

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences



Czech University of Life Sciences Prague

**Faculty of Tropical
AgriSciences**

**Does resource dispersion drive leopard habitat
selection?**

MASTER'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled “Does resource dispersion drive leopard habitat selection?” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague, the 14th May 2020

Kamila Jandová

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Abstract

Leopards (*Panthera pardus*) are known to be obligate carnivores with large variety of prey species and unlike other large felids they can survive in human modified habitats. The main goal of this thesis was to answer the question: “Does resource dispersion drive leopard habitat selection?” To answer this question, possible prey species were firstly identified from camera trap data and then for each prey species the habitat suitability model was built using MaxEnt software. Output habitat suitability maps of prey species then served as the input data for modelling the leopard habitat suitability. The modelling was done by using eight potential prey species – common duiker, bushbuck, cape grysbok, porcupine, baboon, mongoose, genet and hare, together with environmental variables (land cover, aspect, slope, cattle and sheep density, river, roads, protected areas) and GPS collar data from leopards from the Western and Eastern Cape Provinces. The most important finding of this thesis was that habitat suitability of leopard is increasing with habitat suitability of prey species and that prey species have individually higher gains in predicting leopard occurrence than environmental variables and thus the hypothesis that resource dispersion has greater influence on leopard distribution than environmental factors was confirmed.

This result has far reaching consequences for leopard conservation and wildlife management plans. More conservation actions should be done on protecting prey species in order to better maintain long term leopard survival.

Key words: MaxEnt, *Panthera pardus*, prey species, South Africa, species distribution modelling, wildlife conservation.

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1. Introduction and Literature Review

Resource selection in large felids is driven by many environmental and ecological factors such as climate, landscape cover, prey species and their abundance and anti-predatory behaviour. Presence of congeners or other competitors might also play a limiting role in resource selection (Sunquist & Sunquist 1989). It was proven that on the broad scale, abundance of large carnivores is driven by distribution or abundance of herbivores. But it was found that at fine scale African lions in Serengeti are not selecting hunting areas according to high prey densities but according to where it is easier to catch the prey (Hopcraft et al 2005). The same was found in leopards in Phinda Private Game Reserve in South Africa (Balme 2007).

Leopards inhabit large scale of habitats from woodlands, grassland savannah and mountains to shrublands, semi-deserts and coastal scrub (Swanepoel et al. 2016). They can live in almost every habitat (Sunquist & Sunquist, 2002) even in human modified ones unlike other large felids (Ray et al. 2005). Leopards are obligate carnivores with large variety of prey species - 92 (Ray et al. 2005, Hayward et al. 2006) from small to medium-sized ungulates to rodents, rabbits, birds or arthropods (Nowak 2005).

Habitat and prey losses are major threats to leopards. Human population is increasing and so is demand for habitat and resources usage. Even though leopards are still widely distributed, African leopards have lost 36.59% of their range during the past 100 years (Ray et al. 2005). Situation in South Africa is such, that only 20 % (248 770 km²) of the South African range is suitable for leopards as their habitat and is also fragmented into four major areas which are including Eastern and Western Cape Provinces (Swanepoel et al. 2013).

Increasing human demand for habitat and resources is often leading to wildlife having to be in involuntary close contact with humans, and competition for food resources and space is rising. The result of this rivalry is often human wildlife conflict, a major cause of carnivore extinctions at local scales (Ray et al. 2005).

Carnivores have higher tendency to get into conflict with humans because of their large home ranges and dietary habits (Inskip & Zimmermann 2009). Occurrence of

leopards in areas managed by humans will always lead to predation on livestock (Athreya & Belsare 2007). People who are dependent on livestock and game animals are in a position, where predation on their livestock is causing them economical costs (Constant et al. 2015). But leopards might be unfairly persecuted for livestock losses which they did not caused, but were committed by other predators such as jackal or caracal (Ott et al. 2007).

1.1. Why Carnivores?

Large terrestrial carnivores are important group of animals which have ecological effects on their environment. Many animals from this group are directly affecting their prey, which may lead to indirect effect as well. As an example can be declining population of leopards in West Africa. Decline in leopard's population is coinciding with increase abundance of olive baboons (*Papio anubis*) (Wolf and Ripple 2016). As a result prey of baboons, other primates, birds and ungulates has rapidly declined. Baboons might also get into a conflict with local people, since they feed on their agricultural crops and livestock (Soulé 2010).

Large carnivores are important drivers of wildlife tourism and they bring economic and social human benefits with them (Wolf and Ripple 2016).

1.2. Solitary Carnivores

Solitary species are those species which have limited social interactions with their conspecifics. They avoid them and by this, they gain a greater fitness benefit in contrast to social animals (Logan & Sweanor 2001). It is known 179 solitary living carnivores from total number of 247 carnivores. These 179 carnivores are facing competition between conspecifics which also brings with it some limitations, such as getting to the shared resources is harder, stalking prey in different habitat types, where is it sometimes hard to be inconspicuous or undetected. Solitary carnivores have separated territories or they temporary avoid each other. Times when they meet together are when there is territorial conflict or during courtship season. Resource dispersion,

animal spatial distribution or kinship are principles which explain occurrence of social interactions between solitary carnivores. (Elbroch et al 2017).

Savanna is a type of habitat which can with its rich vegetation support herbivores of different sizes in high densities and carnivores can be occurring there in high numbers too, due to wide range of prey presence. That might be also reason, why are interaction between carnivores more frequent there than in other habitats (Hunter & Hilde 2005).

1.2.1. Resource dispersion hypothesis

Resource dispersion hypothesis (RDH) assumes that places with patchily distributed resources across space and/or time will have reduced resource-based costs of sharing territory with conspecific (Johnson et al. 2002). When the RDH is applied to solitary species it predicts that places with highest richness of resources became zones where territories of individuals might overlap, even though they are remaining behaviourally solitary. Pumas had higher chance to hunt in overleaping home range areas in the winter than in areas without overlaps. Overlaps between home ranges might be higher on places where migratory prey aggregates (Elbroch et al. 2016).

When young pumas are trying to search for a place to settle, females behave differently from males. Females are searching for a place which is closer to their mother and to place where they were raised. This behaviour leads to life where home ranges of related females often overlap or are next to each other. And in addition leads to benefits to share resources with relatives. Leopard's females are also showing this kind of tendencies (Sunquist & Sunquist 2014).

1.2.2. Resource selection function

Resource selection function (RSF) is a function by which it can be described distribution and abundance of a species, since each species is dependent on some resources which are somehow distributed (Boyce & McDonald 1999).

Species will be selecting resources which are the most likely to satisfy their needs for surviving, as it is presume now, and high quality will be selected more compare to the lower quality resources. Optimal foraging theory predicts that if the

availability of resources changes so the usage of resources by the animals might change as well, hence comparison of available resources with their usage or non-usage is important to get useful conclusion, how is the resource selection working for particular species. The amount of resources which is exploited by the animal in certain period of time is usage of resources. The amount of resources which is accessible to the animal in that same period of time is availability of resources (Manly et al. 2002) Resource selection function models have its use in conservation and management and they have its implications, therefore the key stone of resource selection models is their prediction reliability (Boyce et al. 2002).

1.2.3. Habitat selection

Habitat selection is a process which includes behavioural decisions with innate and learned origin which animals make in order to decide which habitat to use at different scales of the environment (Krausman 1999).

Individuals of all species need to fulfil two fundamental things- to survive and reproduce. To make that happen they require resources which also include variations in landscape features such as vegetation cover, den sites, water, places to hide from predators and food. Availability of food is one of the most important features of all (Hunter & Hinde 2005).

Habitat selection affects species interactions, population dynamics and long term survival (Morris 2003). Investigating how environmental changes affect individual behaviour, as well biological dynamics can improve our understanding of species biology and evolution, as well as guide conservation management decisions (Johnson et al. 2006; Takahata et al. 2014).

RSFs have been developed to help us understand and underpin how organisms use environmental indicators which drive their choices in order to select habitat. If we understand, how animals are selecting their habitats, we can then find ways how to improve and restore environments which were damaged due to bad influence of humans on them. Poor habitat selection choices made in quickly changing environments may lead the species to select habitat with ecological traps (Schlaepfet et al. 2002).

One individual species can show significant diversity in its spatial ecology across different sites (Bothma et al. 1997; Mizutani & Jewell 1998; Marker & Dickman 2005). To fully grasp the species ecology, the research on a broad scale is needed to provide precise data. A leopard is a good example of such species as it is geographically widespread and can be found in various habitats across African and Asian continent. (Nowell & Jackson 1996). It is especially important to understand how and why species are moving, and are disturbed within human dominated environments (Bothma et al. 1997; Mizutani & Jewell 1998; Marker & Dickman 2005). Leopards in the Western and Eastern Capes are an example of a top level predator surviving in and around heavily modified human environments. Identifying how they select their habitat is crucial for their long term survival.

RSFs models can be based on scales defined by Johnson (1980). First order selection (the entire species range), second order selection (home range of individual or group), third order selection (resource or habitat usage within individual's home range or group's home range) and fourth order selection (resource availability at the sites within home range).

1.3. Leopard Ecology and Behaviour

1.3.1. Morphology

Leopard morphology varies greatly in South Africa with smaller animals occurring further south. The head and body length of leopard is 91-191 cm, tail is 58-110 cm long and shoulder height is 45-78 cm. Males are heavier than females with weight between 37-90 kg and between 28-60 kg for females. Fur has many variations of colours and patterns. The base colour ranges from pale yellow straw to brownish yellow. Belly with inner parts of limbs are white. Back with shoulders, upper legs are covered with black spots arranged into rosettes. Head with throat and chest are covered with small black spots and belly with large black spots (Figure 1) (Nowak 2005).

Small male individuals with weight about 31 kilograms and females with weight about 21 kilograms could be found in mountainous area of the Cape Province in South Africa (Sunquist & Sunquist 2002).



Figure 1. Male leopard on the road in Kgalagadi Transfrontier Park, South Africa (author: Matthew Schurch 2020).

1.3.2. Habitat and geographic distribution

Leopards are found from the southern-most points of Africa through to the Middle East Asia to the Amur Peninsula in the Russian Far East (Stein & Hayssen 2013). In Arica they are distributed in Southern Africa, East Africa, Central Africa, West Africa and North Africa (Figure 2). Only isolated populations of leopards are occurring in North Africa due to restriction of their former range by 97 %. In contrary probably the healthiest populations of leopards are occurring in Southern Africa, when we look at their entire distribution (Stein et al. 2020).

Leopards inhabit large scale of habitats from woodlands, grassland savannah and mountains to shrublands, semi-deserts and coastal scrub, but they prefer rocky and wooded habitat types (Swanepoel et al. 2017). The possible reason why leopards use mountainous area is that they can hide from human persecution and do not have to compete so much for the space with people there, as in less rugged human used areas (Swanepoel et al. 2013).

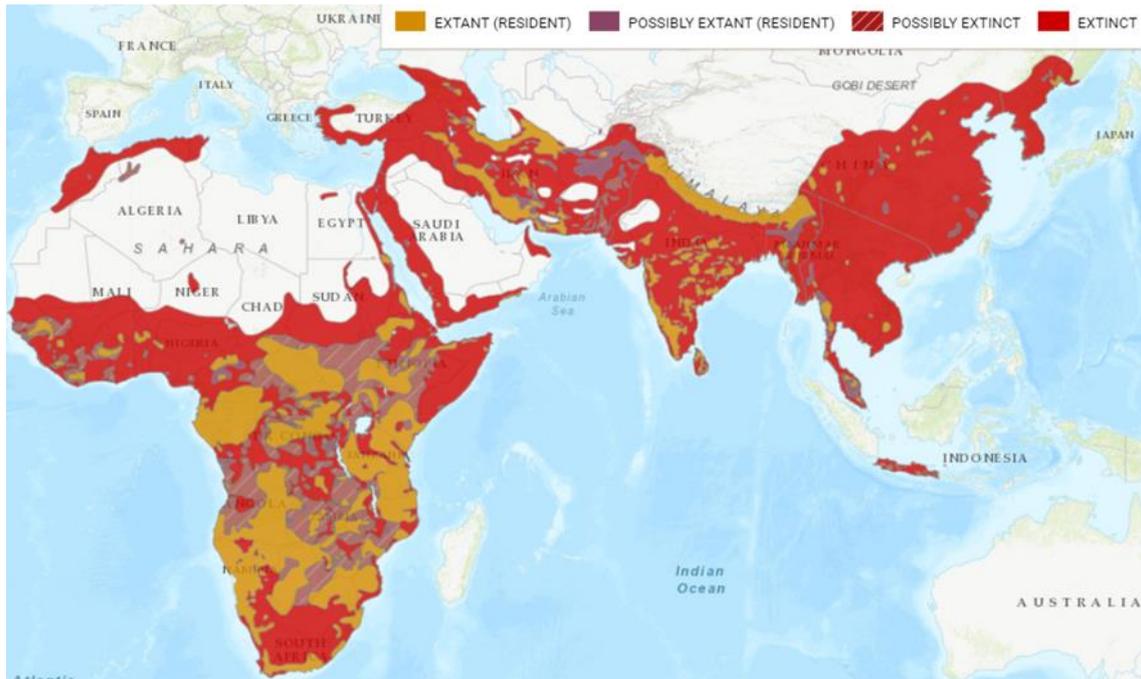


Figure 2. Geographical distribution of leopard (Source: Stein et al. 2020).

1.3.3. Range and space usage

Leopards are territorial solitary animals (Macdonald & Loveridge 2010). Only period to be seen together with others is when mating or mother with cubs, however male leopards are often in touch with females and cubs they know and they are even tolerant to the cubs of a female they have mated with before. Territorial fights between leopards are unusual, mainly between neighbours which know each other for a long time and are aware of each other presence (Hunter 2015). Bond between mother and daughters is really strong and permanent, that might explain tolerance of daughters on overlapped ranges (Estes 1991). Territories of daughters contain parts of mother's range and they share it (Stein & Hayssen 2013).

Habitat, prey availability and threats are influencing leopard's density, from 1 to more than 30 individuals per 100km² (Macdonald & Loveridge 2010). Leopards in the Congo Basin are occurring in small numbers or are even absent in areas where human villages are. The reason why is so, is that local people are hunting leopards prey and so the resources for the leopard are depleted (Pitman 2012).

The centre area of a home range is defended by adult individuals against same kind and sex. There is some sort of tolerance between leopards when it comes to edges of ranges which overlap with edges of neighbour's territory (Hunter 2015). Large overlaps between ranges are in areas where prey resources are not abundant so much. How much the neighbouring ranges overlap is influenced by prey resources and by presence of other large competitors in the area (Bothma & Walker 1999). Males have larger range than females which leads to, that one leopard's range contains a number of females' ranges. Size of male range depends on number of females inside it, however, females' home range size is influenced by availability of suitable prey (Hunter & Hinde 2005). Small ranges are found in areas with prey abundance and larger ranges are found in areas with lower prey abundance (Stein & Hayssen 2013).

1.3.4. Prey and suitable habitat for hunting

Leopards are like other large cats obligate carnivores however they are also opportunistic generalists. Their diet is composed from large variety of prey species but predominantly they hunt medium-sized ungulates (Ray et al. 2005).

Because leopards are solitary, they usually avoid hunting species which pose high risk of injury to them. Species to which they avoid to prey on are elephant, hippopotamus (*Hippopotamus amphibius*), Cape buffalo (*Syncerus c. caffer*) and eland (*Tragelaphus oryx*) (Hayward et al. 2006). Small animals like Rock hyrax (*Procavia capensis*) or klipspringer antelope (*Oreotragus oreotragus*) are usual prey for leopard in mountain and rocky areas (Swanepoel et al. 2016).

Mongoose was recorded as potential prey item for a leopard in 7 studies, as an actual prey item in 4 studies and 6 times in leopard scats (Hayward et al. 2006; Martins et al. 2011). Porcupine was recorded as a potential prey item in 1 study and there was no record of being an actual prey item in used studies (Hayward et al. 2006). However, porcupine was recorded to be occurring 2 times, 1 time and 5 times in leopard scats (Martins et al. 2011; Fischer & Schwarz 2006; Williams et al. 2018) and 5 times as a feeding remains (using clusters of GPS locations) (Martins et al. 2011). Hares (*Lepus* sp.) were report as a potential prey item in 9 studies and as actual prey item in 4 studies (Hayward et al. 2006). Lagomorphs were reported to be occurring 10 times and 7 times in scats (Martins et al. 2010; Fischer & Schwarz 2006) and 1 time in feeding remains (using clusters of GPS locations) (Martins et al. 2011). Baboon was recorded as potential prey item in 10 studies and as actual prey item in 5 studies (Hayward et al. 2006). It was recorded 4 times, 12 times, 4 times and 17 times in scats of a leopard (Martins et al. 2011; Fischer & Schwarz 2006; Norton et al. 1986; Williams et al. 2018). Common duiker has been reported as possible prey item in 11 studies as well as actual prey item. It was recorded 20 times, 2 times, 3 times, 3 times and 16 times in scats (Fischer & Schwarz 2006; Otto et al. 2007; Norton et al. 1986, Martins et al. 2010; Williams et al. 2018) and 4 times as feeding remains (using clusters of GPS locations) (Martins et al 2011). Cape grysbok was reported as potential prey item in 1 study and in no study as actual prey item (Hayward et al. 2006). It was reported to be occurring 3 times, 4 times and 29 times in scats (Martins et al. 2011; Otto et al. 2007; Norton et al.

