cat *(Felis catus)* (Letnic and Dworjanyn 2011). Mohammadi *et al.* (2017) recently observed one of the first instances of interspecific killing between a gray wolf *(Canis lupus pallipes)* and a golden jackal *(Canis aureus)* in Iran.

Interspecific killing describes the killing of one species by another, where the victim is not consumed (de Oliveira and Pereira, 2014). There are various reasons this may occur, such as territorial disputes, or minimising competition for resources, such as food and water (Shen, 2011). Interspecific killing can be symmetrical, where an interaction may result in the death of either species; or asymmetrical, where only one species is likely to be killed in the interaction (Palomares and Caro, 1999). Group size, age, sex, physical condition, body mass, prey abundance and resource availability are factors which may influence interspecific killing (Palomares and Caro, 1999).

Intraguild predation occurs when the predator that has been killed is subsequently consumed for energetic gain (de Oliveira and Pereira, 2014). Intraguild predation simultaneously reduces competition for resources, and provides energetic gain. This is more likely to occur when food resources are scarce, or are disputed (Polis *et al.*, 1989; Palomares and Caro, 1999). Examples of intraguild predation include red foxes and feral cats being consumed by dingoes in Australia (Letnic and Dworjanyn, 2011; Brook *et al.*, 2012), gray foxes *(Urocyon cinereoargenteus)* and bobcats *(Felis rufus)* being killed and consumed by coyotes in California (Fedriani *et al.*, 2000), and swift foxes *(Vulpes velox)* depredated by coyotes in Colorado (Thompson and Gese, 2007). Through interspecific killings and intraguild predation, apex predators can elicit a numerical response in the population of mesopredators (de Oliveira and Pereira, 2014). However, apex predators can also alter the spatial behaviour and activity patterns of mesopredators (Palomares and Caro, 1999).

Mesopredator suppression describes the regulation of the range, population or behaviour of a mesopredator, through the presence of an apex predator (Prugh *et al.*, 2009). The mesopredator release hypothesis describes the impact that removing an apex predator from an ecosystem will subsequently have on the range, population or behaviour of the mesopredator, where one or more of these factors were previously regulated by the presence of the apex predator (Ritchie and Johnson, 2009; Wallach *et al.*, 2015a). When one or more regulating factors are removed, there is potential for range expansion, rapid population increase, and behavioural change in the

mesopredator. A combination of these factors can decimate the prey species of the mesopredator, as increased food resources are required to sustain the artificially inflated mesopredator population (Prugh *et al.*, 2009). Mesopredator release increases predation pressure on lower trophic levels, whilst overall biodiversity can be reduced with a risk of local species extinction (Prugh *et al.*, 2009; Wallach *et al.*, 2015b). As well as the ecological impacts, mesopredator release can also have socioeconomic impacts on local communities (Prugh *et al.*, 2009).

<u>1.2.3 Case Study: Australia</u>

Understanding the principles of mesopredator suppression and release is important when making management decisions regarding predator control. Removal of an apex predator, such as the removal of dingoes around ranches and farmland in Australia, can have cascading impacts on lower trophic levels (Brook *et al.*, 2012).

The dingo is the largest terrestrial predator in Australia (Allen, 2012). Through their suppression of introduced mesopredators such as the red fox and feral cat, they protect Australia's native, and often endemic, biodiversity (Allen, 2012). However, dingoes are also considered to pose a threat to livestock, which leads to their persecution around ranches and farmland, as a method of mitigation to prevent or minimise livestock loss (Allen, 2012; Wallach *et al.*, 2017). In the absence of dingoes, populations of red foxes and feral cats become largely unregulated, resulting in increased predation pressure on prey species (Gordon *et al.*, 2015). Feral cats are generalist and opportunistic predators; with a varied diet consisting of birds, small mammals and marsupials, lizards, and invertebrates (Paltridge *et al.*, 1997). The red fox is also a generalist predator, sharing a similar prey base to the feral cat, but also depredating small to medium-sized macropods (Coates and Wright, 2003). The red fox reportedly depredates up to 77 native Australian species; ten of which are threatened species (Tasmanian Government, 2018).

The introduction of these mesopredators has already had a negative impact on Australia's native species. The desert rat-kangaroo *(Caloprymnus campestris)* is an example of a native species which has become extinct in Australia, due to predation pressure from introduced red foxes and feral cats (Woinarski and Burbidge, 2016a). Terrestrial species are most at risk, such as the endangered numbat *(Myrmecobius fasciatus)* and the vulnerable bilby *(Macrotis lagotis)*; both of which face decreasing population trends as a direct result of depredation from the red fox and feral cat (Woinarski and Burbidge, 2016b; Burbidge and Woinarski, 2016). Red

foxes have recently been observed for the first time in Australia climbing eucalyptus trees *(Eucalyptus spp.)* to hunt juvenile koalas *(Phascolarctos cinereus)* (Mella *et al.*, 2018), highlighting a possible risk to arboreal species too.

Research has shown, however, that in the presence of dingoes the population of red foxes and feral cats can be supressed; alleviating the pressure on prey species. Letnic and Koch (2010) showed that the abundance of the vulnerable dusky hopping-mouse *(Notomys fuscus)* decreased in the absence of dingoes; indicating that they benefit from the mesopredator suppression of red foxes and feral cats. It is evident within the literature that dingoes play an important role in structuring the mammal community within their ecosystems; and their interactions with mesopredators are important for overall ecosystem biodiversity (Letnic and Koch, 2010).

Based on this evidence, the introduction or management of apex predators can theoretically be used as a conservation tool, to control the density or alter the behaviour of mesopredators, and protect lower trophic levels from high predation pressure and overexploitation (Lentic and Dworjayn, 2011). This management technique could be important in ecosystems where a non-native mesopredator has been introduced, and endemic species have not developed efficient predator-defence mechanisms; or in ecosystems where the naturally occurring apex predator has been previously extirpated, and subsequently reintroduced.

1.2.4 Contrasting Evidence

While there is evidence that large carnivores are responsible for trophic cascades in other ecosystems, and their ecological importance and conservation priority is not contested (Ripple *et al.*, 2014), contrasting research exists which disagrees with case studies of dingoes in Australia, and wolves in Yellowstone National Park.

Although the use of dingoes to manage introduced mesopredators in Australia is discussed in the literature, Allen *et al.* (2011) has criticised many of these studies for their flawed methodology. Allen *et al.* (2011) reviewed studies that investigated the effects of dingoes on introduced mesopredators (i.e. the red fox and feral cat) and also on endemic threatened species, using track-based activity indices. It was concluded that 75% of the studies that were reviewed contained serious methodological weaknesses. These flaws include failing to account for seasonal variations in predator activity, and using binary observations where continuous observation would be more appropriate.

Fleming *et al*. (2012) outlined seven considerations that must be taken into account when managing mesopredator populations with dingoes, including the role that humans play within the environment as an apex predator. They state that managing dingoes to conserve biodiversity, whilst ignoring these seven factors, is likely to be unsuccessful and even counterproductive, with potential negative effects on overall ecosystem biodiversity. Fleming *et al*. (2012) emphasises the requirement for an adaptive management framework, to increase the likelihood of success.

There is also research that contests the reported impact of the reintroduction of wolves into Yellowstone National Park. Despite reports of increased vegetation growth, Marshall *et al.* (2013) reported that willow *(Salix spp.)* has not recovered within Yellowstone as previously stated. Marshall *et al.* (2013) showed that altering the browsing habits of elk alone was not sufficient to restore riparian vegetation to conditions prior to the extirpation of wolves from Yellowstone. They conclude that the reintroduction of wolves into Yellowstone was not capable of reversing the disturbance caused by their removal, with respect to riparian vegetation (Marshall *et al.*, 2013).

Middleton *et al.* (2013) states that long-term behaviour monitoring suggests that elk rarely alter their browsing patterns in response to wolves. The reintroduction of wolves may not be the only factor influencing elk populations. Other factors have contributed to the decline in elk populations which are not widely acknowledged; including human hunting, increasing bear populations and severe periods of drought (Middleton, 2014). Middleton *et al.* (2013) concludes that there is therefore not a clear link between the reintroduction of wolves and the reported ecosystem changes, such as the re-establishment of riparian vegetation or altered elk behaviour, although wolves do influence elk survival through direct depredation. This contrasting evidence does not disagree with the underlying theories behind the mesopredator release hypothesis or the landscape of fear, but instead states that the particular examples that have been discussed do not have enough evidence to support them. Further research considering these criticisms are therefore likely to be required, in order to validate these examples.

1.2.5 Occupancy Analysis in Conservation

Understanding the ways in which predators interact with one another, and with their environment, is important for making conservation decisions (Guisan *et al.*, 2013). Occupancy analysis is a valuable tool for ecologists, in that it can be used to interpret and understand the

distribution of a species, in relation to various factors such as habitat, and the presence of other species.

Occupancy describes the proportion of an area occupied by a species (Mackenzie *et al.*, 2006). Naïve occupancy can provide an estimate of species occupancy, where it has been detected at the site at least once. Naïve occupancy, however, does not consider the species detection probability.

