Final Year Project Report

University of Brighton 2019

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Using Camera Trapping to Assess the Influence of Habitat, Prey and Competitors on African Leopard Occurrence.

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A Research Article: Journal Style: **Biological Conservation**. Author's guidelines can be found at: https://www.elsevier.com/journals/biological-conservation/00063207/guide-for-authors

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Glossary of acronyms and Abbreviations

CITES	Convention on International Trade in Endangered Wildlife
IUCN	International Union for the Conservation of Nature
KNP	Kruger National Park
KWS	Kenya Wildlife Service
MC	Mara Conservancy
MMNR	Maasai Mara National Reserve
NACOSTI	National Council for Science and Technology

Abstract

The African leopard (*Panthera pardus*) has lost over half of its former range in recent decades, with national parks and reserves maintaining vital source populations, particularly in East Africa. Protected areas are increasingly acting as critical refugia for wildlife, serving as protection for extensive ecological processes and ecosystem functions. Due to increasing human encroachment into the remaining habitat of large predators, there is an urgent need to understand the underlying processes which drive co-occurrence among apex predators. Camera traps are increasingly being used to determine relationships between sympatric mammals and environmental characteristics, often with a view to inferring interspecific interactions. In this context, this study aimed to investigate the environmental factors influencing leopard occurrence from photographic data collected across 34 camera stations, over a single season, in the Masai Mara National Reserve, Kenya. Logistic regression modelling indicated that leopard occurrence was significantly influenced by the presence of spotted hyeanas (*Crocuta crocuta*) (Wald χ^2 (1) = 6.526, p = 0.011). These findings suggest that lion presence, prey, and habitat did not have a strong influence on the occurrence of leopards. Lions (*Panthera leo*) and hyeanas pose a threat to individual leopards, yet, relatively little is known of the processes facilitating co-occurrence between carnivore guild members, particularly leopards. Further research should investigate how resilient leopards are to the effects of intra-guild competition, particularly in areas used intensively by leopards and hyeanas. Understanding intra-guild interactions is key to conserving one of last intact carnivore guilds in the world, within the boundaries of one of Africa's most outstanding protected areas.

Keywords: camera trapping, leopard, spotted hyeana, protected area, co-occurrence

1. Introduction

1.1. Protected areas

Protected areas, such as national parks and game reserves, serve as crucial safe havens for large predators and, in so doing, provide protection for ecological processes and ecosystem functions (1, 2). However, increasing human activities beyond park boundaries drives their fragmentation (3), creating mosaics of small and isolated protected areas ineffective for conserving wide-ranging large mammal species (4, 5). Further, land use change beyond protected area boundaries can negatively impact immigration/emigration rates (6, 7), restricting the genetic diversity of animal populations (8), and ultimately population dynamics (6). For instance, agricultural expansion may restrict a number of predators to smaller areas of protected land. This limits spatial partitioning between competitors, driving more overlap than may have previously existed (9). Understanding the consequences of this is vital because competition can influence distribution, species' densities, and reproductive success (10). Thus, where the dynamics of competitor encounters change, protected populations may be placed at risk of extinction (11, 12). In Africa, where human population growth has intensified habitat conversion and the fragmentation of protected areas, these issues are particularly apparent (3). As a Consequence, large predator populations have declined by almost 60 % during the past four decades (7, 13).

The African leopard exists within a complete predator assemblage, within which interspecific competition is fierce. As such, the leopard serves as a valuable ecological case study on the question of how competitors might coexist under conditions of forced proximity (14). Until recently, leopards were assumed to be resilient to interspecific competition and, consequently, have been omitted from research that is focused on interspecific competition (15). However, evidence now suggests that dominant competitors – such as lions do in fact pose a threat to leopards (16, 17). Enforced proximity with dominant competitors could influence leopard behaviour and impact reproductive success. Their survival is important from an ecological perspective because intact predator assemblages are essential for optimal ecosystem function (18).

Protected areas may be key to the leopards' survival because outside of these areas they suffer higher mortality rates (19). Therefore, it is important to understand the factors that enable coexistence between leopards and their competitors inside protected areas (9). Beyond caching their prey in trees, not much is known about the mechanisms that facilitate co-occurrence between the leopard and its competitors (20, 21).

1.2. Importance of apex predators as ecosystem engineers

Large predators play a vital role in regulating and structuring ecosystems (22, 23). The strength and nature of their impacts are influenced by various factors, including body size, metabolic needs, density, sociability and hunting strategies. Larger predators tend to have increased energetic limitations, longer lifespans and low population densities, and roam extensively in search of larger prey (24, 25). As a consequence, these biological characteristics lead them into direct conflict with humans and livestock, placing them at greater risk of persecution (23), and ultimately local extirpation (26).

Despite existing at low densities large predators can still exert ecological effects (27), however persecution may influence their ecological role and impact their social structure and stability (28). Typically, the impacts of large predators are known to extend down through the food chain to herbivores and plants, but it is becoming increasingly evident that their influences spread broadly to other species facilitated by their regulatory effects on mesopredators (29, 30). Large predators have the dual function of regulating herbivores through predation and mesopredators through interspecific competition and, consequently, structuring ecosystems along numerous food-chain pathways. Combined, these effects influence the strength and nature of ecosystem function. Thus, the conservation of large carnivores is particularly important, both because of their vulnerability to extinction and for their role in the structure, function and stability of the ecosystem (23, 29).

Leopards are one of several large predators associated with recognised trophic cascades and are known to have a cascading influence on ecosystems and ecological communities (23). Indeed, where leopards and lions occur sympatrically they exert control on mesopredators. For example, an increase in the abundance of baboons (*Papio anubis*) in West Africa, was linked with declines in these predators relative to other explanatory environmental factors that might explain range use and abundance of baboons. This is important because among large mammals baboons pose a significant threat to crops and livestock. Indeed, in certain areas it is common for children to be kept out of school to protect crops from baboon raids (23).

1.3. Conservation status of the African leopard

The leopard's ability to adapt to changing environments and to varying habitats, has enabled them to survive in regions where other large felids have been eradicated, or severely isolated (31, 32). However, this adaptability has not habituated the leopard against all levels of threat (33). Leopards, like many large carnivores that are in decline (34), face a number of significant and ongoing threats, which aside from habitat loss and prey base depletion, include human-leopard conflict, poaching for skins and body parts, unregulated trophy hunting and retaliatory killing (35-40).

The leopard is a solitary and reclusive felid that despite being one of Africa's most widespread large cats, have lost between 63 – 75 % of their historical range (41) (Table 1). Following a recent up listing, the International Union for the Conservation of Nature (IUCN) and the Convention of International Trade in Endangered Species (CITES), classify the leopard as Vulnerable (33, 42). The IUCN recognises nine subspecies (43, 44) (Table 1).

Robust population estimates and demographics and a greater understanding of the threats facing the leopard requires more research (33). With the exception of the Phinda Game Reserve, South Africa (45), long-term data on leopard populations is almost entirely absent (33). While the leopard attract considerable interest from researchers and conservationists, some regions and subspecies are studied with greater intensity than others, thus more comprehensive research efforts should be prioritised (33).

Table 1. IUCN classification and range estimates for leopard subspecies. Subspecies are listed in order of least extant range to most. Values in bold indicate greatest threat. Source: Jacobson et al., (33)

Panthera pardus subspecies	Common name	IUCN classification	% Range loss	% remaining range
Panthera pardus orientalis	Amur leopard	Critically Endangered	**97 - 98**	< 5
P.p. nimr	Arabian leopard	Critically Endangered	**98**	< 5
P.p. melas	Javan leopard	Critically Endangered	84	< 5
P.p. kotiya	Sri Lankan leopard	Endangered	63	< 5
P.p. japonensis	Chinese leopard	Near Threatened	**96 – 98**	< 5
P.p. delacouri	Indochinese leopard	Near Threatened	**93 – 96**	
P.p. saxicolor	Persian leopard	Endangered	72 – 84	10 – 15
P.p fusca	Indian leopard	Vulnerable	70 - 72	< 5
P.p. pardus	African leopard	Vulnerable	63 – 75	**15 - 20**

1.4. The African predator guild

Wilson (176) defines a species guild as a collection of species, within a community, that compete for the same resources. The African large predator guild (hereafter, large predator guild) embodies the last intact guild of large predators (14) and includes the lion, leopard, cheetah, (*Acinonyx jubatus*) spotted hyeana and the African wild dog (*Lycoan pictus)* (14, 46). The predator guild is characterised by intense intra-guild competition, which has implications for the life history traits, use of space, and activity budgets of co-occurring species (24, 46, 47).

The Leopard is a mid-sized member of the large predator guild, while smaller than lions and hyeanas, they have on average, a greater body mass than both cheetahs and wild dogs (48). However, when considering that the combined body mass of a pack of wild dogs provides a distinct competitive advantage, it is likely that the leopard, out of all guild members, is competitively superior only to the cheetah (48).

Leopards are known to exhibit high levels of dietary overlap, home range and habitat preference with the other members of the predator guild, suggesting that potential competition for resources is likely to be high (48, 49). Indeed, Balme et al. (17) found that in certain areas lions and hyeanas together, were the highest cause of mortality for leopard cubs. Leopard and lion interactions have been relatively well studied (16, 50), at population level, within productive habitats, leopards are not affected by intra-guild competition with lions (50-52), whilst, at the habitat-scale, competitor risk is shown to influence leopard behaviour and space use. For instance, leopards are known to be highly susceptible to losing their prey to competitors, particularly by spotted hyeanas (49), and thus caching their prey within trees has been strongly linked to kleptoparasitism-avoidance (20, 53). Furthermore, when lions are nearby leopards move into denser habitat (16), they are more likely to avoid areas recently occupied by lions (54) and they become more vigilant when perceiving lions to be nearby (9).

1.5. Habitat and prey preferences of the African leopard

Landscape characteristics and prey abundance appear to be the causal factors driving resource selection in large predators (55, 56). A predator's choice of feeding habitat may simply be ruled by where the prey abundance is highest (prey abundance hypothesis) (57), or alternatively, where prey is easier to catch (landscape hypothesis). In the Serengeti Hopcraft et al. (57) found that lions selected areas with good cover in which to hunt rather than areas where prey were more abundant. Lion's improved their hunting success by making use of fine-scale landscape features (e.g. eroded areas, thick vegetation and drainage lines), they also spent less time in short grass than expected. Wolves (*Canis lupis*) have also been found to favour habitat where it was easier to kill prey. However, in this case, wolves selected habitat where prey detectability and encounter rates were higher, rather than providing greater cover (58). Balme, Hunter and Slowtow (56) found that leopards in the Phinda Private Game Reserve, South Africa, selected areas where prey was easier to catch rather than where prey was more abundant, and habitats with intermediate cover were favoured for hunting. In these studies habitat covariates that enhanced prey vulnerability to predation were attributed to the results. Landscape features differed within selected habitats according to the preferred hunting techniques of the predators (56).

However, other studies have found that feeding habitats are selected according to prey abundance by some predators (59-64). In these cases, predators simply hunted in areas where prey was more abundant, and ‘catchability’ was not significantly influenced by the landscape. Hayward and Kerley (151) outlined the theory behind both hypotheses; predators should choose to hunt in habitats where energy needs can be met with minimum energy expenditure, and that pose the least risk. The prevailing factor driving decisions on where to hunt is likely to be prey catchability or abundance (or a combination of both), depending on the payoff realised by the predator.

Leopards tolerate a wide range of habitats (65), ranging from tropical forests, alpine mountains, semi deserts, to grassland regions (33, 66), they may also persist near major cities (67). The leopard is the most widespread of all large felids, occurring throughout much of Asia, sub-Saharan Africa and the Middle East (66). This ability to persist in such a wide variety of landscapes is primarily due to their extremely adaptable hunting strategy. Leopards have a highly catholic diet, in sub-Saharan Africa alone they have been recorded feeding on over 90 species, including arthropods, birds, reptiles, and small mammals to large ungulates weighing twice their body weight e.g. eland (*Tuarotragus oryx*). Leopards are also opportunistic feeders (68-70) and have been observed scavenging on elephant (*Loxidonta africana*) and giraffe (*Giraffa camelopardalis*) carcasses (21). While, the leopards preferred prey range is between 10 – 40 kg (71), to maintain bodyweight they require between 1.6 and 4.9 kg of meat each day (20, 65, 70). Leopards employ a range of hunting techniques to capture their prey that vary according to habitat type and target species, but almost certainly depend on some form of cover to conceal their approach (72). For any chance of success, they must get close to their prey (mean ± SE: 4.4 ± 0.25 m) in savanna woodland in Kaudom, Namibia (73) before launching a strike. Thus, leopards are reliant on some form of cover, although vegetation as low as 200 mm has been found to effectively conceal them (70). Successful hunting attempts are remarkably low, only 5 % of hunts in the Serengeti ended in kills (74), 16 % in in the Kruger National Park (20) and 38 % in Kaudom, Namibia (73). Moreover, between 5 and 10 % of kills are stolen by other predators, particularly lions and spotted hyeanas (20).