1986). Bushbuck was reported as potential prey in 13 studies and as actual prey item in 12 studies (Hayward et al. 2006). It was reported to be occurring 6 times, 81 times and 81 times in scats (Otto et al. 2007; Fisher & Schwarz 2006; Williams et al. 2018). Genets were reported to be potential prey item in 7 studies and as actual prey item in 4 studies (Hayward et al. 2006).

Hayward et al. (2006) were using data from published and unpublished sources ranging from years 1960 to 2005, from different African countries. Martins et al. (2010) were collecting data in Western Cape (South Africa) in Cederberg Mountains, where scats were collected between 2004 and 2008, resulting in 93 leopard scats. Leopard feeding remains located by cluster of GPS localities are coming from 10 adult leopards collared between 2005-2009. Otto et al. (2007) were working with 40 scat samples collected in Baviaanskloof regions and adjacent rangelands in Eastern Cape (South Africa) from April till September 2004. Fischer and Schwarz (2006) were working with 179 scat samples collected in Soutpansberg (South Africa) between 1999 and 2003. Norton et al (1986) were working with 237 scats collected in south – western Cape mountains. Williams et al. (2018) were working with 237 scat samples collected in Soutpansberg Mountains in Limpopo province (South Africa) between July 2011 and December 2015.

All publications mentioned above, which recorded bushbuck as a prey item or its occurrence in the leopard scats, have the highest accounts of being a leopard prey. Moreover bushbuck is significantly preferred prey with impala and common duiker by leopard (using Jacob's index) (Hayward & Kerley 2008). Common duiker has the second highest account of being a prey item, and as it was written it belongs between the species which are significantly preferred, but common duiker is more frequently taken as prey item than bushbuck (Hayward et al 2006). However, looking at the studies which were focusing on Western and Eastern Cape (Martins et al. 2010; Otto et al. 2007; Norton et al. 1986), the highest number of occurrences in the scat analyses had cape grysbok. That might be caused by the fact that Cape grysbok is an endemic species to the South Africa and is widespread and locally common within its historical range in the Eastern and Western Cape provinces (Castelló 2016), so no records of cape grysbok could be made in studies which were not focused on Western and Eastern Cape. Common duiker is on the second place and bushbuck on third.

Baboons are known to attack and kill leopards in order to defend the trope. Two studies with focus on Western Cape are recording occurrence of baboon in the scats. Two remaining studies with focus on northern part of South Africa are recording higher numbers. According to Hayward et al. (2006), leopards significantly avoid preying on baboons (based on Jacobs's index) and are taken significantly less frequently than expected based on their abundance. This might be caused into some degree by risk of being injured or even killed (Kiffner et al. 2013). Leopards might prey on baboons when larger prey is less abundant (Sedensticker 1983), but new findings are showing that female leopards in Welgevonden Private Game Reserve in Waterberg Mountaintains in South Africa are predated on baboons unusually high and their diet was consisting of 20.2% from baboons, and it have become the highest value of predation on baboons ever recorded (Jooste et al. 2013). However Ott et al. (2007) in their study focused on Baviaanskloof region, disprove the claim that leopards are easily preying on baboons, even if the baboons are abundant in the region.

Porcupine was most abundant prey item from the all articles in the study which was conducted in Cederberg mountains in Western Cape. Porcupines are taken as prey in accordance to their abundance (Hayward et al. 2006). But Fisher and Schwartz (2010) found that leopards are taking porcupines less frequently even though they are widespread species in Lajuma Mountain Retreat, Soutpansberg in South Africa. Leopard individuals might develop preference for certain type of prey and specialize on its hunting and it might be learned. Such example could be a leopard male from Kalahari Desert, which developed a technique to ambush porcupines when they walked out from their dens. (Sunquist & Sunquist 2002).

Genet, mongoose and hare are all taken as prey in accordance to their abundance (Hayward et al. 2006). Lagomorphs accounted the highest occurrence in leopard scats in the study conducted in Cederberg mountains in Western Cape. This area is also the only one, compare to other areas from other publications mentioned above, with focus on South Africa, which has reports of mongoose being found in leopard scats

It was found that leopards in Phinda nature reserve in Kwa-Zulu Natal, South Africa hunt in less dense vegetation. Ideal habitat to hunt for leopards should be dense enough to provide them safe approach and distance to attack without being spotted by

the prey, but at the same time it should not slow down the stalking process or reduce encounter rates with the prey (Balme et al. 2007). Smaller groups of herbivores occur in the dense vegetation which might yield benefits for the prey, such as lower probability of being detected and collide with a predator (Dehn 1990). Animals which are gathered in small herds in habitats with dense vegetation are also the preferred prey species of leopard, because they pose lower threat of injury (Hayward et al. 2006). Hunting technique - stalk, chase and kill might change into different technique in dense vegetation, e.g. hiding close to the food source of the prey and then ambush it from a short distance (Hart et al. 1996). In case of South African leopards it was recorded that they prefer ambush-pounce technique in dense, riverine woodland (Balme et al. 2007) and in contrary north eastern Namibian leopards use stalking phase in an open area (Stender et al. 1997). Phinda nature reserve in Kwa-Zulu Natal, South Africa leopards avoided grassland the most. Prey such as nyala and impala are occurring on grassland in larger herds than in denser vegetation, which is increasing the probability that the predator will be spotted before making its move (Dehn 1990). Another reason why leopards might avoid grasslands is that lions and other competing carnivores have increased occurrence there (Balme et al. 2007). Impala, bushbuck and common duiker are living in small herds in dense habitats which are ideal place for hunting (Hayward et al. 2006).

1.3.5. Relationships with other carnivores

Leopards are sometimes killed or their catch is taken by other larger carnivores (Ray et al. 2005). They tend to hoist their killed prey when dominant competitors are around, especially when hyaenas come to the kill side. If leopards with a kill are in presence of lions, they immediately run away after giving up their catch. Females are hoisting lower proportion of kills than males (Balme et al. 2017). Trees are really important for leopards since they are using them as a safe spot to hide when larger competitors are around (Sunquist & Sunquist 2014). Options to climb large trees in dense vegetation are richer than in open habitats. In northern Namibia where large trees are sparsely distributed, one leopard was killed by lions after running and hiding himself in a tree which was not high enough to protect him against lions (Hunter & Hide 2005). Leopards are often followed by black-backed jackals (*Canis mesomelas*) when

hunting, keeping from them specific distance 20-30 m. Jackals bark at leopard in specific way and might even end up like leopards prey (Bothma & Walker 1999).

Presence of other larger competitors is not always connected to changes in leopard's population. Reduction in lion population on places where spotted hyenas (*Crocuta crocuta*) were still present did not show an increase in leopard population (Stein & Hayssen 2013).

Confrontations between felids are hostile and driven by dominance, larger dominate smaller ones. Lions pose a threat not only to leopards but to all other cats. They are responsible for most of the deaths of cubs of cheetah and leopard. On the other hand leopard is an only feline which is recorded as killing lion's cubs (Hunter &Hinde 2005).

2. Aims of the thesis

The aim of the thesis was to determine the distribution of the leopard habitat in the Eastern and Western Cape provinces of South Africa as a relation to food resources. To achieve the aim, following objectives were formulated:

1) To evaluate the presence of various types of prey for leopards in the study area.

2) To evaluate the criteria for habitat selection in terms of environmental factors (vegetation type, slope, aspect) compared to resource dispersion (prey distribution).

3. Materials and Methods

3.1. Study area

Study area is situated in the Western Cape Province in South Africa (Figure 3). Within this area, four specific areas of interest were selected: Garden Route, Klein Swartberg, Overberg and “Winelands”. Three of four areas include sub-site areas; namely for Overberg it is De Hoop, Hermanus and Agulhas; for Garden Route – Craggs and SANParks (South African National Parks); for Winelands - Robertson and Greyton.

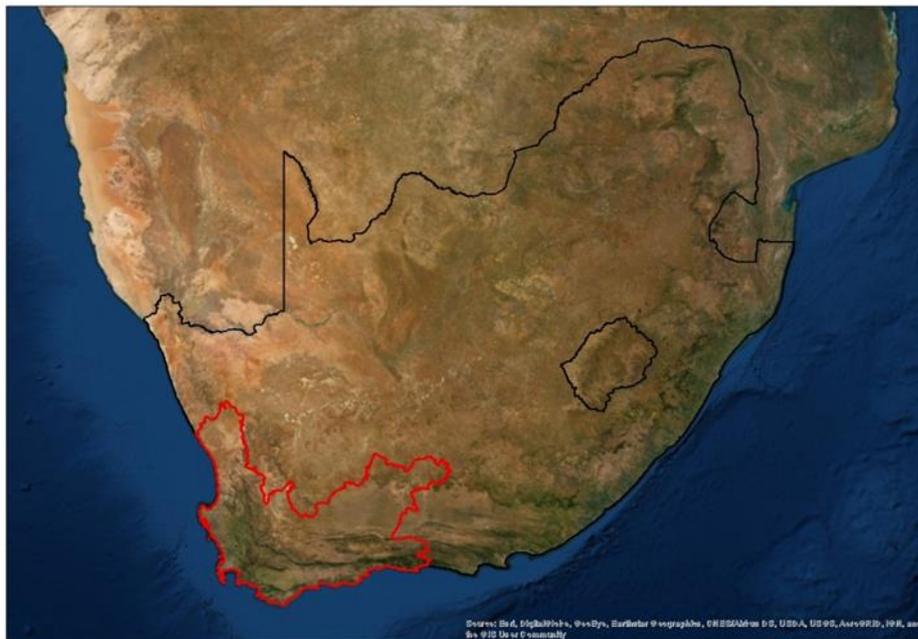


Figure 3. Study area- black colour is showing borders of South Africa and red colour borders of Western Cape Province.

Diverse plant communities such as fynbos (Figure 4), succulent Karoo, Nama Karoo (Figure 5), patches of Albany Thicket and forest can be found in Western Cape (de Villiers et al. 2016). Indigenous forest vegetation which is found in Garden Route makes this area a holder of an important portion of remaining indigenous forest in the country. Fynbos vegetation type is mostly found in mountains and coastal plains (CNdV Africa 2005).



Figure 4. Fynbos(Source: GSDB 2020).

Figure 5. Nama Karoo (Source: Dumbacher et al. 2012).

Topography of the Western Cape province territory extends from coastal plains bounded by steep cliffs and sandy beaches, often through mountain ranges bounding distant valleys, to wide empty inland plains of Karoo areas (CNdV Africa 2005).

Western Cape landscape is changing from semi-deserts in the west and north to forest bounding the south coast. Mountain ranges are found through Western Cape Province and mountains with elevations between 900-2300 m a.s.l. could be found in southwest (CNdV Africa 2005; Thompson et al. 2020).

Warm temperate Mediterranean type of climate is found in Western Cape. It is characteristic with its cool and wet winters and relatively hot and dry summers (Bargmann 2003). Most of the rains are received in winter and early spring (May to August). Western Cape has variations in mean annual rainfall across its range, with up to 3000 mm of rain in mountainous regions and in contrary <200 mm of rain in lowlands (40 m) (Lakhraj-Govender & Grab 2019).

3.2. Data collection and processing

The data for the research were collected using various techniques. The data on prey species were collected using a set of camera traps across the study area, the data on leopard occurrence were collected using GPS collars with satellite receivers, and the environmental data over the study area were obtained from public databases of remote-sensed environmental parameters.

3.2.1. Camera traps

Camera trap data were collected over the years by Landmark Foundation in the focus area. Only one type of camera was used for data collecting, Cuddeback Attack IR trail camera 1156. The total number of selected camera sites for the thesis was 128 (Figure 6). Camera sites were selected according to a number of camera trap days in four mentioned areas.

Fifty four cameras were coming from Winelands (Robertson 50, Greyton 4), 29 from Overberg (De Hoop 6, Hermanus 6, Agulhas 17), 38 from Garden Route (Craggs 14, SANParks 24) and 17 from Klein Swartberg. Cameras were set in 3 minutes interval and checked every 70 – 90 days.

Cameras at selected sites were working in different periods in different areas. From November 2011 till August 2013 in Overberg (De Hoop, Hermanus, Agulhas) from March 2012 till November 2014 in Garden Route (SANParks, Craggs), from May 2012 till August 2012 in Winelands (Robertson, Greyton) and from June 2015 till July 2016 in Klein Swartberg area (Table 1).

For the first objective camera sites with 76 camera trap days were selected to get the highest number of different camera sites as possible because more presence points is better for species distribution modelling (Watt 2018).

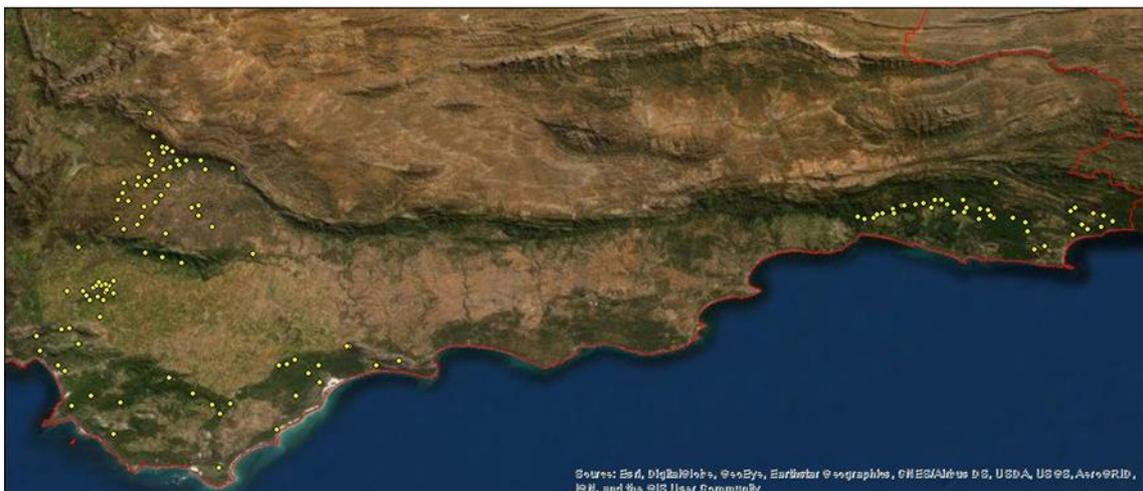


Figure 6. Yellow points indicate selected camera sites with 76 camera trap days.

Table 1. Information about selected cameras in different areas and the period of their records.

Research site	Camera trap days	Duration	Number of Camera Sites
De Hoop	76	November 2011 - January 2012	1
	76	November 2011 - February 2012	1
	76	March 2012 - May 2012	4
Hermanus	76	November 2011 - February 2012	1
	76	March 2012 - May 2012	5
Agulhas	76	March 2013 - May 2013	8
	76	June 2013 - August 2013	9
SANParks	76	March 2014 - May 2014	17
	76	June 2014 - August 2014	5
	76	August 2014 - November 2014	2
Crags	76	March 2012 - May 2012	3
	76	June 2013 - August 2013	9
	76	March 2014 - May 2014	1
	76	May 2014 - August 2014	1
Klein Swartberg	76	June 2015 - August 2015	5
	76	March 2016 - May 2016	9
	76	May 2016 - July 2016	3
Robertson	76	May 2012- July 2012	4
	76	June 2012 - August 2012	9
	76	October 2012- December 2012	27
Greyton	76	May 2012 - August 2012	4
Total			128

3.2.2. Collar data

Data from the sampled leopards used in this study form part of a broader leopard conservation project initiated in 2004 in Eastern and Western Cape, South Africa. Collars were set for some individuals with 6 hour data collection interval (*) and for some with 4 hour data collection interval (Table 2). GPS or satellite collar was used (Vectronic-aerospace, berlin, Germany, or Animal Wildlife Tracking, South Africa). Data were downloaded remotely, using an ultra-high receiver (UHF), or by satellite transmission.