Detectability describes the likelihood of encountering a species when it is present during a survey (Mackenzie et al 2006). Imperfect detectability occurs when the likelihood of encountering the species is less than 1. If a species is detected at a site, this means that the species occurs at that site, and the species has been detected by the researcher. If a species is not detected at a site, this can mean that either the species does not occur at that site, or the species does occur at that site, but was not detected by the researcher. Therefore, the non-detection of a species at a sample site does not necessarily mean that it is absent from that site, unless the probability of detection is 1 (MacKenzie *et al.*, 2002). Sites can therefore appear to be unoccupied, when the species is actually present, but has not been detected. Detection probability *(p)* describes the probability of detecting a species, if it is present in the environment. The detection probability for most mammal species is $p < 1$. If the detection probability is not accounted for, the species occupancy will likely be underestimated, creating a bias in the research results (Zylstra, 2009).

Occupancy analysis is a valuable tool for ecologists who are trying to understand the way species exist within their environments, and how they interact with other species, and various environmental factors. Conservation management decisions can be informed by occupancy analysis, as this is a more reliable method than working from invalidated indices of abundance (Hayward *et al.*, 2015). Indices of abundance rely on various assumptions being met. Mackenzie *et al.* (2006) state that as these assumptions are unlikely to be true, indices therefore have limited use, and estimates of abundance should consider detectability. Occupancy models produce estimates of occupancy, factoring in species detectability (MacKenzie *et al.*, 2002).

1.2.6 Study Area: Zambezi National Park, Zimbabwe

The Zambezi National Park (Figure 1), and adjacent Victoria Falls National Park, cover a total area of 56,000 hectares in Matabeleland North Province, in the western tip of Zimbabwe (Victoria Falls River Lodge, 2017). Victoria Falls, known locally as Mosi-oa-Tunya, is a UNESCO World Heritage Site, and is the world's largest sheet of falling water (UNESCO

World Heritage Centre, 2018). This protected area traverses Zambia and Zimbabwe; protecting 2340 hectares of Victoria Falls National Park, and 741 hectares of the Zambezi National Park, along the banks of the Zambezi River (UNESCO World Heritage Centre, 2018).
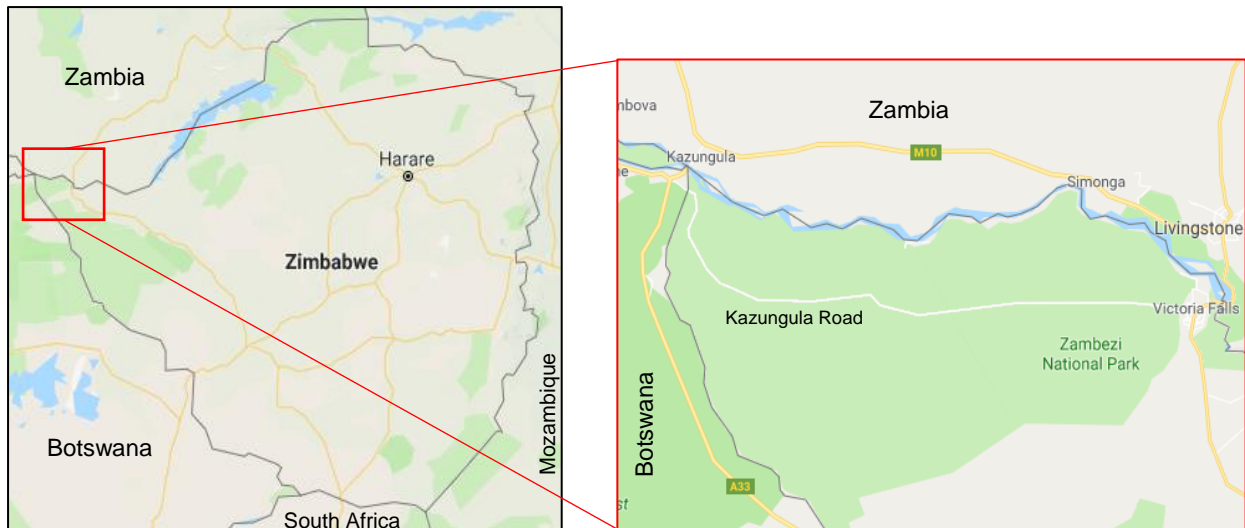
Figure 1. Zambezi National Park, Zimbabwe (Google Maps, 2018).

Zambezi National Park is divided into two distinct habitats by the Kazungula road that leads to the Zimbabwe/Botswana border (Victoria Falls River Lodge, 2017). The northern area of the park bordering the Zambezi River is comprised of riverine habitat and floodplains, with riverine shrubs and extensive open mopane *(Colophospermum mopane)* woodlands (Bhejane Trust, 2015). The remaining area of the national park, bisected by the Kazungula Road, is the Chamabonda Vlei (Bhejane Trust, 2015). The Chamabonda Vlei, in the southern area of the park, is characterised by large, open grass plains bordered by areas of Zambezian teak *(Baikiaea plurijuga)* woodland (Bhejane Trust, 2015; World Wildlife Fund, 2017).

The mopane woodlands within Zambezi NP are heavily coppiced, due to the browsing activities of African elephants *(Loxodonta africana)*. *Colophospermum mopane* is a primary component in the diet of African elephants here (Smallie and O'Connor, 2000), and their feeding habits result in stunted growth and occasional damage. Browsing by elephants can also cause the death of *C. mopane*; directly through uprooting, or indirectly through excessive browsing (Lewis, 1991).

The climate in Zimbabwe varies considerably according to altitude and topography. There is a rainfall gradient, decreasing from east to west across the country. Land at lower altitudes experiences higher temperatures and less rainfall (Nations Encyclopedia, 2018). The

westernmost tip of Zimbabwe, encompassing Zambezi NP, has a warm, semi-arid climate, experiencing temperature highs of up to 38°C in the summer months (Peel *et al.*, 2007).

African lion *(Panthera leo)*, spotted hyena *(Crocuta crocuta)* and black-backed jackal *(Canis mesomelas)* are regularly sighted in Zambezi NP. More elusive resident carnivores include leopard *(Panthera pardus)*, cheetah *(Acinonyx jubatus)* and the African wild dog *(Lycaon pictus)* (Peel and Peel, 2017). Herbivores such as the African elephant *(Loxodonta africana),* Burchell's zebra *(Equus quagga burchellii)*, greater kudu *(Tragelaphus strepsiceros)*, giraffe *(Giraffa camelopardalis)*, waterbuck *(Kobus ellipsiprymnus)*, impala *(Aepyceros melampus)* and Cape buffalo *(Syncerus caffer)* can all be found within the national park (Peel and Peel, 2017).

Zambezi National Park's expansive range and diverse species composition create an ideal research environment. The African Lion and Environmental Research Trust (ALERT) is an organisation in Zimbabwe, which has various ongoing research projects within Zambezi National Park. The main aim of ALERT is to facilitate and promote conservation and management plans for the African lion, and the ecosystems in which it occurs. Whilst the African lion is the focal species for a lot of the work that ALERT does, other species that coexist alongside the African lion are also studied. Research examining the coexistence of species within Africa's large predator guild is carried out by ALERT within Zambezi NP (African Lion and Environmental Research Trust, 2018).

ALERT engages in, and supports projects to: protect and restore habitat for lions, assess and monitor population size and health, mitigate the conflict between lions and communities, improve understanding of lion ecology and behaviour, and assist wildlife authorities to develop and implement appropriate policies to conserve lions (African Lion and Environmental Research Trust, 2018). ALERT also engages in activities that promote functional and diverse ecosystems, and incorporate inter-related ecological, social and economic issues.

The African Lion and Environmental Research Trust have been instrumental in their facilitation of this research work, and have shared their knowledge and resources to allow primary data collection to take place, addressing the aims and hypotheses of this research (1.3).

1.2.7 Threats to Africa's Predators

Africa supports the only intact large predator guild on the planet, and so represents the original state of apex predator – mesopredator interactions, compared to the simplified systems in the

America's or Australia, since the Pleistocene (Van Valkenburgh *et al.*, 2016). With each member of Africa's large predator guild threatened with varying levels of extinction pressure (Kissui, 2008; African Wildlife Foundation, 2017; IUCN, 2018), there is a need to understand the roles that each species has in interactions between guild members, to drive future conservation efforts. Occupancy analysis is crucial for ecologists to working to conserve Africa's large predators. It is important to have robust methods for measuring occupancy of a species, before conservation management decisions can be put in place.

1.2.8 Thesis Statement

This research aims to identify how the occupancy of apex predators influences the occupancy and spatial behavior of mesopredators within a landscape; specifically focusing on the community of predators in the Zambezi National Park ecosystem, in Zimbabwe, Africa. The wider implications of mesopredator spatial behavior will also be discussed, with respect to mesopredator suppression, and informing conservation management decisions.

1.3 Aims and Hypotheses

This aim of this research is to determine whether the presence of apex predators using a track or road, will elicit a micro-scale spatial response from mesopredators, using the same track or road. Data will be collected using camera traps, and occupancy analysis will be used to address the following hypotheses:

Hypothesis 1: Apex predator occupancy will be higher along tracks, whereas mesopredator occupancy will be higher in adjacent off-track habitat.