1.6. Methods of monitoring leopards

The leopard is arguably the least studied of all African guild members and this is a likely consequence of the difficulty in collecting data on a species that is elusive, solitary and wide-ranging - and thus difficult to observe directly (48). Furthermore, for a species that, until recently, was of low conservation concern (33, 42), the high costs associated with acquiring ecological data, particularly with the use of GPS radio collars - a tool often used to obtain data on cryptic species (75), may have led to resources being directed towards species perceived to be of greater conservation concern (48). However, advances in digital photography and infrared sensor technology has led to a cost-effective, non-invasive, means of gathering reliable information on elusive species, with the use of camera trap methodology (76, 77). Following the recent up-listing of the leopards conservation status this is a timely opportunity to acquire the knowledge urgently required in order to implement effective conservation actions, where needed (48).

1.6.1. Camera trapping

A variety of techniques have been developed to study and monitor large mammals such as leopards. Techniques that include the use of the presence of signs, such as prey availability (20); kill sites and spoor (78); interviews with local people (79); and more direct survey techniques, for instance, the collaring of individuals within a population (80, 81). There are limitations to all these techniques and, in particular the collaring of animals which is constrained by the small number of individuals that can be tagged simultaneously, the ambiguity of how many untagged individuals are present within the population, and the high costs and ethical issues associated with collaring animals (82). Over the past two decades camera traps have considerably advanced our ability to study rare and elusive species (83). They have the advantage of being non-invasive and appropriate for use over large areas with relatively minimal effort (84) and expertise. Where species have uniquely identifiable coat patterns or markings, for example bobcats (*Lynx rufus*) (85), tigers (*Panthera tigris*) (86), ocelots (*Leopardus paralis*) (87), jaguar (*Panthera onca*) (88), and leopard (89), capture-mark-recapture (CMR) models can be used to estimate population densities using camera trap data (90). Today camera trapping is also used to study various aspects of wildlife ecology including species inventory, distribution, population structure, habitat use and behaviour (91).

This study, for the first time, uses camera trapping to assess the influences of leopard occurrence in the Maasai Mara National Reserve (MMNR), Kenya. Two main questions are addressed: (1) do leopards choose certain habitat types in which to hunt and, if so, (2) what factors determine whether an area is preferred or avoided? For instance, do leopards select habitats where prey species richness/category (i.e. prey weight) are optimum? Or, do they select habitats which increase the probability of prey capture, such as semi-open habitats which provide a level of concealment. Furthermore, does the presence or absence of intra-guild competitors (e.g. lions, hyeanas) drive whether an area is selected by leopards?

1.7. Project aims and objectives

1.7.1. Project statement

Habitat loss and human conflict have led to the unprecedented decline of large predators. The function of apex predators on ecosystem structure and regulation is well-known. This study will use camera trap technology to investigate the factors (e.g. habitat type, prey species richness and interspecific competition) influencing leopard occurrence in the Maasai Mara National Reserve.

1.7.2. Objectives and hypothesis

1. Determine whether there is a correlation between habitat type and leopard occurrence

- H_0 – Leopard occurrence is not influenced by habitat type.

- H_1 – Leopard occurrence is more likely in semi-open rather than open habitat types.

2. Determine whether species richness is related to leopard occurrence.

- H_0 – There is a positive correlation between leopard occurrence and species richness.
- H_1 – There is no correlation between species richness and leopard occurrence.

3. Determine whether sympatric carnivore occurrence is related to leopard occurrence.

- H_0 – There is a positive correlation between leopard occurrence and sympatric carnivore occurrence.
- H1 – There is no correlation between leopard occurrence and sympatric carnivore occurrence.

2. Study Area

This study was conducted in the Mara Triangle Conservancy, Kenya 1°24'23.58" S 34°54'23.58" (Fig. 1), from March 2019 to June 2019. The Mara Triangle comprises approximately one third (482 km^2) of the Maasai Mara National Reserve (hereafter the Reserve). The Reserve is a designated protected area located in the south-west of Kenya and it is bounded by the Serengeti National Park to the south, private group farms to the north and east, and by the Siria escarpment to the west. The Talek, Mara and Sand rivers subdivide three regions of the Reserve, Sekenani, to the east, Musiara, to the north, and the Triangle, to the west (92). The Mara Triangle is managed independently of the Reserve by the Mara Conservancy (MC), which has been responsible for the management of the Triangle since 2001. At the request of the Kenyan government the MC was tasked with tackling increases in poaching and wildlife declines (93, 94). Through implementing regular anti-poaching patrols, restricting livestock grazing within the Reserve, and the dispersal of tourism revenues throughout the community, the MC has made marked improvements to conditions in the Triangle. Furthermore, anthropogenic disturbance of wildlife is limited by controlled visitation by tourist vehicles (94).

Land use within the Reserve is restricted to wildlife viewing and photographic tourism (95). Tourism is one of the leading industries in Kenya, contributing > 13 % of the GDP, and > 10 % of the national employment sector. For example, in 2011 alone wildlife safari's contributed > USD1 billion to Kenya's national revenue (96).

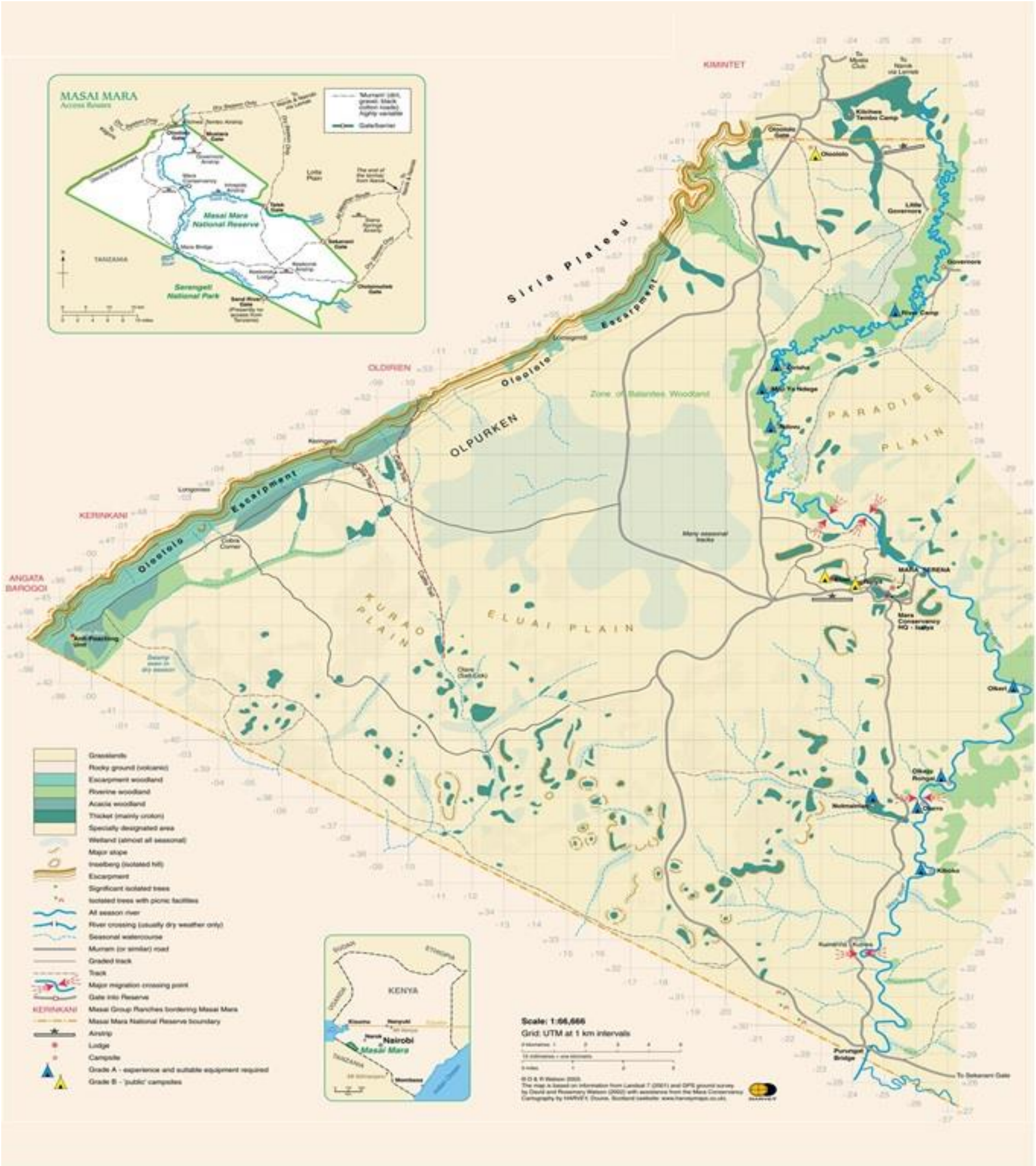

Figure 1. Map of study area Mara Triangle Conservancy. Inset shows location of the study site within the Maasai Mara National Reserve, Kenya. Source: Watson (97).

2.1. Habitat

Six habitat types characterise the Mara Triangle (Table 2) (97) consisting primarily of tall, open grasslands interspersed with Acacia gerrardii and Terminalia trees, shrub lands and riverine forest (98). Poor draining soil and low average elevation combine to cause waterlogging during the wet season. Rainfall forms a bimodal pattern, with the wet season occurring from November – June and the dry season from July – October. The wet season has two distinct phases, the long rains which span March – June, and the short rains which span November – December (99, 100).

2.2. Prey species and carnivore guild

Large herds of migrating wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and Thomson's gazelle (*Gazella thomsoni*) are attracted to the Reserve from the Serengeti by the long rains with numbers generally peaking in July, by November most of the migrating herds have returned to Tanzania (100, 101). The study area is home to non-migratory populations of all three species while also supporting an abundant and diverse community of resident herbivores, including browsers and grazing species (102). These range in size from; elephant Cape buffalo (*Syncerus caffer*), and giraffe, to smaller ungulates such as impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and common duiker (*Sylvicapra grimmia*) (Table 3). There is a full guild of large carnivore species present in the area, including lion, leopard, cheetah, spotted hyeana and the African wild dog (90). Mesopredators, including serval (*Felis serval*) and black backed jackal (*Canis mesomelas*) are also common.

3. Methods

Ethics statement

Non-invasive methods were used to collect data in this study and therefore ethics committee approval was not required. Permits to conduct the study were issued to Eve M. Hills by the Kenya Wildlife Service (KWS), and the National Council for Science and Technology (NACOSTI). Permission to conduct research within the Mara Triangle Conservancy was granted by Brian Heath (CEO Mara Conservancy).

3.1. Pilot study

Following Wang and Macdonald (112), a pilot study was conducted during a two week period (September 2018), using 3 Spypoint™ Solar, 2 Browning™ Strike Force, 2 Browning Dark Ops HD Pro and 4 Bushnell™ HD (digital) remote cameras, which enabled battery life and camera effectiveness in the Reserve's environment to be tested.

3.2. Preliminary survey

With the assistance of local rangers, a preliminary survey was conducted in the study area to identify sites where there was evidence (or prior knowledge) of leopard presence or activity, including, spoor, scratch marks (103), existing photographic record, and places where leopards might be expected to pass. Animal trails leading towards, or near to permanent water, drainage lines and potential cache/marking trees were selected as potential camera points. Thus, ensuring that sampling effort covered all habitat types and areas where leopards were likely to be present (104). Both old and recent leopard signs were recorded to help gauge the likelihood of capturing the focal-species at each point (105). Spacing between potential points during the preliminary survey was measured using a handheld GPS unit. In agreement with a MC management request, camera-traps were not placed in areas where they would be easily seen by visitors to the Reserve. Consequently, although leopards are known to utilise road networks (90, 105-107) camera traps were not placed on roads during this survey.

3.3. Camera trap placement and spacing

It is important that the entire survey area is covered by camera traps, with no gaps large enough for an individual of the focal-species to exist without encountering a camera-trap for the duration of the survey (86, 104, 108). Karanth et al. (86) further recommend that survey areas are kept as circular as possible, to improve tractability for analysis, and to avoid survey designs with high perimeter to area ratios.