Data were then mapped in ArcGis to see if any obvious outliers existed. If they did, they were removed. Then points with a Degree of Precision of more than 20 metres were excluded from the analyses as well. Data were then saved as excel sheet csv format.

Table 2. List of collared leopards with information about place of collaring, sex, tracked period, collar number and number of positions (data points).

Location	Province	Collar number	Period tracked	Sex	Data points
Baviaanskloof	Eastern Cape	1015*	Jan. 2015 - Feb. 2016	M	230
Addo	Eastern Cape	2996	Dec. 2006 - Dec. 2007	M	1875
Cockscomb	Eastern Cape	2997	Jun. 2007 - May 2008	M	2504
Swartberg	Western Cape	3805*	Sep. 2012 - Oct 2014	M	1133
Baviaanskloof	Eastern Cape	3809*	Jan. 2008 - Apr. 2009	M	1828
Baviaanskloof	Eastern Cape	6776*	Apr. 2009 - Sep. 2010	M	2222
Baviaanskloof	Eastern Cape	6667*	Jan. 2009 - Jul. 2010	M	2457
Garden Route	Western Cape	6666*	Mar. 2009- Jun. 2010	M	1368
Langeberg	Western Cape	8182*	Jun. 2010 - Mar. 2011	M	1053
Ceres	Western Cape	8578*	Jun. 2011 - Aug. 2012	M	1384
Ceres	Western Cape	8677*	Nov. 2012 - Jun. 2014	M	376
Hermanus	Western Cape	9536*	Jun. 2011 - Sep. 2011	M	377
Hermanus	Western Cape	9648*	Feb. 2012 - Apr. 2012	M	472
Baviaanskloof	Eastern Cape	1412	Jun. 2014 - Jan. 2016	F	2439
Baviaanskloof	Eastern Cape	3704	Sep. 2007 - Jul. 2008	F	2388
Baviaanskloof	Eastern Cape	3710	Aug. 2007 - Dec. 2007	F	649
Garden Route	Western Cape	3809*	Sep. 2009 - Jun. 2010	F	997
Cockscomb	Eastern Cape	3805*	Jan. 2009 -Aug 2009	F	1126
Baviaanskloof	Eastern Cape	6775*	Apr. 2009 - Aug 2009	F	457
Cockscomb	Eastern Cape	6777*	Jul. 2009 - Sep. 2009	F	2013
Baviaanskloof	Eastern Cape	8183	Jun. 2010 - Jul. 2011	F	876
De Hoop	Western Cape	8294*	Mar. 2011 - Jan. 2012	F	1363
Rooihoek	Eastern Cape	8642*	Jan. 2011 - Mar. 2012	F	1384

3.2.3. Environmental variables

Following environmental layers were used: land cover of South Africa consisting of 46 classes (FAO 2009); roads (Meijer et al. 2018); rivers (DIVA-GIS, 2003); protected areas consisting of formally protected areas (type A and B) and informally protected areas (CapeNature 2017, SANParks/SANBI 2010); cattle and sheep density map (heads/100km²) (FAO 2014) and DEM layer (DIVA-GIS 2003) from which slope and aspect were created. DEM raster layer was first re-projected from Geographic Coordinate System WGS84 to Projected Coordinate System WGS84 World Mercator in ArcMap10.7.1. to create Z factor parameter, which is needed for correct creation of a slope and an aspect (Frye 2007). Both aspect and slope were created in QGIS 3.12.1. (QGIS Development Team 2020), using analysing raster tools. After creating slope and aspect, both layers were then re-projected back to WGS84 in ArcMap10.7.1. Values in aspect layer were additionally reclassified in QGIS 3.12.1. from 0-360 degrees to values 10-80 where 10 indicates North (0-22.5; 337.5-360), 20 Northeast (22.5-67.5), 30 East (67.5-112.5), 40 Southeast (112.5-157.5), 50 South (157.5-202.5), 60 Southwest (202.5-247.5), 70 West (247.5-292.5), 80 Northwest (292.5-337.5) (Reades 2016). Formally protected areas of a type A are those which are

managed by government. Formally protected areas of a type B are those areas which are managed by shared management (e.g. collaboration of institutions or trans-boundary states) (Mitchell et al. 2018).

3.3. Data analysis and building the model

digiKam (digiKam team 2001-2020), R-studio (RStudio Team 2015) and MaxEnt- (maximum entropy modelling) (Phillips et al. 2017) softwares were used for the first objective, i.e. to identify the prey species within the area of interest. Some of the camera trap data were already sorted into a species files by Landmark Foundation. These data were then double checked and tagged with remaining unsorted data in digiKam software. To extract all necessary information about camera trap data from digiKam and putting them into a excel sheet format, R software package (R Core Team, 2020): camtrap R (Niedballa et al. 2016) was used. Camtrap R package was also used for eliminating possible repeated records of the same individual of the same species within one hour set interval. Individual prey species records were then filtered and saved in csv format. It was filtered 12 possible prey species using various publications (Hayward et al 2006; Martins et al 2010; Fischer & Schwarz 2006; Williams et al. 2018; Norton et al., 1986) as a reference. Individual species records were then adjusted so they would contain in first column only name of the species, in second column longitude and in third column latitude.

All environmental layers were aligned into same resolution (1km) and extent in QGIS 3.12.1. and saved into ASC format, which is required by MaxEnt.

To build the best model for each species, some of the settings stayed the same through whole building process and some settings were changed due to different number of individual species occurrence points and changes in replicate run types. Following settings remained the same the whole time: number of background points (default 10 000), maximum iterations (set 5000) and regulation multiplier (default 1). Maximum iterations was set to 5000 because it gives the model satisfying amount of time for convergence. If number is set low the model might not have enough time to converge and as a result it may produce over or under predicted relationships (Castilho, 2015). Default 10 000 background points was left as it was found that with 10 000

background points more accurate results are obtained (Barbet-Massin et al. 2012). Regularization multiplier was left to default 1 because it is known for well performing and its reliability (Elith et al. 2011). Number of replicates was set to 10 as it is common value in the literature and random test percentage was set to 20 (Castello 2019). Depending on the number of occurrence points of each species different features types were used. For species with at least 10 points linear and quadratic feature type were used. For species with at least 15 points linear, quadratic and hinge feature types were used. (Elith et al. 2011). Default replicate type (crossvalidation) was used in the first runs for each species and variables with low gain or those which were reducing predictive performance were excluded from the model. After having selected variables other two replicate types were used as well (subsample and bootstrap) and model with the best performance was then selected.

Habitat suitability maps were created as an output of final run of Maxent for individual species, where 1- red colour, represented the greatest habitat suitability, 0- dark blue colour represented the lowest habitat suitability.

To avoid spatial autocorrelation, GPS collar data were spatially thinned, using spThin R package (Aiello-Lammens et al. 2015). The thinning parameter was set to 800 m distance. Then the data were used as an occurrence points into the MaxEnt with habitat suitability maps for individual prey species as input environmental layers together with other environmental layers mentioned above, to generate model for leopards. To get the best model, same procedure as for prey species was applied.

4. Results

Twelve possible prey species were captured on the camera traps, however only eight of them had enough occurrence points to build a good model. Those are common duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), cape grysbok (*Raphicerus melanotis*), porcupine (*Hystrix africae australis*), baboon (*Papio cynocephalus*), mongoose (*Herpestes* sp.), genet (*Genetta* sp.) and scrub hare (*Lepus saxatilis*). Potential prey species with low number of occurrence points were bat-eared fox (*Otocyon megalotis*), kudu (*Tragelaphus strepsiceros*), grey rhebok (*Pelea caprelous*) and klipspringer (*Oreotragus oreotragus*). All final MaxEnt models were produced by subsample replicate type. Roads and rivers were only variables which were always excluded from the analyses after first run of MaxEnt, as their gains were low and the variables by themselves were not useful for estimating prey species occurrence.

Common duiker was caught at 43 camera sites in total and final model was built from 5 environmental layers, which included: land cover, cattle and sheep density, slope and aspect. Cape grysbok was caught at 61 camera sites in total and the model was built from 6 environmental layers in total. Five of them were matching to those used in common duiker and one additional was protected areas. Bushbuck was caught on 40 camera sites in total and the model was built from 5 environmental layers, which included land cover, protected areas, aspect, slope and cattle density. Porcupine was caught at 84 camera sites in total and the model was built from 5 environmental layers including land cover, sheep and cattle density, slope and protected areas. Baboon was caught on 76 camera sites in total and the model was built from 5 environmental layers which included land cover, protected areas, sheep and cattle density and slope. Mongoose was caught at 55 camera sites and final model was built from 5 environmental layers, where 4 of them were matching to those used for bushbuck, and one additional was sheep density layer. Genet was caught at 49 camera sites in total and 4 environmental layers were used to build the model. The layers were matching to those, used to build a model for mongoose, except the slope layer. Hare was caught at 35 camera sites in total and only 3 environmental variables were used to build the final model, slope, land cover and cattle density (Table 3).

The AUC (area under the curve) values for all modelled prey species were close to 1 (Table 3.), which indicates that the model performance was good. AUC value is one the most important evaluation of a model performance. If the value is closer to 0.5, it is an indication that the model has no ability to distinguish between presence and absence. (Narkhede 2018).

Table 3. AUC values with layers used in modelling for individual species and number of camera capture sites

Species	AUC	Environmental Layers	Number of Sites
Common duiker	0.968	land cover, cattle density, sheep density, slope, aspect	43
Bushbuck	0.986	land cover, cattle density, slope, aspect, protected areas	40
Cape grysbok	0.972	land cover, cattle density, sheep density, slope, aspect, protected areas	61
Porcupine	0.969	land cover, cattle density, sheep density, slope, protected areas	84
Baboon	0.965	land cover, cattle density, sheep density, slope, protected areas	76
Genet	0.966	land cover, cattle density, sheep density, protected areas	49
Mongoose	0.966	land cover, cattle density, sheep density, slope, protected areas	55
Strub hare	0.939	land cover, cattle density, slope	35

The variables which contributed the most (when all the variables were run together while building the model) and therefore had the highest impact on predicting prey species occurrence of all mentioned potential prey species, except for hare, was the land cover. Layers with the second highest impact on predicting prey species occurrence were cattle density (porcupine, hare) or sheep density (common duiker, cape grysbok) and protected areas (bushbuck, baboon, genet, mongoose). The highest impact on hare occurrence had the slope layer. The lowest impact on predicting species occurrence varies among the species: slope layer for common duiker, aspect layer for bushbuck and cape grysbok, sheep density layer for baboon and genet, cattle density layer for mongoose, and finally land cover layer for hare.

The greatest habitat suitability for all prey species was found at four land cover types: closed needleleaved deciduous or evergreen forest, closed broadleaved deciduous forest, open broadleaved deciduous forest and closed to open broadleaved evergreen or semi-deciduous forest. Habitat suitability was greatest at protected area category type B for all species, except for bushbuck where it was category type A. Habitat suitability was greatest at slope with orientation (aspect) to South. With increasing slope habitat suitability was increasing for the species, except for hare and bushbuck. Bushbuck's habitat suitability was increasing with an increasing slope till the value of slope reached around 3.5 degrees, then the habitat suitability started to decreasing. Same trend was seen in hare when the slope reached value around 3 degrees. All habitat suitability maps can be found in Appendix 1.

The final model for the leopard was also produced by using subsample replicate run type and roads with rivers were excluded from the analyses for the same reasons as in prey species together with aspect layer. The model was built from 13 layers which included eight habitat suitability maps of a prey species (porcupine, mongoose, scrub hare, genet, common duiker, bushbuck, cape grysbok and baboon), five environmental layers (slope, aspect, land cover, sheep and cattle density) and 2201 GPS points, derived from the collared leopards. Habitat suitability output map of the final model for leopard can be seen in Figure 8.

The AUC value was 0.989, which once again indicates good model performance. The variables which contributed the most (when all the variables were run together while building the model) and hence had the highest impact on predicting the occurrence of the leopard, were: mongoose, porcupine, scrub hare and baboon. The lowest impact had genet, bushbuck and land cover.

The environmental variable with the most useful information by itself (when it was run in isolation and then was compared to training gain, when it was run with all other variables) and which contributed the most individually on predicting leopard occurrence was: porcupine, followed by mongoose, baboon and other prey species (Figure 7). What can be seen from the Figure 7 resource dispersion has greater influence on predicting leopard distribution than environmental factors.

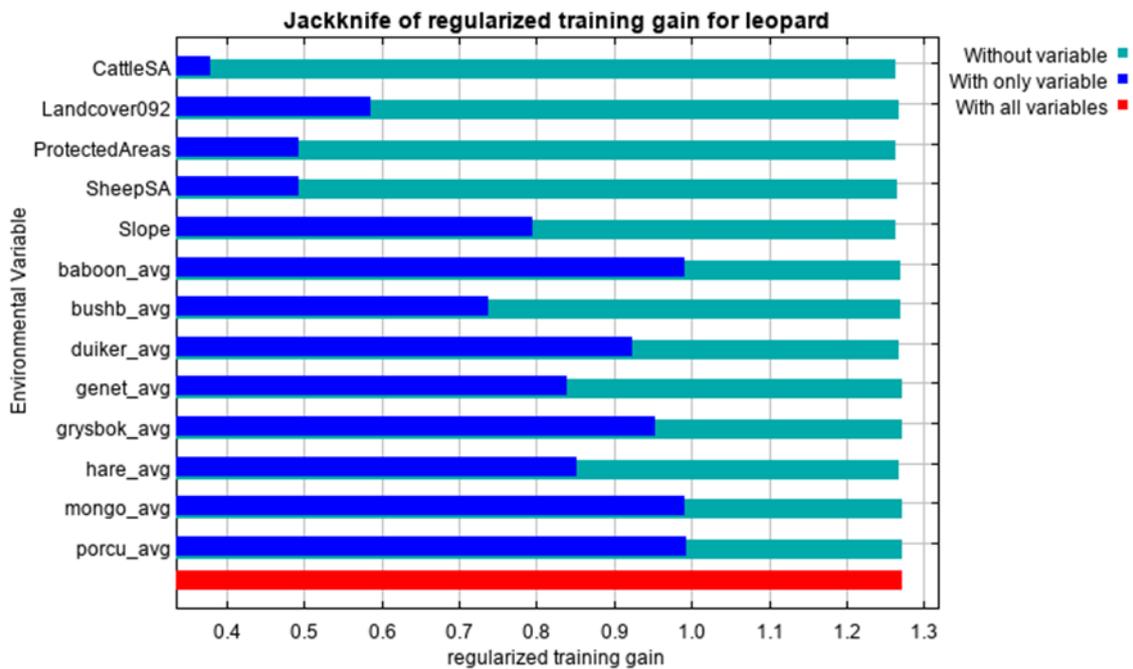


Figure 7. Jackknife of regularized training gain for the leopard (bushb-bushbuck, mongo- mongoose, porcu- porcupine, landcover092- landcover2009).

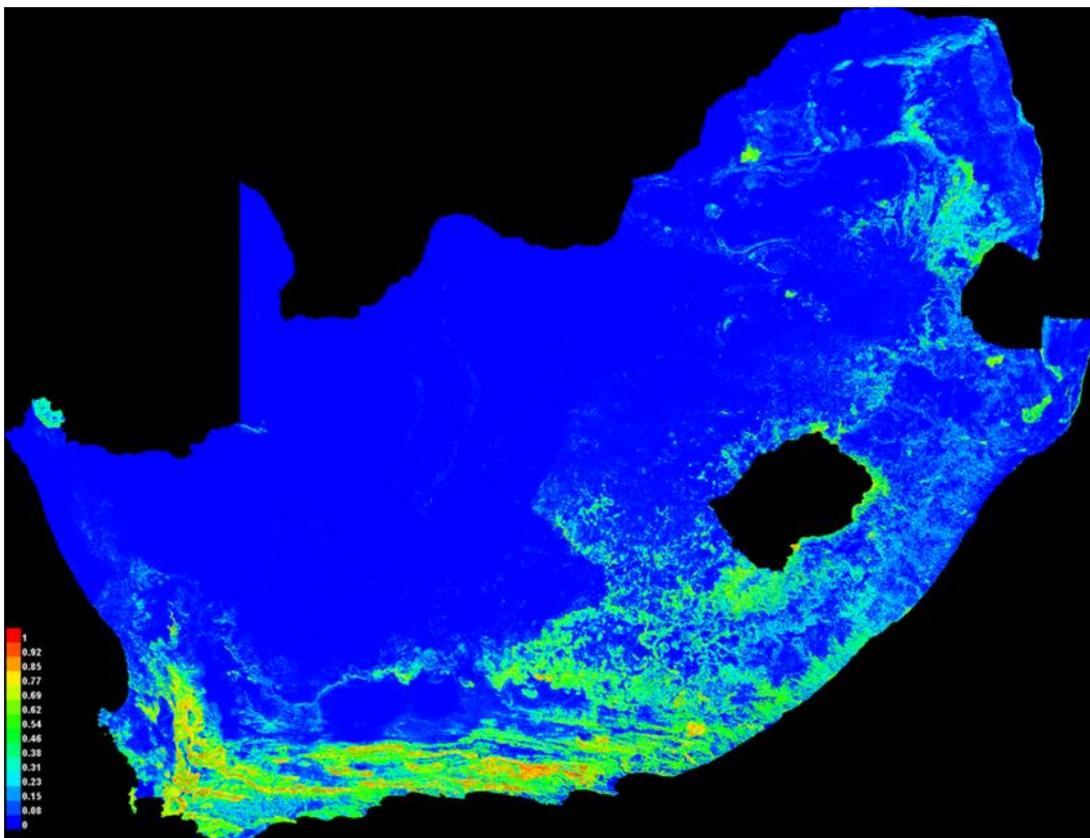


Figure 8. Habitat suitability map of leopard (red- greatest habitat suitability, blue- lowest habitat suitability)

Habitat suitability for a leopard was increasing with the increasing habitat suitability for all mentioned prey species (Appendix2: Chart graphs A). It indicates that where the habitat suitability for the prey species is higher, so is the probability of finding the prey species on those places and so is the probability of finding a leopard there as well. Figure 9. shows how the habitat suitability of a leopard is influenced by habitat suitability of a common duiker.