Hypothesis 2: Mesopredators will avoid areas frequently used by apex predators.

Hypothesis 3: Apex predators influence the spatial behavior of mesopredators.

1.4 Methods

<u>1.4.1 Data Collection</u>

Camera traps were used to collect data on the spatial behaviour and use of habitat features in apex predators and mesopredators, within Zambezi National Park, Zimbabwe. Data collection took place across June and July 2017, during the country's cool, dry season (Peel *et al.*, 2007). Data collection was observational only; no baiting occurred and there was no experimental manipulation.

The cameras were set out in a grid pattern, as shown in Figure 2, to enable systematic sampling. This layout was replicated at two independent sites, and each site comprised a total area of 12,000m^2 (Figure 2). Data collection using camera traps is non-invasive, and is not species-specific.
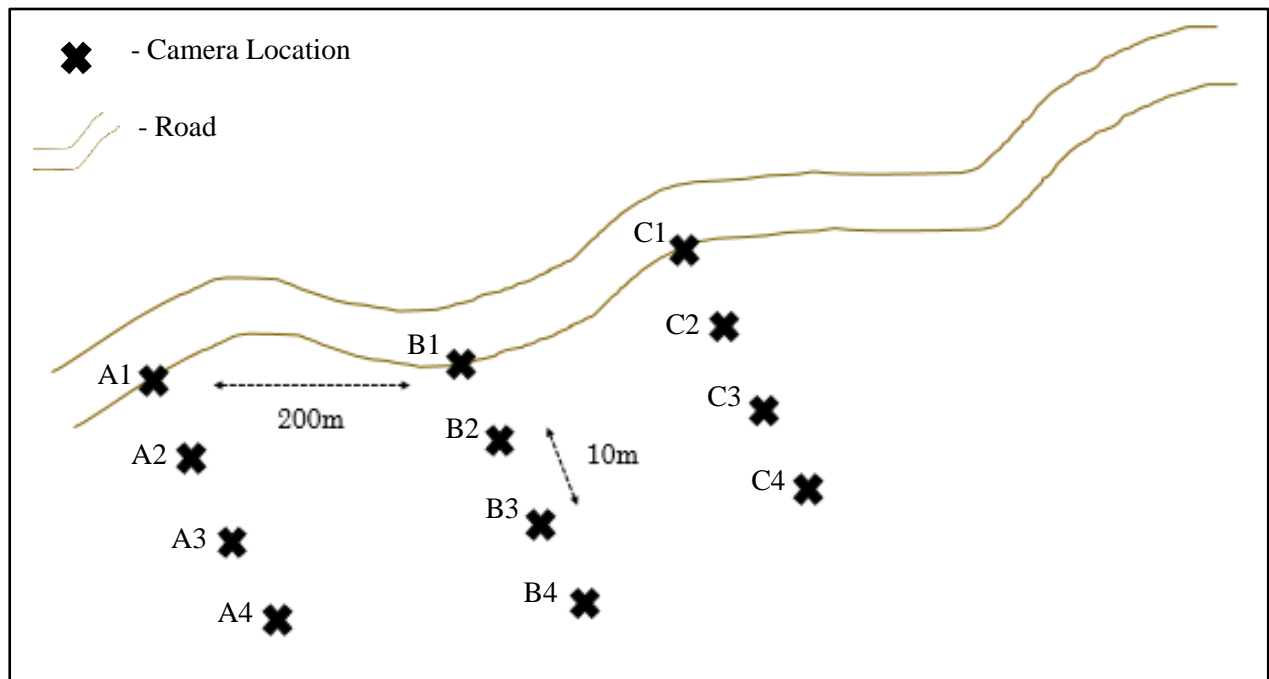
Figure 2. Layout of the camera traps along a road at each survey site. Each "X" represents an individual camera trap. The camera located on the road is 0m, and each camera is located at a 10m interval perpendicular to the road thereafter. This set up is replicated three times (A, B and C) along the road, at intervals of 200m. Each site comprised an area of 12,000m^2.

Reconyx HC500 HyperFire Semi-Covert Cameras (Reconyx, 2015) and UWAY VH400HD Trail Cameras (UWAY Outdoors Canada, 2015) were used.. The cameras were secured to vegetation using the Python Lock by Master Lock (Master Lock Company LLC, 2017), approximately 0.5m above ground level.

The cameras were active continuously for a ten-day period. They took a burst of three photos when triggered, and there was a 30 second quiet period between photo bursts and reactivation. The sites were surveyed consecutively, with a day in-between to allow for image retrieval and battery-charging. The spacing of cameras perpendicular to the road was measured with an open reel tape measure, whilst the odometer of the research vehicle was used to measure the distance along the road.

Two different camera models were used as these were the only available resources. The cameras were configured to the same capture and sensitivity settings. Both camera types are of similar size and shape, both have infrared capability and are equally camouflaged and non-obtrusive.

1.4.2 Study Sites

Two sites were selected to provide independent replicates of the data collected. Figure 3 shows the location of the study sites within Zambezi National Park. The sites were comparable in their expected species composition, as well as their distance from the Zambezi River. Appendix I shows a vegetation map of Zambezi National Park.

Figure 3. Location of data collection sites within Zambezi National Park. Markers represent the camera trap located on the road, at 0m.

Mopane *(Colophosphermum mopane)* scrub habitat was dominant across both sites (Figure 4a and 4b). The mopane shrub covering was denser at Site 1 (Figure 4a), and less dense at Site 2

(Figure 4b). Site 2 had larger areas of open scrub and grass. Site 1 was more accessible by road, and had a higher volume of traffic compared to Site 2.

Figure 4. Mopane *(Colophosphermum mopane)* scrub habitat present at Site 1 (a) and Site 2 (b). Site 2 (b) had a less dense mopane shrub covering, and more open, grassy areas.

As this research is focused on predators, there was a list of predetermined target species. The eleven target species are: African lion *(Panthera leo)*, African wild dog *(Lycaon pictus),* leopard *(Panthera pardus)*, cheetah *(Acinonyx jubatus)*, spotted hyena *(Crocuta crocuta)*, black-backed jackal *(Canis mesomelas)*, caracal *(Caracal caracal)*, serval *(Leptailurus serval)*, African wildcat *(Felis lybica)*, African civet *(Civettictis civetta)*, and large-spotted genet *(Genetta tigrina)*. All of these species have been recorded within the Zambezi National Park, although some are more frequently sighted than others (Mandinyenya, *pers. comm.*, 2017).

1.4.4 Data Analysis

The data was analysed using Program PRESENCE, to create occupancy estimates for each species, at each distance from the track (Program PRESENCE 2.12.26, 2019). This was replicated for both survey sites.

Program PRESENCE provides a naïve occupancy estimate, which shows the proportion of sites that were surveyed, where the focal species was detected at least once. The following equation can be used to calculate the naïve occupancy estimate:

Occupancy (Ψ) = x/y

Where x is the number of sightings of a species, and y is the total number of sighting periods.

Naïve occupancy does not, however, consider the detectability of the species. Occupancy modelling is more robust, as it acknowledges differential detectability, which may drive differences in occupancy, rather than a species simply being present or absent.

1.5 Results

African wild dog *(Lycaon pictus)* and leopard *(Panthera pardus)* were target species of this research, but were not detected by the camera traps; although tracks and spoor of both species had been identified near data collection sites. Cheetah *(Acinonyx jubatus)* was also a target species, however this species was not detected by camera traps, and there was no physical evidence to indicate their presence near the data collection sites at the time of data collection.

Eight of the 11 target predator species were therefore captured by the camera traps, moving along or adjacent to the track, during the data collection period. Camera trap images of the focal species can be found in Appendix II.

Species that were detected by the camera traps, but were not relevant to the aims of this research included: aardvark *(Orycteropus afer)*, Cape porcupine *(Hystrix africaeaustralis)*, impala *(Aepyceros melampus)*, greater kudu *(Tragelaphus strepsiceros)*, African elephant *(Loxodonta africana)*, giraffe *(Giraffa camelopardalis)*, Burchell's zebra *(Equus quagga burchellii)*, and warthog *(Phacochoerus africanus)*. See Appendix III for details of non-target species encounters.

A series of tables (1-4) and figures (5-7) summarise the results of the occupancy modelling carried out on the data collected from the first data collection site (Site 1) using Program PRESENCE (Program PRESENCE 2.12.26, 2019).

Each table shows the occupancy estimates for eight species of predators, on a track at a 0 metre distance, and then at 10 metre increments moving away from the track, up to a 30 metre distance. The naïve estimate shows the proportion of sites that were surveyed, where the species was detected at least once. Detectability describes the likelihood of encountering that species during a survey, if it is present at the site. Occupancy (Ψ) describes the proportion of an area occupied by a species, where the detectability of that species is accounted for (Mackenzie *et al.*, 2006). Standard error and 95% confidence intervals (95% CI) are also shown for each occupancy estimate.

Each figure shows a visual comparison between the naïve occupancy estimate for the species, and the observed occupancy (+1SE).