Placement of camera-traps depends greatly on preliminary investigation of the survey area to find areas of concentrated use by the focal-species (104, 105). The necessity to ensure that every individual in the survey area has the opportunity to encounter a camera-trap throughout the survey determines the distance between camera points and defines the extent of the area sampled by each camera-trap (108). Thus, it is the minimum home range of the focal-species which determines the spacing of camera-points required to avoid gaps in the survey area, and ensure all individuals are potentially exposed to a camera-trap (86, 108). Generally, the female minimum home range is used for spacing camera points as this ensures that all classes of the population, including transient juveniles, and adult males (who often have home ranges that are 3 - 5 times larger than females (109, 110)) have a good chance of encountering a number (> 1) of camera points (86, 105).

3.3.1. Camera set-up

Following du Preez et al (105), all potential camera-trap points identified in the preliminary survey were plotted onto a GIS map, and to ensure maximum spacing was not violated, all points were placed within a grid with a cell size of 5.25 km^2, which corresponds to approximately half the diameter of the smallest recorded home range for a female leopard (10 km^2 (111), before the final camera points were selected. The total number of grid cells for the entire survey area was ~17. Taking into account the results of the preliminary sign survey and following previous survey design guidelines (82, 104, 112), thirty four suitable camera points were identified across the study area. Spacing was based on the diameter of the smallest home range 3.6 km, although in practice the availability of suitable camera sites resulted in spacing of ~2 – 5 km. With 70 camera-traps available 1-2 camera-points were placed within each grid cell, one cell did not contain a camera point due to a lack of suitable sites at the location. A micro-habitat survey was conducted at each camera point and habitat type recorded.

Logistical issues meant camera trapping was conducted in two phases, although these ran largely concurrently (between April 2019 and June 2019). The north and north-west region (phase I) was surveyed for 63 days, and the north eastern and southern regions (phase II) were surveyed for 56 days (Table 2). The total period for each trapping phase was within a time frame generally accepted as satisfying demographic population closure for a large carnivore (90, 113).

3.3.2. Camera location

Sixty Browning Strike force, 2 Browning Dark Ops, 3 Spypoint solar and 7 Bushnell HD cameras were used during the survey, and aside from the Spypoint cameras which were solar powered, the remaining cameras were powered by alkaline batteries, all were digital. Cameras were housed in protective metal cases and placed between 30 and 70 cm above the ground, they were secured to natural fixtures (e.g. trees) or, in order to facilitate optimal positioning (105), fixed to custom-made metal posts of approximately 1 m in length. Almost sixty percent of camera traps were placed near large trees, while the remainder were placed on existing animal trails. Cameras were placed in pairs opposite each other so as to capture both flanks of a passing leopard, and slightly offset so that the flash from one camera would not overexpose the images captured from the other (16). Cameras were positioned 2-6 m from where a leopard was expected to pass (89), and were set for 24 hrs. Spypoint camera sensitivity was set to normal (to prevent thousands of false triggers by moving vegetation - as experienced during the pilot study) Once triggered, the cameras took a series of 3 photographs followed by a 1 minute delay, before being triggered again. The cameras were monitored (where logistically possible) once a week to replace SD cards, check battery power and positioning (baboons, elephants, hyeanas and other wildlife are known to damage/move cameras – as revealed in the pilot study).

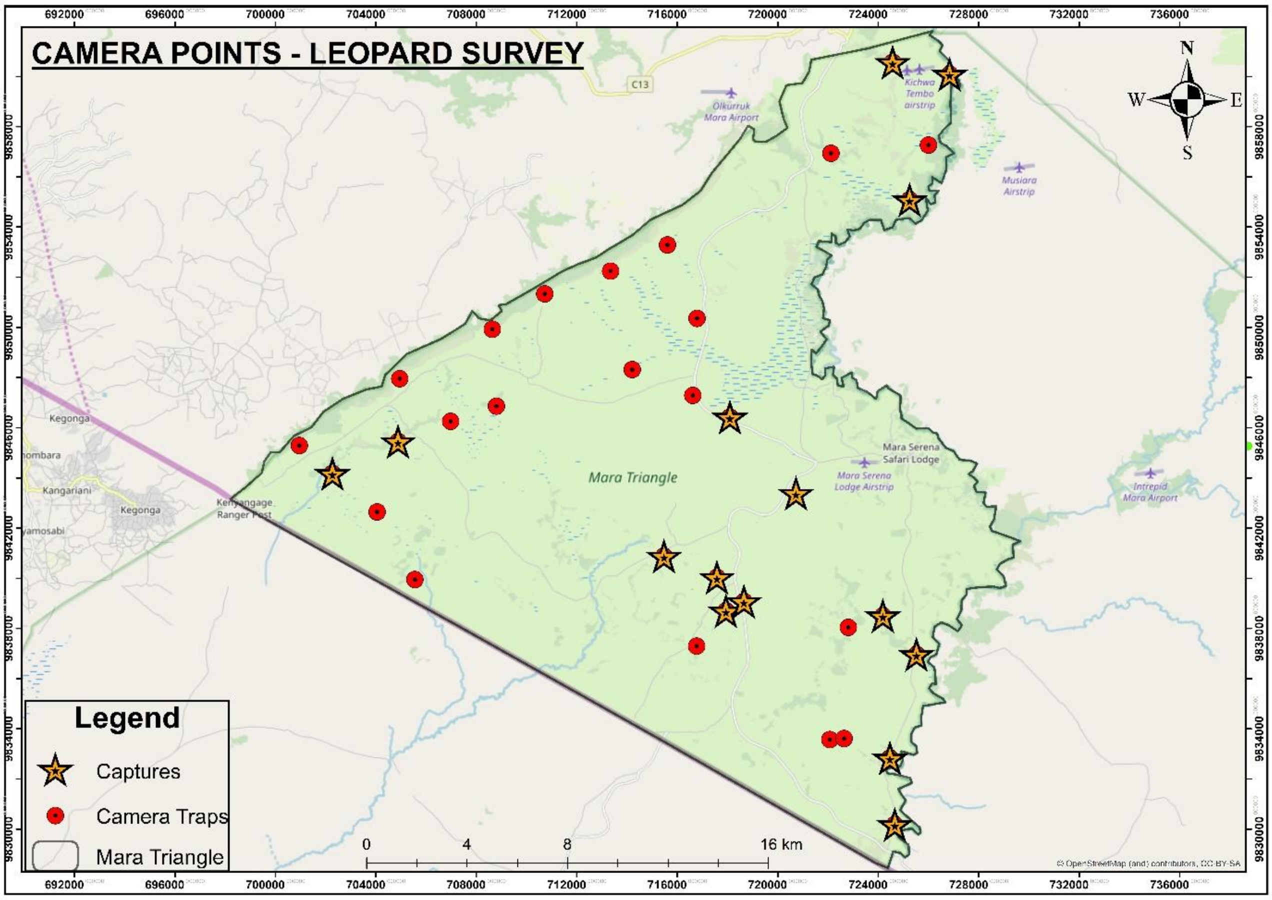

Figure 2. Location of camera-trap sites within the Mara Triangle, displaying where leopards were photo-captured. Red circles indicate camera locations and gold stars indicate camera locations where leopard occurrence were recorded. Map source: ArcMap 10.6.1

3.4. Trapping occasions

As leopards are largely active between dusk and dawn each trapping occasion was defined as the twenty four hour period beginning and ending at noon (114-116), thus, the trapping occasion reflects the active period of the leopards daily cycle. The rare events where leopards were captured within 3 hours before or after noon were not considered separate trapping occasions (105).

3.5. Habitat categories

Habitat comprised three categories; open, semi-open and closed (Table 2). Open habitats were comprised predominantly of grasslands, and included wetland and balanite zones, semi-open habitats included Acacia woodland and thicket, and closed habitats comprised pockets of dense riparian forest. Following Madsen and Broekhuis (117) closed habitats were merged with semi-open as the proportions of closed habitats were relatively low (Fig. 1) and thus using semi-open to predict leopard presence would result in increases in both open and closed habitats.

Table 2. Summary of habitat types found in the study area. Habitat classification was based on the three habitat structures found in the Mara Triangle; open, semi-open and closed. Adapted from: Broekhuis, Cushman and Elliot (175).

Habitat structure	Characteristic species	Classification
Riverine forest	Warburgia ugandensis, Acacia xanthophloe	Closed
Grassland	Themeda triandra, Hyparrhenia rufa	Open
Wetland/swamp	Grasses, mixed small flowering plants, herbs and shrubs	Open
Woodland/bush	Acacia brevispica, Acacia drepolobium	Semi-open
Escarpment	Mixed habitats: wetland/thicket/ravine	Semi-open
Thicket	Croton dichogamus, Euclea divinorum	Semi-open

4. Data analysis

4.1. Leopard occurrence

Individual leopards were identified by examining unique spot patterns on their pelage, facial scarring and/or any other distinctive features (Fig. 3) (112, 40). The sex of leopards was determined by following guidelines from Balme et al. (17) using the presence of or lack of dew laps and external genitalia, and overall size of the leopards to sex individuals (40). At the study site there was an existing database of leopard photographs taken by visitors, photographers and guides which aided the identification and confirmed the sex of any individuals that were only partially photographed or captured from one angle. The majority of leopards were identified (and triple checked) by the same person although a second opinion was sought where there was any doubt in the matching process.

Next, a leopard detection history at each camera trap location was created, consisting of binary values with '1' indicating leopard presence and '0' indicating leopard absence (118). Each trap night (24- hour period) was considered a single sampling occasion and each camera location considered an independent site, therefore each sampling occasion was a temporal repeat of the survey (91, 119).

To measure camera trapping success for leopards in the study area a Relative Abundance Index (RAI) was calculated (120, 121). Thus, the total number of leopard captures were divided by survey effort (i.e. total number of trap nights) and multiplied by 100. To determine variation in capture success across the study area RAI's were calculated for the northern region, the southern region and for the study site as a whole.

4.2. Prey species and sympatric carnivore occurrence

Prey species identity and weight range were confirmed using Kingdon and Hoffman (72). Prey data were categorized according to body weight as follows; category 1 (small prey) = (0.1 - 10 kg), category 2 (medium) = (11 – 40 kg), category 3 (large prey) = (41 – 450 kg), and category 4 (mega-herbivores) = (> 451 kg) (Table 3). Adapting methods used by Skinner and Chimimba (13) prey weight were categorized by adding the mean values of adult weights for all species detected on a single sampling occasion. Species richness was categorised according to the number of prey species detected on each sampling occasion (24 hours) and ranged between 0 and 6. Sympatric carnivore presence or absence was recorded using binary values '1' for presence and '0' for absence.

Using the Generalized Linear model a binary logistic regression was applied to model the relative probability of leopard presence occurring in the two remaining habitat types (i.e. open and semi-open) and to predict leopard occurrence when considering prey species richness, prey weight and presence/absence of sympatric large predators, as influencing factors. Included in the model were five variables; habitat type, lion presence, hyeana presence, prey species richness and prey category. The logistic regressions used the stepwise backward-elimination method based on the Wald statistic (56). The Wald statistic and the corresponding significance level test the significance of each of the independent variables in the model (122). The ratio of the slope coefficient β to its standard error, squared, equals the Wald statistic. If the Wald statistic is significant, then the parameter is considered significant in the model (56). Significance was set at p = 0.05. All variables were initially included in the model before sequential removal of non-significant variables at the 95 % level, based on lowest coefficient (β) values (123). All statistical tests were conducted using program Excel 2013 (Windows Office, 2013) and SPSS 25.0 (SPSS, Chicago, IL, U.S.A).

Table 3. A summary of the species richness, weight range and prey categories of small to large terrestrial mammal species photo-captured in the Mara Triangle.

