CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences

Small-carnivores population survey in Southern Namibia

MASTER'S THESIS

Prague 2020

Author: Bc. Alba Andrés Criado

Chief supervisor: doc. Ing. Karolína Brandlová, Ph.D.

Consultant: Ing. Viktor Neštický

Declaration

I hereby declare that I have done this thesis entitled "Small-carnivores population survey in Southern Namibia" 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, 13th of May, 2020

A. Andrés

....

Alba Andrés Criado

Acknowledgements

First of all, I would like to thank my supervisor Dr. Ing. Karolína Brandlová, Ph.D. for giving me the opportunity of working on this topic and helping and supporting me during the process of the elaboration of this thesis. I would like to show my gratitude to my teachers and other members of the department, thanks to whom I have learned much more than what was offered in the study program.

I would also like to show my gratitude to the Faculty of Tropical Agrisciences and the Czech University of Life Sciences in Prague, which provided me with the financial support for the realization of the fieldwork and gave me the opportunity to travel to the real Africa I always dreamed of.

I would also like to mention in these acknowledgements all the people I shared my life with during the trip to Namibia, wonderful people always willing to help us and share their immense knowledge with us: Gabriel, Monika and Jan, the O'Connell family and the two Petrorius families, people who love and transmit their love, passion, and dedication for the land they live and work on. Last but most important is my gratitude to the Morkel family, who offered us this wonderful opportunity, welcoming us into their home and sharing their life, stories and adventures with us. Estelle and Pete are incredible and strong people, who dedicate their entire lives to the defence of wildlife. In these acknowledgements I would like to show them all my support and send them my best wishes and hope for the battle they are fighting these days.

Thanks to my consultant Viktor Neštický who helped us with the design of the methodology and all the data collection, being our guide in Namibia. To him I add my other travel partners, Clara Koch Jimenez, Germán Franco Polo and Adrián Martín Taboada with whom I shared many laughs, braai nights and unforgettable experiences.

Carlos Castillo deserves a special mention in this section, without him you wouldn't be reading this thesis. Thanks to him I discovered this master's degree and his support has always been present during these two years.

Thanks to my family, friends and classmates. My most special gratitude goes to Daniel Hernández Alonso, my life partner, with whom I not only share all my good and bad moments, but also my vocation and admiration for wildlife. Together we decided to face the challenge of coming to the Czech Republic and leaving our comfort zone, an experience I do not regret for a second.

Last but not least I want to express my gratitude to everyone that is reading this thesis, to which I have dedicated a lot of my time and illusions, enjoying and learning with it in the same way that I hope you will.

Abstract

Small carnivores represent a group of species with great ecological plasticity, present in all continents and habitats, exhibiting a wide range of adaptations that allow them to survive from different food resources and in the most extreme situations. These adaptations place them in intermediate positions in the food chain, playing vital roles in the maintenance of ecosystem communities by regulating the levels of primary consumers, feeding the larger predators and also participating indirectly in their regulation through disease transmission.

The framework of this thesis was focused on a study of the diversity of small carnivores in a private reserve located in the arid Nama-Karoo of southern Namibia. The data collection took place during the winter of 2019, using 30 camera traps that operated continuously over the period of one month. The main objective of this thesis was to describe the species richness and diversity of small carnivores in the area by studying their distribution patterns, abundance and diurnal activity. Ten species of small carnivores belonging to the families Felidae, Canidae, Hyaenidae, Mustelidae, Viverridae and Herpestidae were detected in the area, being uniformly distributed throughout the study area, with differences in the choice of habitat by the different species, according to their vital needs. Almost all species except Cape grey mongoose (*Herpestes pulverulentus*) showed a nocturnal pattern of activity and overlapped in time with other species, indicating a low level of competition.

This thesis is presented as a first approach to the study of small carnivores in the area, creating a basis of knowledge for the proper management and conservation of these species in desert lands where resources are limited.

Key words: camera traps, diversity, species richness, occupancy, activity pattern.

Contents

1. Introduction and Literature Review ... 1

1.1. Small Carnivores ... 3

1.1.1. Small Carnivore Families ... 5

1.1.2. Ecological roles of small carnivores ... 8

1.1.3. Conservation Status of Small Carnivores ... 9

1.1.4. Research on Small Carnivores ... 12

1.2. Camera traps in wildlife surveys ... 15

1.2.1. Advantages and disadvantages of Camera traps ... 15

1.2.2. Approaches of Camera trap surveys ... 17

2. Aims of the Thesis ... 20

3. Methods ... 22

3.1. Study area ... 22

3.2. Data collection ... 26

3.3. Data analysis ... 28

3.3.1. Diversity and species richness ... 29

3.3.2. Relative Abundance Indices ... 31

3.3.2.1. Photographic Camera Trapping Rate Calculation ... 31

3.3.2.2. Modelling Occupancy and Detection Probabilities ... 32

3.3.3. Activity pattern ... 34

4. Results ... 35

4.1. Diversity and species richness ... 36

4.2. Relative Abundance Indices ... 40

4.2.1. Photographic Camera Trapping Rate ... 40

4.2.2. Occupancy and detection probability ... 42

4.3. Activity pattern ... 48

5. Discussion ... 52

6. Conclusions ... 58

7. References ... 59

List of tables

Table 1. Small Carnivore species expected and observed 35

Table 2. Individuals sampled in the study area, species richness estimates and diversity indexes.. 36

Table 3. CTR results for small carnivore species 41

Table 4. Model estimation for occupancy and detection probability for each species of small carnivore ranking the models by the lowest AIC 44

Table 5. Occupancy and detection probability values estimated (± SE) for the model with the best fit 47

Table 6. Summary table of circular descriptive statistics. 50

Table 7. Temporal overlap of the small carnivores in the area of study....................... 51

List of figures

Figure 1. Area of study, located in the most southern part of Namibia........................ 22

Figure 2. Picture of KumKum Farm.. 24

Figure 3. Selected habitats in KumKum and Pelgrimsrust farms................................ 27

Figure 4. Accumulation and rarefaction curves of small carnivore species detected over time in the whole study area.. 38

Figure 5. Accumulation and rarefaction curves of small carnivore species detected over time in the rocky mountain habitat.. 38

Figure 6. Accumulation and rarefaction curves of small carnivore species detected over time in the milky shrubland habitat.. 39

Figure 7. Accumulation and rarefaction curves of small carnivore species detected over time in the sandy plain habitat.. 40

Figure 8. CTR mean vales and SE bars represented for each species across the different habitats... 42

Figure 9. Bar Graph representing the values of calculated Naïve Occupancy for the small carnivore species for the whole area and each habitat........................... 43

Figures 10(a-h). Graphs representing the estimates of occupancy and detection probabilities obtained for the model that best fit the distribution of each species of small carnivore... 46

Figures 11 (a-j). Circular plots representing the circadian activity pattern of the small carnivore species 49

List of the abbreviations used in the thesis:

AIC: Akaike Information Criteria

CR: Critically Endangered

CSD: Circular standard deviation

CTR: Camera Trapping Rate

EN: Endangered

HWC: Human Wildlife Conflict

IUCN: International Union for Conservation of Nature's Red List

LC: Least Concern

m a.s.l: meters above sea level

MS: Milky Shrubland

mya: million years ago

NT: Near Threatened

OSG: Otter Specialist Group

RM: Rocky Mountain

SCR: Spatial Capture-recapture m

SCSG: Small Carnivore Specialist Group

SD: Standard Deviation of the mean

SE: Standard Error of the mean

SH: Shoulder Height

SP: Sandy Plain

VU: Vulnerable

WA: Whole study Area

1. Introduction and Literature Review

The world is changing. During the last 50 years, human beings have experienced an exponential increase in their population, which requires the exploitation of the natural resources for their development. This situation generates an impact on the ecosystems that affects the rest of life on Earth. Habitat loss and fragmentation, climate change, overexploitation of natural resources, introduction of invasive species and diseases and anthropogenic pressures are the main threats that biodiversity is facing nowadays (Sechrest & Brooks 2002).

Carnivorous mammals are particularly sensitive to these threats, as they require larger territories to satisfy their needs, share and compete for the same resources with humans (entering into conflict with them), or simply their way of life is not compatible with urban life. In addition, any change in their environment not only has a direct impact on carnivores, it also impacts the lower levels of the trophic chain on which they rely for their survival (Purvis et al. 2000; Cardillo et al. 2004).

The efforts that conservation biologists are making to measure and understand these threats and their consequences on carnivore populations are not uniformly distributed: large carnivores have always attracted more attention to the society, either because of their majesty and beauty (in the positive and negative sense for them), or because of the conflict they generate for humans by being large predators. However, their smaller relatives seem to be less interesting despite their greater number of species, variety of niches and habitats or their complex lifestyles (Roemer et al. 2009).

Africa is home to one third of the world's small carnivores, yet it is a continent where research focused on small carnivores is low compared to other continents (González-Maya & Ramírez-Chaves 2017) or compared to large carnivores (Do Linh San et al. 2013). One of the causes may be that a large number of small carnivore species are not threatened and have wide distribution ranges or maybe, they are not interesting enough to be studied as they are not as annoying as large carnivores are for humans (Brooke et al. 2014).

The importance of small carnivores in ecosystems, their value as indicator or keystone species and our relationship with them deserve much more understanding than is devoted to them. To do this, it is important to know the life history of the species, their distribution, their role in the community and how people are influencing them and vice versa.

When studying species, it is common for researchers to choose protected nature reserves or parks to carry out their studies, as these are relatively controlled areas where access to information and the research process may be relatively comfortable (Brooke et al. 2014). However, life in these places may be slightly different from life outside them, due mainly to human action and environmental modification it produces outside these protected areas. Small carnivores are able to live especially well outside of these reserves as they are able to adapt to anthropogenic areas, finding places where the conflict of humans with large carnivores has eliminated their main predators, creating relatively safe areas for them (Bateman & Fleming 2012). In those areas, several species of small and medium carnivores can live together, establishing very complex relationships among them and the rest of the species, including domestic species. For these reasons, there is a need to understand the fauna beyond the large reserves, to areas not so well studied, to degraded habitats and see how life develops in these regions.

Remote and hard-to-reach areas such as deserts and rocky areas are particularly difficult to do research as it is uncomfortable to move around them and are often places where there are no adequate facilities or means to research or live. In these places, where active methods can be tedious and ineffective, passive sampling methods such as camera traps can provide information on wildlife that would otherwise be almost impossible to record. Camera traps, in exchange for a relatively low economic investment and simple installation and handling, make it possible to detect a wide range of species, to know their behaviour, their activity patterns, their life traits and even to identify individuals. They stand out from other methods in their ability to sample elusive and nocturnal individuals, species that live in low densities or are difficult to detect, features that perfectly define small carnivores.

1.1. Small Carnivores

The Small Carnivores, better called Small Carnivorans and also called Mesocarnivores, represent the smaller members of the Carnivora order. Despite the fact that their morphologies, sizes and habits vary between groups, any species whose average weight is less than 15-20 kg is considered a small carnivore in opposition to large carnivores (Buskirk & Zielinski 2003; Roemer et al. 2009). These species are widely distributed throughout the order, being present in 12 from a total of 13 current terrestrial Carnivora families.

All these families are grouped into two distinct suborders. The suborder Feliformia includes species with certain "cat-like" appearance: Felidae (small and big cats), Hyaenidae (hyaenas and aardwolf), Herpestidae (mongooses), Viverridae (genets and civets), Eupleridae (malagasy mongooses and fossa), Nandinidae (African palm civet), and the recent Prionodontidae (lisangs). All of them, except Felidae and Hyaenidae, are made up exclusively of small carnivores. On the other side the suborder Caniformia collects "dog-shaped" species: Canidae (dogs, wolves, foxes...), Procyonidae (racoons, coatis, kinkajous...), Ailuridae (red panda), Mephitidae (skunks, stink badgers), Mustelidae (weasels, otters, badgers...) and the families without small carnivores Ursidae (bears), Otaridae (sea lions), Phocidae (seals) and Odobaenidae (walrus) (Hunter 2018).

The main characteristic common to these families appears in the late Paleocene (55-65 mya) in a civet-like mammal (belonging to the Miacoidea group), today considered the common ancestor of the order Carnivora (Macdonald & Kays 2005; Goswami 2010). This characteristic arises as a change from an insectivorous diet to a diet based on larger prey and is called " carnassial pair". It consists of a pair of cheek teeth (usually the last upper premolar and the first lower molar) with a blade-like shape used to cut and tear different animal tissues (Edelman 2019).

This modification in the diet requires other adaptations at a structural level. Life as a predator requires a very defined body design to ensure success in hunting. The senses are highly developed; the eyes are placed in a frontal position increasing the capacity to distinguish depths (Kitchener et al. 2017), the hearing is enhanced, and the sense of smell is developed to the maximum extent known in mammals. All these senses are integrated into a large brain (Edelman 2019), which allows them to develop complex predatory and social behaviours.