Table 1. Results of occupancy analysis from Program PRESENCE for eight predator species, on a track (0m) within Zambezi National Park, Zimbabwe (Site 1).

	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Spotted Hyena	0.3333	0.1683	0.3960	0.3461	0.0370	0.9179
Black-backed Jackal	0.3333	0.2903	0.3445	0.2824	0.0434	0.8591
Caracal	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Serval	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
African Wildcat	0.6667	0.3975	0.6709	0.2740	0.1519	0.9587
African Civet	0.3333	0.1683	0.3960	0.3461	0.0370	0.9179
Large-spotted Genet	0.3333	0.1683	0.3960	0.3461	0.0370	0.9179
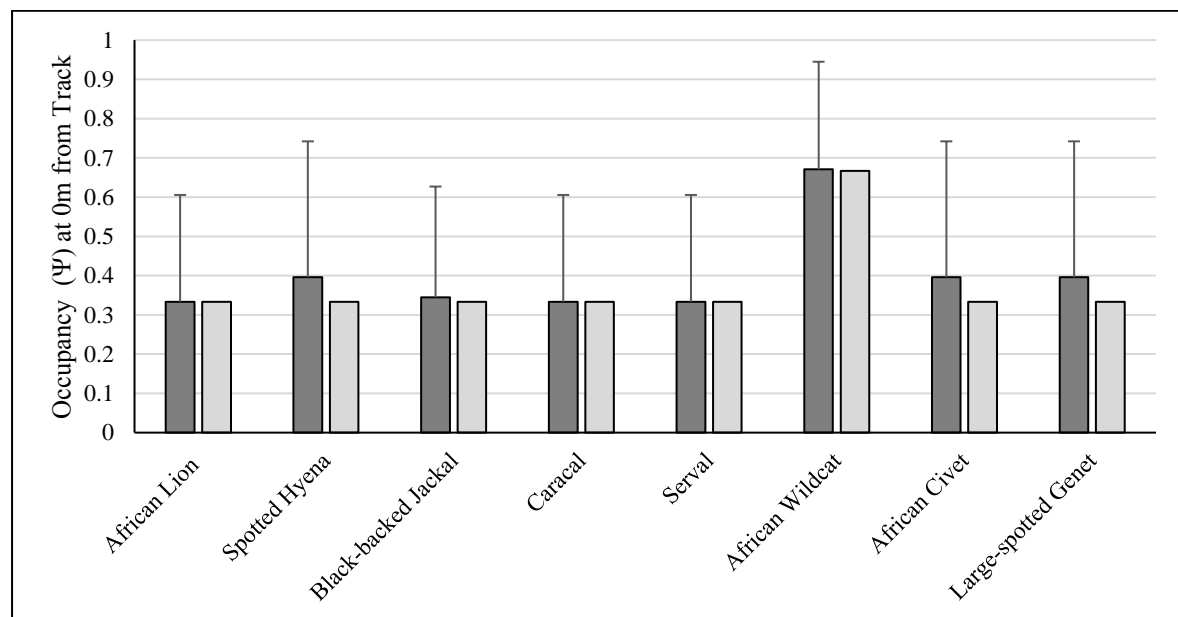
Figure 5. Modelled occupancy estimates (dark grey, +1SE) and naïve occupancy estimates (light grey), for eight predator species, along a track (0m) within Zambezi National Park, Zimbabwe (Site 1).

Table 2. Results of occupancy analysis from Program PRESENCE for eight predator species, 10m from a track, within Zambezi National Park, Zimbabwe (Site 1).

	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Spotted Hyena	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Black-backed Jackal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.3333	0.1683	0.3960	0.3461	0.0370	0.9179
African Civet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
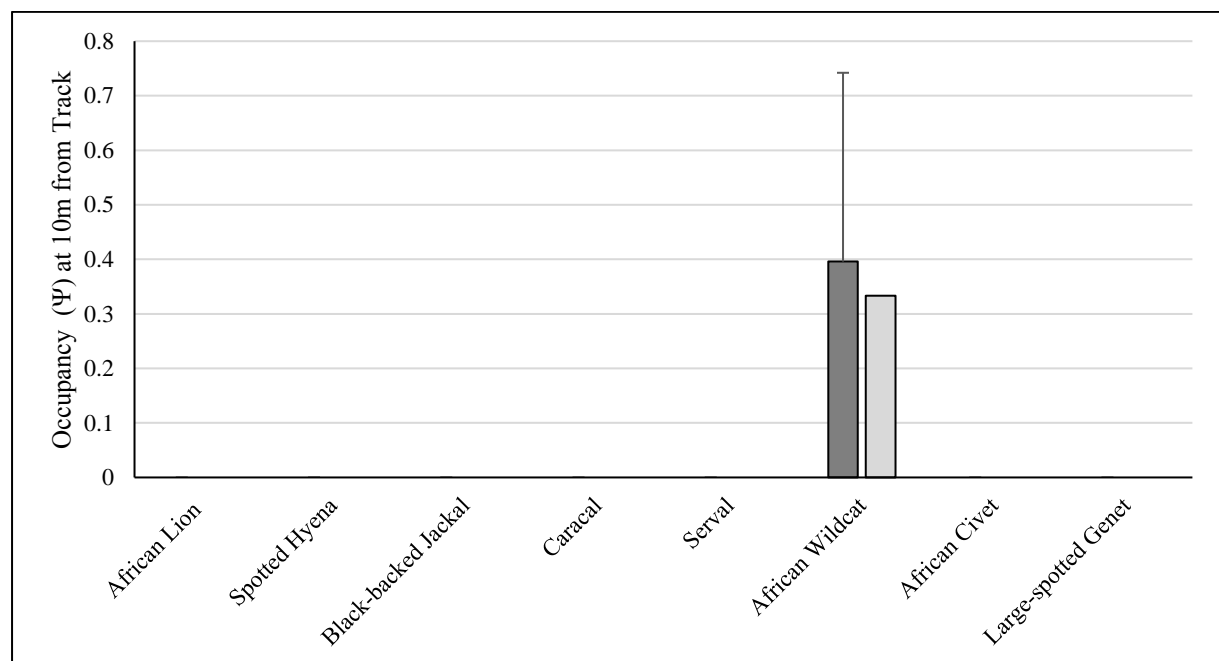
Figure 6. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, 10m from a track, within Zambezi National Park, Zimbabwe (Site 1). Note: The only predator species detected at this sampling point was the African wildcat.

Table 3. Results of occupancy analysis from Program PRESENCE for eight predator species, 20m from a track, within Zambezi National Park, Zimbabwe (Site 1). (No predators were detected at this sampling site during the study).

	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Spotted Hyena	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Black-backed Jackal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Civet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000

Table 4. Results of occupancy analysis from Program PRESENCE for eight predator species, 30m from a track, within Zambezi National Park, Zimbabwe (Site 1).

|	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Spotted Hyena	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Black-backed Jackal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.6667	0.1683	0.7920	0.3675	0.0458	0.9967
African Civet	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
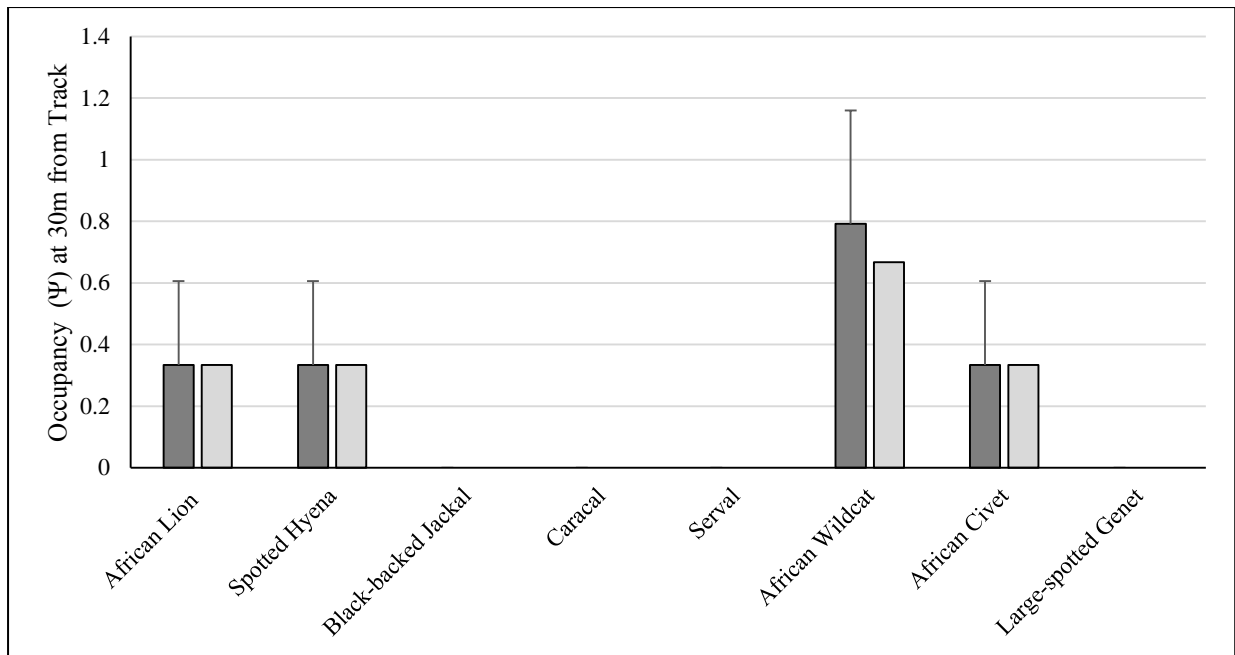
Figure 7. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, at 30m distance from a track within Zambezi National Park, Zimbabwe (Site 1).