Latin name	Common name	Weight range	Mean adult weight	Prey category
Phacochoerus africanas	Warthog	45 - 150 kg	97.5	3
Loxodonta africana	Elephant*	2,200 - 6,300 kg	4,250	4
Aepyceros melampus	Impala	40 - 80 kg	60	2
Modoqua kirkii	Kirks Dik dik	3.8 - 7.2 kg	5.5	1
Kobus ellipsiprymnus defassa	Defassa Waterbuck	160 - 300 kg	230	3
Giraffa Camelopardilis tippelskirchi	Giraffe	450 - 1,930 kg	1,190	4
Lepus microtis	Hare	1 - 5 kg	3	1

Papio cynocephalus anubis	Olive Baboon	11 - 50 kg	30.5	2
Cercopithecus aethiops	Vervet monkey	3,5 - 8 kg	5.75	1
Hippopotamus amphibius	Hippopotamus*	180 - 275 kg	227.5	3
Syncerus caffer	Buffalo*	250 - 850 kg	550	4
Hystrix africanaeaustralis	Porcupine	12 - 27 kg	19.5	2
Bdeogale crassicauda	Bushy tail Mongoose	1.3 - 2.25 kg	1.77	1
Sylvicapra grimmia	Common duiker	12 - 25.5 kg	18.75	2
Bos taurus	Cattle	450 - 1,090 kg	770	4
Damaliscus lunatus jimela	Topi	75 - 160 kg	117.5	3
Alcelaphus buselaphus cokii	Coke's hartebeest	116 - 218 kg	167	3
Gazella thomsonii	Thomsons Gazelle	15 - 35 kg	25	2
Equus burchellii	Burchell's Zebra	175 - 322 kg	248.5	3
Taurotragus oryx	Eland	300 - 942 kg	621	4
Cercopithecus sp.	Blue monkey	5 - 12 kg	8.5	2
Pedetes capensis	Spring hare	3 - 4 kg	3.5	1
Diceros bicornis	Black Rhinoceros*	700 - 1,400 kg	1,050	4
Conochaetes taurinus	Wildebeest	140 - 290 kg	215	3
Oryteropus afer	Aardvaark	40 - 80 kg	60	2
Gazella grantii	Grants gazelle	38 - 81.5 kg	59.75	2
Redunca arundinum	Southern reedbuck	50 - 90 kg	70	3
Oreotragus oreotragus	Klipspringer	8 - 18 kg	13	2
Tragelaphus scriptus	Common bushbuck	24 - 80 kg	52	2
Ourebia ourebi	Oribi	12 - 22 kg	17	2
Genetta genetta	Common genet	1.3 - 2.25 kg	1.77	1
Felis serval	Serval	6 - 18 kg	12	2
Mungos mungo	Banded mongoose	1.5 - 2.25 kg	1.87	1
Canis mesomelas	Black-backed jackal	6.5 - 13.5 kg	10	2

Ovis aries/ Capra aegagrus hircus	Sheep & goats	20 - 160 kg	90	3
Felis silvestris	African wildcat	3.2 - 4.5 kg	3.85	1

* Indicates large mammal species that are considered potential leopard prey although are typically avoided (71).

5. Results

5.1. Camera trapping

The total sampling effort for both phases was 2029 camera trap nights. A total of 91 trap nights were lost due to false triggers as associated with swaying grass and/or damage by wildlife resulting in a total of 1938 trapping occasions.

The survey yielded a total of 725 leopard captures across the study site, which ranged from 58 (8 %) captures in the northern region to 667 (92 %) in the southern region (Table 5). Using unique coat patterns (Fig. 3), 13 individual leopards were identified, 3 (23 %) in the north and 10 (76. 92 %) in the south (Table 4). Six adult males, six adult females and one juvenile were photographed on 35 occasions during the survey. Capture frequencies ranged from 1 – 8 captures per individual. Leopards were captured at 15 of the 34 camera trap stations (Fig. 2). More than half (*n* = 20, 58.82 %) of leopards were captured at trees, while 41.17 % (*n* = 14) were captured on trails. Leopard capture rates were considerably higher in the southern region (RAI = 77.2) when compared to the north (RAI = 5.3), with an average relative abundance-success score of (RAI = 41.25) (Table 5). A total of 41 mammal species were captured during the survey (Table 3). The smallest species considered in the analysis is the common genet (Genetta genetta – mean = 1.77 kg) and the largest, the elephant (mean = 4250 kg).

Figure 3. Two photographs of the same female leopard captured on different trapping occasions. An example of identifying spot pattern is circled on each photograph.

Table 4. Relative abundance index (RAI) of leopard capture success rates (number of leopard captures per 100 camera-trap events) across the study area (121).

Sampled area	Survey duration (mean no of trap days)	Camera trap stations	Camera trap nights	Total leopard pictures	Identified leopards	Capture rate (%)
Northern Triangle	60	18	1,075	58	3	5.3
Southern Triangle	54	16	863	667	10	77.2
Average	57	17	969	362.5	6.5	41.25
Total	-	34	1,938	725	13	

5.2. Univariate comparisons

The number of leopard captures were marginally less than expected in semi-open habitats; closed riverine, woodland/bush and thicket (*n* = 24, 68.57 %). In contrast, more leopard captures than expected occurred in open habitats; grassland, wetland and swamp (*n* = 11, 31.42 %) (Table 5) suggesting that leopards do not always select habitats that provide sufficient cover for hunting prey.

Table 5. Summary of the proportion of leopard presence and absence in each habitat type

Leopard presence/Absence	Open	Semi-open	Total
Presence	11	24	**35**
No. trap nights	850	1086	1938
Proportion %	1.29	2.21	1.81

The number of prey species detected on a single trap night during the camera trap survey ranged from '0' to '6'. As expected, the mean number of different prey species detected in semi-open habitat types was higher (*n* = 1163, 60 %) than those captured in open habitats (n = 775, 40 %) (Table 6). Albeit, the number of prey species captured in open habitat types was not as low as expected. The number of prey detected in semi-open habitats and the number detected in open habitat types, according to prey weight category, followed a similar pattern, small prey (n = 66, 65% and n = 35, 35 %), medium prey (*n* = 100, 71 % and *n* = 40, 29 %), large prey (n = 227, 76 % and *n* = 72, 24 %) and mega-herbivores (*n* = 298. 61 %, *n* = 193, 39 %), respectively.

Table 6. Number of prey species captured within each habitat category (open/semi-open) per trap night, and mean prey species richness by habitat type.

Habitat type	No. of Prey species captured 0 – 6							Total trap nights	Mean/SD
	0	1	2	3	4	5	6		
Open	482	228	54	10	1	0	0	775	110.71/169.67
Semi-open	517	338	176	78	24	24	6	1163	166.14/179.90
Total No. of sightings	999	566	230	88	25	24	6	1938	

When the range of prey species is considered (i.e. 0 – 6), the number of leopard captures were significantly higher where 0 prey species were detected on a single trap night (*n* = 21, 60 %) (Table 7). Proportionally there was a positive significant correlation between leopard captures and the detection of six prey species (33.33 %) albeit the number off detections was small (n = 2) (Table 7). When considering prey weight categories leopard captures were proportionately higher where zero prey were detected (49 %). No leopards were captured where small prey (1 – 10 kg) were detected. The proportion of leopards detected on the same trapping occasion as medium prey (11 – 40 kg) was 7 %, 29 % of captures with large prey (41 – 450 kg), and 15 % with the mega-herbivore category (> 450 kg). Suggesting that leopards did not select hunting areas based on the availability of preferred prey species (i.e. 20 – 40 kg).

Table 7. Summary of species richness and proportion of leopard captures (%)

Leopard Captures (Presence/Absence)	Species Richness							Total	Mean/SD
	0	**1**	**2**	**3**	**4**	**5**	**6**		
Presence	21	8	3	1	0	0	2	35	5.0/6.55
Absence	978	558	227	87	25	24	4	1903	271.8/318.3
No. of trap nights	999	566	230	88	25	24	6	1938	
Proportion (%)	2.10	1.41	1.30	1.14	0	0	33.33		

Four of the five large predator guild members present in the study area were detected during the survey. As cheetah captures were low (*n* = 2), and zero African wild dogs were observed, these species were removed from further analysis. The number of lion and hyeana detections were highly disproportionate (*n* = 32) and (*n* = 153), respectively (Fig. 4)

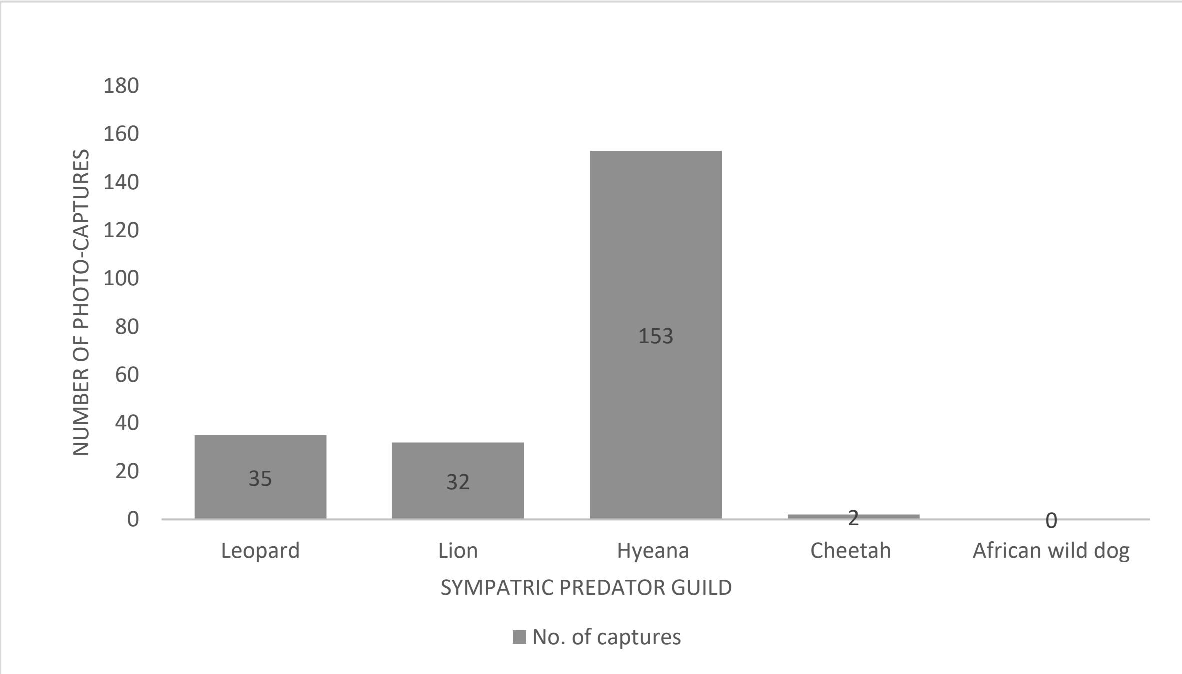

Figure 4. Count of photo- captures of each of the predator guild members detected during the camera survey.

5.3. Multivariate analyses

5.3.1. Influence of prey category on leopard presence

In predicting leopard occurrence across the study area, the initial binary logistic regression model considered five predictive variables, three categorical which included habitat, hyeana and lion, and two continuous variables representing prey species weight and prey species richness. With leopard presence as the dependent variable, all possible comparisons were considered within the model. However, none of the variables were significant parameters in the initial model other than hyeana presence (Wald χ^2 (1) = 6.149, p = .013). Indicating that when accounting for all possible comparisons the model predicted that only hyeana presence had a significant effect on the occurrence of leopards. The parameter with lowest coefficient in the first model was prey weight category (Wald χ^2 (1) = .346, p = 0.556), indicating that prey species biomass did not influence leopard presence or absence. Prey weight was therefore excluded from further analyses.

5.3.2. Influence of lion presence on leopard presence

Again, in the second model, the significant predictor on the presence of leopards was the presence of hyeana (Wald χ^2 (1) = 6.393, p = .011). The parameters of the three remaining variables were non-significant, albeit, species richness was weakly non-significant (Wald χ^2 (1) = 3.058, *p* = 0.080). The parameter in this model with the lowest coefficient (β = .706) and thus the least significant predictor of leopard occurrence, was the presence of lions (Wald χ^2 (1) = .461, *p* = .497). Indicating that there was no correlation between the presence of lions and the presence of leopards. Lion presence was excluded from further analyses.

5.3.3. Influence of habitat on leopard presence

In the next model, in respect of habitat type, the results of the logistic regression were similar to those of the univariate comparisons, in that the model predicted that habitat type had a non-significant effect on leopard presence (Wald χ^2 (1) = .886, *p* = 0.346) (Fig. 5). Indicating that site selection by leopards is not influenced by habitat type. In this model species richness was again non-significant (Wald χ^2 (1) = 2.956, *p* = 0.086) with hyeana presence remaining the most significant predictor of leopard occurrence (Wald χ^2 (1) = 6.436, *p* = .011).