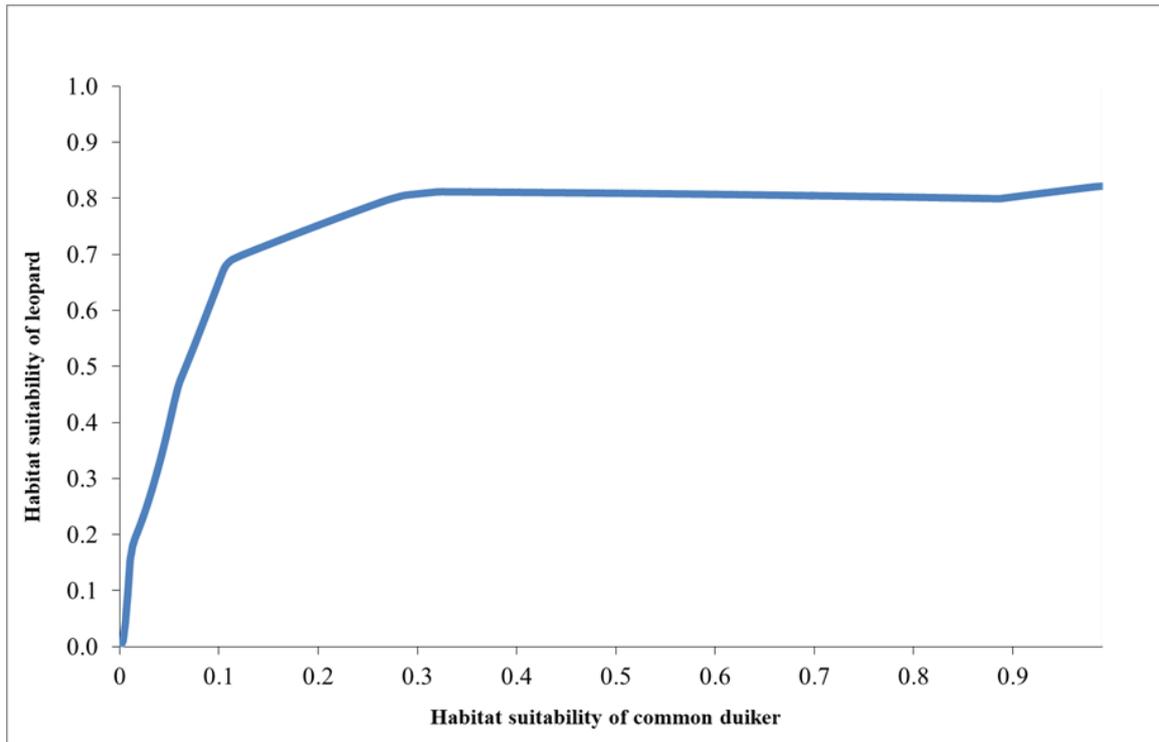


Figure 9. Relationship between the habitat suitability of leopard and habitat suitability of common duiker

The habitat suitability was greatest within protected area category type B, followed by A (Appendix 2: Bar graphs). With increasing sheep density habitat suitability was increasing as well till the density reached around 94 animals per 100km². Then the habitat suitability started to decrease with increasing sheep density (Figure 10). The cattle density showed that with increasing density, habitat suitability for leopard was firstly decreasing, then increasing and once again decreasing after the density reached around 60 animals per 100km² (Appendix 2: Chart graphs B).

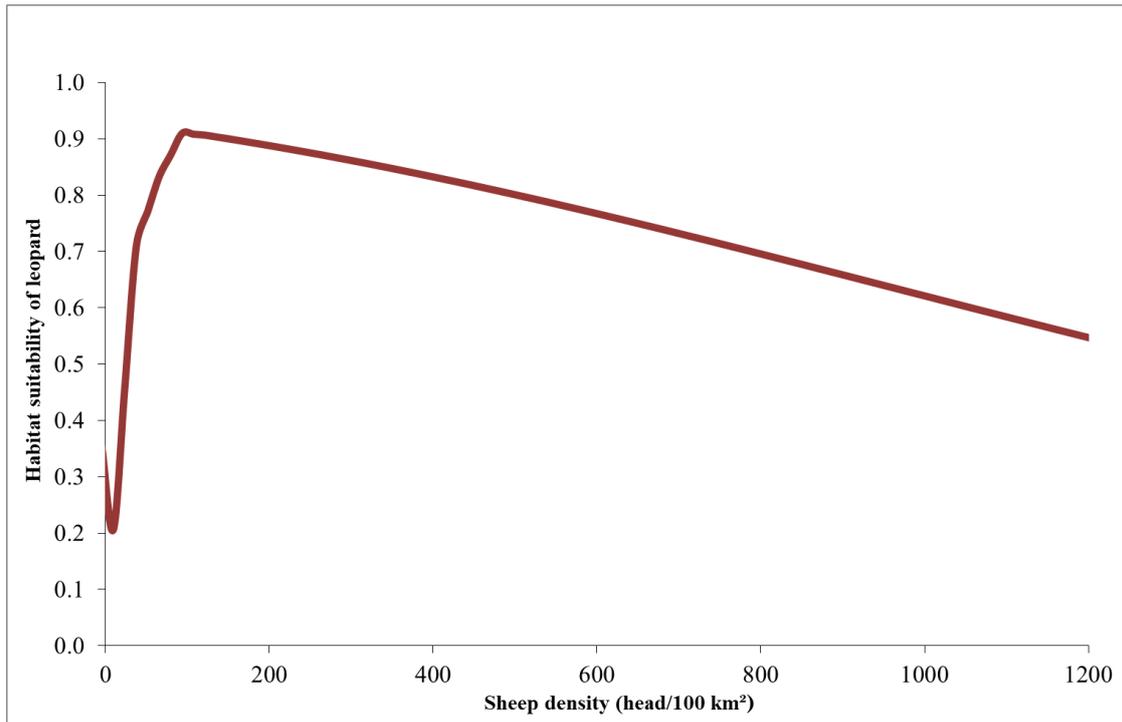


Figure 10. Response of leopard (in terms of habitat suitability) to sheep density (head/100km²).

The habitat suitability was greatest within land cover type: open needleleaved deciduous or ever green forest, followed by open broadleaved deciduous forest and closed broadleaved deciduous forest (Appendix 2: Bar graphs); and with increasing slope habitat suitability for a leopard was increasing as well (Appendix 2: Chart graphs B).

5. Discussion

The results indicate that the habitat suitability for a leopard was increasing with an increasing habitat suitability of prey species. Swanepoel et al (2013) used in their study only environmental variables (such as land cover, surface ruggedness, DEM etc.) to estimate extent of suitable leopard habitat in South Africa. This study has extended these previous analysis techniques by combining prey distribution models with environmental variables. The results indicate that prey species information has a greater contribution in explaining leopard distribution. Therefore my results are supporting the hypothesis that resource dispersion has greater influence on predicting leopard distribution than environmental factors. The probability that leopard could be occurring at some place is increasing with the probability that the prey species will be occurring there as well. This result is supported by the work of Creel et al (2001) and Carbone & Gittleman (2002), where the authors found that great influence on carnivore densities and distributions has distribution and density of prey.

Figure 7 shows that antelope species (cape grysbok, common duiker and bushbuck) explain leopard occurrence in order which can be matched to order of antelope accounts found in leopard scats, where cape grysbok was the most accounted prey item followed by common duiker in Western Cape Province but no records are made for bushbuck (Martins et al. 2010; Norton et al. 1986). However in Ott et al. (2007) the order of antelopes accounts in scats are different and most accounted species in leopard scats was bushbuck, followed by cape grysbok and common duiker.

Non-prey species layers showed (when they were run individually) that the highest gain and therefore contributed the most on predicting leopard occurrence was slope layer. With increasing slope the habitat suitability of leopard was increasing as well. A possible reason why it is so, might be as Swanepoel et al (2013) suggested, that leopards use mountainous areas because those are places where they can hide from human persecution and they do not have to compete so much for the space with people there, compare to less rugged human used areas. The increasing habitat suitability of leopard with increasing slope might have also caused, why bushbuck as a potential prey species, even though to be recorded in high numbers in scats in Williams et al. (2018)

and Fischer and Schwarz (2006), end up in this study between species with lowest contribution in prediction of leopard occurrence, as its habitat suitability was decreasing with increasing slope. Same reason might be stated for hare, as its habitat suitability was decreasing with increasing slope. However, attention should be paid to a fact that, prey species samples for this study were taken only from Western Cape Province and leopard samples from Eastern and Western Cape Provinces.

Closed broadleaved deciduous forest was found to be in all prey species as well in leopard as one of the land cover types with the greatest habitat suitability. Two factors are driving leopard when it comes to hunting – the abundance of prey and satisfying land cover, so that successful hunt would be ensured. Leopards in Welevonden in South Africa accounted most of their hunts in higher levels of vegetation covers like mixed closed woodland, as chances being detected while hunting are lower. This even outweighs that in these habitats number of prey species is low. These factors might have enable leopards to prey successfully upon species which are usually considered as dangerous or hard to catch, such as baboons (Pitman et al. 2013). However, leopards in Phinda Private Game Reserve in South Africa are using less dense vegetation for hunting (Balme et al. 2007).

Species distribution models are based on precondition that the sample data which are used for the modelling are representing the whole ecological range of the species and they are able to predict probability of a species being present at areas which were not sampled (Proosdij et al. 2015). In species distribution modelling, possible lack of data is disturbing, as a creation of good quality models is plainly influenced by number of samples which are used for the modelling (Wisz et al. 2008). Moreover larger sample sizes of occurrence points might be required to describe precisely range of conditions under which the species are occurring (Austin 2002). Besides, the way how the environmental variables interact between each other is in many cases important for characterizing relationships between the species and the environmental variables. With increasing number of predictor variables, the number of parameters to be assessed for interactive effect is exponentially growing (Rushton et al. 2004). However, there are studies which produced models only from small sample sizes 5, 10, 25 which had higher accuracy than models with 100 sample size. On the other hand, it is known that

modelling with small sample size like 20 or 15, decreases model performance (Proosdij et al.2015).

As mentioned above, occurrence points (samples) are meant to reflect the whole ecological range of that species, and with increasing sample size the characterization of the relationships between the environment and species improves. In this study only smaller sample sizes were used ranging from 35 to 84. Therefore the predictions for the prey species or leopards must be interpreted with caution and should be mostly used for leopards in Western and Eastern Cape provinces, as all occurrence points for prey species were derived from areas in Western Cape and leopard occurrences from Eastern and Western Cape provinces. Caution must be taken when interpreting habitat suitability map for cape grysbok as MaxEnt predicted suitable areas outside of its historical range.

Layers which were causing most of the problems in interpretation of results were sheep and livestock density layers. In most of the cases habitat suitability was firstly decreasing with increasing livestock density, which was at really low values, as the density started to increase more, habitat suitability for the species started to be increasing as well and after certain peak of livestock density, value of habitat suitability started to decrease with increasing density. In general expected result for the leopards should be that the habitat suitability is decreasing with increasing density of a livestock from the begging. Especially, when the farmers are posing increasing threat to leopards when they are trying to protect themselves from economical losses. On the other hand the depredation on the livestock and how often it is happening is related to availability of a natural prey and which husbandry approaches are applied by farmer. As an example could be a farm in Kenya which had high numbers of livestock animals but no leopard was accused of any depredation on a livestock. The reason for this was that the availability of natural prey in the area was high and farmers were in addition accompanying their animals on pastures (Pitman 2012). For further investigation, it would be worth trying to use different layer source and compare those results with current ones.

For the future it would be good to try to do same analyses with bigger sample size for the prey species, maybe from different provinces as well, and compare the

results with current ones to see if there was a significant change in habitat suitability for prey species and leopard as well. As significant change in habitat suitability for prey species might influence driving factors in leopard habitat selection. And even though this study has proven that habitat selection of leopard is driven rather by prey distribution than by environmental layers, more studies like this are needed to be fully sure.

6. Conclusion

The goal of this thesis was to answer the question whether resource dispersion drives leopard habitat selection. My results are supporting the hypothesis that resource dispersion has greater influence on leopard distribution than environmental factors. This might have implications to conservation actions and research, as we might start to fully understand what is driving leopards in their habitat selection.

More studies like this should be conducted in order to be truly sure that driving force of leopard habitat selection is resource dispersion. Conservation and land management organizations should take the results of this thesis into account in their long term planning so that prey species and leopard suitable habitat is preserved. More efficient protection of prey species might have a positive outcome on leopard survival and farmer – leopard conflicts, because distribution and abundance of natural prey have an influence on livestock depredation by leopard.

Another reason why the natural food resources should be protected and more research to be done on diet composition of leopard in different areas is that leopards might have changes in their diet depending on how close to human settlements they are. It was found that leopards in the Congo Basin Rainforest increasingly predate on primates and rodents in areas close to settlements, compared to areas which are further away where the diet was dominated by ungulates (Henschel et al. 2011).

When protecting leopard we should not overlook the result that protected areas and higher slope played also an important role in predicting leopard occurrence, because in such places leopards are not facing persecutions and do not have to compete for space with people.

7. References

- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* **38**: 541-545.
- Athreya VR, Belsare AV. 2007. Human - Leopard Conflict Management Guidelines. Kaati Trust, Pune. India.
- Austin MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**: 101-118.
- Balme G, Hunter L., Slotow ROB. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* **74**: 589-598.
- Balme GA, Miller JRB, Pitman R, Hunter LTB. 2017. Caching reduces kleptoparasitism solitary, large felid. *Journal of Animal Ecology* **86**: 634-644.
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**: 327-338.
- Bargmann Ch.J. 2003. Geology and Wine Production in the Coastal Region, Western Cape Province, South Africa.. *Geology and Wine* **7** **30**: 161-182.
- Bothma J du P, van Rooyen N, le Riche EAN. 1997. Multivariate analysis of the hunting tactics of Kalahari leopards. *Koedoe* **40**: 41-50.
- Bothma J du P, Walker C. 1999. *Large Carnivores of the Savannas*. Springer. Verlag Berlin Heidelberg.
- Boyce MS, McDonald. 1999. Relating populations to habitats using resource selection functions. *Trend in ecology and Evolution* **14**: 268 -272.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection function. *Ecological Modelling* **157**: 2281-300.

Carbone C, Gittleman JL. 2002. A common rule for the scaling of carnivore density. *Science* **295**: 2273-2276.

Castelló JR. 2016. *Bovids of the World: Antelopes, Gazelles, cattle, Goats, Sheep, and Relatives*. Princeton University Press.

Castello M. 2019. Tips on “Species Distribution Modelling” using MaxEnt. The University of Auckland New Zeland. Available from: <https://www.oceansofbiodiversity.auckland.ac.nz/2019/04/27/tips-on-species-distribution-modelling-using-maxent/> (accessed March 2020).

Castilho R. 2015. *Species Distribution Modeling*. 101. Basics Hands-On. Experimental work notes.

CNdV Africa. 2005. *Western Cape Provincial Spatial Development Frame Work: The Western Cape Province Today*. Environmental planning, landscape architecture, urban design. Caledon.

Constant LN, Bell S, Hill RA. 2015. The Impacts, characterisation and management of human - leopard conflict in a multi-use land system in South Africa. *Biodiversity and Conservation* **24**: 2967-2989.