The same occupancy analysis was carried out on the data collected from the second sampling site (Site 2). A series of tables (4-8) and figures (8-11) summarise the results of the occupancy modelling carried out on the data collect from the second data collection site (Site 2) using Program PRESENCE (Program PRESENCE 2.12.26, 2019).

Table 5. Results of occupancy analysis from Program PRESENCE for eight predator species, on a track (0m) within Zambezi National Park, Zimbabwe (Site 2).

|	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.3333	0.2903	0.3445	0.2824	0.0434	0.8591
Spotted Hyena	0.3333	0.4995	0.3337	0.2724	0.0434	0.8468
Black-backed Jackal	0.3333	0.5999	0.3334	0.2722	0.0434	0.8465
Caracal	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Serval	0.3333	0.2903	0.3445	0.2824	0.0434	0.8591
African Wildcat	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Civet	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Large-spotted Genet	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465

Figure 8. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, at 0m on a track within Zambezi National Park, Zimbabwe (Site 2).

Table 6. Results of occupancy analysis from Program PRESENCE for eight predator species, at 10m from a track, within Zambezi National Park, Zimbabwe (Site 2).

|	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Spotted Hyena	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Black-backed Jackal	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Civet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000

Figure 9. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, at 10m from a track within Zambezi National Park, Zimbabwe (Site 2).

Table 7. Results of occupancy analysis from Program PRESENCE for eight predator species, at 20m from a track, within Zambezi National Park, Zimbabwe (Site 2).

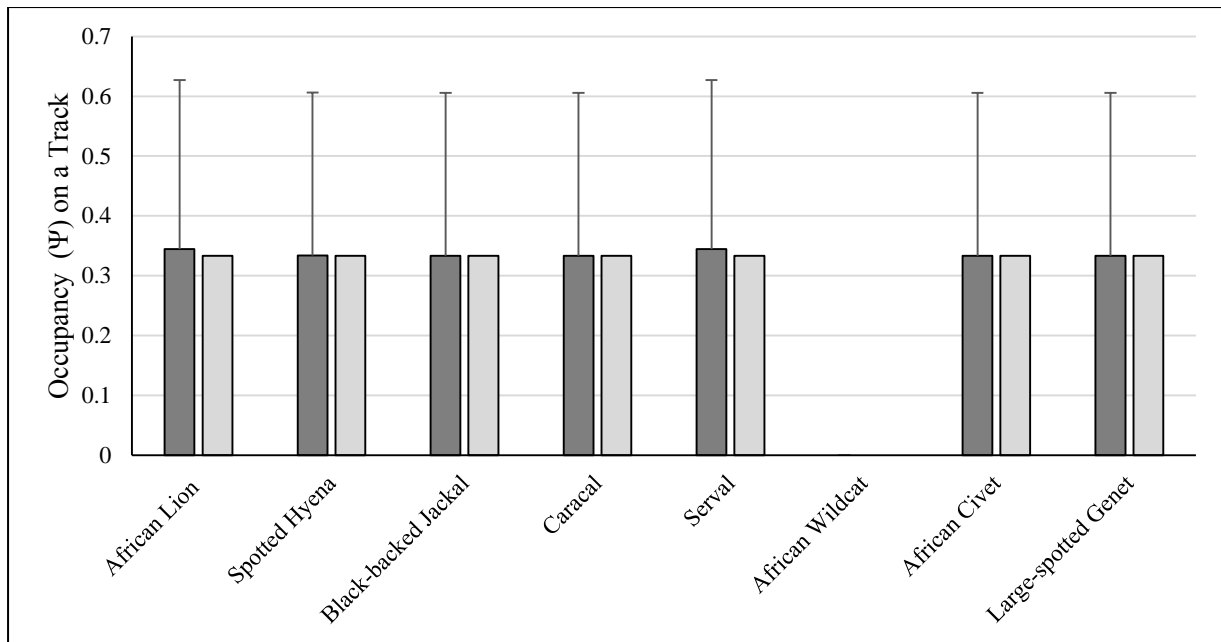|	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Spotted Hyena	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
Black-backed Jackal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Civet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000

Figure 10. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, at 20m from a track within Zambezi National Park, Zimbabwe (Site 2).

Table 8. Results of occupancy analysis from Program PRESENCE for eight predator species, at 30m from a track, within Zambezi National Park, Zimbabwe (Site 2).

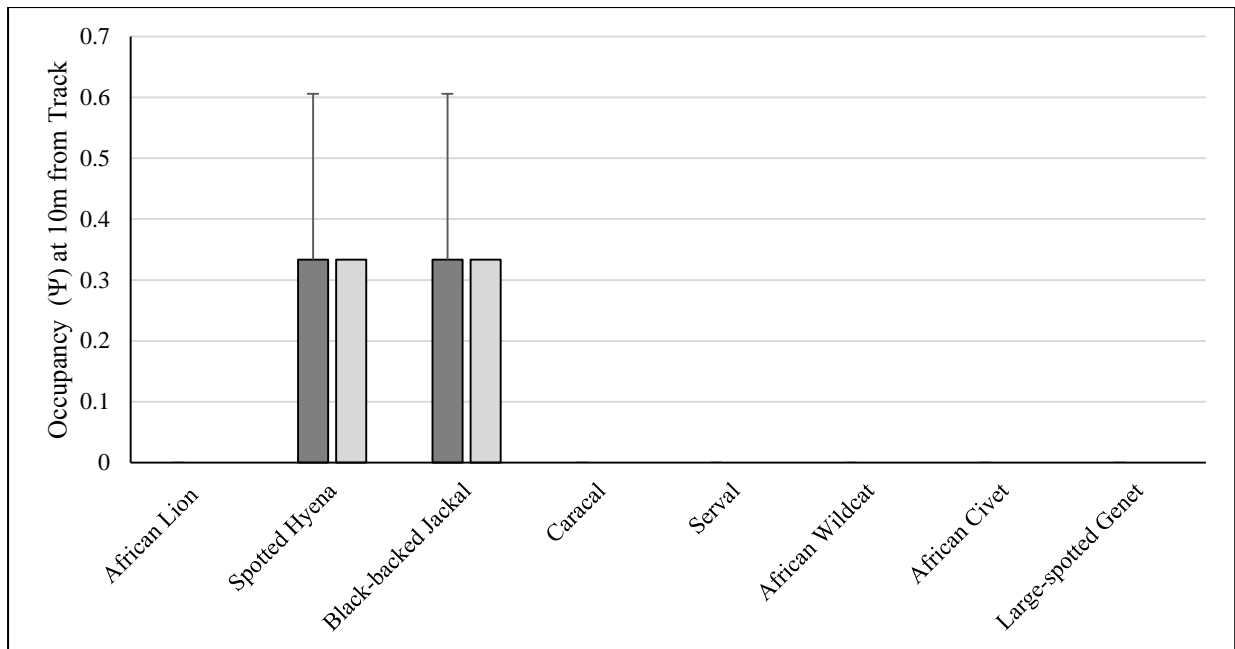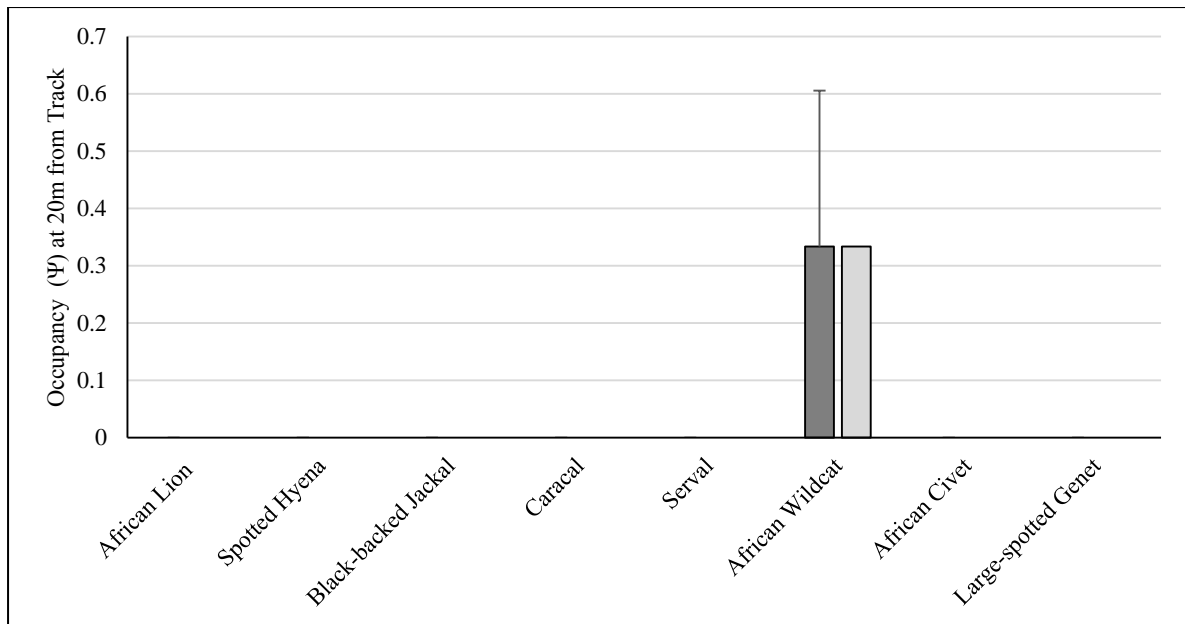|	Naïve Estimate	Detectability	Occupancy (Ψ/psi)	Standard Error	95% CI (Lower)	95% CI (Upper)
African Lion	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Spotted Hyena	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Black-backed Jackal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Caracal	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Serval	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
African Wildcat	0.3333	0.0333	0.3333	0.2722	0.0434	0.8465
African Civet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Large-spotted Genet	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
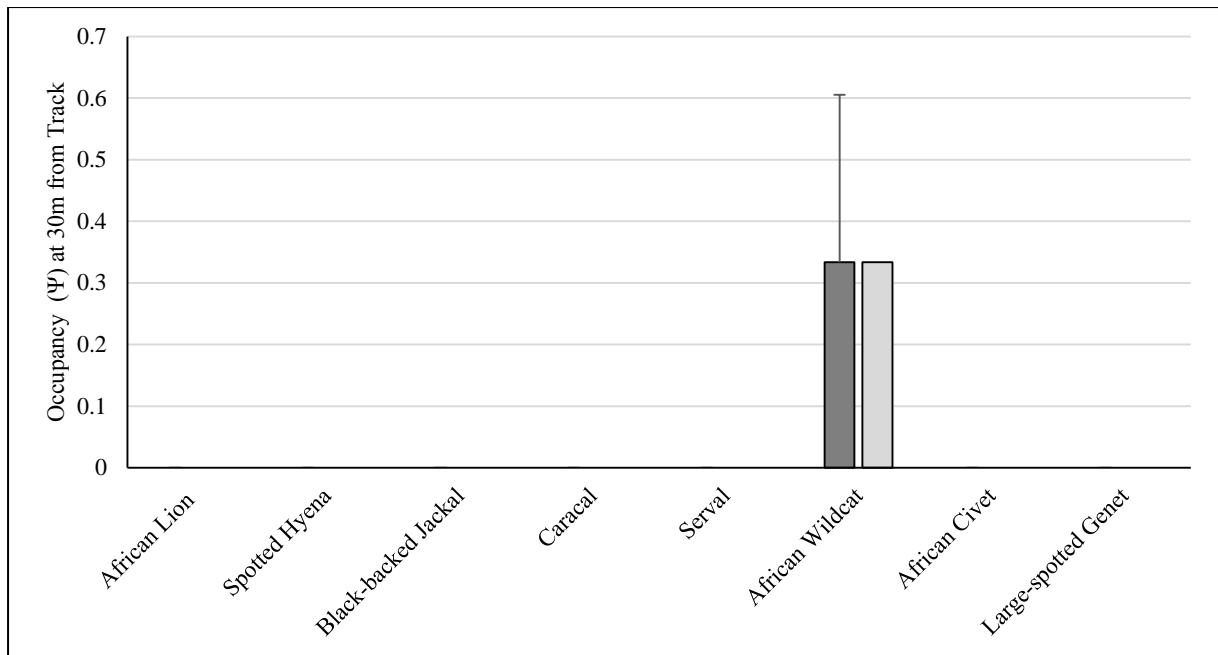
Figure 11. Modelled occupancy estimate (dark grey, +1SE) and naïve occupancy estimate (light grey), for eight predator species, at 30m from a track within Zambezi National Park, Zimbabwe (Site 2).