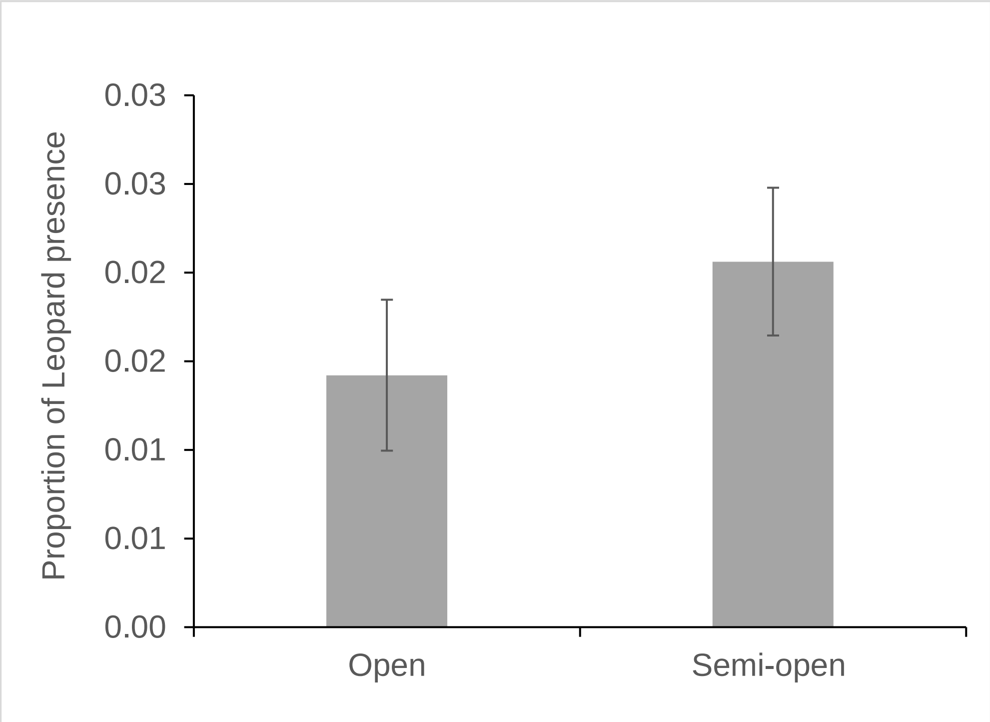

Figure 5. Total proportion of Leopard sightings in relation to habitat type ±SEM. Total camera trap nights: 1938. Leopard presence was not significantly influenced by habitat type

5.3.4. Influence of species richness on leopard presence

One categorical and one continuous predictor variable remained in the penultimate model, (hyeana and species richness, respectively). In contrast to the univariate analyses, the model did not consider species richness to be a significant predictor of leopard presence

(Wald χ^2 (1) = 2.518, p = .113), indicating that there was no correlation between prey species and the presence of leopards. Hyeana remained the variable most likely to predict leopard presence (Wald χ^2 (1) = 7.899, p = .005).

5.3.5. Influence of hyeana presence on leopard presence

The predictor variables excluded from the final model were lions, habitat, prey category, and prey species richness. The logistic regression model which best predicted leopard occurrence was the presence of hyeana (Wald χ^2 (1) = 6.526, p = 0.011) (Fig. 6). For hyeana, the coefficient is β = 1.101 with a 95 % confidence interval from .256 to 1.947, therefore the model predicts the presence of hyeana has a positive and significant effect on the presence of leopards. Interestingly, while hyeana presence had a significant impact on leopard presence there were no hyeana sightings captured within open habitat (Fig. 7). An interaction between habitat type and hyeana presence may have influenced leopard presence, however the number of sightings were too low to analyse statistically.

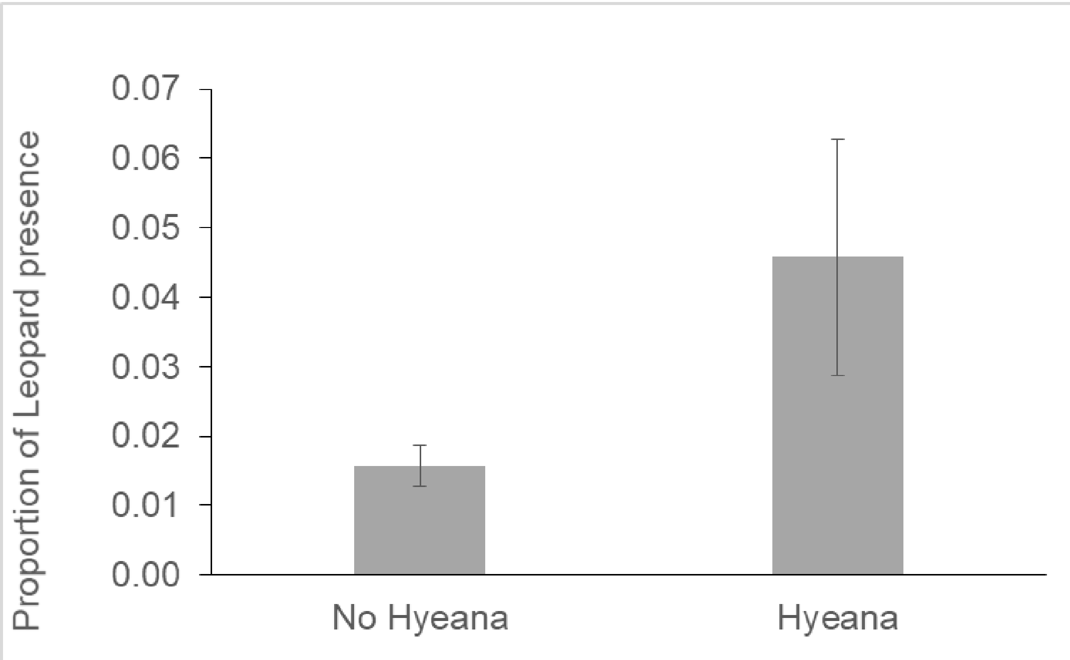

Figure 6. Total proportion of Leopard sightings in relation to hyeana presence ±SEM. Total camera trap nights: 1938. Leopard presence was found to be significantly greater in the presence of hyeanas compared to hyeana absence

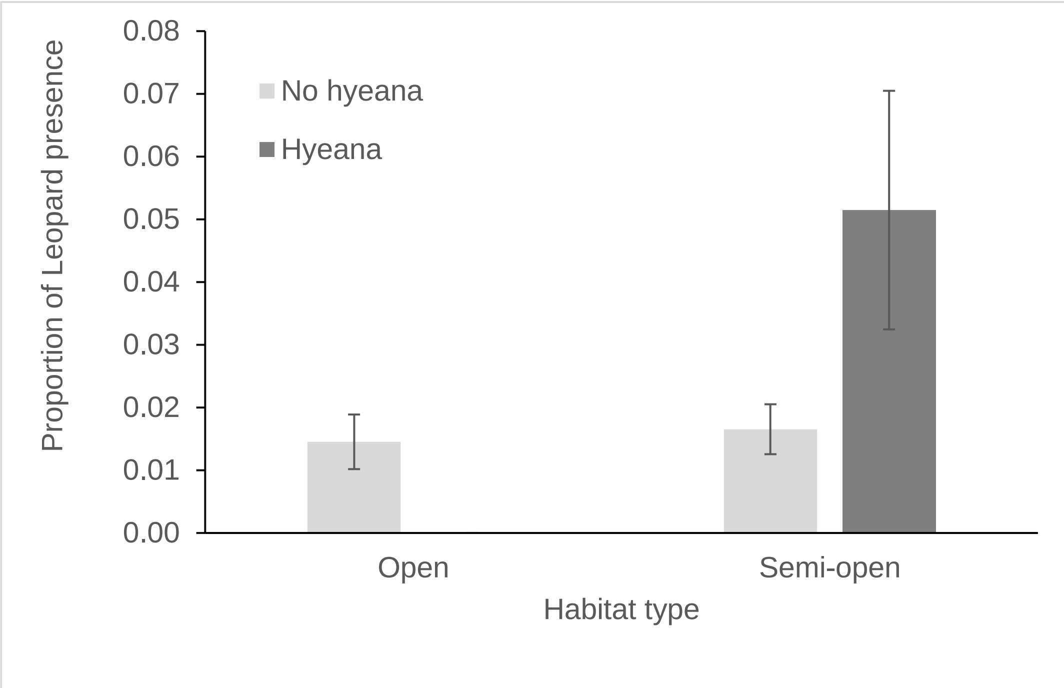

Figure 7. Total proportion of leopard sightings in relation to hyeana presence and habitat type ±SEM. Total camera trap nights: 1938. Leopard presence was found to be significantly greater in the presence of hyeanas, whereas habitat type was not found to significantly influence Leopard presence.

6. Discussion

Recent advances in camera-trap technology have opened up a non-invasive method of researching large elusive predators that would otherwise be impossible (124). In this study, camera trapping was used to assess whether habitat type, prey species richness and preferred prey weights, and the presence of guild competitors influenced the occurrence of leopards within a protected area.

6.1. Camera trapping and leopard occurrence

The Browning™ and SpyPoint™ camera trap equipment proved reliable and produced high quality photographs of leopards which could be used for individual recognition. The equipment was robust and worked effectively even after being trampled by elephants or bouts of heavy rain (125). In general, traps were checked weekly during this study, although for logistical reasons there were a few occasions when this was not possible. While it is difficult to determine a minimum interval for checking traps once every 5 – 7 days should be adequate. It is impossible to predict when a trap might be hampered by wildlife or how much battery life will be used over a certain period of time. These factors are dependent on the trapping site with capture rates of all species and interference by wildlife/people/vegetation being important variables (e.g. lions resting at the trapping site all day could fill an SD memory card or exhaust battery life) (125).

Following Karanth & Nichols (113) traps were placed within a grid format using sites that had the greatest likelihood of obtaining leopard photographs. However, placement of the camera traps proved difficult due to the logistical problems in finding cache/marking trees and animal trails regularly used by leopards (125). It is proposed for future studies, in the absence of radio-telemetry movement data on leopards; where sites regularly used by leopards can be easily identified (88), that extended preliminary surveys of the study areas are conducted to increase the number of trapping locations frequently used by leopards. Additionally, although it was usually possible to place the cameras opposite each other at most locations, it was not always the case, as a result, photographs of just one flank of a passing leopard were taken. However, although a leopards spot markings vary bilaterally it was, nevertheless, generally possible to match both sides as invariably more than one photograph was taken of each leopard during one trapping occasion (125). Identification was further aided by an existing photographic database of leopards present in the study area.

From a sampling design and effort perspective the use of trees and animal trails as sampling points proved to be successful. For instance, placing cameras at trees and on trails captured an equal proportion of the population. This is interesting because male leopards are known to cover greater daily distances than female leopards (20), males are also more likely to use roads (45). Thus, a greater number of female captures might have been expected here. Chapman and Balme, (89) placed 97 % of camera-stations on road networks in a private reserve in South Africa, and detected equal numbers of male and female leopards. They presumed that male leopards had a higher probability of being detected than females. Indeed, two males comprised 68 % of all captures, indicating an unnatural skew towards males in the population. In contrast, this study found that females comprised 62 % of all detections, indicating an unnatural skew towards females in the population. However, because male leopards typically have larger home ranges than females, they are expected to spend a proportion of their time outside of sampling point areas, thus reducing their encounter rates (20). Alternatively, female home ranges are generally smaller which could have led to the higher encounter rates experienced in this study (90).

Three of the thirteen individuals identified during the survey were captured in the northern half of the Reserve (Fig. 2) and ten individuals were captured in the southern half of the Reserve (one recapture from the north). Sampling effort and methodology remained consistent throughout the survey, therefore, the number of individuals captured in the north could be presumed to reflect a lower number of leopards inhabiting the northern part of the Reserve (89). However, false–negatives are not accounted for in this study and on two occasions leopards were observed within 2-300 m of a trap location, and on two further occasions, fresh leopard spoor was detected at the trapping location, although individuals were undetected by the cameras. Consequently, it is possible that there are more leopards in the area other than those that did encounter a camera. Historically, illegal hunting has been greater along the western border of the northern Serengeti National Park adjoining the Mara Triangle (96, 126, 127), which has been linked with dramatic declines in numbers of waterbuck, topi, buffalo and giraffe (126, 128). Furthermore, high levels of poaching activity in the north have also been recorded (129), and which have been explicitly linked to wildlife declines in the area (128).

Reductions in prey numbers may in turn influence the number of leopards. Indeed, a review on predator abundance correlates by Carbone et al. (130) found that a reduction in prey numbers led to a five- six times greater reduction of large predators (130). Earlier studies have shown that energetic costs may limit body mass in large predators (131). For instance, large predators have bigger home ranges (132, 133) and hunt for longer (68) in areas where prey numbers are low. Under these conditions, it would be expected that large predators work harder to maintain their energy budgets, which in turn may influence their population numbers. In this case, leopards with very high hunting costs will be particularly vulnerable to environmental changes that influence feeding ecology, because increased time spent hunting greatly adds to overall energy costs. Energetically stressful situations can lead to lower reproduction and survival rates, for large predators this situation could be exacerbated by life-history traits that already render them vulnerable to extinction (131). Although the Mara conservancy's regular anti-poaching patrols deter illegal hunting activities along the border it remains a problem. Controlling poaching and illegal hunting inside the Reserve will ultimately reduce impacts on leopards and their prey.