Although these adaptations seem to be common to all species, adaptive radiation has made carnivorans really flexible in terms of diet. Some families such as felids and mustelids are almost exclusively carnivorous, others contain species that rely on a large percentage of invertebrates (aardwolf, bat-eared fox, otter), are omnivorous in a higher or lower degree (foxes, civets, raccoons) or even almost totally herbivorous (red panda, kinkajou) (Macdonald & Kays 2005). Most of the species are highly generalists eating almost everything they can catch or prey and provides a source of energy, but also, some species are very specialist, using mainly one type of prey (e.g. Ethiopian wolves' preys are mainly small rodents (Macdonald & Kays 2005), red panda's diet is about 95 % of bamboo (Hunter 2018)) . These dietary adaptations are closely related to the lifestyle and habitat of each species.

Carnivores have been able to colonise all continents except Antarctica, being present in very diverse habitats; from vast, bare lands such as arctic areas and deserts, to areas of exuberant tree cover as the jungles of equatorial zones (Macdonald & Kays 2005; Edelman 2019). In these various habitats, different lifestyles arise as a result of adaptation to the environment, the climate and the relationship with other members of the community. The small carnivores can be terrestrial, fossorial, arboreal and even closely related to aquatic environments. Most of them are nocturnal but there are also some diurnal species.

Regarding their social organization, the majority of species are solitary. This behaviour is justified for several reasons, including competition for resources (food and breeding pair), the small size of their prey (it makes it unnecessary to require help to hunt it and sharing is not worth) and that in most cases the females do not need the male to raise their offspring and even avoid him. Nevertheless, some species have assumed the costs that a life in company requires in order to obtain a series of benefits such as the defence of greater territories (European badgers), to prevent being predated (meerkats), to increase their hunt efficiency (mutualism between coyotes and American badgers) or to increase their biological effectiveness (cooperative breeding in dwarf mongooses) (Macdonald & Kays 2005).

Solitary or not, each individual depends on the relationship with the rest of the inhabitants of his environment for survival. Carnivores have developed a complex communication system, integrated by different visual (facial expressions, body postures), acoustic and olfactory signals that allow the messages to be transmitted in time and space (Macdonald & Kays 2005). Odorous signals play a very important role for carnivores, since their communicative function allows them to mark their territories, indicate their reproductive state, identify themselves as members of a group or deter possible aggressors (Edelman 2019). These signals are found in urine, faeces and in secretions formed by different odoriferous glands. Among them, the anal glands seem to play a very important role in communication, as they can be found highly developed in some species, forming sacs or pouches that can be used to spray substances in several circumstances (Gorman & Trowbridge 1989).

Once the main common characteristics of this group are known and the great variability of life traits observed, it is pertinent to describe the characteristics that unify the members of the different families, focusing mainly on the families with representatives in the African continent.

1.1.1. Small Carnivore Families

As seen in the introduction to this subchapter, within the order Carnivora there are two taxonomic divisions according to the morphological similarity with felids (Feliformia) or canids (Caniformia). These groups, now supported by genetic data (Agnarsson et al. 2010), classified the species by matching their morphological features with the general descriptions that defined the different taxa.

The main group that defines the appearance of the suborder Feliformia is the family Felidae, which are easily recognizable since all their species have great similarities with the domestic cats. Almost all its morphology reveals their predatory and hypercarnivorous lifestyle (Hunter 2018). They have triangular heads with short, flattened snouts that increase the power of biting. The eyes are large and in a frontal position, giving them excellent depth perception as well as excellent night vision. The ears are large and very mobile, able to detect the slightest sound. They have a slender body and strong forelimbs armed with powerful retractile claws (except for the cheetah) that facilitate the grip of the prey once it has been reached (Kingdon & Hoffmann 2013). This perfect killer design is culminated by a variety of fur patterns that allow them to camouflage in the different environments where they live (Sunquist & Sunquist 2002; Nowak 2005).

Within the family Hyaenidae there is only one species of small carnivore, the aardwolf (*Proteles cristata*). The most notable characteristic of this group is the digestive ability which allows them to digest substances from carrion (hyaenas) to toxic terpenes produced by termites (aardwolf) (Kingdon & Hoffmann 2013; Hunter 2018). The aardwolf in appearance reminds of a striped hyena (*Hyaena hyaena*), but smaller in size and weaker in body structure, having the same curved appearance caused by having the front legs longer than the hind ones. Despite having highly developed jaws like its larger relatives, the aardwolf lacks a developed carnassial pair due to its almost exclusive diet of termites and insect larvae. It inhabits mainly in open sandy plains or shrubby areas, using old aardvark burrows as shelter (Macdonald & Kays 2005).

The herpestids (Herpestidae) and viverrids (Viverridae) are families whose species have a similar body pattern: elongated body with short legs and long tail, long and pointy head and presence of developed anal glands. Viverrids have more striking coat patterns, often with spots and stripes (e.g. civet and genet), while herpestids (mongoose and meerkats) have more discreet and uniform patterns. Herpestids are slightly smaller, have shorter and bushier tails and significantly smaller and more rounded ears (Kingdon & Hoffmann 2013). Another difference among them lies in the habitat preference: viverrids prefer to live in areas with dense vegetation while herpestids live in more open places (Nowak 2005; Edelman 2019).

The other three families, Eupleridae, Nandinidae and Prionodontidae, are much more limited in species and geographical distribution. All of these families resemble in appearance to the viverrids, reason why they were grouped within this family for a long time, but now current molecular studies show that they are different families (Agnarsson et al. 2010; Hunter 2018). Euplerids form a group endemic to Madagascar with only eight species (Edelman 2019), the family Nandiniidae has only one species restricted to equatorial Africa, *Nandinia binotata* (African palm civet) and Prionodontidae is a family made up of two arboreal species distributed in Southeast Asia (Hunter 2018).

The most representative family within Canifomia at all levels is Canidae. The morphology of its members is modelled by the process of adaptation to the rapid pursuit of their prey during prolonged periods of time, providing them with great stamina. Its body is flexible and muscular, with a deep chest with long limbs and a generally bushy tail (Kingdon & Hoffmann 2013). Unlike felids, canids base their capture of prey on bites with their sharp canines, instead of claws, so their nails can be blunt and not retractable, more useful for running. The snout and skull are elongated, with large erectile ears and the sense of smell is extraordinarily developed (Edelman 2019). This group counts with several social species that live and hunt in a cooperative way in very complex hierarchical systems, whereas other species, generally the smaller ones, hunt in a solitary way (Nowak 2005).

The elongated morphological pattern observed in viverrids and herpestids is also shown in the families Mustelidae and Mephitidae, which allows them to chase their prey in burrows or provide them with a suitable body shape for aquatic lifestyle (otters, included in Mustelidae). In these families this structure is accompanied by a flexible torso and small eyes and ears. The coat pattern is very varied, ranging from completely plain to striped or spotted patterns with highly contrasting colours (warning coloration). The claws are not retractable and can be very developed for burrowing. These two families are remarkable for their highly developed anal glands, which are used to eject secretions with a generally defensive component. While mustelids are widely distributed around the world, mephitids are restricted to the American continent and islands of Southeast Asia (Nowak 2005; Kitchener et al. 2017; Edelman 2019).

The procyonids (Procyonidae) are distributed in America and are characterized by their facial markings, plantigrade walking and the possession of long tails, used for balancing. They live mainly in forests and their diet varies between highly omnivorous and herbivorous. All of these features fit with the description of the red panda (*Ailurus fulgens*), an exclusively herbivorous species inhabiting the forests of East Asia, previously included within Procyonydae family but currently listed as the unique species of the family Ailuridae (Nowak 2005; Edelman 2019).

Small carnivores are found mostly in the intermediate levels of trophic chains and communities. This is because they are predators, but they are also be predated by larger carnivores. This intermediate position has shaped their life forms and placed them into a strategic position in the ecological communities, giving them tremendously versatile functions in the ecosystems (Palomares & Caro 1999; Buskirk & Zielinski 2003; Roemer et al. 2009).

1.1.2. Ecological roles of small carnivores

The role of small carnivores in ecosystems is more complex than might initially be thought (Roemer et al. 2009). Due to the great variety of diets and sizes present in this group, the roles that they can play are also very varied and what is more remarkable, the same species may play different roles according to the circumstances and the environment in which it lives (Buskirk & Zielinski 2003).

When several species of carnivores live together in the same community, it is likely that there is competition for resources between them or even that one may be prey of the other. This situation is known as “intraguild predation” and constitutes a form of regulation of the lower levels of carnivore populations. In it, the larger predators exert direct pressure on the smaller ones, preying on them, or in an indirect manner, forcing them to modify their social, temporal or spatial distribution, constituting the only way to avoid these potential predators (Palomares & Caro 1999; Buskirk & Zielinski 2003).

In areas where large carnivores are absent, smaller carnivores rise to the apex predator range, controlling the exploitation of plant resources by reducing the number of primary consumers or affecting their behaviour (Palomares & Caro 1999; Terborgh et al. 2001; Edelman 2019). The areas where small carnivores play this role are mainly insular systems where most species are small size. This also occurs in urban or disturbed areas, where habitat fragmentation increases the proportion of land considered as edge areas, where survival for large carnivores is more difficult (Macdonald & Kays 2005). In these fragmented and heterogeneous habitats, the community is altered in a way that the regulation processes that modelled the species composition in the past have now changed, and the absence of former apex predators is one of the key changes. The mesopredator release hypothesis explains that the sudden elimination of an apex predator (either large or small carnivore) in a community produces an increase in smaller carnivore numbers, putting primary consumer populations at risk of overexploitation and extinction with the following consequences that may occur (Crooks & Soulé 1999).

The ingestion of plant matter gives small carnivores another function, which is seed dispersal. Although hypercarnivores can disperse seeds indirectly by consuming the digestive content of their prey (Hämäläinen et al. 2017), the species that play a very important role dispersing seeds are the omnivorous and frugivorous ones (Herrera 1989; Escribano-Ávila 2019). One of the reasons that justify their value as seed dispersers include the greater size of home ranges in comparison with granivorous birds and mammals, allowing the seeds to go further, and even colonize new habitats. In addition, small carnivores preserve the viability of the seeds as they do not mechanically damage them during the ingestion process (González-Varo et al. 2015) and they also favour embryo germination after chemical digestion of some of its protective coatings (Escribano-Ávila 2019).

Small carnivores may also act as reservoirs of disease. The pathogens that most seriously affect large carnivore populations (parvovirus, rabies and canine distemper) are generalists affecting a large number of carnivore taxa. These pathogens are maintained in the populations of smaller species due to the higher density of individuals, and in case of an encounter with a large carnivore, the spillover will occur. This is a particular case in which species from a lower trophic position can limit populations from the highest level of the community (Roemer et al. 2009; Edelman 2019).

For all of these reasons, small carnivores seem to have an enormous weight in the regulation of ecosystems and their correct management can be decisive in preserving an area and the biodiversity that lives in it.

1.1.3. Conservation Status of Small Carnivores

According to data from the IUCN Red List (IUCN 2020b), there are currently 235 species of small carnivores worldwide, of which, three species are in the category of Critically Endangered (CR), 22 species Endangered (EN) and 30 species in Vulnerable (VU) status, making a total of 55 threatened species (23.41 % of the total). Although most species are categorized as Least Concern by IUCN, assessments show that the populations of 117 species are declining (49.79 %), a number that could be higher given that the trend of 47 species (20 %) remains unknown. These percentages show that the current categories may change in the coming years, and that non-threatened species, which are shown to have little conservation attention, may be at greater risk than estimated (Do Linh San et al. 2013). According to Cardillo et al. (2004), it is possible that by 2030 several carnivore species, especially several Viverridae species, could move into threatened categories solely due to human expansion and its impacts. Most of these species in potential future danger are located in Africa, continent that is experiencing a high population growth.

Africa is home for 8 of the 12 families of small carnivores (Felidae, Canidae, Mustelidae, Viverridae, Hyaenidae, Herpestidae, Eupleridae and Nandiniidae) (Hunter 2018), containing a total of 88 species, more than one third (37 %) of the global diversity of small carnivores. The families with the largest number of representatives in Africa are Herpestidae (27 species), followed by Viverridae (18) and Mustelidae (13). Of these African species, 17 are threatened (4 EN, 13 VU) and 35 are experiencing population decline. These data may give visibility to a reality, but they are far from accurate as many of the African small carnivore species require updated population and threat assessments (Do Linh San et al. 2013).

The main threats facing carnivores are habitat loss and fragmentation, human persecution and introduction of invasive species and diseases (Macdonald & Kays 2005; Schipper et al. 2008; Purvis et al. 2000; Edelman 2019). These threats are common to almost all of the biodiversity worldwide, but in species that occupy high trophic levels and rely on large territories the effects are doubled. On the one hand, these threats attack carnivores directly, on the other, the attack is indirect by putting the lower trophic levels at risk and with them, also the carnivores that depend on them for their survival.