At Site 1, African wildcat showed the highest occupancy estimate at the 0m, 10m and 30m sampling points, with an occupancy of 0.6709, 0.3960, and 0.7920 respectively. No predator species were detected at the 20m sampling point.

At Site 2, African wildcat was absent from all but the 30m sampling point. African lion and serval both produced occupancy estimates of 0.3445 at the 0m sampling point. Spotted hyena and black-backed jackal produced equal occupancy estimates of 0.3333 at the 10m sampling point, and spotted hyena produced an estimate of 0.3333 at the 20m sampling point. African wildcat produced an estimate of 0.3333 at the 30m sampling point.

Site 2 appeared to have lower occupancy across all predators, compared to Site 1. Large herbivores, for example African Elephant, were much more numerous at Site 2 (100 detections) compared to Site 1 (4 detections) (Appendix III).

Across both sites, the total number of species detected was greatest at the 0m sampling point, and the frequency of each species was also greatest at the 0m sampling point.

1.6 Discussion

To support the hypotheses of this research, it would be expected that lion and hyena would show the highest occupancy at 0 m sampling points, with a negative gradient in occupancy towards the 30 m sampling point. The opposite would be expected of the smallest mesopredators; showing the highest occupancy at the 30 m sampling points, with a negative gradient in occupancy towards the 0 m sampling points.

Table 1 and Figure 5 show the occupancy estimates for eight predators sampled at a 0m point on a track at Site 1. Table 5 and Figure 8 show the same analysis for Site 2. Compared to the other measuring distances (10m, 20m and 30m) the on-track sampling point showed the greatest amount of species present at one location. The number of detections for each species was also greatest at the 0m sampling point. This data shows that tracks are attractive places to all species as a transport route through their habitat, and does not appear to show a clear preference for apex predators over mesopredators. The occupancy estimates for all species is generally greatest on the road at the 0 m sampling point (Figure 5, 8), indicating that this location produced the highest number of detections for all species. The occupancy estimates for all species are greatest at the 0m sampling point, and decrease or remain constant away from the road (Figures 5 – 11). This provides further evidence that the road is the preferred movement route for all species, regardless of whether they are an apex predator or mesopredator.

The data does not show that apex predators occupy on-track habitat (i.e. the 0 m sampling point) at a significantly higher level than mesopredators (Figures 5 - 11); but rather that both predator groups have a similar occupancy response within their environment. These results do not appear to align with the hypotheses of this research.

Detectability may vary between apex predator species and mesopredator species. Mesopredators are likely to be more numerous, and occur in greater densities, than apex predators (Carbone *et al.*, 1999). Mesopredators have a smaller body mass, and often have smaller territories and lower prey requirements, allowing more individuals to exist within the same area (Carbone *et al.*, 1999). Apex predators typically have a larger body mass, which requires greater energetic intake, necessitating a larger land area to support prey resources (Ordiz *et al.*, 2013). Mesopredators may also be more active and less elusive than apex predators, further increasing their detection probability. A combination of these factors mean

that apex predators occur at lower densities than mesopredators, and may also have a lower probability of detection (Duffy, 2003; Ordiz *et al.*, 2013).

Hypothesis 1 states that apex predator occupancy will be higher at the 0 m sampling point, whereas the occupancy of mesopredators will be highest at the sampling points further away from the road. This data shows that at all distances apart from the 20 m sampling point, mesopredator occupancy is greater, and at the 20 m sampling point, apex predator and mesopredator occupancy is equal.

There are several factors that may be responsible for the differences in occupancy between apex predators and mesopredators. Detectability varies enormously between species, and there are various factors that can affect the detectability of a species, beyond differences in abundance (Schlossberg *et al.*, 2018). Difficult habitats with overgrown vegetation, for example, may conceal the movement of smaller predators (Government of Saskatchewan, 2014). The time of year that data collection occurs may also need to be considered. If a target species give birth to young during a specific time period, or if habitat range changes due to resource availability, this may affect species detectability (Government of Saskatchewan, 2014). The time of day when data collection occurs can also affect the composition of species detected in a sample; influenced by diurnal, crepuscular, or nocturnal behaviour patterns. The use of camera traps that are continuously active and have infrared capabilities eliminate this factor from this research, although it is still important to consider. It is important to identify any factors, either environmental or in the research method, that may affect detectability, and account for those factors in the data analysis (Wilson *et al.*, 2011).

Only eight of the 11 target species were captured by camera traps during this study. The African wild dog, leopard and cheetah were absent from the data collected. Although these three species were absent within the data, they were sighted in and around the research location in the days and weeks following data collection (African Lion and Environmental Research Trust, *pers. comm.*, 2017). This indicates a false absence recording for these three species; whereby a species that may be elusive or scarce is incorrectly recorded as absent in a location, as it was not detected during the data collection period (Gotelli and Colwell, 2011). Imperfect detection creates a bias when the data is modelled, and therefore inferences from this data are unreliable (MacKenzie, 2005).