6.2. Determinants of leopard occurrence

The logistic regression model clearly showed that leopard occurrence was most strongly influenced by the presence of spotted hyeanas. This is interesting because apex predators typically exert direct competitive interactions with co-occurring apex predators for space and food resources (54, 134, 135). Thus, where similar-sized predators consume the same prey species interspecific competition is more prevalent (136). Leopards vary highly morphologically (71) with adults weighing between 20 and 90 kg (137). Although, leopards in the north of their African range are twice the size of their southern conspecifics (e.g. Western Cape of South Africa) (71). Whether this is simply due to latitudinal body mass variation or a response to the availability of larger prey species, or both, is unknown. However, as the spotted hyeana weighs between 45 and 80 kg, and, to maintain condition both predators need between 1.6 - 4.9 kg, and 3.8 - 4.0 kg, respectively, of meat daily (71, 138), this suggests that there is a degree of dietary overlap between both predators. Indeed, the hyeanas flexible foraging strategy means that almost any living, or non-living thing, is potential food (139). Spotted hyeanas, like leopards, have a catholic diet and have been recorded preying on a range of species from fish (139) up to prey the size of Cape buffalo (140) and the calves of giraffe and rhinoceros (138). Notwithstanding their scavenging behaviour, hyeanas are effective hunters, stealing carcasses from other predators or cooperating to bring down larger prey (141). This dietary flexibility makes spotted hyeanas the most successful large predator in Africa (142). Furthermore, co-occurrence between kleptoparasitic species, such as hyeana (143) and their victims can be expected more often than just by chance, either because they come together at kill sites, or the because the former follow and harass the latter (144).

In contrast to findings presented here, analyses of camera trap data collected from five protected areas in KwaZulu-Natal Province, South Africa, observed that hyeana and leopard were less likely to be co-detected at the same site, appearing to avoid interference encounters (135). Their findings supporting the view that co-occurring apex predators avoided interference competition with their nearest dietary competitors by decreasing the probability of being co-detected at the same sites (135). The apparent site-avoidance behaviour by leopards or hyeanas was likely an effect of intra-guild killing out of resource overlap, for instance fights over kills that end in fatality (68). An important determinant of the abundance and distribution of large carnivores is interspecific interaction, changes in the numbers of one carnivore species can lead to direct increase or decrease in the numbers of others by mesopredator release (136). As an example, and of significance here, is the recent doubling in size of one spotted hyeana clan in the Talek region of the Maasai Mara National Reserve (145), becoming one of the largest hyeana clans ever documented in Africa (n = 113) (146).

Hyeana clans in the Reserve are already comparatively large, ranging from 38 to 74 individuals (145), whereas elsewhere in Africa clan size averages 29 individuals (146). Notably, in Talek, the rapid growth in the population of hyeana was concurrent with the striking decline of the lion population. Indeed, lion numbers in the Reserve are thought to have declined by 40 % (147), since Ogutu and Dublin (155) estimated the population 13 years earlier. Green et al (145) suggest that anthropogenic disturbance along eastern edge of the Reserve may be causing a mesopredator release of spotted hyeana through decreased lion-caused mortality among juvenile hyeanas (top-down effects) and an increased availability of livestock (bottom-up effects). Presently, we know nothing about the possible long-term effects of a predator guild in the Reserve that contains fewer lions and more hyeanas than found historically, or the degree to which other species in this ecosystem, including leopards, might be influenced by an increase in hyeanas (145).

Consistent with work in the Kruger National Park (KNP) (148), the regression model indicated that lion presence did not influence the occurrence of leopards. One possible reason for this is that there were not enough data to draw outright conclusions (148), indeed, univariate comparisons showed that co-detections of lions and leopards on the same trapping occasion were extremely low (n = 1). However, lion presence appears to have conflicting effects on the occurrence of leopards wherever the two predators occur sympatrically. For instance, Du Preez at al. (105) found that given lion presence, leopards were more likely to move away. While, Vanak et al. (54) determined that leopard movements were only marginally influenced by lions. Results from the Timbavati Nature Reserve, South Africa, paint a different picture. The length of stay and rate of visitation by leopards were significantly correlated with the length of stay and rate of visitation by lions, meaning the likelihood of interference encounters between leopards and lions in the area was relatively high; thus allowing leopard movements there to be strongly affected by lions. This was shown by the markedly shorter duration of visits in the Kruger study area (148), and could be an example of top predator avoidance by leopards. Indeed, in various African studies high occurrence of lions has been shown to decrease the occurrence of other sympatric predators including wild dogs and cheetah (47, 132, 149).

It is important to note that as leopards are the focal study species the survey design and methodology used in this study aimed to enhance the capture of leopards. Thus, a lack of co-detections of lions and leopards could simply be due to the different sampling methods used. For example, in a recent study by Abade et al. (7) camera traps were used to evaluate lion occurrence in Tanzania’s Ruaha landscape. The study found that lion detections were higher when camera traps were placed on roads and animal trails when compared to lion detections at cameras placed off-trail. In contrast, in this study a greater proportion of camera traps were placed ‘off-trail’ at potential marking trees (59 %) and no camera traps were placed on roads.

While there is some overlap, dietary partitioning between lions and leopards is quite profound (150). Indeed, research from KNP found that lions had a prey base totalling 15 species, 11 of which were seldom shared by other species (150). Analysis of the lion throughout its range shows that it preferentially selects prey within a weight range of 90 – 550 kg, with a preferred weight of 350 kg (151). Among the lions preferred species are buffalo, wildebeest and zebra (151) all species that typically occupy open grassland habitats (98). In contrast, leopards preferentially select smaller species including impala and bushbuck and common duiker that prefer denser habitats (71).

Lions are primarily nocturnal hunters (68) showing a preference for grassland habitats (152), where the dark provides adequate concealment for hunting (153). When lions do hunt during the day they require cover to conceal their approach (153). For instance, bushy habitats (154) and tall grass (153). This indicates a degree of spatial overlap between leopards and lions. Indeed, within similar landscapes to this study, leopards have been found to select areas of semi-open habitat types associated with high prey density and prey catchability, independent of lion occurrence, while lions select for open habitats with higher densities of larger prey (48, 50). Interestingly, this study showed no evidence that the presence of lions influenced the occurrence of leopards. Which might suggest that despite the fact that lions pose a threat to leopard survival (17), that these two predators can co-exist within the same protected area without interference interactions contributing to the leopards decline (50).

Leopards in the Mara Triangle do not appear to preferentially select for habitats that might be expected to enhance prey catchability. In contrast to expectations, habitat type did not influence the occurrence of leopards. This is interesting because leopards are widely perceived to prefer the densest available habitats for hunting (20, 50, 56). For instance, in KNP 46 % of recorded kills were in dense riparian habitats, 44 % in medium to dense thorn-bush thickets and 10 % in open grassland habitats (20). Similarly, Hayward et. al. (138) found that leopards preferred to hunt in dense environments. Whilst, kills were not recorded during this study, univariate analysis suggest the probability of a kill occurring in semi-open habitat was not significantly greater than a kill occurring in open habitat types (69 % and 31 %, respectively), when considering leopard presence in these areas.

Open grasslands dominate the study area while areas of dense vegetation cover are the lowest found in the Reserve (155). It may simply be an absence of preferred habitat types that has resulted in detecting a greater number of leopards in open habitat types. The lack of population data for leopards in the Reserve means it is not possible to determine whether leopards are selecting open habitats by choice or whether they are being forced to occupy less favourable hunting areas because patches of preferred habitats are already occupied by other leopards (20), or indeed, other guild competitors. For instance, spotted hyeanas are known to strongly avoid open habitats (102), and findings in this study support this (Fig. 7). However, as ambush predators leopards require minimal cover to conceal their approach (156), and as such, tall grasses coupled with the leopard's natural camouflage (56), provide sufficient concealment. It is notable that in areas of open grassland camera traps were placed at trees, which are known to be used by leopards to cache prey and provide vertical refuge from aggressive intra-guild encounters (21, 48). Although the number of kills found cached in trees were not recorded during the survey, both fresh and old carcasses were observed. As habitat features and the degree of intra-guild competition determine the probability of a kill being cached (56), this may be a response to relatively high densities of lion and hyeana in the study area.

Prey abundance is believed to be one of the proximate factors driving resource selection in large predators (55). Furthermore, it is also known that prey size is an important consideration for leopards when choosing their prey (157). One of the objectives of this study was to determine whether prey species richness and/or prey biomass influenced the occurrence of leopards in the study area. The leopards preferred prey species occur in small herds (i.e. impala), or are solitary (i.e. duiker), in dense habitats and are common in the study area (Table 3). Interestingly, when included in the logistic regression model neither species richness nor prey weight were found to significantly influence leopard presence. This is presumably due to the low numbers of leopard detections in each category (Table 7). However, Abade et al. (174), also found a weak association between prey availability and leopard site-use in Tanzania's Ruaha landscape, and highlight that prey depletion is one of the main limiting factors to leopard occurrence and population density throughout their range (33, 158, 159).

Patterns revealed in the univariate analyses were more informative. For instance, the data showed that leopard captures and the detection of six prey species was proportionately high, however, the overall the number of captures was extremely low (n = 2) (Table 7). Perhaps predictably, the greatest proportion of leopard captures were found to in the absence of any prey species at all (Table 7), which may suggest prey species were avoiding areas where leopards were present (143), or that prey species did not encounter the cameras (143). The number of leopard captures in relation to prey weight categories was interesting. For instance, only 7 % of leopard captures were detected on the same trapping occasion as medium prey. Given that this is the frequently reported preferred weight range for leopards (20, 71, 142), this result is surprising. However, the greatest proportion of leopards (29 %) were detected on the same trapping occasion as prey in the large category (41 – 450 kg) which could suggest that leopards in the study area are selecting for larger prey. Indeed, Stander et al. (106) suggest a prey weight preference for leopards of 15 – 60 kg. Reanalyses with the 10 – 40 kg weight range, or against leopard biomass in the study area, might yield improved results.

To further improve knowledge and understanding of which prey species leopards prefer and which are avoided within a study area, Hayward et al. (46) recommend using a combination of sampling methods. For example, continuous follows and search-encounter methods are both considered effective ways to determine the diet of a predator (160, 161). However, both methods are challenging when studying shy and elusive predators such as leopards. Faecal analysis is another valuable technique used to ascertain a predator's diet (162). While, aerial counts and line transects are also known to be reliable methods of estimating wildlife densities (94, 98). Combining camera trapping with one or more of these techniques would increase the probability of identifying the majority of the leopards prey species (71).

From a practical viewpoint, using a camera trap survey to yield sufficient detections of multiple species to infer relationships between multiple species is problematic. For instance, occasion length has been found to determine the precision and accuracy of derived estimates (163). Cusack et al. (143) found that while both lion and prey detection had seemingly no effect on hyeana presence during one survey when an occasion length of 24 hours was used, once the occasion length was increased their importance changed considerably. Spatiotemporal correlations between lions and herbivores were similarly influenced by occasion length, with the effect of each herbivore species varying strikingly across occasion length (143). Yet, even an occasion length of 24 hours is unlikely to be suitable for detecting patterns of behaviour that have been shown to occur over an interval of just a few hours (143). Recently, Courbin et al. (164) showed that zebras fled from areas after encountering lions within a couple of hours of the encounter happening. Unless camera traps are installed at very high densities, such a reaction is likely to be undetected. However, the costs of installing more equipment could exceed that of fitting GPS- collars to a subset of individuals, from which more precise data may be obtained (143). Finally, Guillera Arroita et al. (163) recommend that where camera traps are used to detect patterns of behaviour, caution is used when defining what constitutes a trapping occasion, as well as other issues that may need to be incorporated into the study design process, such as the minimum number of sites and the costs of each survey.

7. Conclusions

Results from this study raise the question of whether interactions with hyeanas are having a negative effect on the population of leopards. While caution should be given before drawing inferences about the patterns of behaviour observed from the data. It is important to note that a recent study by Green et al. (145), indicated that populations of lions and hyeanas within the Reserve were changing in opposite directions, suggesting that the large predator guild inside the Reserve is being severely disrupted (165). In other parts of Africa, both lion and leopard populations are declining due to widespread habitat loss, poaching, retaliatory killing, prey depletion and poorly regulated trophy hunting (38, 166-169). A lack of data on the Reserves leopards' hinders the chances of identifying trends in the status of leopards inside the Reserve. However, if we hope to preserve the MMNR as an iconic sanctuary for large predators, we need to perform a rapid and accurate assessment of the leopard population, examine in greater detail the changes that are happening within the large predator guild and their underlying causal factors, and evaluate the impacts of this altered predator community on ecosystem function (145).