Many regions of the Earth are changing rapidly and dramatically due to deforestation, desertification and climate change. All these processes are caused in a greater or lesser extent by the action of humans, who use the land for their own benefits, often without taking into account how these modifications affect the rest of life around. Many species of carnivores avoid these altered habitats, as their proximity to humans represents a vital threat to them and in most cases the characteristics of these new habitats are unfavourable to their survival (Crooks 2002; Łopucki et al. 2019). When this happens, carnivore populations are displaced to undisturbed areas, which are increasingly smaller and more fragmented. This results in higher densities of carnivores in these areas, which will compete for increasingly limited resources, leading to a decline in the numbers of these populations (Macdonald & Kays 2005).

Some species of small carnivores are able to survive in urban or anthropogenic areas due to their great ecological plasticity (Schipper et al. 2008). Being generalists of diet and habitat, they find in urban areas a habitat that provides them with multiple food and shelter resources, adding the advantage of not having larger predators around as they are eliminated from urban habitats (above mentioned as mesopredator release) (Bateman

& Fleming 2012). However, in these areas, mesocarnivores also face new risks that are not so common in the wild; the presence of roads represents a great risk for medium and small-sized mammals, being one of their main causes of death and fragmentation of territories nowadays (Grilo et al. 2009; Kiros et al. 2016).

In rural areas, small carnivores can be a nuisance to humans, so they are persecuted and sometimes killed. The main cause of conflict between humans and wildlife is the damage that they cause to livestock or game species. The impact that mesocarnivores can generate on livestock is estimated to be even greater than the one generated by large carnivores. This is due to the fact that large carnivores defend larger territories than small ones, which implies a lower density of predators per area. As the number of small predators in an area increases, the amount of prey they will take is greater (Macdonald & Kays 2005).

Carnivores can also be chased due to their commercial uses (Kruuk 2002). They can be used to obtain skins and hides, traditional medicines (Alves et al. 2013), cosmetic products or as bushmeat. In some cases, commercial production is regulated and the animals are mainly raised on farms for exploitation. In many others, their exploitation is a consequence of illegal harvesting and trade, where animals and their products are highly demanded and without a correct management, certain species are threatened by over-exploitation. This situation stands out mainly in the Asian continent (Hunter 2018), where exploitation is so frenetic that it even requires the export of products from other continents, such as Africa, putting species from both continents at risk (Do Linh San et al. 2013).

One of the consequences of the use of small carnivores for our benefit is their introduction on non-native areas, acting as invasive species that sometimes are able to adapt fiercely to new territories, entering into competition with native species. The result of this conflict is often unfavourable for the indigenous species, which is directly attacked, displaced or has its prey reduced in its home range, making its survival even harder (Roemer et al. 2009). This introduced species, wild or domestic, may bring with them several pathogens that can cause serious damage to local species. Diseases like rabies, mange, canine distemper are thought to be widely distributed along small carnivores, causing high mortality among them (Bateman & Fleming 2012; Edelman 2019).

Despite their great resilience, these threats appear to cause some impact on small carnivore populations, species that are currently in good condition may soon no longer be so. Actions are needed in order to preserve this group of mammals, not only to recover threatened populations but to prevent others from becoming threatened. Carnivore conservation efforts are particularly complex, since in order to protect them it is necessary to protect their entire environment and the living creatures that live in it, taking also into account intra- and inter- guild relationships. Unfortunately, small carnivores have not attracted as much attention as their larger relatives, so some aspects of their life history are not well understood due to lack of research on them.

1.1.4. Research on Small Carnivores

As it has been shown in the previous chapters, the relationship of man with the small carnivores is closer than one might think they can be in our clothes, perfumes, stealing our "prey", controlling the plagues in the countryside or even cohabiting with us as pets. Human beings have always been attracted to carnivores, beautiful but lethal creatures, intelligent and incredibly capable of confronting even the great predator, the human being.

In an effort to understand these creatures, biologists and naturalists have dedicated themselves to studying and understanding these species around the world, discovering new aspects about their lives every day. Currently the IUCN Species Survival Commission has four specialist groups dedicated to small carnivores' conservation by building knowledge about them and their threats (IUCN 2020a). One of these groups is the Small Carnivores Specialist group (SCSG), created in 1989 and devoted to the research and conservation of Mustelids and Viverrids (excluding otters), groups that at that time included species from the families Nandiniidae, Prionodontidae, Herpestidae, Eupleridae, and Mephitidae (IUCN/SSC 2020). The remaining specialist groups have fewer species of small carnivores, with the Otter Specialist Group (OSG) for fresh and saltwater otters, Cat Specialist Group (Cat SG) for large and small cats, Canid Specialist Group (CSG) for the entire family Canidae and Hyaena Specialist Group (HSG), which includes all 3 species of hyenas and the aardwolf (*Proteles cristata*). Other organizations, such as ASCaRIs in Africa, bring together all the small carnivores of the continent, investing their funds to promote research and dissemination of their knowledge (ASCaRIs 2020).

Among the different families of mesocarnivores, Mustelidae, Canidae and Felidae have the largest number of publications per family, while Herpestidae, Mephitidae, Nandiniidae, Viverridae, Prionodontidae and Eupleridae have the least (Brooke et al. 2014, Pérez-Irineo & Santos-Moreno 2013). The most studied species are the European badger (*Meles meles*), the coyote (*Canis latrans*) and the fox (*Vulpes vulpes*), highly synanthropic species, abundant in developed countries of the northern hemisphere, which indicates a more or less clear bias in the research of small carnivores (Pérez-Irineo & Santos-Moreno 2013).

The research effort is biased towards critically endangered and common species with large ranges that somehow conflict with humans and their interests. There also seems to be a tendency for researchers to carry out their projects in areas with easy access to information or areas with available means and infrastructure for data collection and management, including protected areas, locations where research institutions exist or highly populated areas (Brooke et al. 2014).

For these reasons, the distribution of research at the global level is very heterogeneous. Pérez-Irineo & Santos-Moreno (2013) point out that a great variety of species is not studied in the continents where they are abundant, highlighting the example of viverrids, herpestids and euplerids in the continents of Africa and Asia, where species have all or a high percentage of their ranges of distribution.

Among the reasons to study small carnivores are their wide diversity, their role in ecosystems and the relationship between them and humans, all of them already seen in the past sections. Other reasons that should be mentioned are those that are useful for conservation experts when monitoring and implementing an environmental management plan: mesocarnivores can be used to measure changes in ecosystems or act as protectors of biodiversity in an area. This is because some carnivores are particularly sensitive to change due to some of their ecological characteristics: relatively large territory ranges, low population density and slow-life histories (low reproduction rate) (Cardillo et al. 2004; Purvis et al. 2000). These characteristics make them perfect environmental indicators and markers of ecosystem integrity (Buskirk & Zielinski 2003), since their survival depends in many cases on the abundance of small rodents, which are good indicators of ecosystem quality (Avenant 2011). In addition, this sensitivity requires the protection or restoration of entire communities to guarantee their survival, acting as an umbrella species or, in the case of being essential for the maintenance of the ecosystem, they would play the role of Keystone species, being crucial tools in conservation or restoration plans (Buskirk & Zielinski 2003; Macdonald & Kays 2005).

The field methods used to collect information on small carnivores are very variable depending on the objectives of the study (Lyra-Jorge et al. 2008), and can be invasive (involving direct handling of the animal, e.g. traps, marking of animals) or non-invasive (not requiring capture or handling of the animal, e.g. direct observation, hair snares) (Gompper et al. 2006). However, when planning research in a new area, it is necessary to carry out a baseline study or inventory, which has the function of detecting the species that live in the area, as well as obtaining initial data on their distribution and relative abundance (Morrison et al. 2001; McComb et al. 2010). The most commonly used methods for carnivores in this type of study are those that take into account their cryptic and mostly nocturnal habits, based on the indirect detection of the species from the signs they leave in the environment, whether they are footprints, faeces, marks, hair or burrows by means of track, faecal, hair counts, transects or track stations (Wilson & Delahay 2001; Silveira et al. 2003; Lyra-Jorge et al. 2008). These methods tend to be highly efficient but have certain disadvantages such as terrain-type dependency, very high sampling effort and the requirement for experienced researcher able to identify the species that leave each type of trace (Lyra-Jorge et al. 2008; Long & Zielinski 2008).

Advances in technology allow new techniques that facilitate field work, reducing the effort of the researcher, allowing him to sample territories that are hard to cover, and even allowing behavioural observations of rare or especially elusive species in the wild. One of these techniques is camera trapping, which have increased their presence as the methodology of choice in the recent years (Rowcliffe & Carbone 2008), due to its versatility that allows to sample a wide variety of species from different groups in very diverse habitats, recording information that can be used in many types of studies, all in exchange for a relatively low effort and moderate economic costs.

1.2. Camera traps in wildlife surveys

Camera trapping emerged as a tool for discovering wildlife in 1890 by George Shiras, who managed to get the animals photographed by themselves by using trip wire connected to a flash and a camera (O'Connell et al. 2011). Since then, the use of remote photography has evolved in all its aspects, becoming easier and better to use for wildlife research. Today camera traps are available in a wide variety of brands and types, specialized for different functions and with very competitive price ranges, making them accessible to a large public, both scientific and general (O’Connell et al. 2011).

The functioning of current camera traps is based on the remote capture of wild animals by detecting them through an infrared sensor that detects the temperature changes between the environment and the animal, triggering the activation of the camera (Rovero et al. 2010). When light conditions are low, many cameras have LED infrared lights as a flash, hardly visible to most wildlife, reducing the likelihood of the animal being scared by the flashing light. In addition, the sizes, shapes and colours of the camera frame allow them to be placed on almost any structure without being conspicuous. Most cameras on the market today are digital, with large storage capacity thanks to internal memories or SD cards and high durability powered by several batteries that allow them to last for weeks or months depending on the number of captures made (O’Connell et al. 2011).

Empirical studies with camera traps themselves provide information on the strengths and weaknesses of their use, which results in a positive feedback allowing these strengths to be reinforced and the weaknesses to be solved, making this methodology in continuous improvement (Meek et al. 2015).

1.2.1. Advantages and disadvantages of Camera traps

Camera traps are very helpful in field sampling and include many features that make them the method of choice in a variety of studies (O'Connell et al. 2011). However, far from being a perfect sampling tool, they have certain disadvantages that must be taken into account in any research design, as they can alter results or entail problems during sampling (Meek et al. 2015).

The great variability of brands, models, types of sensors, lenses and flashes, as well as the characteristics that define a greater or lesser sensitivity, durability and quality of the camera constitute a double-edged sword. Having a great variability of options when choosing a camera is a favourable aspect, making possible to choose models that are more competent and resistant to the conditions of the study and budget available. On the other hand, the advances in models and the multiple parameters that can be adjusted to increase the detection probability of the species make it very difficult or almost impossible to standardize and compare methods and results between different studies or between different types of cameras (Kays & Slauson 2008; Meek et al. 2014; Meek et al. 2015).

Among the clear advantages offered by camera traps is the ability to detect elusive species common in almost any type of habitat, with reduced effort, without the presence of the researcher and causing minimal disturbance. In addition, the information that can be obtained from the images, not only allows the identification of the species, but also provides objective and complete information about the presence, behaviour and identity of the animal, which can be stored for later review or analysis (Kays & Slauson 2008; Rovero et al. 2010; O'Connell et al. 2011). The value of these photographs goes beyond the scientific field and can attract the attention of the general public and in some way be used to promote certain species, which can influence interest in their conservation (Kays & Slauson 2008).

On the other hand, entrusting research to electronic equipment may be too risky. The equipment is not completely reliable, as there can be human or mechanical mistakes that prevent the camera from working properly. These can include problems in detecting individuals (false negatives) or captures where there are no individuals (false triggers) due to the action of wind, sun, temperature or a too fast movement of the animal to be captured. Another situation that can occur is that the film, the memory storage or the battery of the cameras may be depleted, and they can also be damaged by the animals, humidity or dust or be stolen (Kays & Slauson 2008; O'Connell et al. 2011). Furthermore, the animal detected may be difficult to identify at an individual or species level if the differences are not very conspicuous. Depending on the type of flash, the animals are likely to detect the camera and startle and may even avoid crossing in front of them. (Meek et al. 2015).

It is essential to study the pros and cons when designing a research in order to prevent possible failures that will negatively affect the results, leading to a loss of time, effort and money.

1.2.2. Approaches of Camera trap surveys

Among the study designs in which we can find camera traps as a method of choice are those focused on species occurrence and distribution, occupancy, population abundance and density, and behavioural studies (Kays & Slauson 2008; Rovero et al. 2010). Although the vast majority of studies are focused on medium to large mammals, camera traps are capable of detecting different groups of vertebrates (Kays & Slauson 2008; Meek et al. 2015). They are especially useful for sampling carnivorous mammals that are often difficult to catch or observe directly (Burton et al. 2015).