It is important to consider if there are other factors that may influence the spatial behaviour in apex or mesopredators. The body mass of each species is a potential factor that may influence

spatial behavior, and species avoidance (Carbone *et al.*, 1999). Whether a predator consumes small or large prey may influence the species that it is likely avoid or interact with (Carbone *et al.*, 1999; Owen-Smith and Mills, 2008). As an example, lion and hyena are more likely to have dietary niche overlapping (Hayward and Kerley, 2008), than a lion and a smaller mesopredator species such as the African wildcat. Hyenas are traditionally regarded as kleptoparasites, but they frequently hunt and kill their own prey (Kruuk, 1966; Trinkel, 2010). Hayward (2006) reports a 68.8% overlap in the preferred prey species of the spotted hyena and the lion. Whilst lions and hyenas both consume prey species such as gemsbok *(Oryx gaxella)*, wildebeest *(Connochaetes taurinus)*, buffalo *(Syncerus caffer)* and waterbuck *(Kobus ellipsiprymnus)* (Hayward, 2006), African wildcat diets comprise primarily of rodents such as hyraxes *(Procavia capensis)* (Palmer, 1988), as well as birds, reptiles and invertebrates (Herbst, 2010). A wildcat is physically incapable of killing the prey species that lions and hyenas predate on. As a wildcat is unlikely to compete with these larger predators for resources, it may be less likely to actively avoid them. This study found that African wildcats had one of the highest occupancy estimates at the 0 m sampling point (Table 1, Figure 5), and therefore frequently moved along the road. This could be interpreted as the wildcat not showing spatial avoidance.

Human presence may also influence the species that are detected during a sampling period (Barbet-Massin *et al.*, 2012). Repeating the data collection in various national parks with different levels of human disturbance, would provide evidence to investigate this theory further.

3.6.1 Discussion of Hypotheses

The first hypothesis states that apex predator occupancy will be higher along tracks, whereas mesopredator occupancy will be higher in adjacent off-track habitat. Occupancy analysis for the target species of this research provides no evidence to support this hypothesis. Occupancy analysis shows that occupancy is higher for all species along the track, and lower off-track. There is no strong support, based on this sampling effort at either site, to support this hypothesis.

Hypothesis 2 states that mesopredators will avoid areas frequently used by apex predators. Data from the camera traps showed that mesopredators, such as black-backed jackal and African wildcat, move through the same areas as apex predators, such as lion and hyena. These data did not show a measurable level of avoidance by mesopredators. Habitat portioning between apex predators and mesopredators in this environment may be temporal, rather than spatial; however further research and data analysis is required to provide empirical evidence to support this claim.

The final hypothesis of this research states that apex predators influence the spatial behaviour of mesopredators. There is evidence within the literature of the influence that apex predators have on mesopredators, and how spatial behaviour can be influenced (Mahon *et al.*, 1998; Switalski, 2003; Allen, 2012). The data from this research, however, has not been able to further substantiate this hypothesis. This data collection was carried out on a small scale and a restricted duration. Improving these aspects of data collection may yield results that align with results published in the literature. Both apex predators and mesopredators showed a similar response in occupancy at each distance.

1.7 Conclusions

The role of apex predators within an ecosystem is context dependent, and there are various influencing factors that may alter their impact. This research showed that all sampled predators exhibited higher levels of occupancy on the track, than in adjacent off-track habitat. This suggests that the track is the preferred route of travel for all species, whether they are an apex predator or mesopredator. This route offers the least resistance, compared to moving through thick or difficult bush and undergrowth habitats. Species will have less resistance using the track, so therefore it seems logical that they should travel along the track if possible.

The data collected during this research period did not support the hypotheses of the research. There was no evidence of mesopredators changing their spatial behaviour to avoid interacting with an apex predator; the data showed no spatial partitioning between apex predators and mesopredators. The data also showed no avoidance by mesopredators of areas frequently used by apex predators; these results show that apex predators and mesopredators frequently use the same tracks, although temporal habitat partitioning could be investigated during future research. The data showed that at the 0 m sampling point, which represents the track, mesopredator occupancy was greater than apex predator occupancy; therefore, providing no support for the hypothesis that apex predator occupancy is higher along tracks. The data also showed that occupancy estimates for every target species is greatest along a road, indicating that the road is the preferred movement route for all species, regardless of whether or not they are an apex predator or mesopredator.

This research has provided evidence that predators that are generally elusive and rarely seen, such as caracal and serval, are present within the Zambezi National Park. This information will be useful when making conservation decisions. Although the data collected did not provide support for the hypotheses of this research, the data will be useful as an educational and promotional tool. Evidence of species in the park that are not often encountered, may also be useful for informing management decisions, or developing responsible wildlife tourism. Camera trap images from this research have been shared with researchers working within the national park, and members of the local community.

1.7.1 Future Scope

This research has highlighted several areas that could either be improved, or could be examined further with future research. The most obvious improvement would be to repeat the data collection process, but extend the period of data collection. A larger dataset is more likely to produce more accurate occupancy estimates, and give a more detailed idea of the interactions within that environment . This could be more likely to provide conclusive evidence to support or reject the hypotheses of the research. Evidence-based conservation decisions are crucial in conservation management decisions, and a larger dataset is essential to providing this evidence.

As an observation of the data, it appears that smaller mesopredators, such as African wildcat, were less influenced by the presence or movement of apex predators, such as lion or hyena, compared to relatively larger mesopredators, such as jackal. This may indicate that mesopredators further away from the mean body mass of an apex predator, who are potentially less competitive for shared resources, are less likely to avoid the apex predator. Further and more detailed research may also look for overlaps in diet or prey preference; predators with a similar prey base, which are more likely to be in direct competition with one another over a limited resource, may have a greater chance of conflict, and therefore may be more likely to actively avoid one another. The average body mass of the apex predators and mesopredators within the environment could be ranked and compared, and used to identify species which are most likely to avoid one another, based on potential for competition or conflict. The bodyweight ranges of the target species in this research, categorized by sex, are available in Appendix V.

Recording and modelling the occupancy of prey species would also be beneficial, as predator occupancy could be compared to prey species occupancy. This could provide information on why a predator is moving through a certain habitat, or if the occupancy of predator and prey or dependent on one another, and in which direction.

Another factor that could be investigated further is the habitat preferences of each species. Factors other than the presence of an apex predator, such as habitat preference for example, may influence whether a mesopredator moves along a track, or in the adjacent bush.

The human influence on predator behavior is another potential influencing factor that should not be overlooked. There is evidence that the spatial behaviour of meopredators is influenced by the presence of humans, and human development of the landscape, as well as the presence of larger, apex predators (Wang *et al.*, 2015). Recording human land-use patterns within

Zambezi National Park, and comparing this with the spatial movements of predators within the same area, may be insightful. This could lead to further investigation into whether the level of disturbance in a national park affects the spatial behaviour of predators, and whether predators from different parks use their environments differently. Kruger National Park is one of the most visited parks in Africa, and receives approximately 950,000 visitors annually (Siyabona Africa, 2017). Zambezi National Park is also a popular tourist destination, but on a much smaller scale – although an official figure of annual visitors has not been released from Zimbabwe Parks and Wildlife Management Authority. Research could establish if road-use patterns of apex predators and mesopredators differ in areas that have a high level of disturbance and human presence.