Protected areas in sub-Saharan Africa are fast becoming isolated land masses bordered by degraded rangelands and expanding human populations (170). The future preservation of large predators depends on the efficiency of sanctuaries to protect species, like leopards, that are particularly sensitive to loss of habitat and at high risk of persecution by people (19, 171). Effective community conservation programs can help alleviate conflicts outside of protected areas (172), and is crucial to long-term conservation of large predators (145). However, if sensitive species are allowed to decline within protected areas, not even the most resourceful conservation initiatives outside of them will be able to sustain large predator populations into the future (143).

Acknowledgements

This study was supported by sponsorship from the Speed Group, the University of Brighton and the Roman Wildlife Foundation. I am also indebted to the Kenya Wildlife Service, the National Commission for Science, Technology and Innovation and The Mara Conservancy for granting permission to undertake the research. This study would not have been possible without the efforts of my field assistant Jackson Okute, Alfred Betts (Mara Conservancy Tourism Warden), and William Nailenya senior rangers for their invaluable assistance and support. Thanks also to Adam Bannister for sharing his Mara Triangle leopard photo database and for his assistance with leopard identification. Finally, I would like to thank Dr Elena Chelysheva and Dr Bryony Tolhurst for their guidance, support and encouragement.

Role of the funding source(s)

The study sponsors had no involvement in the study design, collection, analysis or interpretation of the data, or in the writing of the report.

Conflicts of interest:

None declared.

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8. Appendices

Appendix A – Kenya Wildlife Service (KWS) research permit

KENYA
WILDLIFE
SERVICE

ISO 9001:2008 Certified

KWS/BRP/5001

Ms Eve Marie Hills
P.O.Box 1611-00606
NAIROBI
e-mail: eve.africa@yahoo.co.uk
mobile: 0705138175

Dear Ms Hills

PERMISSION TO CONDUCT RESEARCH IN MAASAI MARA ECOSYSTEM

We acknowledge receipt of your application requesting for permission to conduct research on a project titled: **'Comprehensive Leopard Population Survey in the Mara Using Non-invasive Survey Methods'**. The study will generate data and information to enhance conservation and management of the species in Maasai Mara Ecosystem.

You have been granted permission to conduct the study from **January – December 2019** upon payment to KWS academic research fees of **ksh.52,000** (Masters Study). You will abide by the set KWS regulations and guidelines regarding carrying out research in and outside protected areas. You will also be required to work closely with our Senior Scientist in-charge of Central Rift Conservation Area (CRCA), whom you will give the research project proposal and progress report on the study.

You will submit a bound copy of your MSc thesis to the KWS Director, Biodiversity Research and Planning on completion of the study.

Yours Sincerely,

PATRICK OMONDI, PhD, OGW
Ag. DIRECTOR
BIODIVERSITY RESEARCH AND PLANNING

Copy to:

- AD, CRCA
- Senior Warden, Narok Station
- Senior Scientist, CRCA
- Research Scientist, Maasai Mara Station

P.O Box 40241-00100, Nairobi, Kenya.
Tel: +254-020-2379407/8/9-15. Mobile: +254-735 663 421, +254-726 610 508/9.
Email: kws@kws.go.ke Website:www.kws.go.ke

Appendix B – NACOSTI research permit

THE SCIENCE, TECHNOLOGY AND INNOVATION ACT, 2013

The Grant of Research Licenses is guided by the Science, Technology and Innovation (Research Licensing) Regulations, 2014.

CONDITIONS

1. The License is valid for the proposed research, location and specified period.
2. The License and any rights thereunder are non-transferable.
3. The Licensee shall inform the County Governor before commencement of the research.
4. Excavation, filming and collection of specimens are subject to further necessary clearance from relevant Government Agencies.
5. The License does not give authority to transfer research materials.
6. NACOSTI may monitor and evaluate the licensed research project.
7. The Licensee shall submit one hard copy and upload a soft copy of their final report within one year of completion of the research.
8. NACOSTI reserves the right to modify the conditions of the License including cancellation without prior notice.

National Commission for Science, Technology and innovation
P.O. Box 30623 - 00100, Nairobi, Kenya
TEL: 020 400 7000, 0713 788787, 0735 404245
Email: dg@nacosti.go.ke, registry@nacosti.go.ke
Website: www.nacosti.go.ke

REPUBLIC OF KENYA

NACOSTI

National Commission for Science, Technology and Innovation

RESEARCH LICENSE

Serial No.A 22474

CONDITIONS: see back page

THIS IS TO CERTIFY THAT:
MS. EVE MARIE HILLS
of UNIVERSITY OF BRIGHTON, 41 Hollingbury Gardens-BN14 0EE Worthing,has been permitted to conduct research in *Narok County*

on the topic: *COMPREHENSIVE LEOPARD POPULATION SURVEY IN THE MARA USING NON-INVASIVE SURVEY METHODS*

for the period ending:
18th December,2019

Permit No : NACOSTI/P/18/52242/26906
Date Of Issue : 18th December,2018
Fee Recieved :Ksh 35278

....
Applicant's Signature

....
Director General
National Commission for Science, Technology & Innovation

NATIONAL COMMISSION FOR SCIENCE, TECHNOLOGY AND INNOVATION

Telephone:+254-20-2213471,
2241349,3310571,2219420
Fax:+254-20-318245,318249
Email: dg@nacosti.go.ke
Website : www.nacosti.go.ke
When replying please quote

NACOSTI, Upper Kabete
Off Waiyaki Way
P.O. Box 30623-00100
NAIROBI-KENYA

Ref: No. **NACOSTI/P/18/52242/26906**

Date: **18th December, 2018**

Eve Marie Hills
University of Brighton
ENGLAND.

RE: RESEARCH AUTHORIZATION

Following your application for authority to carry out research on ***"Comprehensive leopard population survey in the Mara using non-invasive survey methods"*** I am pleased to inform you that you have been authorized to undertake research in **Narok County** for the period ending **18th December, 2019.**

You are advised to report to **the County Commissioner and the County Director of Education, Narok County** before embarking on the research project.

Kindly note that, as an applicant who has been licensed under the Science, Technology and Innovation Act, 2013 to conduct research in Kenya, you shall deposit **a copy** of the final research report to the Commission within **one year** of completion. The soft copy of the same should be submitted through the Online Research Information System.

Kalerwa

GODFREY P. KALERWA MSc., MBA, MKIM
FOR: DIRECTOR-GENERAL/CEO

Copy to:

The County Commissioner
Narok County.

The County Director of Education
Narok County.

Appendix C – Emergency Response Plan

Emergency Response Plan

The aim of this document is to collate key information into a simple format for use by project personnel in the event of an emergency.

Produced by: Eve Hills (MRes Ecology Student UoB)	**Date completed**: 18 March 2019
Project: Density and Distribution of Leopards in the Maasai Mara National Reserve	**Country**: Kenya

Project Supervisor: Dr. Bryony Tolhurst (University of Brighton) Contact: b.tolhurst2@brighton.ac.uk Tel: **07766 875629**

Field Supervisor: Dr. Elena Chelysheva (Mara-Meru Cheetah Project) contact: cheetah9@mail.ru Tel: +**254 704 361069**

Country International dial out code: 00	**Time Zone**: GMT + 3 hours

Location	**Address (including GPS location where possible)**	**Telephone (including country code)**
Research and Accommodation Site	**G & G Hotel** **C14 Talek** **Kenya**	**Josef Tira (proprietor) + 254 721 633864** **Elena Chelysheva + 254 704 361069**
Project Management Plan	1) Assess situation and decide whether the incident is a crisis (threatens serious damage to human welfare) or non-crisis situation 2) Administer first aid 3) Contact field supervisor (if not present) 4) Contact additional specialised help (if required) GW Traveller (see information below). emergencies: +44 (0) 203 829 6745, 5) Contact UoB 6) Ensure someone is keeping a record of incident events 7) Complete Incident Report, send to Project Supervisor as soon as possible	
Transport	**Primary**: Private vehicle **Secondary**: Helicopter in extreme emergency	
	Address (including GPS location where possible)	**Telephone (including country code)**
Accident & Emergency Service	**AMREF** Flying Doctor Services	**+ 254 (0) 731 811 811 / 706 811 811 / 20 699 2000** ***Radio Frequencies:*** HF: 9116kHz LSB / 5796 kHz LSB ***Call Sign:*** Foundation Control
Nearest Medical Centre	**Shepherds Medical Centre** (24 hrs) Narok Distance from site approx. 2.5 hrs	+ 254 722 519 169

Nearest Fully Equipped Hospital	**The Aga Khan University Hospital** 3rd Parklands Avenue, Nairobi, Kenya	+ 254 20 366 2000
Nearest Airport	**Olkiombo** Airstrip Distance from site approx. 30 mins.	
	Wilson Regional Airport Off Airport North Road. P.O Box 19001 (00501) Nairobi Kenya Distance from Olkiombo approx.30 mins **Jomo Kenyatta International Airport** Embakasi, Nairobi, Kenya Distance from site approx. 1.5 hrs (road and air)	+ 254 724 256 837 + 254 724 255 343 +254-020-6822111/ Mobile: +254 722 205
Local Emergency Evacuation Service	**AMREF Flying Doctors** Summit Center, 2nd Floor West Wing Block A, Sokoine Road ***Emergency Contacts:*** +255 718181318. +255 789133133 ***General Contacts*** + 255 719881887, +255745716581, + 255684818071 Email: marketing.arusha@flydoc.org	
Support Embassy	**British High Commission** Upper Hill Rd, Nairobi, Kenya	+ 254 20 287 3000

24-Hour Emergency Medical & Evacuation Assistance	**Go Walkabout Travel Insurance** IF YOU NEED EMERGENCY MEDICAL ASSISTANCE ABROAD OR NEED TO CUT SHORT YOUR TRIP: contact Emergency Assistance Facilities 24 hour emergency advice line on: **+44 (0) 203 829 6745**

Appendix D – Risk Assessment

SCHOOL OF PHARMACY AND BIOMOLECULAR SCIENCES GENERAL RISK ASSESSMENT FOR ALL ACTIVITIES

Date: 15/03/2019	Assessor:	Location:	Assessment No.	Review date:
			To be completed by Chair of Safety Committee	

Risk Category: high/med/low* High	Activity to be assessed: Field Research Trip Maasai Mara National Reserve

HAZARD Look only for hazards which could reasonably expect to result in significant harm under the conditions in your workplace	**WHO MIGHT BE HARMED?**	**IS THE RISK ADEQUATELY CONTROLLED?**	**WHAT FURTHER ACTION IS NECESSARY TO CONTROL RISK?**	**RESULT****
List hazards here:	List groups of people who are especially at risk from the significant hazards which you have identified:	List existing controls here or note where the information may be found:	List the risks which are not adequately controlled, and the action you will take where it is reasonably practicable to do more. You are entitled to take cost into account, unless the risk is high:	
Transportation: Road hazards: fast/reckless drivers, pot holes, wildlife, rain/mud, dust, poor lighting, poorly maintained tarmac or dirt/gravel (corrugated) roads.	Students, field assistants, reserve visitors and employees (rangers and camp staff)	When dangerous wildlife are present, only closed-topped vehicles are used. Vehicles used for fieldwork should travel at no more than 50km/hr (30mph) but usually around 30km/hr (20mph). Only qualified drivers can drive the vehicles. Ensure project vehicles are well maintained. Seatbelts must be worn whenever available. Restrict driving at night to only when necessary for the research related tasks. Avoid driving in the rain or while tired. Maintain appropriate distance between vehicles and travel at safe speeds (particularly on unpaved roads) to allow stopping when necessary. Carry cell phone and emergency equipment, such as GPS unit, first aid kit and water in case of accident/break down on road.	N/A	A

*Refer overpage for Departmental guidelines to risk category

**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

Environment & Geographic: Dehydration / Sun / Heat exposure; sudden storms or drops in temperature	Student/field assistants	Bring and utilize adequate clothing (including wide-brimmed hats, long sleeves and sunglasses), high-factor sunscreen, drink plenty of water and eat enough food throughout the day, stay in the shade as much as possible, and leave strenuous tasks until cooler times of day whenever possible. Take appropriate precautions to avoid over-exposure to the sun and dehydration; have frequent "water and snack breaks" to stay replenished during active field work. Exercise precaution even when the sky is overcast. Dress warmly for early morning activities or evenings; recommend clothing that can be layered. Monitor local media for current weather conditions. Monitor participants for general health at all times and have appropriate materials in First Aid kits (rehydration salts, etc.).	N/A	A
Wildlife: Wildlife encounters	Student, field assistants	Be aware of the risks and necessary precautions associated with living and working in the midst of a wilderness area, particularly when walking in the open bush. Never wander off alone or beyond the camp perimeter. Adhere to correct field practice and safety procedures: field communication, use of hand-held radios, and response to wildlife in close proximity, etc. remain alert and aware of your surroundings at all times, and to carefully follow	N/A	A