Creel S, Spong G, Creel N. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35-60 in Gittleman JL, Funk SM, Macdonald D, Wayne RK, editors. *Carnivore conservation*. Cambridge University Press, Cambridge.

de Villiers Ch, Holmes P, Rebelo T, Helme T, Brown DE, Milton BCS, Dean WD, Brownlie S, Snaddon K, Day L, Ollis D, Job N, Dorse C, Wood J, Harrison J, Palmer G, Cadman M, Maree K, Manuel J, Holness S, Ralston S, Driver A. 2016. *Ecosystem Guidelines for Environmental Assessments in the Western Cape*. Fynbos Forum. Cape Town.

Dehn MM. 1990. Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* **26**: 337-342.

digiKam team. 2001-2020. digiKam, Professional Photo Management with the Power of Open Source. Available from: <https://www.digikam.org/> (accessed August 2019).

Elbroch LM, Lendrum PE, Quigley H, Caragiulo A. 2016. Spatial overlap in a solitary carnivore: support for land tenure, kinship or resource dispersion hypotheses? *Journal of Animal Ecology* **85**: 487-496.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for Ecologists. *Journal of Conservation Biogeography* **17**: 43-57.

Environmental Systems Research Institute (ESRI).2019. ArcGIS Desktop 10.7.1.

Frye Ch. 2007. Setting the Z Factor parameter correctly. ArcGIS Blog: Imagery and Remote Sensing. Available from: <https://www.esri.com/arcgis-blog/products/product/imagery/setting-the-z-factor-parameter-correctly/> (accessed April 2020).

Hart JA, Katembo M, Punga K. 1996. Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology* **34**: 364-379.

Hayward MT, Kerley. 2008. Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research* **38**: 93-108.

Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GIH. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* **270**: 298 - 313.

Henschel P, Hunter LTB, Coad L, Abernethy KA, Mühlenberg M. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology* **285**: 11-20.

Hopcraft JGC, Sinclair ARE., Packer C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* **74**: 559-566.

Hunter L.2015. *Wild Cats of the World*. Bloomsbury Publishing, London.

Hunter L.Hinge G. 2005. *Cats of Africa, Behavior, Ecology and Conservation*. Struik Publishers.Cape Town.

Inskip Ch, Zimmermann A. 2009. Human- felid conflict: a review of patterns and priorities worldwide. *Fauna & Flora International Oryx* **43**: 18-34.

Johnson CJSE, Nielson EH, Merrill TL, McDonald, Boyce. 2006. Resource selection function functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* **54**: 89-91.

Johnson DDP, Kays R, Blackwell P, Macdonald DW. 2002. Does resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution* **17**: 563-570.

Johnson DH. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. 1980. *Ecology* **61**: 65-71.

Jooste E., Pitman RT., van Hoven W., Swanepoel, LH. 2012. Unusually High Predation on Chacma Baboons (*Papio ursinus*) by Female Leopards (*Panthera pardus*) in the Waterberg Mountains, South Africa. *Folia Primatologica* **83**: 353–360.

Kiffner Ch, Ndibalema V, Kioko J. 2013. Leopard (*Panthera pardus*) aggregation and interactions with Olive baboons (*Papio Anubis*) in Serengeti National Park, Tanzania. *African Journal Ecology* **51**: 168 – 171.

Lakhraj-Govender R, Grab SW. 2019. Rainfall and river flow trends for the Western Cape Province, South Africa. *South African Journal of Science* **115**: 1-6.

Logan K.A, Sweanor LL. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, California.

Macdonald DW, Johnson DDP. 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. *Journal of Zoology* **295**: 75-107.

Macdonald DW, Loveridge AJ, Nowell K. 2010. *Dramatis personae: an introduction to the wild felids*. Pages 3-58 in Macdonald, D.W., Loveridge, A.J, editors. *The Biology and Conservation of Wild Felids*. Oxford University Press, Oxford.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer, Netherlands

Marker LL, Dickman AJ. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *Southern African Journal of Wildlife Research* **35**: 105-115.

Martins G, Horsnell WGC, Titus W, Rautenbach T, Harris S. 2010. Diet Determination of Cape Mountain Leopard using global positioning system location cluster and scat analysis. *Journal of Zoology* **283**: 81-87.

Mitchell BA, Stolton S, Bezaury-Creel J, Bingham HC, Cumming TL, Dudley N, Fitzsimons JA, Malleret-King D, Redford KH, Solano P. 2018. Guidelines for privately protected areas. Best Practice Protected Area Guidelines Series. Gland, Switzerland: IUCN.

Mizutani F, Jewel PA. 1998. Home ranges and movements of Leopards (*panther pardus*) on livestock ranch in Kenya. *Journal of Zoology* **244**: 269-286.

Morris DW. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**: 1-13.

Narkhede S. 2018. Understanding AUC - ROC Curve. Towards data science. Available from: <https://towardsdatascience.com/understanding-auc-roc-curve-68b2303cc9c5> (accessed April 2020).

Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016. camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution* **7**: 1457-1462.

Norton PM, Lawson AB, Henley SR, Avery G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Journal of Wildlife Research* **16**: 47-52.

Nowak RM. 2005. Walker's Carnivores of the world. The Johns Hopkins University Press, Baltimore, London.

Nowell K, Jackson P, 1996. Wild Cats, Survey and Conservation Action Plan. IUCN/SSC Cat specialist group. IUCN

Ott K, Kerley GI, Boshoff AF. 2007. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *African Zoology* **42**: 31-37.

Phillips SJ, Dudík M, Schapire RE. 2017. Maxent software for modeling species niches and distributions (Version 3.4.1). Available from: http://biodiversityinformatics.amnh.org/open_source/maxent/ (accessed August 2019).

Pitman RT, Kilian PJ, Ramsay PM., Swanepoel LH. 2013. Foraging and Habitat Specialization by Female Leopards (*Panthera pardus*) in the Waterberg Mountains of South Africa. *South African Journal of Wildlife Research* **43**: 167–176.

Pittman RT, 2012. The conservation biology and ecology of the African leopard *Panthera pardus*. *Pardus*. *The Plymouth Student Scientist* **5**: 581-600.

QGIS Development Team. 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from: <http://qgis.osgeo.org> (accessed March 2020).

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from: <https://www.R-project.org/> (accessed January 2020).

Ray CJ, Hunter L., Zigouris J. 2005. *Setting Conservation and Research Priorities for Large African Carnivores*. Wildlife Conservation Society, New York.

Reades J. 2016. Aspect – Slope Maps In QGIS. *King's Geocomputation: Data Analytics and simulation for environment and society*. Available from: <https://kingsgeocomputation.org/2016/03/16/aspect-slope-maps-in-qgis/> (accessed on April 2020).

RStudio Team. 2015. *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA. Available from: <http://www.rstudio.com/> (accessed January 2020).

Rushton PS, Ormerod SJ., Kerby G. 2004. New paradigms for modelling species distributions? *Journal of Applied Ecology* **41**: 193-200.

Schlaepfer M, Runge M, Sherman P. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* **17**: 474-480.

Schwarz S, Fischer F. 2006. Feeding ecology of leopards (*Panthera pardus*) in the western Soutpansberg, Republic of South Africa, as revealed by scat analysis. *ECOTROPICA* **12**: 35-42.

Seidensticker J. 1983. Predation by *Panthera* cats and measures of human influence in habitats of South Asian monkeys, *International Journal of Primatology* **4**: 323-326.

Soulé ME. 2010. Conservation Relevance of Ecological Cascades. Pages 337–353 in Terborgh J, Estes JA, editors. *Trophic Cascades: Predators, Prey, And Theand the Changing Dynamics Of Nature*. Island Press, Washington, DC.

Stander PE., Haden PJ, Kagece II, Ghau II. 1997. The ecology of asociality in Namibian leopards. *Journal of Zoology* **242**: 343-364.

Stein AB, Athreya V, Gerngross P, Balme G, Henschel P, Karanth U, Miquelle D, Rostro-Garcia S, Kamler JF, Laguardia A, Khorozyan I, Ghoddousi A. 2020. *Panthera pardus* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020: e.T15954A163991139. . Available from: <https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T15954A163991139.en>. (accessed on May 2020).

Stein AB, Hayssen V. 2013. *Panthera pardus* (Carnivora: Felidae). *Mammalian Species* **900**: 30-48.

Sunquist F, Sunquist M. 2014. *The Wild Cat Book*. The University of Chicago Press, Chicago.

Sunquist ME, Sunquist FC. 1989. Ecological Constraints on Predation by Large Felids. Pages 283-301 in Gittleman JL, editor. *Carnivore Behavior, Ecology, and Evolution*. Springer, Boston.

Swanepoel LH, Lindsey P, Somers MJ, van Hoven W, Dalerum F. 2013. Extent and Fragmentation of suitable leopard habitat in South Africa. *Animal Conservation* **16**: 41-50.

Swanepoel LH, Williams S, Gaigher I, Child MF. 2017. A Conservation assessment of *Panthera pardus*. *The Red List of Mammals of South Africa, Lesotho and Swaziland 2016*. 1-13.

Takahata Ch, Nielsen SE, Takii A, Izumiyama S. 2014. Habitat Selection of a Large Carnivore along Human-Wildlife Boundaries in a Highly Modified Landscape. *PLOS ONE* **9**: 1-13.

Thompson LM, Bundy CJ, Hall M, Gordon DF, Nel A, Lowe ChC, Vigne R, Mabin AS, Cobbing JRD. 2020. Encyclopedia Britannica. South Africa. Available from: [//www.britannica.com/place/South-Africa/Relief](https://www.britannica.com/place/South-Africa/Relief) (accessed on February 2019).

van Proosdij ASJ, Sosef MSM, Wieringa JJ, Raes N. 2015. Minimum required number of specimen records to develop accurate species distribution models. *ECOGRAPHY* **39**: 542-552.

Watt D. 2018. Preparing Data for MaxEnt Species Distribution Modeling Using R. Azavea: Blog- Spatial Analysis. Available from: <https://www.azavea.com/blog/2018/10/09/preparing-data-for-maxent-species-distribution-modeling-using-r/> (accessed on February 2019).

Williams KS, Williams ST, Fitzgerald LE, Sheppard EC, Hill RA. 2018. Nrown Brown hyena and leopard diets on private land in the Soutpansberg Mountains, South Africa, *African Journal of Ecology* **56**: 1-7.

Wisn MS, Hijmans RJ, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distribution Working Group. 2008. Effects of sample size on the performance of species distribution model. *Diversity and Distribution* **14**: 763-773.

Wolf C, Ripple WJ. 2016. Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science* **3**: 1-12.

Figure 2. Stein AB, Athreya V, Gerngross P, Balme G, Henschel P, Karanth U, Miquelle D, Rostro-Garcia S, Kamler JF, Laguardia A, Khorozyan I, Ghoddousi A. 2020. *Panthera pardus* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020: e.T15954A163991139. . Available from: <https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T15954A163991139.en>. (accessed on May 2020).

Figure (3; 6) Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 4. GSDB .2020. Genome size database of the Greater Cape flora: Fynbos. Institute of Botany, Czech Academy of Sciences. Available: <https://botany.natur.cuni.cz/gsdb/> (accessed on April 2020).

Figure 5. Dumbacher JP, Rathbun GB, Smit HA, Eiseb SJ. 2012. Phylogeny and Taxonomy of the Round – Eard Sengis or Elephant Shrew, Genus *Macroscelides* (Mammalia, Afrotheria, Macroscelidea. Plos One 7: 1-12.

Figure (7; 8; 11-18) Phillips SJ, Dudík M, Schapire RE. 2017. Maxent software for modeling species niches and distributions (Version 3.4.1). Available from: http://biodiversityinformatics.amnh.org/open_source/maxent/ (accessed August 2019).

Figure (9; 10; 19-29) Microsoft Corporation, 2010. Microsoft Excel, Available at: <https://office.microsoft.com/excel>.

Tables (1; 2; 3) Microsoft Corporation, 2010. Microsoft Excel, Available at: <https://office.microsoft.com/excel>.

Figure 29. FAO. 2009. GeoNetwork: Land Cover of South Africa – Globcover Regional. FAO, Rome. Available from: <http://www.fao.org/geonetwork/srv/en/metadata.show?currTab=simple&id=37221> (accessed March 2020).

Environmental variables

CapeNature. 2017. WCBSP Protected Areas. 2017. Available from: <http://bgis.sanbi.org/SpatialDataset/Detail/649> (accessed March 2020).

DIVA-GIS, free, simple and effective. 2003. Available from: <https://www.diva-gis.org/datadown> (accessed March 2020).

FAO. 2009. GeoNetwork: Land Cover of South Africa – Globcover Regional. FAO, Rome. Available from: <http://www.fao.org/geonetwork/srv/en/metadata.show?currTab=simple&id=37221> (accessed March 2020).

FAO. 2014. GeoNetwork: Cattle Distribution – Gridded Livestock of the World V 2.01. FAO, Rome. Available from:

<http://www.fao.org/geonetwork/srv/en/metadata.show?id=47949&currTab=simple>
(accessed on March 2020).

FAO. 2014. GeoNetwork: Sheep Distribution – Gridded Livestock of the World V 2.01. FAO, Rome. Available from:
<http://www.fao.org/geonetwork/srv/en/metadata.show?id=48050&currTab=simple>
(accessed on March 2020).

Meijer JR, Huijbegts MAJ, Schotten, CGJ, Schipper AM. 2018. Global patterns of current and future road infrastructure. *Environmental Research Letters*, 13-064006. Available from: www.globio.info (accessed March 2020).

SANParks/SANBI. 2012. NPAES Protected Areas - Informal 2010. Available from: <http://bgis.sanbi.org/SpatialDataset/Detail/144> (accessed March 2020).

DIVA-GIS, free, simple and effective. 2003. Available from: <http://www.diva-gis.org/datadown> (accessed on April 2020).

Appendices

List of the Appendices:

Appendix 1

Habitat suitability maps of prey species:

- 1- red colour represent the greatest habitat suitability
- 0- dark blue colour represents the lowest habitat suitability

Appendix 2

1) Chart graphs:

- A) Relationships between habitat suitability of leopard and habitat suitability of prey species
- B) Relationship between habitat suitability of leopard and continuous environmental variables

2) Bar graphs:

- Relationship between habitat suitability of leopard and categorical environmental variables

Appendix 3

Land cover types within South Africa

Appendix 1: Habitat suitability maps of prey species

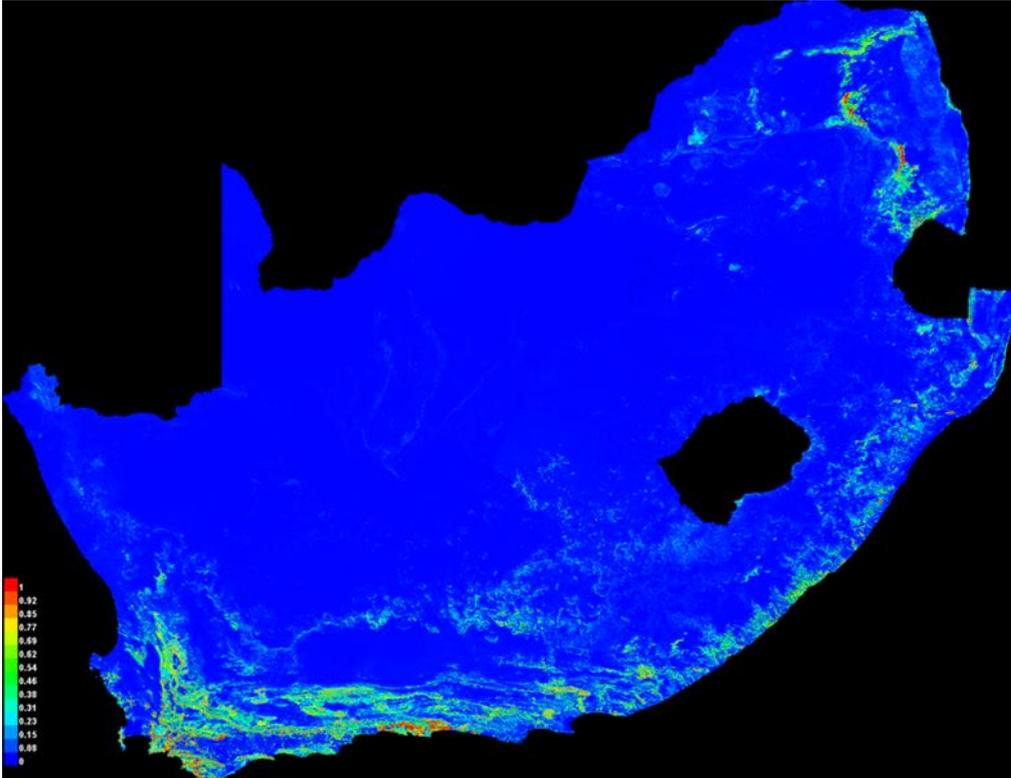


Figure 11. Habitat suitability map of a baboon.