The effectiveness of the camera traps has been compared in several studies (Silveira et al. 2003; Barea-Azcón et al. 2006; Gomper et al. 2006; Long et al. 2007; Lyra-Jorge et al. 2008), elucidating that there are no perfect methods and that the efficiency of one or another depends on the area of study, the species to be sampled and the research team, since, where some are more efficient at detecting species in a shorter time than camera traps (scent stations and sign surveys in Barea-Azcón et al. 2006, detection dogs in Long et al. 2007, track-plots in Lyra-Jorge et al. 2008), are also more costly in effort or are more limited by climatic conditions, type of terrain or personal field experience. Camera traps appear to be particularly useful in remote areas of large size and/or difficult access where other methodologies such as indirect signal-based methods can be very laborious (Silveira et al. 2003; Sunarto et al. 2013).

In studies of occurrence and distribution, camera traps are used to show the species living in a given geographical area, accompanied by data on their relative abundance, their habitat preferences and their distribution in the study area. The repetition of these surveys enables the monitoring of a community, showing the changes in the communities over time (Kays & Slauson 2008). An example of these inventories is the one carried out by Tobler et al. (2008) in the Tropical Forest of south-eastern Peru. They showed the efficiency of camera traps in detecting medium to large mammal richness, collecting a total of 24 species out of the 28 observed in the area (86 %). Other studies such as the one of Bengsen (2014) consisted of species monitoring, in this case measuring the effects of pest control on invasive species such as the wildboar (*Sus scrofa*), the cat (*Felis catus*) and the fox (*Vulpes vulpes*) in Australia, showing a sharp reduction in their detection. Some studies focusing on small carnivores such as that of Johnson et al. (2009) and Mudappa (2007) offered pioneering inventories in rainforest regions of Laos and India respectively. While Johnson focuses mainly on the presence of 13 species of small carnivores along The Nam Et-Phou Louey National Protected Area (Laos), Mudappa focuses on seeing the effects of fragmentation of rainforest areas in the southern region of the Western Ghats (India) by combining camera traps with line transects, demonstrating a decrease in the number of nocturnal small carnivores in disturbed areas compared to undisturbed areas.

Occupancy surveys can focus on the ranges of distribution of one or several species, functioning as abundance estimators and allowing the calculation of the detection probabilities of the species (Sunarto et al. 2013; Burton et al. 2015). In addition, these studies show occupancy models in which covariates are included, indicating the degree to which both abiotic and/or biotic factors affect the presence and detectability of species (Rovero et al. 2010; Sunarto et al. 2013). Rovero et al. (2014) focused their study of habitat preference in the Udzungwa Mountains, in Tanzania, addressing how different abiotic variables (habitat, distances to rivers, forests, slopes...) affect the distribution of species, as well as the different groups of mammals (carnivores, insectivores, omnivores and herbivores) have different probabilities of being detected, with herbivores having the higher detectability than the rest of groups, and carnivores, the lowest. Some others, such as Satterfield et al. (2017) focus on comparing how the use of different types of baits can modify the probability of detection of different carnivores, concluding that there are differences between baits that should be used for large carnivores (meat) and those that attract small carnivores (fat rags).

Abundance and density assessments are usually carried out on species with identifiable individuals, either by coat pattern, significant markings or artificial markings made by previous capture, giving information not only about the number of individuals in a population but also about their territories (Kays & Slauson 2008; Burton et al. 2015). Jackson et al. (2006) measured the density of snow leopards in Hemis National Park, India, using capture-recapture methods (SCR) in two successive years. The results showed that the density of tigers experienced a marked reduction because an error within the study design when the second year the area of study was twice as big as the previous year, reducing the density of camera traps per sampling area. Capture-recapture techniques have been used mainly for large carnivores, however, a large amount of small carnivores possess coat patterns that allow their identification for density analysis, such as those of Msuha (2009) and Rich (2016), who presented in their theses how the SCR method can be applied to several species of small carnivores: serval, aardwolf and large spotted genet in Msuha (2009) and serval, aardwolf and African civet in Rich (2016).

Some other studies provide insight into the behaviour of the animals; their activity patterns and their feeding or breeding behaviours (Kays & Slauson 2008). Studies such as the one done by Leuchtenberger et al. (2018) show patterns of species activity, with respect to the circadian rhythm of several species in the Brazilian Pampas. Others, such as de Satgé et al. (2017) study the spatio-temporal distribution of the small carnivore guild in the Succulent Karoo, showing that there was a distribution in activity periods among the species and that those that shared the same range of activity dealt with the overlap by reducing their co-ocurrence, avoiding conflict and possible intra-guild predation. Other authors such as Caravaggi et al. (2017) focused on compiling different behavioural studies carried out with camera traps, presenting a very complete review showing the various applications of these in the field of ethology.

As can be seen, the applications of camera traps in wildlife research are practically infinite and especially useful in areas where research is not particularly accessible. Among these areas there are arid ecosystems in areas with low human densities and adverse climatic conditions.

2. Aims of the Thesis

This thesis focuses on the design, implementation and analysis of a species inventory of small carnivores in a private reserve in the arid Nama Karoo in southern Namibia with a view to its use for further studies focusing on the conservation and management of this area and the diversity inhabiting it.

The main aim of this thesis was to identify and describe the diversity of small carnivores in the area, studying their distribution, abundance and activity over the space and time.

To achieve this, different perspectives of analysis were used, compiling the information provided by thirty camera traps placed in the area over a period of one month. In this way, the main objective can be divided into three objectives:

First, the study of species diversity and richness throughout the area and within it, their variation between the different main habitats of the area: rocky mountain, milky shrubland and sandy plains.

Second, the study of their relative abundance in terms of camera trapping photographic rate, occupancy and detection probability, which were used to measure which species were more frequent and more distributed throughout the study area, once again, providing data for the whole area and its subdivision into habitats.

These two objectives provide information on which habitat is preferred for a larger number of small carnivore species or if a species is only found in one type of habitat, identifying features about the ecology of small carnivores.

The third and final objective was focused in observing the activity pattern of each species, identifying its activity ranges and comparing them with other small carnivores' activity patterns.

As this was the first study on small carnivores carried out in the area, predictions were made based on the characteristics of the species reported as present according to field guides (Stuart & Stuart 2015; Kingdon 2015; Hunter 2018) and a previous study aimed at identifying suitable spots for detecting leopards (Table 1) carried out by Viktor Neštický.(unpublished). It was predicted the presence of at least, the most common species, in absence of species never seen in the study area before but present in surrounding zones; the black-footed cat (*Felis nigripes*), yellow mongoose (*Cynictis penicillata*), meekat (*Suricata suricatta*), marsh mongoose (*Atilax paludinosus*) and clawless otter (*Aonyx capensis*), the latter two being semi-aquatic species only detected in the vicinity of the Orange River.

Due to the great plasticity of most of the small carnivores previously found in the study area, it was estimated that almost all species would be present in all habitats, adapted to the arid conditions and foraging in these circumstances. A greater abundance of species and individuals was expected in the plains and shrub areas, which have more vegetation indicating a more complex habitat in which a greater number of preys such as rodents, small reptiles and invertebrates could survive.

3. Methods

3.1. Study area

The study on which this thesis is focused took place in a private wildlife reserve in the extreme south of Namibia, on the border with South Africa, delimited by the Orange River (28° 45' 26.8956" S, 18° 52' 30.8316" E). It constitutes an area of about 460 km^2 subdivided into 4 parcels: KumKum Farm, Pelgrimsrust, Kambreek and Pelladrift (Figure 1) with an elevation between 300 and 900 m a.s.l. This reserve is located in the province of Karasburg within the administrative district of Karas, in a remote area quite far from urban settlements, being Warmbad the nearest, 40 km away. The land surrounding this reserve consists of sheep-breeding farms, the main economic resource of the region (Mendelsohn et al. 2003), all of them protected with fencing systems (some of them electrified) in order to prevent the access of predators including leopards, caracals, and especially, black-backed jackals.

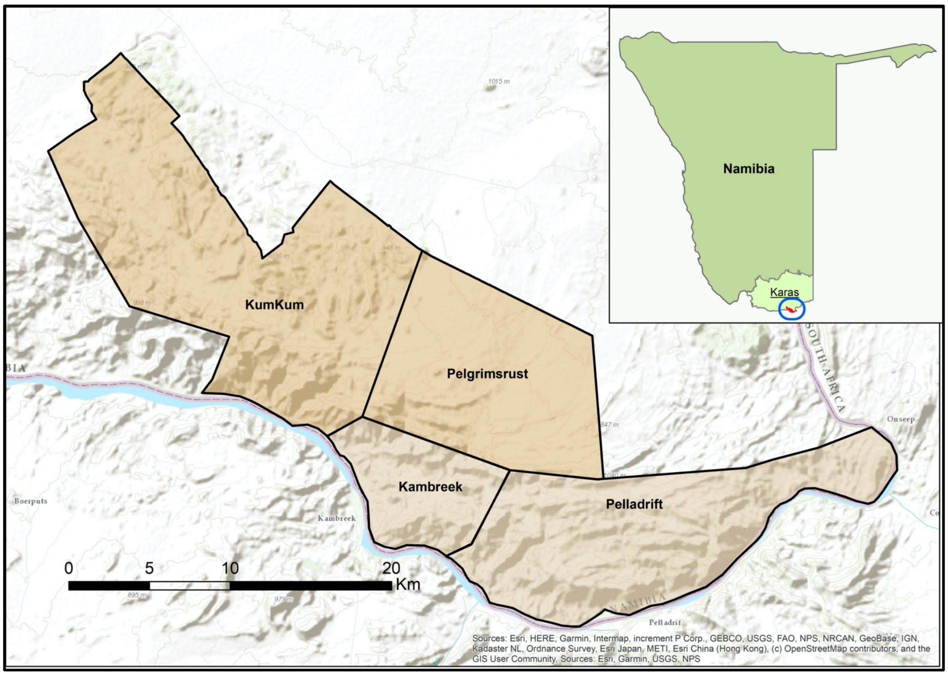


Figure 1. Area of study, located in the most southern part of Namibia. Divisions of the reserve: KumKum, Pelgrimrust, Kambreek and Pelladrift.

The reserve was used as a game reserve until not so many years ago. The management of the territory was based on its division into fenced plots that controlled the movement of the animals to facilitate their tracking. In 2012 the land was bought by Dr. Peter van der Byl Morkel and Ian Craig in order to protect the territory and create a wildlife reserve, where human actions were minimal to preserve the natural environment as much as possible (Mikslová 2019). The current management of the area is very limited and focused mainly on removing fences to allow animals to have free movement throughout the area, avoiding the depletion of the food sources in the most densely populated areas. Currently the area is still in a recovery period. The periods of drought that have been occurring in recent years and a possible high density of herbivores difficult the growth of vegetation, affecting the entire ecological community of the area.

Geomorphologically, the reserve comprises a fairly heterogeneous landscape, made up predominantly of rocky and abrupt areas (Figure 2), in which two mountainous formations can be seen, one in the north of KumKum Farm of clearly volcanic origin and the other covering the entire southern belt delimiting the northern side of the Orange River valley, of metamorphic origin, occupying the south of KumKum Farm, Kambreek and Pelladrift. Between both formations, a narrow valley opens up to the west into a large sandy plain that extends beyond the boundaries of Pelgrimrust to the north and east. This region is located within the geological area known as the Namaqua Metamorphic Complex, which is composed mainly of granite gneisses, quartzite, schists and amphibolites, as well as some plutonic rocks such as those observed in the KumKum Mountains (Moore 1981). The soils are poorly developed, shallow and slightly alkaline, mainly red and yellow in colour as a result of the oxidation of iron minerals (Watkeys 1999).

Figure 2. Picture of KumKum Farm, showing the north mountain ridge, the appearance of the sandy plain and few Euphorbia sp shrubs.

The climate is continental, classified as Hot arid desert according to the Köppen-Geiger climate classification (Beck et al. 2018). The closest climatic records are found in the Tantalite Valley, which registers temperature ranges between 6º and 35ºC and an average annual precipitation of 45.8mm in the last 10 years (World Weather Online 2020). Precipitation are mostly distributed in summer (December-April), mainly in March. Drought periods are unpredictable and often prolonged for years (Mucina et al. 2006).

Climatic and geological features frame the study area within an ecological gradient zone between the Nama-Karoo biome and the desert biome that ascends through the Orange River valley giving rise to the Gariep Desert. The main factor affecting the vegetation of the area is the distribution of rainfall, not only along the year but also between years, where periods of rain are preceded by years of drought of variable duration (Cowling 1986). The vegetation pattern alternates patches where dwarf shrubs and bushes (up to 1 m tall) intermix with grasses and succulents, patches where "white grasses" (Poaceae) cover the sandy plains creating open grasslands, and rocky areas where milky shrubs of the genus Euphorbia (*E. degreana, E.gregaria*) are the dominant species (Figure 2). Some phanerophytes can also be observed, mainly in drainage zones (*Acacia mellifera*, invasive *Prosopis* species) or rocky areas (*Aloidendrum dichotomum*) (Jürgens et al. 2006; Mucina et al. 2006).