*Refer overpage for Departmental guidelines to risk category

**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

		instructions of project supervisor (Dr Elena Chelysheva). Adhere to project rules and protocols at all times. Research will be conducted from closed-topped vehicles at all times when dangerous wildlife are present. Wear appropriate footwear and long pants for protection from snakes, insects or vegetation. Utilize armed rangers to accompany field tasks where dangerous animals are present (participants are NEVER permitted to touch or handle firearms).		
Health: Biting insects (mosquitoes, ticks, etc.)	Student, field assistants	Avoid insect bites wherever possible: use insect repellent (20 – 30% DEET is generally recommended) and wear neutral-coloured field clothes, including long trousers tucked into socks. Pack appropriate medication for allergic reactions to insect bites to (e.g. antihistamines). Be aware of the possibility of ticks, where they might be found, and how to avoid them. Check skin and clothes for ticks daily. If a tick is found, remove it using fine-point tweezers, grasping the tick as close to its mouth as possible, slowly pulling the tick straight out; immediately wash the area with soapy water.	N/A	A
Environment & Geographic: Terrain: uneven, rocky, steep, dusty or muddy ground, dense vegetation (thorn bushes), animal burrows and other holes.	Student, field assistants	Walk slowly and carefully along tracks and paths where possible, and be aware of your surroundings at all times. Wear high quality, well broken-in walking boots with ankle protection and wear long trousers to avoid scratches from thorny vegetation. Carry a personal First Aid kit and	N/A	

*Refer overpage for Departmental guidelines to risk category

**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

		mobile phone at all times, and never work alone. Take regular breaks to avoid overexertion and contact supervisory staff if feeling unwell.		
Wildlife: Venomous snakes: spitting cobras, vipers	Student, field assistants	Be aware of the possibility of snakes, where they might be found, and how to avoid them. Wear sturdy, ankle-high footwear for protection when working in the field and closed-toe shoes at all other times. Follow project supervisor's advice in snakebite prevention and what to do in the event of an incident prior to fieldwork.	N/A	A
Personal Safety/Security: Firearms: armed guards accompany teams in the field	Student, field assistants	Only qualified, regularly trained, authorized field rangers may handle firearms or act as armed guards. Guards must keep their weapons unloaded when not required and within their possession at all times. Guns must have a safety catch. Participants are NEVER permitted to touch or handle firearms.	N/A	A
Plants: Dangerous vegetation: poisonous if ingested or in contact with open wounds, thorns (acacia), allergies	Student, field assistants	Identify potentially harmful plants and take action to avoid contact. Carry medication (antihistamines) in case of contact and allergic reactions. Wear appropriate clothing in the field: long trousers, ankle-high hiking boots, etc.	N/A	A

*Refer overpage for Departmental guidelines to risk category

**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

Personal Safety/Security: Theft / petty crime	Student, field assistants	Take standard precautions such as not traveling alone, never walking around alone (especially after dark), storing passport and money safely, avoid wearing expensive jewellery and flashing money or electronics, leaving unnecessary valuables at home, and to guard against pickpockets, particularly when in urban centres during recreational time or before/after the team. Only use official taxis and to agree on a price in advance.		A
Health: Anaphylactic Shock or other allergic reaction to stings / food / pets at the field site	Student, field assistants	Carry antihistamines, etc. in case of an allergic reaction.	N/A	A
Health: Disease	Student, field assistants	Be aware of the diseases found in Africa: hepatitis, schistosomiasis, trypanosomiasis, filariasis, leishmaniasis, chikungunya, Rift Valley fever, tick bite fever, dengue, West Nile virus, brucellosis, rabies, HIV/AIDS, tuberculosis, cholera, plague, and typhoid. Seek medical advice prior to travelling and have appropriate inoculations and up-to-date immunizations including tetanus. Only use potable/treated water for consumption. Wear protective gloves if collecting scat samples and wash hands after all field excursions. The project site is not in a malaria area.	N/A	A

*Refer overpage for Departmental guidelines to risk category

**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

Health: Gastrointestinal illness / diarrhoea	Student, field assistants	Ensure good hygiene practices are maintained at camp and during field work. Have an ample supply of potable water. Bring a personal first-aid kit including stomach illness relief and prescribed antibiotics. Always wash hands with soap and water or a hand sanitizer before eating, and drink filtered or bottled water. Prior to travel, seek GP's advice about options for treating travellers' diarrhoea.	N/A	A
Health: Allergy, scratch or bite from a domestic animal.	Student, field assistants	Avoid contact with unknown cats and dogs.	N/A	A

* As far as the Department is concerned the levels can be defined generally as follows:

High Very likely to cause multiple/single death or serious injury. It is highly unlikely that this category will apply to any activities within this Department

Medium Quite possible to cause injury or disease capable of keeping an individual off work for a period of one hour or more

Low No or very low risk of injury or disease as long as all reasonable precautions have been taken so far as is reasonably practicable

A low risk category for all operations should be the normal state of the Department

If you have any further queries please do not hesitate to contact either Professor Adrian Bone, Dr R W Daisley or Dr K J Rutt.

FILE COPY WITH CHAIR OF THE SAFETY COMMITTEE

*Refer overpage for Departmental guidelines to risk category
**Key to result: T = trivial risk; A = adequately controlled risk; N = not adequately controlled; U = unable to decide, further action required.

Appendix E – SPSS Data Output

Model Information

Dependent Variable	Leopard[a]
Probability Distribution	Binomial
Link Function	Logit

a. The procedure models 0 as the response, treating 1 as the reference category.

Case Processing Summary

	N	Percent
Included	1938	100.0%
Excluded	0	0.0%
Total	1938	100.0%

Categorical Variable Information

			N	Percent
Dependent Variable	Leopard	0	1903	98.2%
		1	35	1.8%
		Total	1938	100.0%
Factor	Habitat	1	774	39.9%
		2	1164	60.1%
		Total	1938	100.0%
	Lion	0	1905	98.3%
		1	33	1.7%
		Total	1938	100.0%
	Hyeana	0	1785	92.1%
		1	153	7.9%
		Total	1938	100.0%

Continuous Variable Information

		N	Minimum	Maximum	Mean	Std. Deviation
Covariate	Cum Prey Weight kg	1938	0	6897	838.23	1591.268
	Sp, Richness	1938	0	6	.90	1.133

Goodness of Fit[a]

	Value	df	Value/df
Deviance	91.555	387	.237
Scaled Deviance	91.555	387	
Pearson Chi-Square	676.510	387	1.748
Scaled Pearson Chi-Square	676.510	387	
Log Likelihood[b]	-56.712		
Akaike's Information Criterion (AIC)	125.425		
Finite Sample Corrected AIC (AICC)	125.468		
Bayesian Information Criterion (BIC)	158.841		
Consistent AIC (CAIC)	164.841		

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Cum Prey Weight kg, Habitat , Sp, Richness

a. Information criteria are in smaller-is-better form.

b. The full log likelihood function is displayed and used in computing information criteria.

Omnibus Test[a]

Likelihood Ratio Chi-Square	df	Sig.
9.860	5	.079

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Cum Prey Weight kg, Habitat , Sp, Richness

a. Compares the fitted model against the intercept-only model.

Tests of Model Effects

	Type III		
Source	Wald Chi-Square	df	Sig.
(Intercept)	28.879	1	.000
Lion	.451	1	.502
Hyeana	6.149	1	.013
Cum Prey Weight kg	.346	1	.556

Habitat	.815	1	.367
Sp, Richness	1.623	1	.203

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Cum Prey Weight kg, Habitat , Sp, Richness

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval Lower	95% Wald Confidence Interval Upper	Hypothesis Test Wald Chi-Square	Hypothesis Test df	Hypothesis Test Sig.
(Intercept)	1.951	1.1130	-.230	4.133	3.073	1	.080
[Lion =0]	.699	1.0405	-1.341	2.738	.451	1	.502
[Lion =1]	0[a]	.	.	.	.	.	.
[Hyeana=0]	1.113	.4489	.233	1.993	6.149	1	.013
[Hyeana=1]	0[a]	.	.	.	.	.	.
Cum Prey Weight kg	9.276E-5	.0002	.000	.000	.346	1	.556
[Habitat =1]	.348	.3860	-.408	1.105	.815	1	.367
[Habitat =2]	0[a]	.	.	.	.	.	.
Sp, Richness	.269	.2114	-.145	.684	1.623	1	.203
(Scale)	1[b]						

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Cum Prey Weight kg, Habitat , Sp, Richness

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Tests of Model Effects

Source	Type III Wald Chi-Square	Type III df	Type III Sig.
(Intercept)	28.949	1	.000
Lion	.461	1	.497
Hyeana	6.393	1	.011
Habitat	.950	1	.330
Sp, Richness	3.058	1	.080

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Habitat , Sp, Richness

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval Lower	95% Wald Confidence Interval Upper	Hypothesis Test Wald Chi-Square	Hypothesis Test df	Hypothesis Test Sig.
(Intercept)	1.930	1.1133	-.252	4.112	3.004	1	.083
[Lion =0]	.706	1.0400	-1.332	2.744	.461	1	.497
[Lion =1]	0[a]	.	.	.	.	.	.
[Hyeana=0]	1.132	.4478	.255	2.010	6.393	1	.011
[Hyeana=1]	0[a]	.	.	.	.	.	.
[Habitat =1]	.374	.3835	-.378	1.125	.950	1	.330
[Habitat =2]	0[a]	.	.	.	.	.	.
Sp, Richness	.332	.1899	-.040	.704	3.058	1	.080
(Scale)	1[b]						

Dependent Variable: Leopard

Model: (Intercept), Lion , Hyeana, Habitat , Sp, Richness

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Tests of Model Effects

Source	Type III Wald Chi-Square	Type III df	Type III Sig.
(Intercept)	154.615	1	.000
Hyeana	6.436	1	.011
Habitat	.886	1	.346
Sp, Richness	2.956	1	.086

Dependent Variable: Leopard

Model: (Intercept), Hyeana, Habitat , Sp, Richness

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval Lower	95% Wald Confidence Interval Upper	Hypothesis Test Wald Chi-Square	Hypothesis Test df	Hypothesis Test Sig.
(Intercept)	2.628	.4317	1.782	3.475	37.066	1	.000
[Hyeana=0]	1.135	.4473	.258	2.011	6.436	1	.011
[Hyeana=1]	0[a]	.	.	.	.	.	.
[Habitat =1]	.360	.3824	-.389	1.109	.886	1	.346
[Habitat =2]	0[a]	.	.	.	.	.	.
Sp, Richness	.324	.1887	-.045	.694	2.956	1	.086
(Scale)	1[b]						

Dependent Variable: Leopard

Model: (Intercept), Hyeana, Habitat , Sp, Richness

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Tests of Model Effects

Source	Type III Wald Chi-Square	df	Sig.
(Intercept)	162.497	1	.000
Hyeana	7.899	1	.005
Sp, Richness	2.518	1	.113

Dependent Variable: Leopard

Model: (Intercept), Hyeana, Sp, Richness

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval Lower	95% Wald Confidence Interval Upper	Hypothesis Test Wald Chi-Square	Hypothesis Test df	Hypothesis Test Sig.
(Intercept)	2.697	.4273	1.860	3.535	39.844	1	.000
[Hyeana=0]	1.230	.4378	.372	2.088	7.899	1	.005
[Hyeana=1]	0[a]	.	.	.	.	.	.
Sp, Richness	.295	.1862	-.069	.660	2.518	1	.113
(Scale)	1[b]						

Dependent Variable: Leopard

Model: (Intercept), Hyeana, Sp, Richness

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.

Tests of Model Effects

Source	Type III Wald Chi-Square	df	Sig.
(Intercept)	276.936	1	.000
Hyeana	6.523	1	.011

Dependent Variable: Leopard

Model: (Intercept), Hyeana

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	3.038	.3869	2.279	3.796	61.638	1	.000
[Hyeana=0]	1.101	.4313	.256	1.947	6.523	1	.011
[Hyeana=1]	0[a]	.	.	.	.	.	.
(Scale)	1[b]						

Dependent Variable: Leopard

Model: (Intercept), Hyeana

a. Set to zero because this parameter is redundant.

b. Fixed at the displayed value.