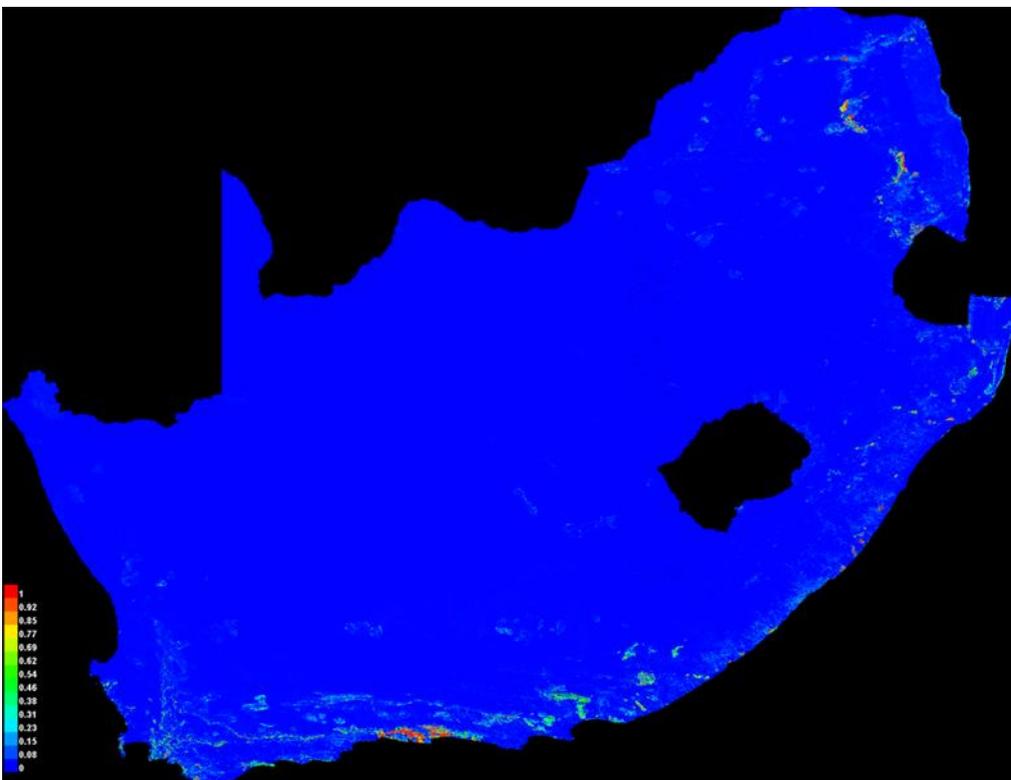


Figure 12. Habitat suitability map of a bushbuck.

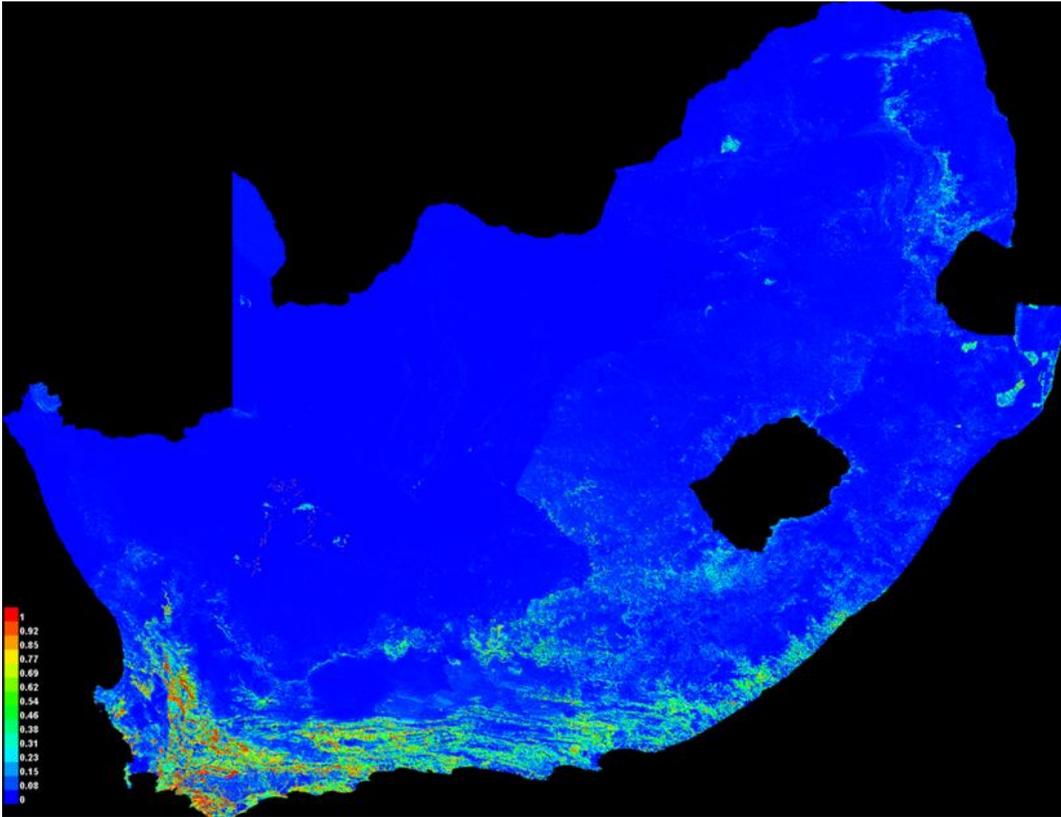


Figure 13. Habitat suitability map of Cape Grysbok.

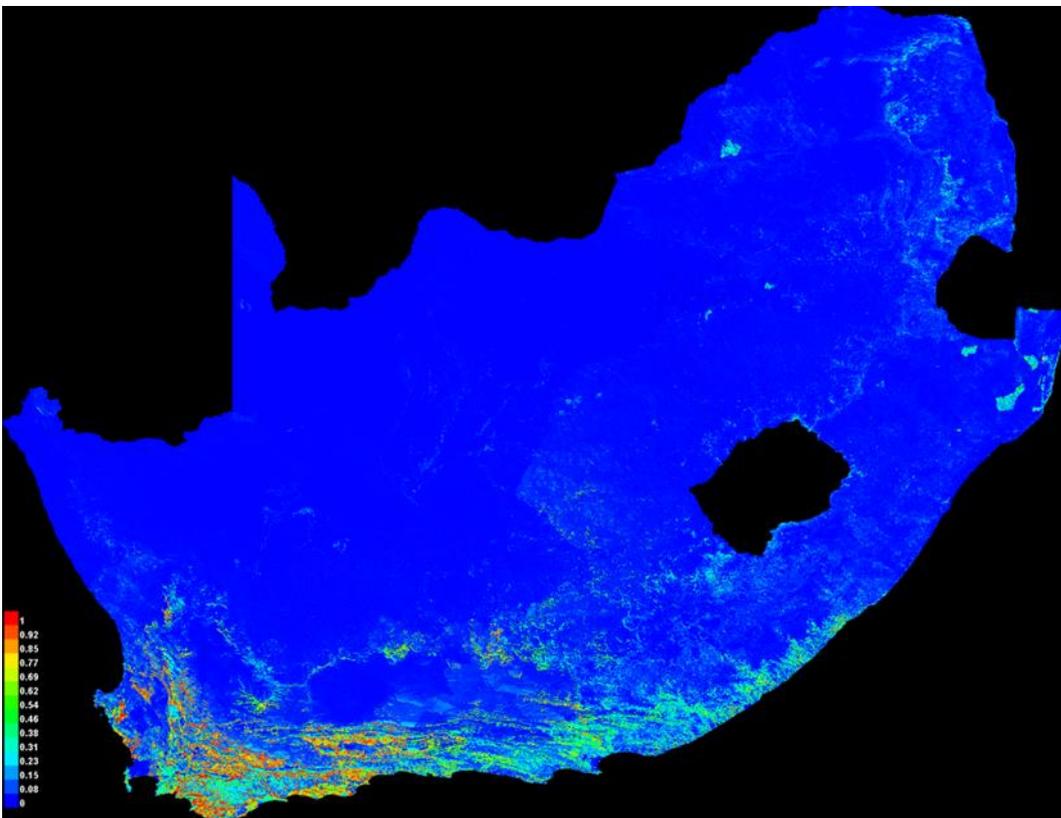


Figure 14. Habitat suitability map of common duiker.

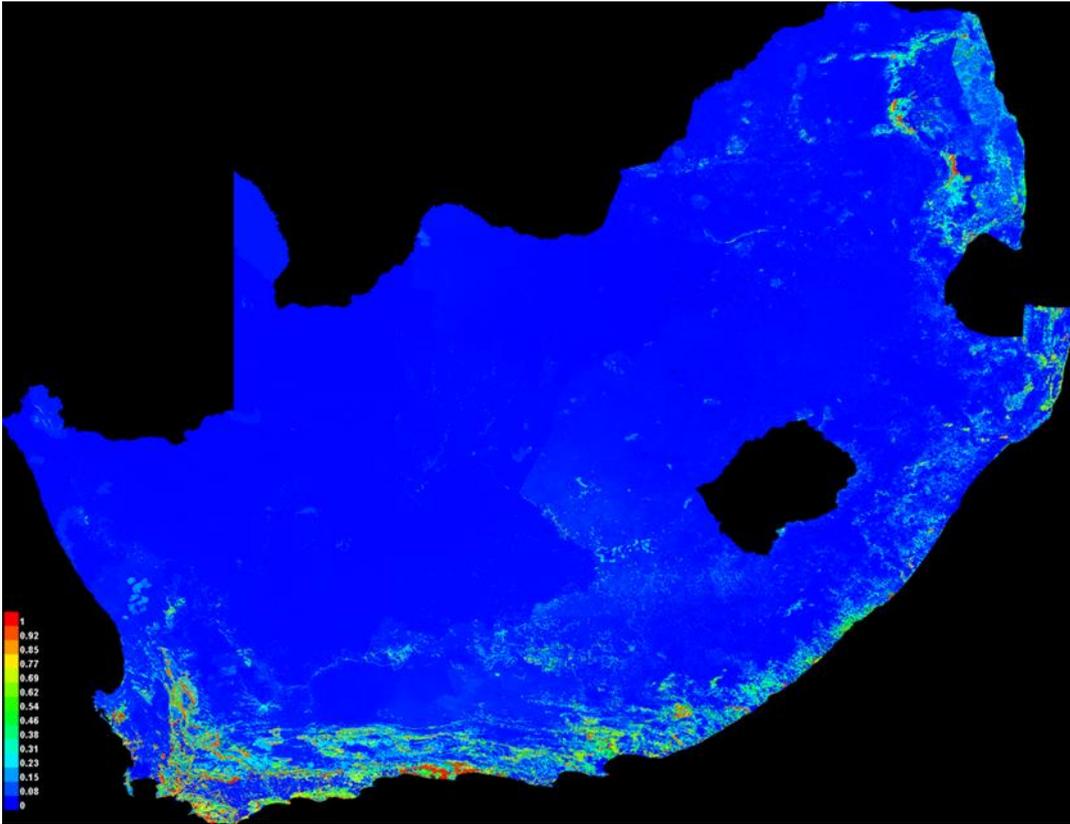


Figure 15. Habitat suitability map of genet.

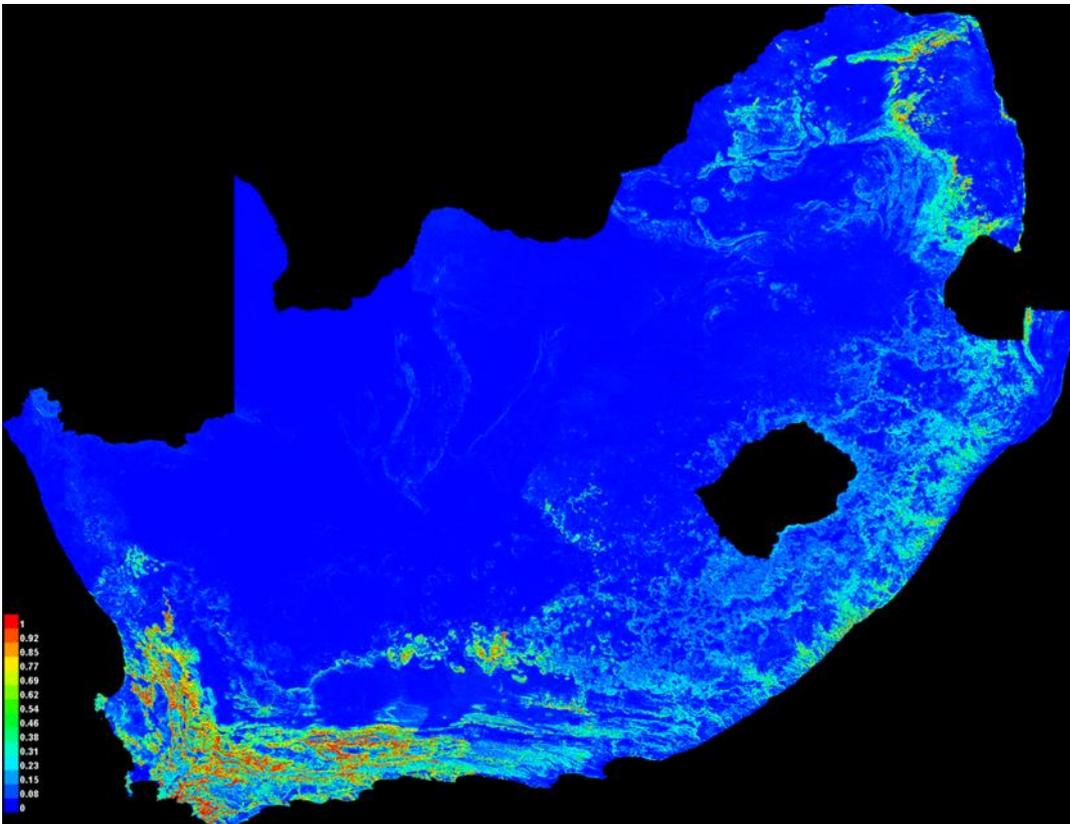


Figure 16. Habitat suitability map of hare.

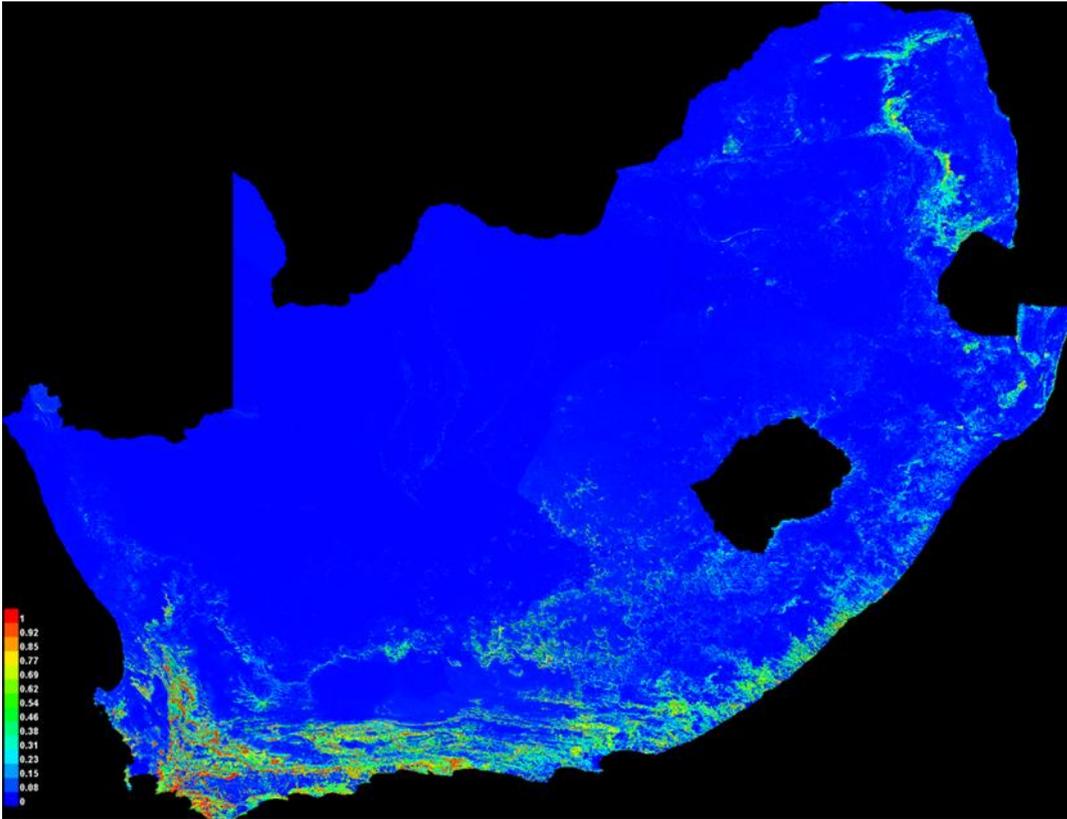


Figure 17. Habitat suitability map of mongoose.