The fauna of the reserve lacks a complete species inventory, only the most common or easily identifiable species have been registered. Among the mammal species observed are twelve species of small carnivores (Table 1) in addition to leopards (*Panthera pardus*), brown hyenas (*Hyaena brunnea*), different species of antelopes including springboks (*Antidorcas marsupialis*), greater kudus (*Tragelaphus strepsiceros*), klipspringers (*Oreotragus oreotragus*) and gemsboks (*Oryx gazella*), mountain zebras (*Equus zebra*), aardvarks (*Orycteropus afer*) and small mammals like springhares (*Pedetes capensis*), Cape ground squirrels (*Xerus inauris*) and Cape crested porcupines (*Hystrix africaeaustralis*), as well as a large number of small rodents, elephant shrews, hares and bats.

The most common birds in the area are the small passerines including the sociable weaver (*Philetairus socius*), the Cape bunting (*Emberiza capensis*), the Karoo scrub-robin (*Cercotrichas coryphaeus*), mountain wheatears (*Myrmecocichla monticola*) and several species of larks (Alaudidae). Other birds are also common, like the Namaqua sandgrouse (*Pterocles namaqua*), Karoo korhaan (*Eupodotis vigorsii*) and some birds of prey such as the pale chanting goshawk (*Melierax canorus*), the Verreaux eagle (*Aquila verreauxii*) and the lappet-faced vulture (*Torgos tracheliotus*). Reptiles are also abundant, with different species of lizards (*Pedioplanis* spp.), geckos (*Pachidactylus* spp., *Chondrodactylus* spp.), agamas (*Agama* spp.), skinks (*Trachylepis* spp.) and snakes (*Psammophis* spp., *Bitis* spp., *Naja* spp.) as well as a wide variety of invertebrates including termites, desert beetles, millipedes, spiders and scorpions.

The history of the area as a wildlife reserve is still very brief and much work remains to be done and research to be conducted. Efforts are needed to understand the ecological carrying capacity of the land, since in such an arid zone the vegetation is scarce and an excess in the number of herbivores can destroy the whole plant community. The geomorphology of the area presents an almost unique location, where mountains arise in a region dominated by vast plains that extend hundreds of kilometres to the north, which may influence the presence of some species of plants and animals that prefer rocky habitats for living (e.g. leopards in Southern Africa (Mann 2014)) or represent a physical barrier for those that inhabit sandy plains.

3.2. Data collection

The data collection period took place during the winter of 2019, between July and August. A total of 30 digital cameras traps (twelve UoVision UV535, ten SiFar 3.0C, seven Browning Prometheus, models BTC-5HDP (one), BTC-5PXD (four) and BTC-6PXD (two), and one Reconyx PC800 Professional) were installed during a period of 38 days (from July 9 to August 16), distributed along the KumKum Farm and Pelgrimsrust terrains.

The selection of the surveyed area was conducted by using satellite images and on-site visual inspection, identifying and delimiting the different habitats and accessible areas. The criteria for selecting the working areas was based on the accessibility either by car or on foot; very steep terrain with difficult access was excluded as it would take a lot of time and effort to get there every 10 days for the camera service. As for the types of terrain, three main habitats were described:

- Rocky mountain (Figure 3b): elevated areas with very little or no vegetation, with soil mainly made up of small or medium-sized dark rocks. This habitat includes the areas of the KumKum mountain ridge.
- Milky shrubland (Figure 3c): areas mainly characterized by the predominance of milky shrubs of the genus *Euphorbia*, with soils that vary from rocky to sandy, mostly adjacent to rocky outcrops. This habitat extends along the sides of the KumKum dry river valley and Pelgrimsrust plains, intercalated with Sandy plain habitat.
- Sandy plain (Figure 3d): sandy areas, with little or no vegetation. Where present, mainly composed by both perennial and annual grasses (white grasses) and woody shrubs. This habitat dominates the centre of the KumKum dry river valley and areas intercropped with milky shrublands in Pelgrimsrust.

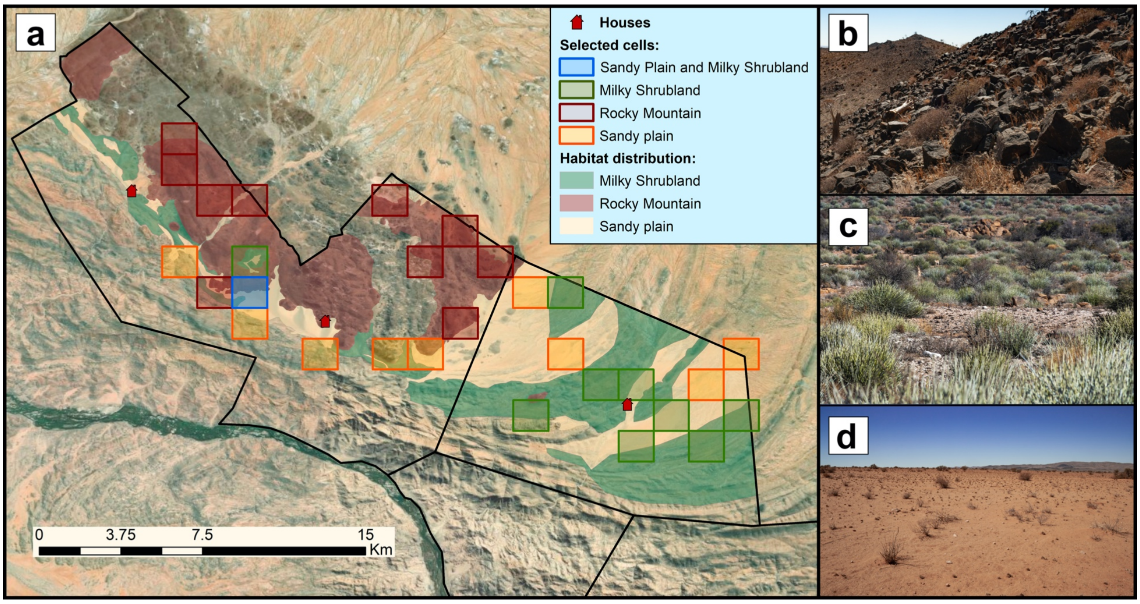


Figure 3. Selected habitats in Kumkum and Pelgrimsrust farms. a: Map of the area representing the habitats in different colours and the selected cells for the camera placing. b: Rocky Mountain habitat. c: Milky Shrubland habitat. d: Sandy Plain Habitat. Pictures by Daniel Hernández.

The distribution of habitats and accessible areas were sketched within ArcMap 10.5.0 (ESRI, CA, USA) (Figure 3a) for the subsequent selection of camera locations, placing a total of 10 cameras per habitat. The sampling points were randomly selected, creating a 2 km^2 grid cells and selecting ten cells by generating 10 random points for each habitat type.

Inside the cell, the camera was deployed within the most suitable spot for detecting fauna (next to animal tracks, water ponds, dry riverbeds) with a minimum space of 1 km between cameras. Each location was recorded using MotionX-GPS application (Fullpower, CA, USA) and at each point the camera identification code, habitat and dates and times of installation, service (every 7-10 days) and camera recovery were recorded.

Each camera trap was placed at a height of 30 – 50 cm from the floor using natural structures such as tree trunks or rock piles or using iron poles. The possible vegetation that could cause false positives by movement was removed from the first 4 m of the camera field of view and the sun triggering was also avoided by placing the camera against the sun trajectory. The cameras were set to work 24 hours per day and to take 3 pictures per trigger, without capture delay and variable sensitivity depending on the model of the camera and the presence/absence of possible false triggers because of plant movement. These settings were adjusted and changed along the survey in stations where the triggering was too high because of animals crossing very often (waterholes), sun or vegetation activating the cameras.

In order to increase the detectability, canned sardines and tuna-oil were used as bait. These baits have been shown to be effective as attractants for small carnivores: kit foxes, fishers, skunks, martens (Schlexer 2008), ocelots (Trolle & Kéry 2003), *Felis* spp. in Namibia (Hanke & Dickman 2013), Iberian carnivores including small-spotted genets (Ferreira-Rodriguez & Pombal 2019) and black-backed jackals (Humphries et al. 2016). The bait was placed impregnating the ground in front of the camera, 2-3 metres apart from it, ensuring the proper framing of the animal in the photograph. The bait was refreshed every 7-10 days when the camera service was performed in order to keep the odour of the bait constantly within the station.

During each service, the camera's remaining battery was checked and replaced if it was low, photographs were downloaded to an external hard disk and the memory card formatted. The photographs from each camera were stored within computer folders named with the reference code of each station for later analysis.

3.3. Data analysis

The data were compiled and analysed mainly by using the free software ZSL-CTAP (Camera Trap Analysis Package), developed by the Zoological Society of London for camera trap data processing. It consists of a tool that not only allows organizing the data to obtain information about the community and species in the study area, but also allows the analysis of the sampling effort and the estimation of the richness, relative abundance, occupancy and activity patterns of the different species in the study (Amin et al. 2017). The first step was the creation of a database based on the information gathered concerning the camera trap itself; brand, reference number, location and description of the habitat, dates and times of services to each camera, as well as the information extracted from the different photographs. The information contained in the photographs was obtained by extracting the metadata (name, date and time) from the ".jpg" file through the free software VIXEN 1.Ocr1 (Ramachandran & Devarajan 2018), obtaining a text file that can be processed in Microsoft Excel (Microsoft, 2020), removing the unwanted extracted metadata and adding the description of each photograph, indicating the presence or not of wildlife, and if so, the captured species. The process of filling out the template provided by the ZSL-CTAP software was tedious as all the required information had to be introduced manually, including the information for every photograph. However, the time spent on such a simple task saved hours of data analysis that were performed directly by the software.

Once the template was created, the information was imported into the ZSL-CTAP software as a new survey, where the program analysed the information according to previously selected parameters. Among them, the most important pattern to be defined was the duration of the event, which indicates the interval of time between consecutive images that the software considers to be a single animal visit (Meek et al. 2014), in this case the duration of the event was determined to 60 minutes.

For the statistical analysis of the data, the software Statistica v10 (Statsoft Inc, Tulsa, USA) was used. The normal distribution of the data was checked by using Kolmogorov-Smirnov's test, allowing the selection of parametric or non-parametric methods when comparing the sample sets, choosing one-way ANOVA for the comparison of those variables with normal distribution, and the Kruskal-Wallis test in the negative case. If significant differences were obtained, subsequent post-hoc analysis was performed in order to identify the origin of these differences. For all these tests the significance level was set at 0.05.

3.3.1. Diversity and species richness

The study of small carnivore diversity and richness was carried out by using diversity indices and accumulation and rarefaction curves. Results were produced for the whole area and for each particular habitat, enabling their comparison at a statistical level.

The calculation of diversity indices was done with Past4.0 software (Hammer et al. 2001), extracting the number of independent events calculated by the CTAP software. As each event is assumed to be a single individual visiting the camera, it is necessary to add individuals in those events with more than one of them, obtaining the total number of individuals sampled per species during the survey. The diversity index chosen was the Shannon-Wiener (H) index, which assumes that individuals are randomly sampled from an infinite size community where all species are represented in the sample (Magurran 2004).

This index is usually supplemented by the Pielou's evenness index (J), which measures the degree of heterogeneity of the Shannon-Wiener index and is defined as the ratio between the calculated index and the maximum value that the Shannon-Wiener index would have in the community if the distribution of species abundance were uniform, being 0 the value with higher heterogeneity and 1 the lower (Niedballa et al. 2015).

One of the problems with the Shannon-Wiener index lies in the interpretation of its results, which express the biodiversity value of an imaginary community in which all species are equally common. For this reason, some studies suggest the use of “D” numbers that measure the "effective number of species" or "equivalent numbers", which would indicate the effective number of species present in a virtual community that shares the value of the Shannon-Wiener Index with the community surveyed. The formula used for its calculation consists of the exponential of the Shannon-Wiener Index: e^H (Jost 2006; Jost & González-Oreja 2012). These values make the comparison between different communities easier, giving them a meaning in a comprehensible scale.

The ZSL-CTAP software provides accumulation curves, calculated for the set of species of a community or certain taxa of interest, in this case, small carnivores. Accumulation curves indicate the rate at which a new species is incorporated into the inventory, providing evidence of its richness and abundance of distribution, showing the cumulative number of species as a function of sampling effort (represented in days) (Magurran 2004). In addition, the software also provides the calculation of the estimated accumulation curve, in this case representing the value of species richness according to the non-parametric Jackknife first order estimator, which takes into account the imperfect detection of species. The rarefaction curves are calculated as the expected number of species based on different sampling combinations (1,000) from the sampling data, allowing to estimate if the duration of the study was sufficient to capture most species when the asymptote is reached in the graph (Amin et al. 2017).

3.3.2. Relative Abundance Indices

Relative abundance indices (RAI) are used to infer the abundance of species according to their capture population (Photographic Camera trapping rate), their detectability and their presence/absence throughout the study area (occupancy).