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1.9 Appendix

Vegetation map of Zambezi National Park, Zimbabwe. Reproduced with express permission from Bob Mandinyenya (Principal Researcher, African Lion and Environmental Trust, 2017).
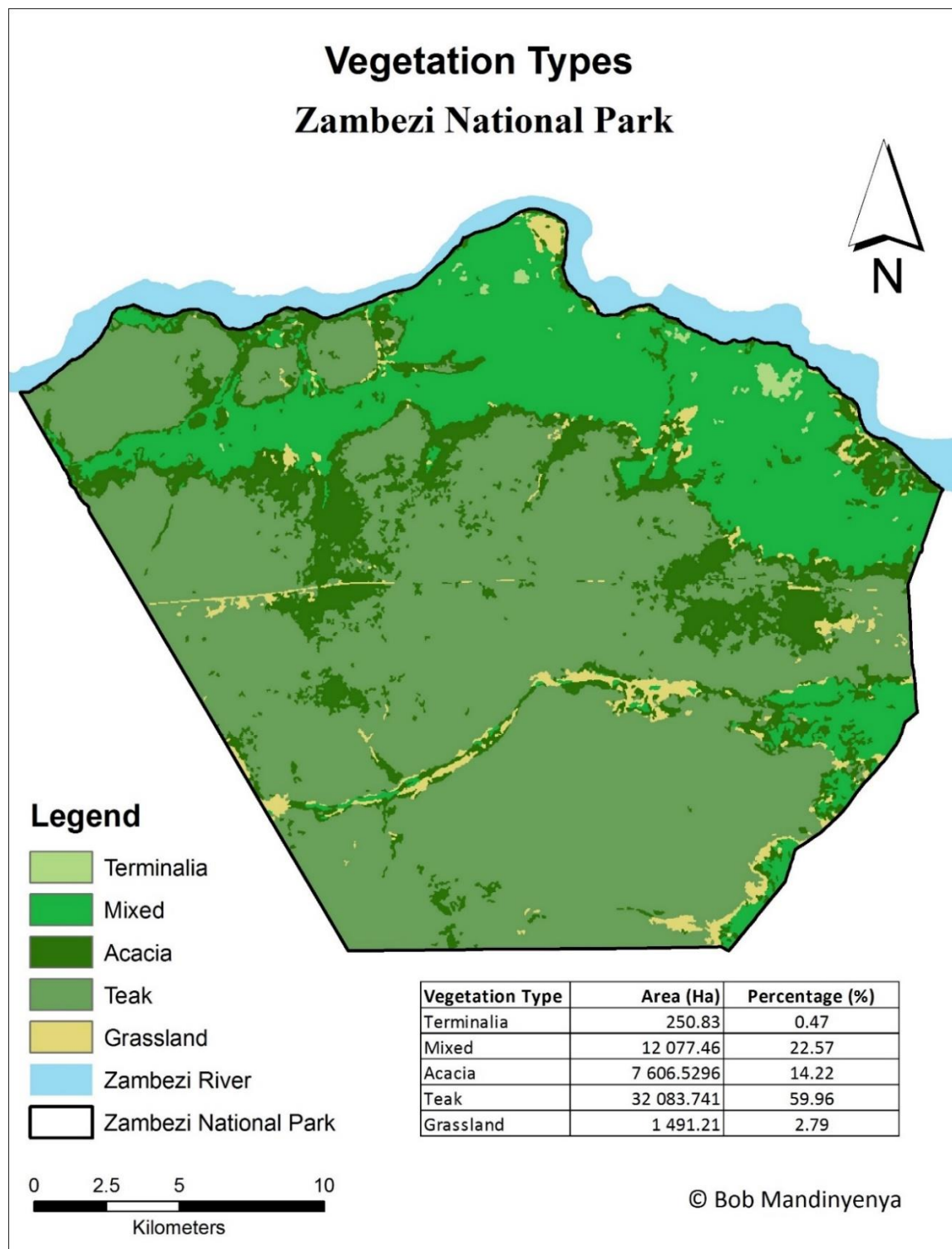
A selection of target species, captured by camera traps during primary data collection, within Zambezi National Park, Zimbabwe. June/July 2017.

African Lion *(Panthera leo)*

Caracal *(Caracal caracal)*

Spotted Hyena *(Crocuta crocuta)*

Large-spotted Genet *(Genetta tigrina)*

Large-spotted Genet *(Genetta tigrina)*

African Wildcat *(Felis silvestris lybica)*

African Civet *(Civettictis civetta)*

Black-backed Jackal *(Canis mesomelas)*

Serval *(Leptailurus serval)*

Appendix III.

A. Number of detections of all species at Site 1 across 120 camera trap nights, within Zambezi National Park, Zimbabwe.

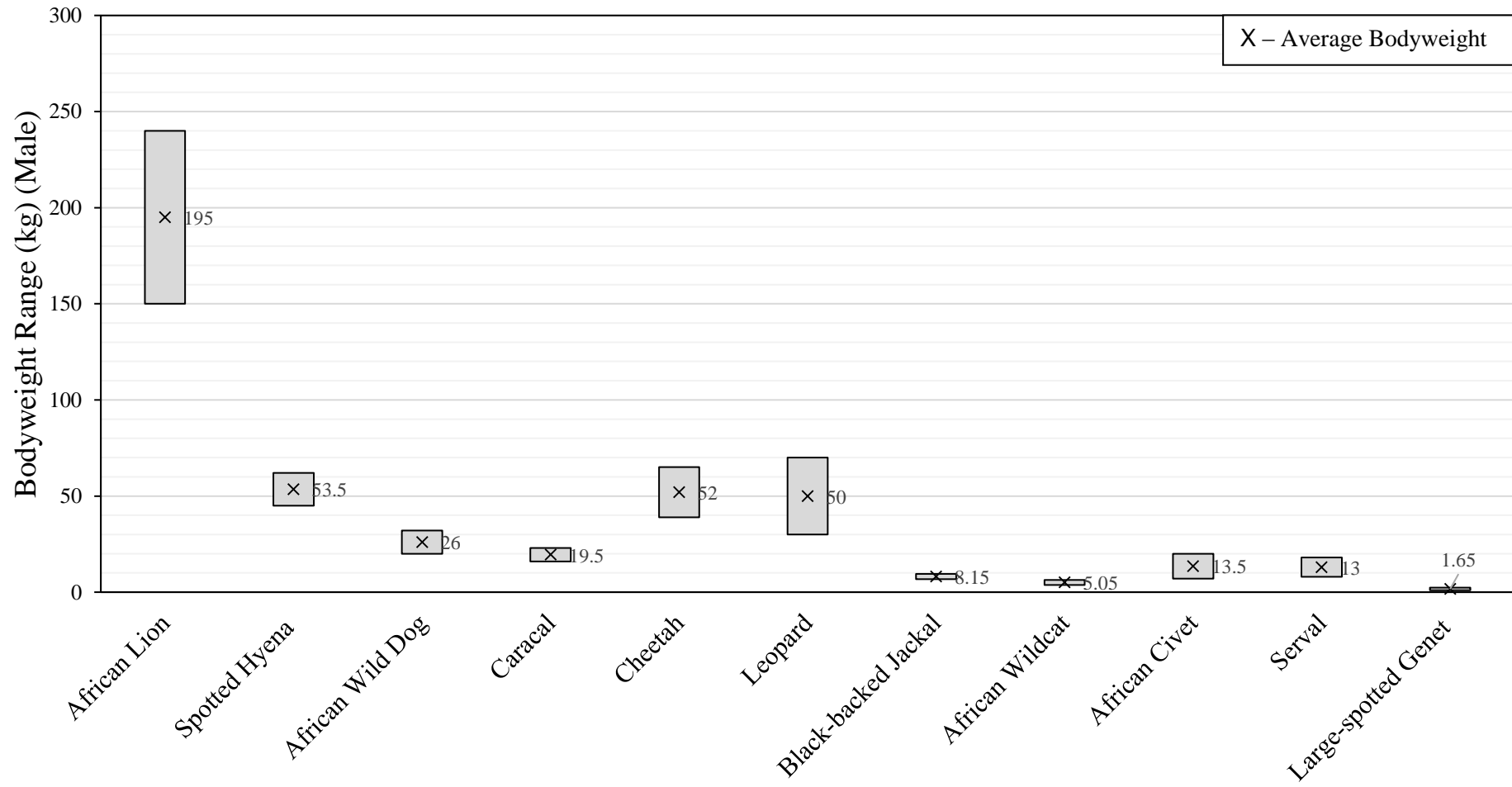| Species	Number of Detections
African Lion *(Panthera leo)*	3
Spotted Hyena *(Crocuta crocuta)*	3
Black-backed Jackal *(Canis mesomelas)*	6
African Wildcat *(Felis silvestris lybica)*	22
Caracal *(Caracal caracal)*	1
African Civet *(Civettictis civetta)*	4
Large-spotted Genet *(Genetta tigrina)*	2
Serval *(Leptailurus serval)*	1
Greater Kudu *(Tragelaphus strepsiceros)*	11
African Elephant *(Loxodonta africana)*	4
Giraffe *(Giraffa camelopardalis)*	6
Burchell's Zebra *(Equus quagga burchellii)*	2
Aardvark *(Orycteropus afer)*	1
Cape Porcupine *(Hystrix africaeaustralis)*	5
Warthog *(Phacochoerus africanus)*	7
Swainson's Spurfowl *(Pternistis swainsonii)*	1
Red-crested Korhaan *(Lophotis ruficrista)*	1
Helmeted Guinea Fowl *(Numida meleagris)*	2

B. Number of detections of all species at Site 2 across 120 camera trap nights, within Zambezi National Park, Zimbabwe.

Species	Number of Detections
African Lion *(Panthera leo)*	4
Spotted Hyena *(Crocuta crocuta)*	8
Black-backed Jackal *(Canis mesomelas)*	10
Caracal *(Caracal caracal)*	1
Serval *(Leptailurus serval)*	3

African Civet *(Civettictis civetta)*	2
Large-spotted Genet *(Genetta tigrina)*	1
African Wildcat *(Felis silvestris lybica)*	2
Elephant *(Loxodonta africana)*	100
Burchell's Zebra *(Equus quagga burchellii)*	11
Impala *(Aepyceros melampus)*	5
Greater Kudu *(Tragelaphus strepsiceros)*	14
Giraffe *(Giraffa camelopardalis)*	9
Warthog *(Phacochoerus africanus)*	5
Chacma Baboon *(Papio ursinus)*	2
Cape Porcupine *(Hystrix africaeaustralis)*	4
Helmeted Guinea Fowl *(Numida meleagris)*	2
Red-billed Hornbill *(Tockus erythrorhynchus)*	1
Swainson's Spurfowl *(Pternistis swainsonii)*	1
Magpie Shrike *(Urolestes melanoleucus)*	1

A. Male bodyweight range (kg) for the target species of this research. X represents average bodyweight (Macdonald, 2006; Encyclopedia of Life, 2011).

B. Female bodyweight range (kg) for the target species of this research. X represents average bodyweight (Macdonald, 2006; Encyclopedia of Life, 2011).