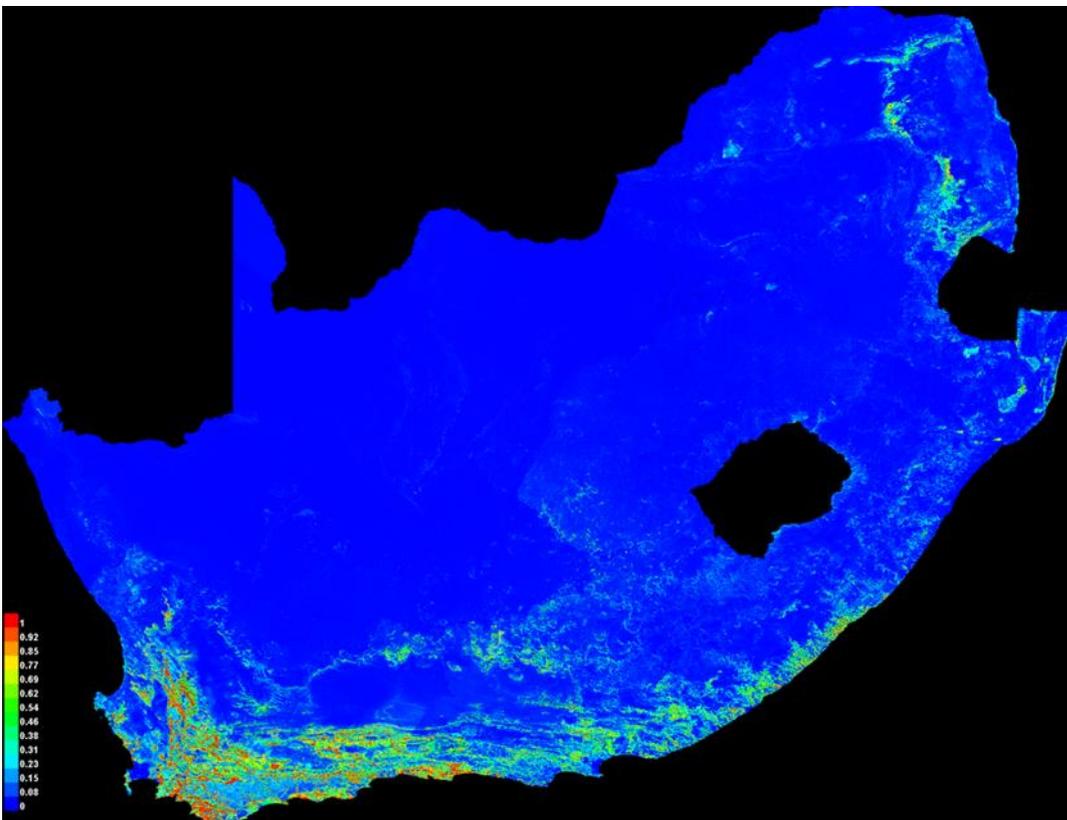


Figure 18. Habitat suitability map of porcupine.

Appendix 2: Chart graphs

A) Relationships between habitat suitability of leopard and habitat suitability of prey species

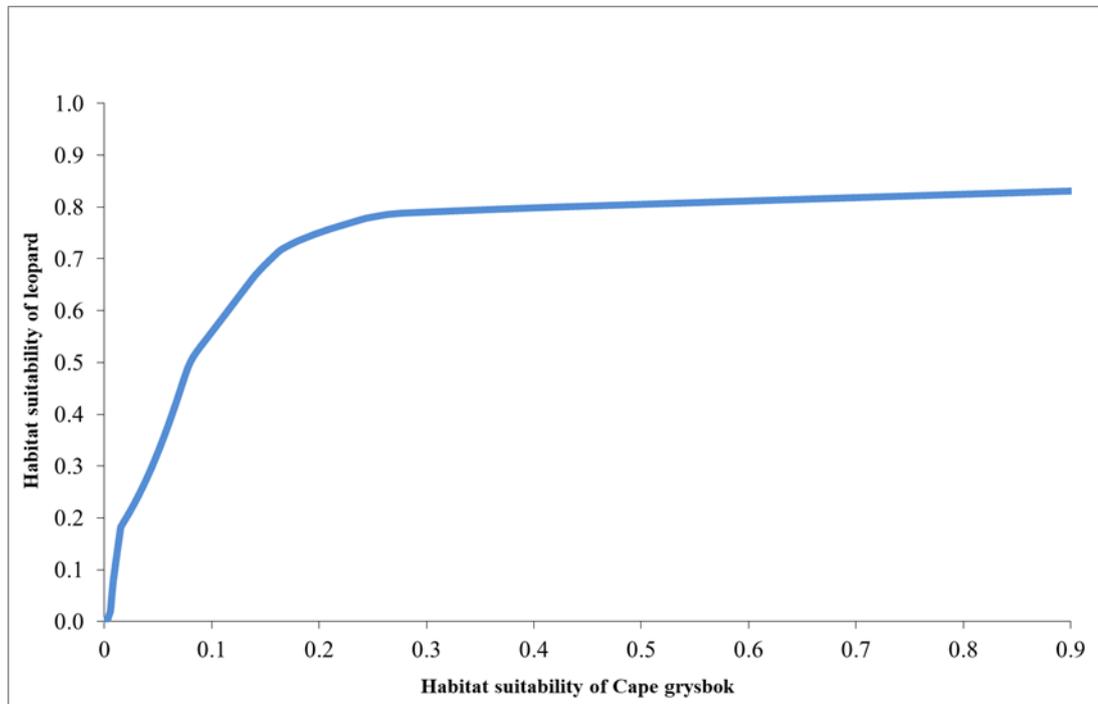


Figure 19. Leopard response to the habitat suitability of Cape grysbok.

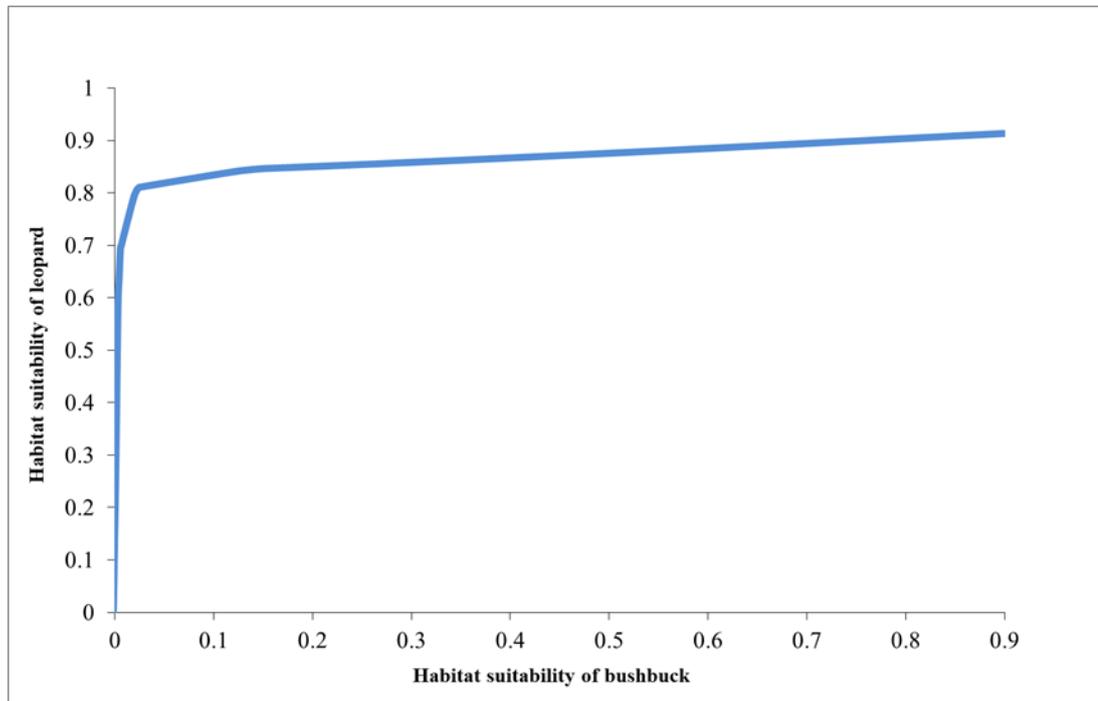


Figure 20 Leopard response to the habitat suitability of bushbuck.

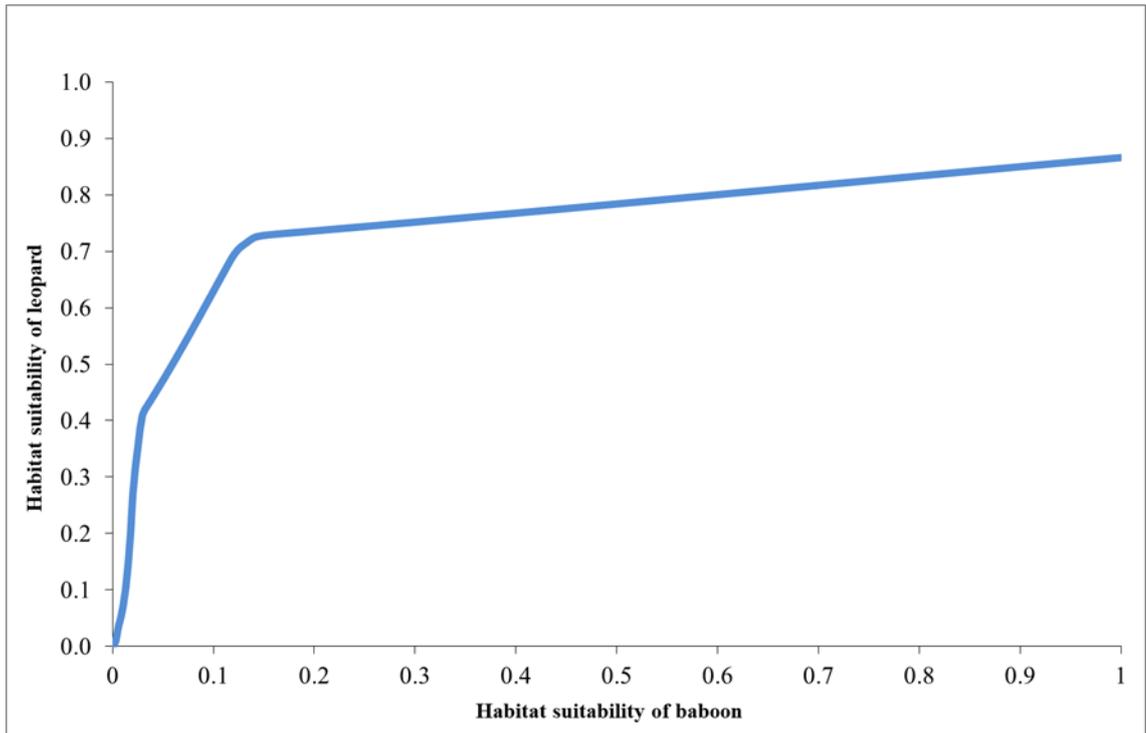
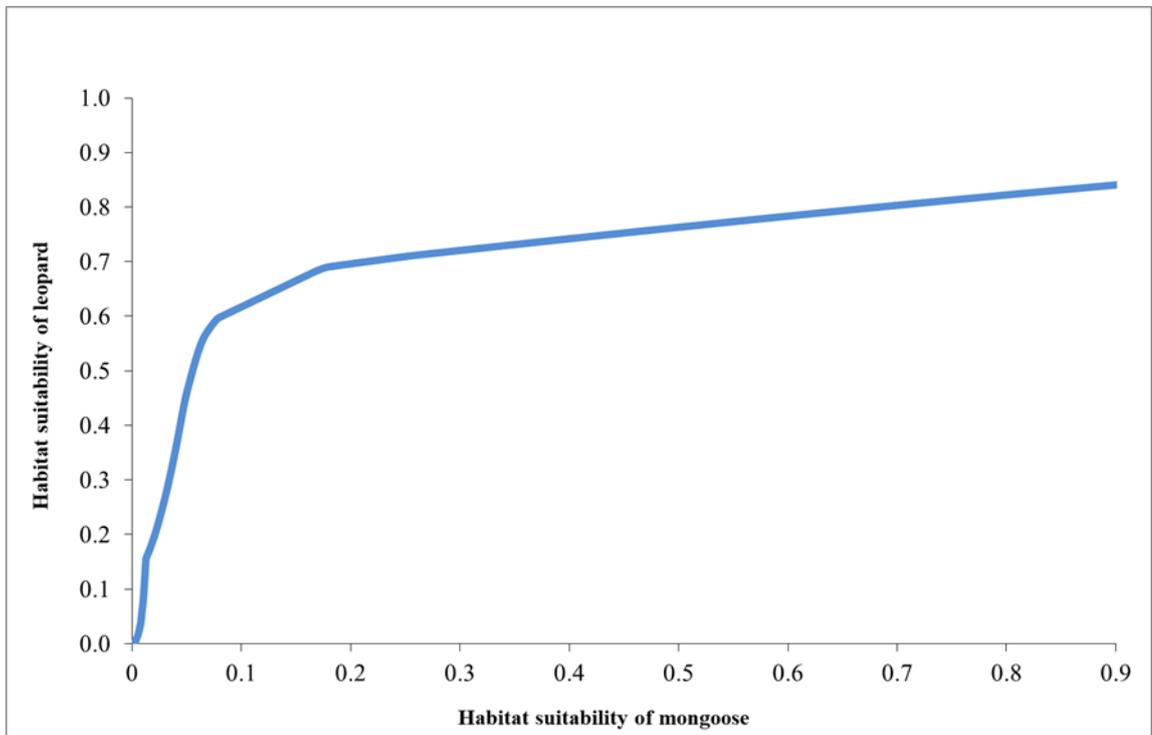


Figure 21. Leopard response to the habitat suitability of baboon.



Graph 22. Leopard response to the habitat suitability of mongoose.

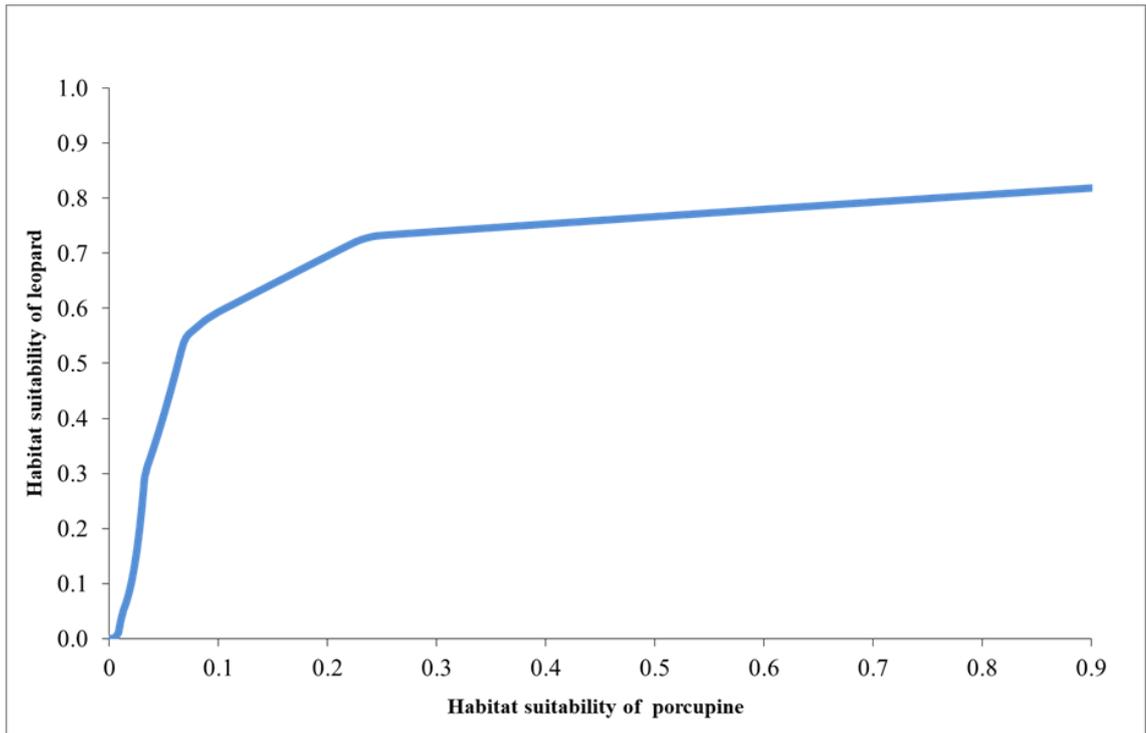


Figure 23. Leopard response to habitat suitability of porcupine.