3.3.2.1. Photographic Camera Trapping Rate Calculation

The ZSL-CTAP software was used again for the calculation of the capture rate. The photographic camera trapping rate (CTR) is defined as the average value of independent photographic "events" per trap day standardized to 100 days (Amin et al. 2017). It can be used as simple relative abundance index, with the assumption that target species will trigger cameras according to their density if all species have similar detectability and camera placement was aleatory (Carbone et al. 2002). However, this index may produce overestimated calculations, since it is likely that the individuals captured of a species in the same camera (or several cameras if the separation of these is lower than their home range) were the same individual, especially in territorial carnivores. This is because repeated visits of a single individual on a continuous basis would increase its capture rate without increasing the abundance of that species within the territory (Silveira et al. 2003).

For the calculation of the CTR and its comparative analysis between habitats, a period of time was selected in which at least 60 % of the cameras were operational. This standardizes the sampling over time, not only referring to the duration of the sampling time interval but also to the exact dates of sampling, which prevents the influence of possible climatic factors that occurred in that time period (rain, sandstorms, sharp drop or rise in temperatures) qualitatively affect all locations simultaneously. In addition, dates when a high percentage of cameras of a habitat were not operational are avoided, which could cause a bias in the CTR estimation as the sampling effort during those days was reduced for that specific habitat.

3.3.2.2. Modelling Occupancy and Detection Probabilities

One of the weaknesses of using the camera trapping rate as an index of relative abundance is the fact that it does not take into account the imperfect detection of species (Rovero et al. 2014). One of the possible alternatives to this method is the estimation of occupancy, which provides information on the proportion of the area occupied by a species and its detection probability (MacKenzie et al. 2002), which can be correlated with the abundance of that species in the study area.

The model for estimating occupancy when the detection probability is ≤ 1 proposed for MacKenzie (2002) is based on the simultaneous estimation of occupancy and detection probability in a maximum likelihood framework, where each sampling unit is visited on multiple sampling occasions, recording in each of them the detection (1) or non-detection (0) of the target species (Rovero et al. 2010; O'Connell et al. 2011). This model assumes that (a), populations are closed (no entry or exit of individuals in the study area, (b), absent species are not detected but a species present may or may not be detected, and (c), the detection of a species at one point is independent of the rest of the points, meaning that they should be separated enough to inference that one specific individual will be only detected in one sample point (MacKenzie et al. 2002; Sunarto et al. 2013).

This model also considers the addition of covariates as factors that can influence the occurrence and detectability of species. Thus, different models can be created to estimate the occupancy and detectability of species according to the effect that a given covariate has in one or both estimators.

The ZSL-CTAP software allows the creation of these models through the creation of detection/non-detection matrices of species, after the adjustment of some parameters such as the size in days of the sampling occasion (in this case defined as 1 per day) and the start and end dates for the analysis among others. Once these matrices were created, the "unmarked" package of the R statistical software (Fiske & Chandler 2011) was used for the single-season occupancy analysis for each species, obtaining the modelled values of occupancy (ψ) and detection probability (p) with and without covariates (Amin et al. 2017).

The complete set of data was used for the analysis of the occupancy and the detection probability, using the complete study period and therefore all the events recorded. The proportion of camera location visited by each species during the study period, termed as Naïve occupancy (MacKenzie et al. 2006) was calculated in order to get a descriptive and visual appreciation of the observed presence of the small carnivores along the cameras before the occupancy modelling analysis. In order to avoid unreliable estimates of occupancy, species with less than 10 events or with a Naïve Occupancy less than 0.1 were discarded from the analysis.

An occupancy analysis framework was used to investigate the influence of the type of habitat as a covariate, creating four different models according to the possible combinations in which the habitat can affect the estimation of occupancy, detection probability or both at the same time. The first was the null model, ψ(.), p(.), assuming that occupancy and detection probability were constant across all cameras. The second represented the contrary model, ψ(habitat), p(habitat), indicating that habitat influenced both the distribution of the species and its probability of detection. The third and fourth models expressed how the type of habitat uniquely influenced the probability of detection of the species (ψ(.), p(habitat),) or the distribution of the species (ψ(habitat), p(.)). The Akaike Information Criteria (AIC) was used to select the best fit model, ordering the models with the lowest AIC value first, and then calculating the difference in value between this and the rest of the models (ΔAIC) in order to calculate their Akaike weights (ω). The calculation of the weight of each model allows us to measure its relative importance, in other words, the percentage in which this model explains the distribution and detection of the target taxon in the real world (Burnham & Anderson 2002). The effect of covariates was analysed in all small carnivore species, indicating the model that best illustrates the distribution and detection probability of each of them. The criteria for selecting the models that best fit the actual distribution of the data for each species was based on different steps. The first step was based on the pool of values obtained for the AIC, using the "thumb rule" of Burnham & Anderson (2002), which indicate that the level of empirical support for a model is "substantial" if the value of its ΔAIC is lower than 2, a fact that made the models be taken into account as a representative model. In the case of not selecting a single model, the second step consisted of observing whether the main model represented 90 % of the relative importance, if not, those models that accumulated a relative weight of 0.90 were taken as relevant ones.

Once the optimal models were selected, the values of the occupancy and detection probability estimates for each species were plotted with the purpose of observing and comparing the differences of these values across habitats.

3.3.3. Activity pattern

ZSL-CTAP software provides circular charts of circadian activity for each species, which indicate the frequency of events detected throughout the survey per hour. This information was exported to Oriana v4.02 (Kovach Computing Services, Anglesey, U.K.), a circular statistics software used for the calculation of descriptive statistics; mean vector (μ), standard deviation and two data distribution tests. The first test was the Rayleigh Uniformity test (Z), which allows to determine whether the data of each species were uniformly distributed, receiving non-significant results when species have a uniform or bimodal pattern of activity (Zar 2010). The second test performed is the Rao's spacing test (U) which is based on the uniformity of the separation of adjacent points, so that non-significant results will only be obtained if the distribution of activity data is uniform throughout the day (Kovach Computing Systems, 2011).

The pattern of activity of each species was represented in the form of a circular histograms, representing the frequency of events for each hour interval, the mean vector, and its 95 % confidence intervals.

Furthermore, the activity patterns of the different species of small carnivores were compared two by two using Watson's U^2 Test (U^2), which provides significant results if the paired species have different activity patterns (Zar 2010; Kovach Computing Systems, 2011).

4. Results

The study period resulted in a total of 935 camera trap days (30 cameras working for 31.6 ± 1.32 days each) and 18,111 photographs, of which 11,673 (64.45 %) showed wildlife. The vast majority of the remaining photographs contained images caused by the false trigger of plant movement or the sun facing the camera due to a wrong placement. A total of 1,031 wildlife events were recorded, involving more than thirty species of mammals. Among them, 329 events were attributed to the presence of ten species of small carnivores (Table 1); aardwolf (*Proteles cristata*), African wildcat *(Felis silvestris lybica*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), Cape fox (*Vulpes chama*), Cape grey mongoose (*Herpestes pulverulentus*), caracal (*Caracal caracal*), honey badger (*Mellivora capensis*), small-spotted genet (*Genetta genetta*) and zorilla (*Ictonyx striatus*). The complete list of species detected by the camera traps during the survey can be found in Appendix 1.

Table 1. Small Carnivore species expected and observed. Previously Observed species were registered by Viktor Neštický during his research on the area (personal communication). Species Status and Population trend extracted from IUCN Red List (IUCN 2020b).

			Previously Observed	**Observed (survey)**	**Status (IUCN)**	**Population trend**	**Home Range Size (km^2)**
Family Canidae	Black-backed jackal	*Canis mesomelas*	✓	✓	LC	Stable	1-24.9
	Cape fox	*Vulpes chama*	✓	✓	LC	Stable	1-32.1
	Bat-eared fox	*Otocyon megalotis*	✓	✓	LC	Stable	0.3-3.5
Family Mustelidae	Zorilla	*Ictonyx striatus*	✓	✓	LC	Stable	Unknown
	African clawless otter	*Aonyx capensis*	✓		NT	Decreasing	17-42
	Honey badger	*Mellivora capensis*	✓	✓	LC	Decreasing	126-541
Family Felidae	Caracal	*Caracal caracal*	✓	✓	LC	Unknown	3.9-65
	Black-footed cat	*Felis nigripes*			VU	Decreasing	8.6-16.1
	African Wildcat	*Felis silvestris lybica*	✓	✓	LC	Decreasing	3.5-13
Family Viverridae	Small-spotted genet	*Genetta genetta*	✓	✓	LC	Stable	0.33-12
Family Hyaenidae	Aardwolf	*Proteles cristata*	✓	✓	LC	Stable	1-6
Family Herpestidae	Marsh mongoose	*Atilax paludinosus*	✓		LC	Decreasing	0.5-2.04
	Cape grey mongoose	*Herpestes pulverulentus*	✓	✓	LC	Stable	0.3-0.92
	Yellow mongoose	*Cynictis penicillata*			LC	Stable	0.1-1
	Meerkat	*Suricata suricatta*			LC	Stable	2-10

4.1. Diversity and species richness

Of the 10 species of small carnivores observed throughout the study area, the vast majority were distributed across all habitats (Table 2). 8 of the 10 species were observed in rocky mountains, with the exception of bat-eared fox and black-backed jackal. Same number of species were found in the milky shrubland, without the detection of bat-eared foxes and honey badgers in this habitat. Sandy plain was the habitat with a highest number of species detected, being the caracal the only species absent from the ten present in the whole study area.

Table 2. Individuals sampled in the study area, species richness estimates (Jackknife 1st Order) and diversity indexes: Shannon-Wiener (H), Pielou's evenness (J) and Effective number of species (D).

	Whole study area	Rocky Mountain	Milky Shrubland	Sandy-Plain
Aardwolf	30	4	7	19
African wildcat	17	4	10	3
Bat-eared fox	29	0	0	29
Black-backed jackal	22	0	6	16
Cape fox	108	4	18	86
Cape grey mongoose	109	54	31	24
Caracal	2	1	1	0
Honey badger	7	5	0	2
Small-spotted genet	14	7	6	1
Zorilla	11	5	4	2
Totals				
Nº Individuals	349	84	83	182
Nº Species	10	8	8	9
Jackknife 1st Order Estimate	10	8.98	8.97	9.98
Shannon-Wiener diversity index (H)	1.81	1.32	1.74	1.56
Pielou's evenness index (J)	0.79	0.63	0.84	0.71
e^H: Effective number of species (D)	6.12	3.73	5.71	4.75

The values provided for the whole study area by the 1st order Jackknife estimator matched with the species richness of mesocarnivores observed (Table 2). However, the species richness estimated for each habitat suggested the presence of one more species, showing that the study period was sufficient to detect the 89 % of carnivore species present in rocky mountain, 89.19 % in milky shrubland, and 90.19 % in sandy plain.

The Shannon-Wiener value for the entire study area was 1.81 with a uniformity value (J) of 79 %, and an effective number of species of 6.12 (Table 2), indicating that the total community in the area has the same Shannon-Wiener diversity value as a virtual community of 6.12 species with a uniform distribution of species abundance (J = 1).

The habitat with the highest diversity value was milky shrubland (H = 1.74), followed by Sandy plain (H = 1.56) and finally the rocky mountain (H = 1.32). Although the number of species was higher in the Sandy plain than in the other two habitats, the Pielou's evenness index shifted the milky shrubland to first place in terms of diversity due to a higher value of evenness (84 %) compared to the 71 % and 63 % estimated for the sandy plain and rocky mountain respectively.

The effective number of species in each habitat showed the same pattern seen above, with milky shrubland being the habitat with the highest effective number of species (D = 5.71). Nevertheless, the results of the one-way ANOVA showed that there were no significant differences between the communities of small carnivores in each habitat ($F_{2.27} = 0.452$, $P = 0.641$).

The Figures 4 to 7 show the accumulation and rarefaction curves for the total area and for each habitat. They show the rate of species recruitment over the sampling days in accumulated (jagged) and rarefacted (smooth) ways, as well as the curve showing the variation in the Jackknife estimator over time.

The graph for the whole study area (Figure 4) shows that both the accumulation curve and the rarefaction curve reach or come close to the asymptote before the first half of the study period, both showing a very steep slope, detecting the first 9 species by day 11. The Jackknife estimator curve reaches the stable value of 10 species from day 20, just the half of the study period.