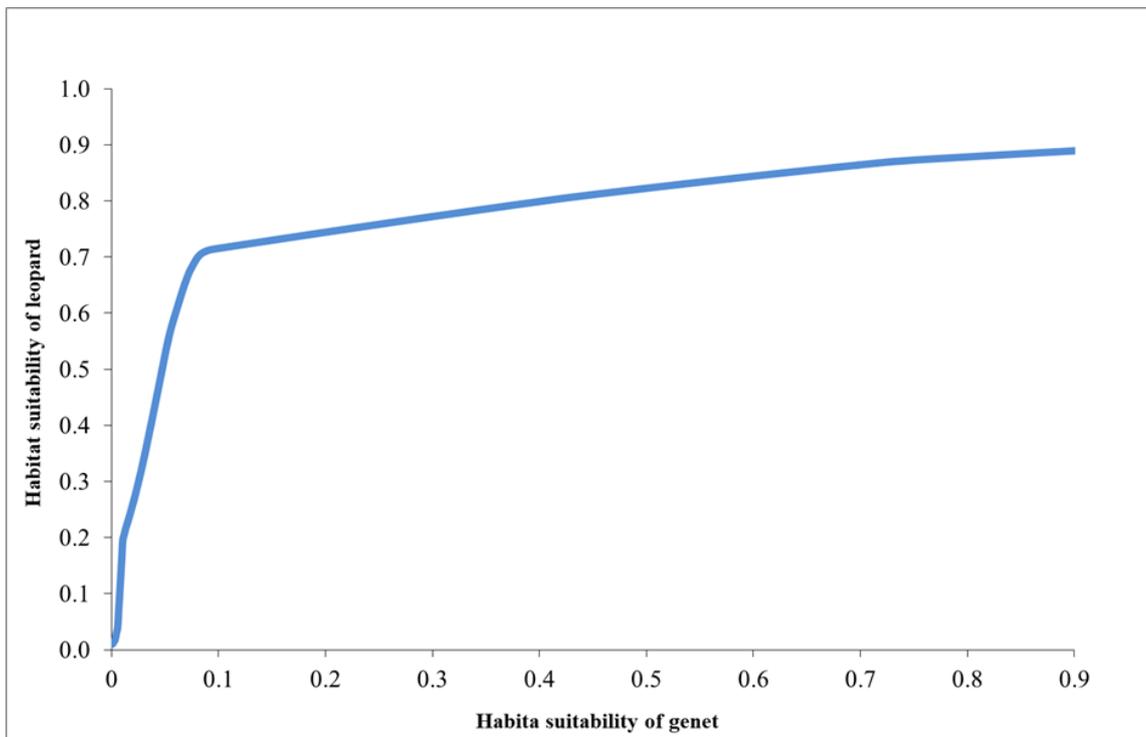


Figure 24. Leopard response to habitat suitability of genet.

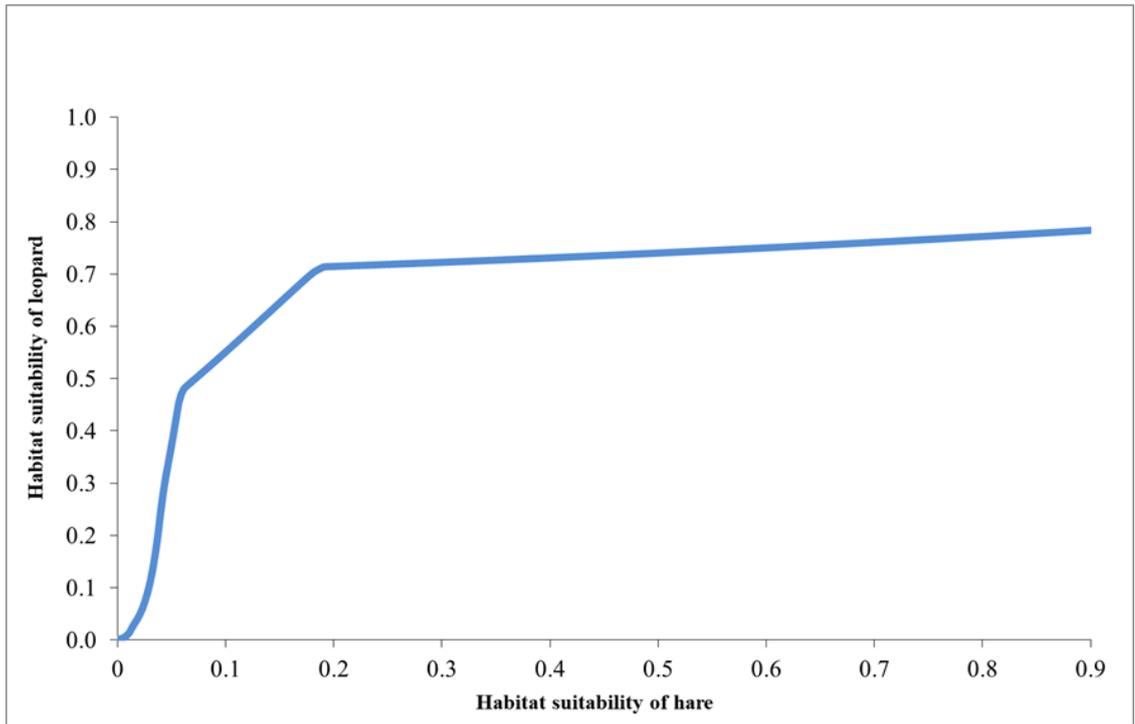


Figure 25. Leopard response to habitat suitability of hare.

Appendix 2: Chart graphs:

B) Relationship between habitat suitability of leopard and continuous environmental variables

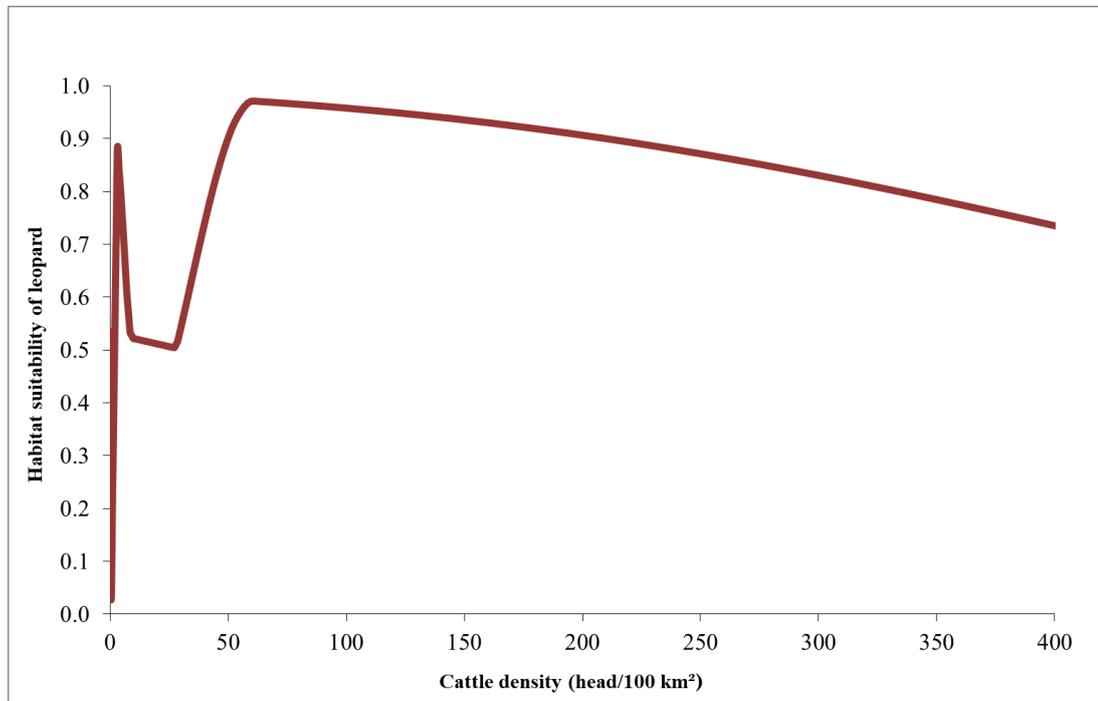


Figure 26. Response of leopard to cattle density (head/100km2).

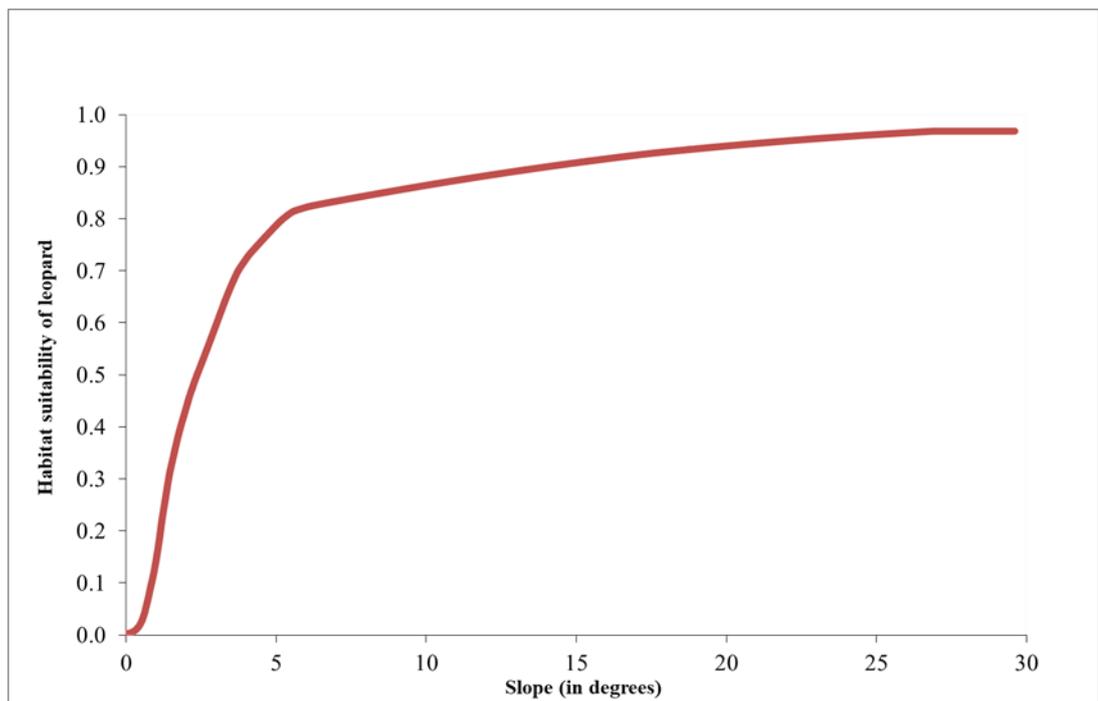


Figure 27. Leopard response to the slope (in degrees).

Appendix 2: Bar graphs:

Relationship between habitat suitability of leopard and categorical environmental variables

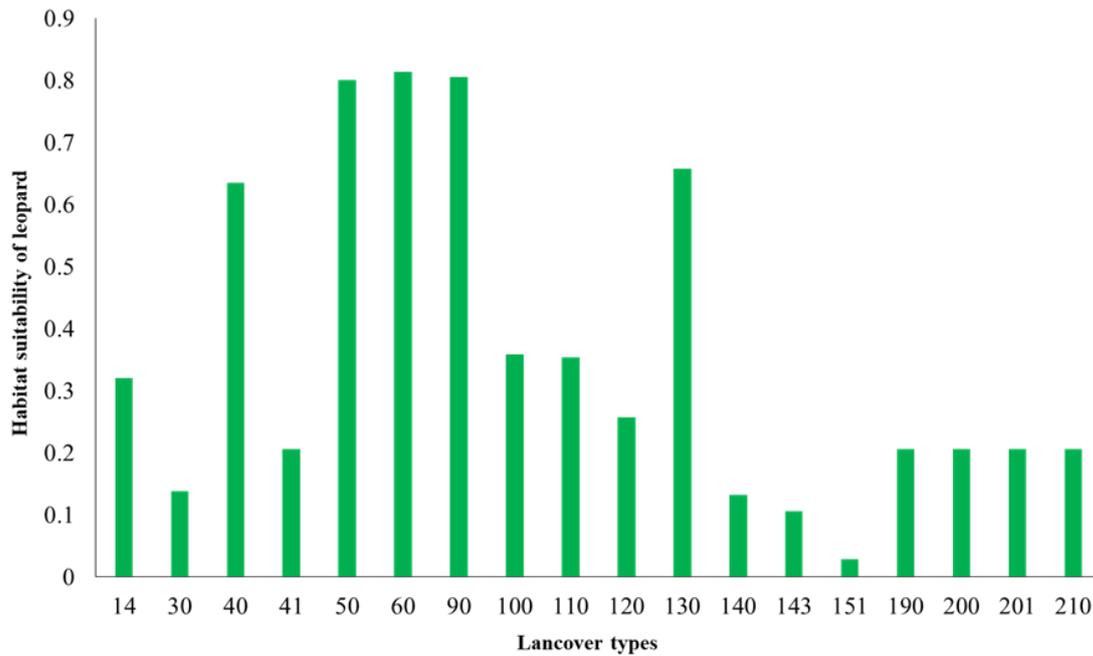


Figure 28. Response of leopard to different land cover types. The greatest habitat suitability was at land cover categories 60, 90 and 50 (chart with land cover category types is in Appendix 3).

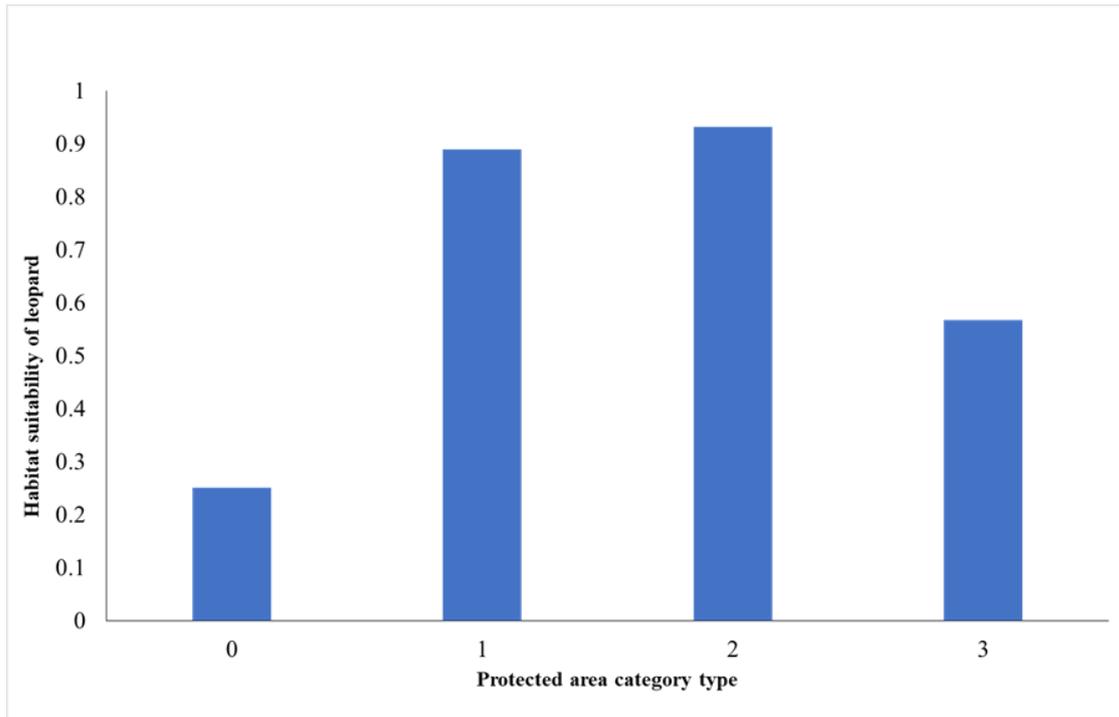


Figure 29. Response of leopard to different protected area category types. The greatest habitat suitability is found in category type 2 (formal protected area type B) followed by 1 (formal protected area type A) and 3 (informal protected area). Type 0 indicates no protect area.