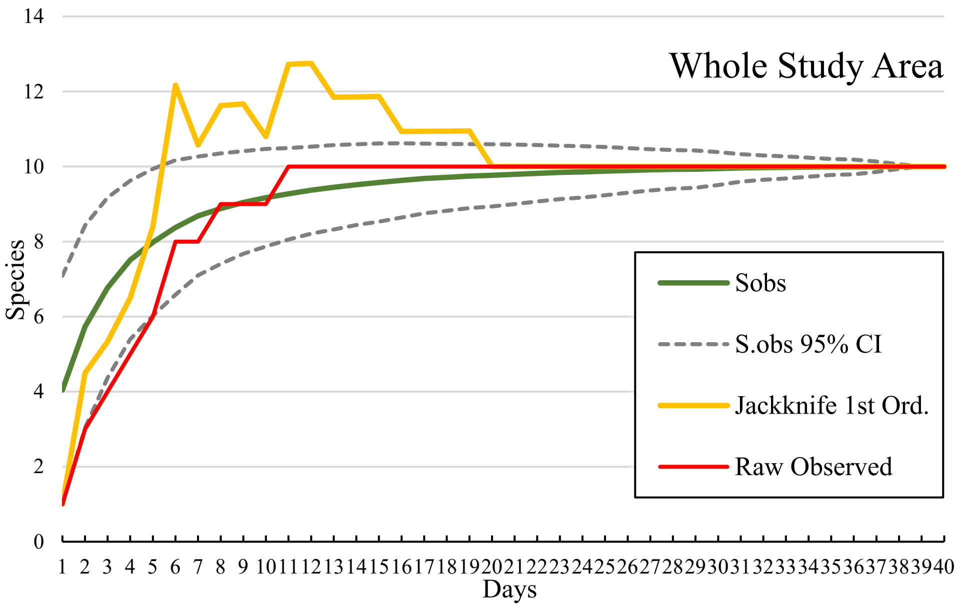


Figure 4. Accumulation (jagged) and rarefaction curves (smooth) of small carnivore species detected over time in the whole study area. Jackknife 1st order estimate curve also represented.

The graph corresponding to the rocky mountain habitat (Figure 5) displays a different trend, since the accumulated curve and the rarefaction curve do not complement each other so much, having the latter a much smoother growth, reaching the first 7 species by the half of the study period, while the raw accumulation curve reaches its maximum on the 11th day. The Jackknife's estimated value is maintained in 9 species from day 24.

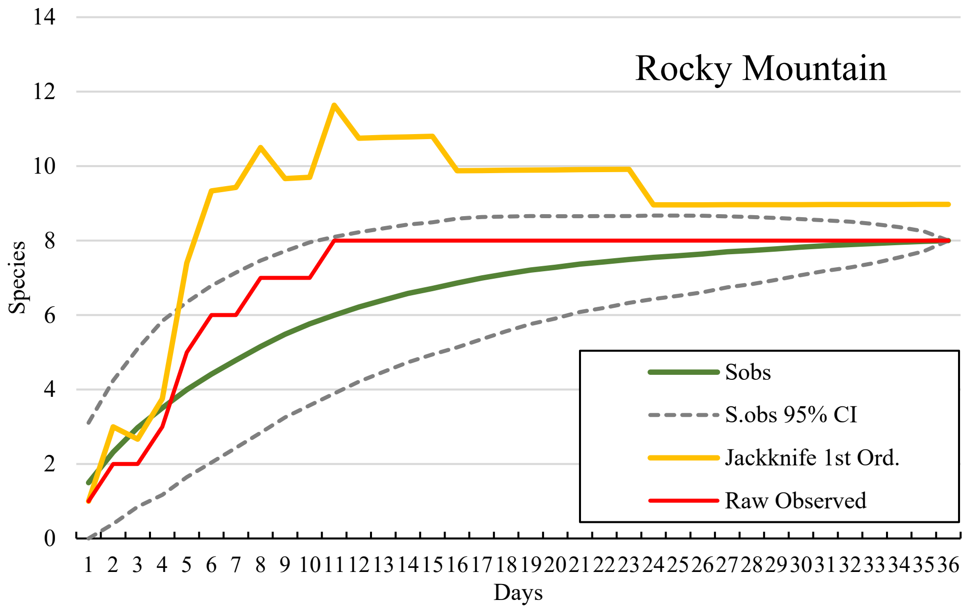


Figure 5. Accumulation (jagged) and rarefaction curves (smooth) of small carnivore species detected over time in the rocky mountain habitat. Jackknife 1st order estimate curve also represented.

The milky shrubland graph (Figure 6) has more parallel structure, with both curves showing a fast growth at the beginning, reaching their maximum values towards the half of the study. For the rarefaction curve, the first 7 species are detected by day 12, 5 days later than the raw accumulation one. The Jackknife's estimated values experience an increase when the last species is detected on day 19, increasing in 2 species the previous estimated number, being placed one species above the ones reported during the survey.

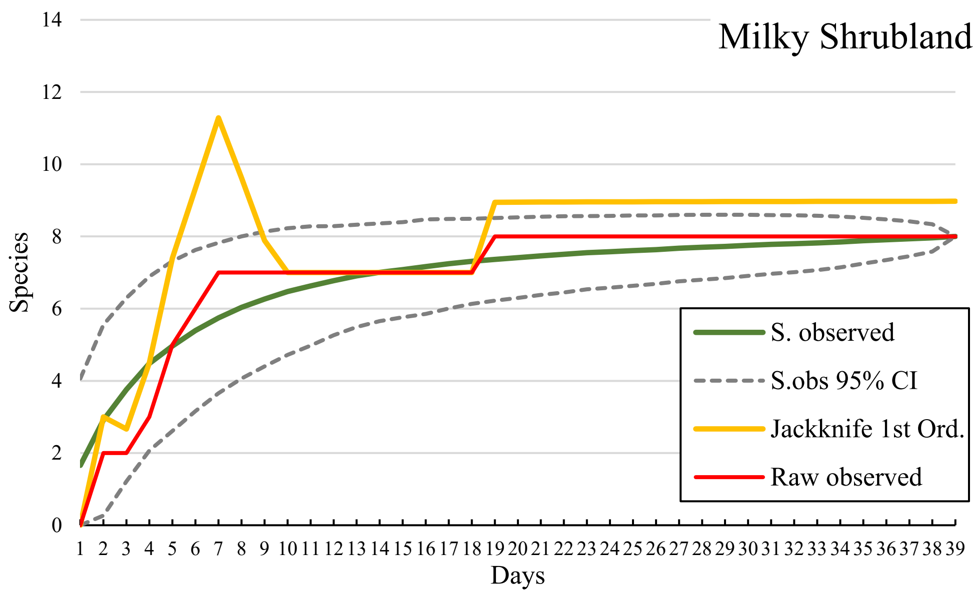


Figure 6. Accumulation (jagged) and rarefaction curves (smooth) of small carnivore species detected over time in the milky shrubland habitat. Jackknife 1st order estimate curve also represented.

The last graph represents the sandy plain habitat (Figure 7), having a much more stepped structure both Jackknife estimator and raw accumulation curves, the latter showing a slow rate of species recruitment, with the last 2 species (out of 9) being recruited in the second half of the study. The rarefaction curve is not very steep, requiring 19 days to recruit the first 8 species. The Jackknife estimator reaches value 9 on day 33 of 39, which is rather late position compared to the rest of the graphs.

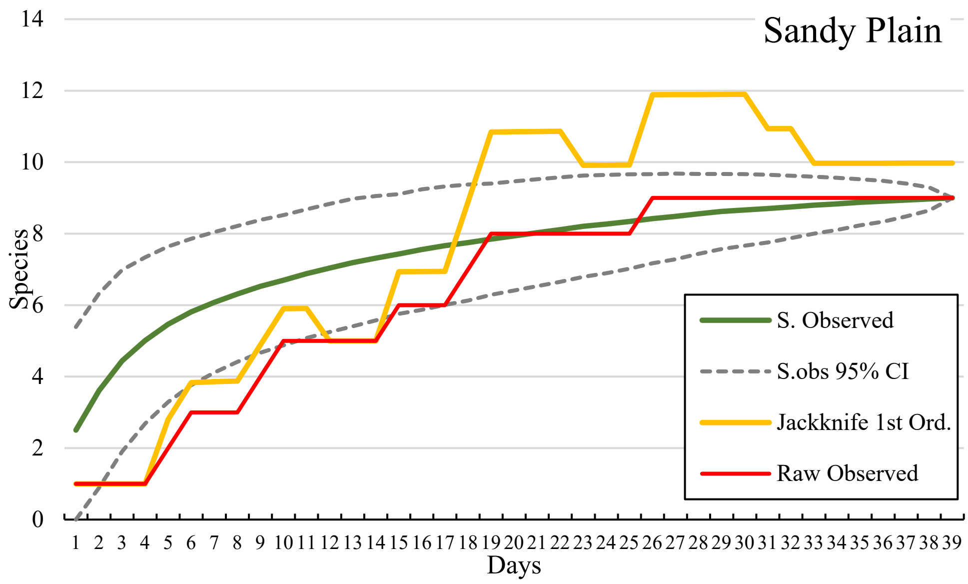


Figure 7. Accumulation (jagged) and rarefaction curves (smooth) of small carnivore species detected over time in the sandy plain habitat. Jackknife 1st order estimate curve also represented.

4.2. Relative Abundance Indices

4.2.1. Photographic Camera Trapping Rate

The time interval used for the CTR calculation comprised the days between 16th of July and 11th of August, both dates included (27 days). The results are shown in the Table 3, containing the mean values of CTR and SD for each species, calculated for the whole study area and each of the habitats. In addition, p-values of the Kruskal Wallis test are also given, as well as the habitats that showed significant differences after the nonparametric post-hoc procedure (Dunn's test).

The species with the highest capture rate was the Cape fox with an average (CTR ± SD) of 11.16 ± 6.11 events per capture day /100 days, followed closely by the Cape grey mongoose with 9.7 ± 6.32 events. The rest of the species presented much lower capture rates between a range of values of 0.12 ± 0.64 and 3.49 ± 3.94, being the caracal the least detected species.

Table 3. CTR results for small carnivore species. Mean (x) and standard deviation (SD) values obtained for the whole area and each habitat, results for Krukal-Wallis test's p-values and habitats that showed significant differences after post-hoc analysis are shown.

Species	Whole Study Area		Rocky Mountain		Milky Shrubland		Sandy Plain		Kruskal Wallis p value	Different habitat
	$\hat{x}$	SD	$\hat{x}$	SD	$\hat{x}$	SD	$\hat{x}$	SD		
Aardwolf	3.49	3.94	1.48	5.34	1.85	3.96	7.15	8.68	0.001	SP
African wildcat	1.76	1.96	1.11	3.20	2.96	4.65	1.11	3.20	0.119	
Bat-eared fox	2.14	3.81	0.00	0.00	0.00	0.00	6.68	12.1	0.000	SP
Black-backed jackal	2.21	3.16	0.00	0.00	1.85	3.96	5.63	7.98	0.001	RM↔SP
Cape fox	11.16	6.11	1.36	4.06	5.19	7.53	27.39	17.5	0.000	SP
Cape grey mongoose	9.70	6.32	14.81	11.37	8.52	10.27	6.83	8.13	0.023	RM↔SP
Caracal	0.12	0.64	0.00	0.00	0.37	1.93	0.00	0.00	0.368	
Honey badger	0.89	1.80	1.85	3.96	0.00	.00	0.78	2.82	0.058	
Small-spotted genet	0.88	1.78	0.74	2.67	1.48	4.56	0.37	1.92	0.571	
Zorilla	1.16	1.67	1.48	3.62	1.11	3.21	0.74	2.67	0.690	

The species that showed significant differences in their CTR across the different habitats were the aardwolf, the bat-eared fox, the black-backed jackal, the Cape fox, and the Cape grey mongoose, with the habitat of sandy plain differing from the other two in most cases, only differing from rocky mountain in the case of black-backed jackal and Cape grey mongoose. The differences between the CTR values can be easily observed in graphs (Figure 8), showing how the sandy plain was the habitat that differs positively in all cases except for the Cape grey mongoose, a species with a higher CTR in rocky mountain habitat. In all species with significant differences observed, the milky shrubland is found in intermediate positions.

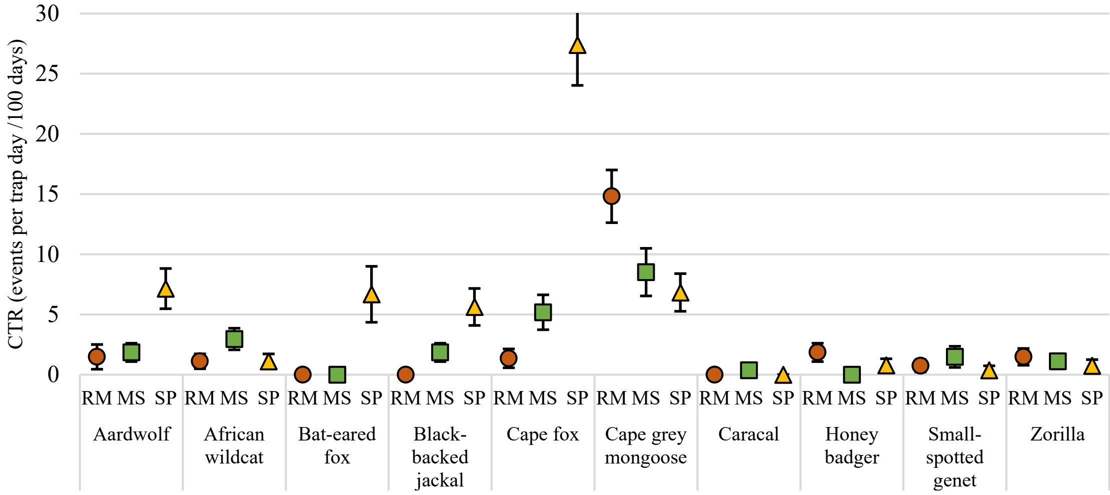


Figure 8. CTR mean vales and SE bars represented for each species across the different habitats. Red circles represent the values for Rocky Mountain (RM), green squares for Milky Shrubland (MS) and yellow triangles for Sandy plain (SP).

4.2.2. Occupancy and detection probability

The species detected in a greater number of cameras was the Cape grey mongoose, with a value of naïve occupancy for the total area of 0.73 being detected in a total of 22 cameras (Figure 9), being sandy plain the habitat with a lower detection for this species, observed in 50 % of the cameras. The next most detected species was the Cape fox, appearing in the 53.3 % of the cameras (16), being sandy plain the most frequent habitat for the species. The species with the lowest total value of naïve occupancy was the caracal, detected only in 2 cameras (Naïve = 0.067). The only species with an exclusive representation in one of the three habitats was the bat-eared fox, with a naïve occupancy value of 0.1 for the total area and 0.3 for sandy plain. The rest of the species were detected in a low number of cameras, between 7 and 12, with naïve occupancy values ranging from 0.23 to 0.4 for the total area.

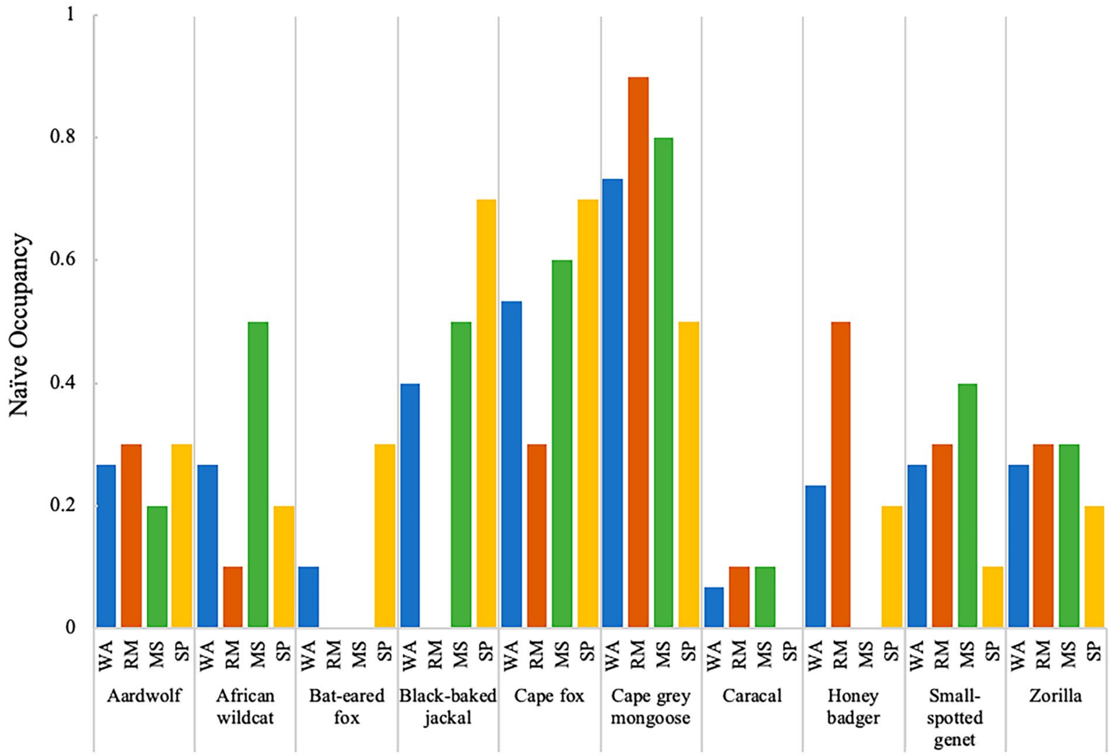


Figure 9. Bar Graph representing the values of calculated Naïve Occupancy for the small carnivore species for the whole area and each habitat. Blue bars indicate the values of naïve occupancy for the whole area (WA), red bars for Rocky Mountain (RM), green bars for Milky Shrubland (MS) and yellow bars for Sandy Plain (SP).

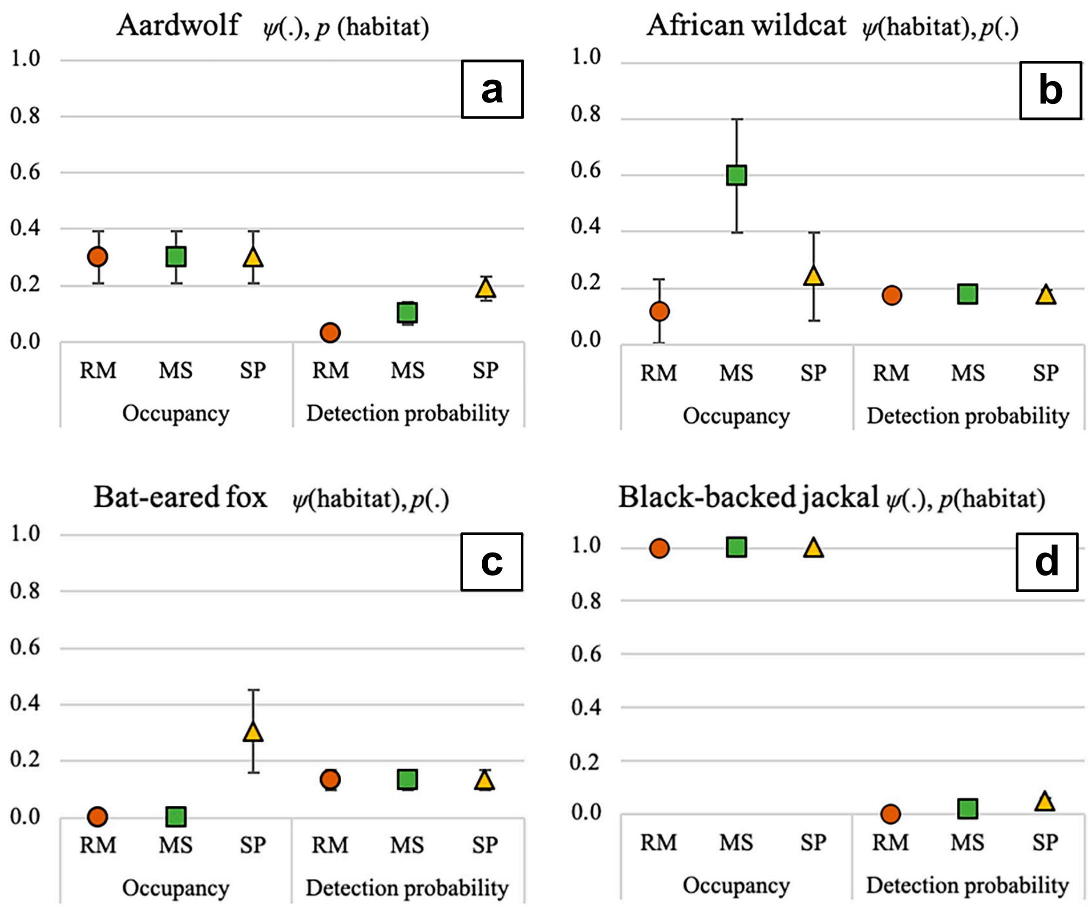
Only two species were excluded for the modelling of occupancy and detection probability estimates; the honey badger and the caracal, with less than 10 events in total (7 and 2 respectively), (Appendix 2(g,h)). The results for the values of the Akaike Information Criterion are represented in the Table 4, as well as the relative weights of each model and the accumulated weight of the models for each species. Observing the models that obtained more weight for each species, it could be inferred that the covariate habitat participated in the distribution of all species in greater or lesser degree.

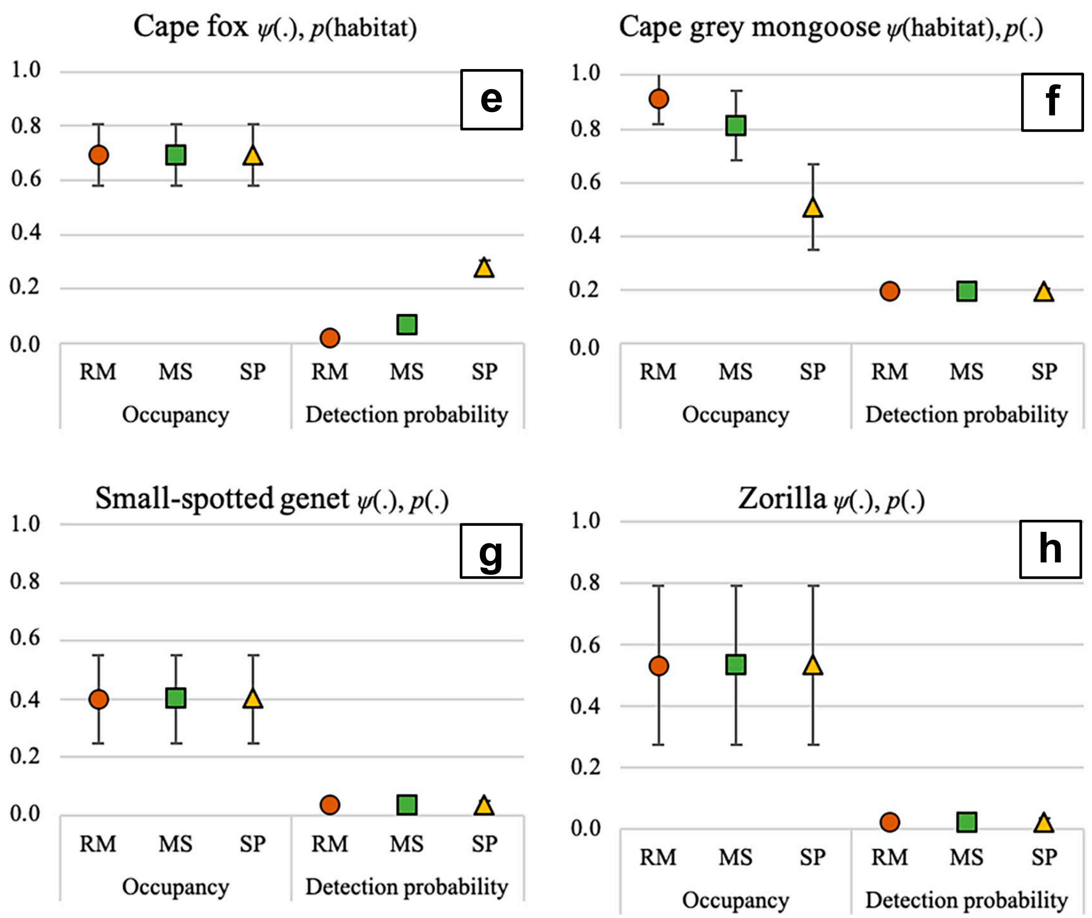
According to the criteria established for the selection of the best model, five of the eight species analysed presented a single model with a substantial level of empirical support (AIC < 2), being ψ(.), *p*(habitat) the model of choice for the aardwolf, ψ(habitat), *p*(.) for the bat-eared fox, ψ(.), *p*(habitat) for the black-backed jackal, ψ(.), *p*(habitat) for the Cape fox, and the null model, ψ(.), *p*(.) for the zorilla. The second step that considered as the best model the one with a relative weight of 0.90 was not useful, because for the three remaining species, the accumulated weight of 0.90 is reached in the third model, indicating that there were no single model that approached the reality of the sampling.

Table 4. Model estimation for occupancy and detection probability for each species of small carnivore ranking the models by the lowest AIC. *Δ*AIC and relative weights (*ω*) used to show the importance of each model.

	Model	AIC	*Δ*AIC	AIC weight (*ω*)	Cumulative weight
Aardwolf	*ψ*(.), *p* (habitat)	206.05	0.00	0.78	0.78
	ψ(habitat), *p* (habitat)	208.65	2.60	0.21	0.99
	ψ (.), *p* (.)	214.23	8.18	0.01	1.00
	ψ(habitat), *p* (.)	217.88	11.84	0.00	1.00
African wildcat	*ψ*(habitat), *p*(.)	161.61	0.00	0.38	0.38
	ψ(.), *p*.(.)	162.04	0.43	0.31	0.68
	ψ(habitat), *p*(habitat)	162.90	1.29	0.20	0.88
	ψ(.), *p*(habitat)	163.96	2.35	0.12	1.00
Bat-eared fox	*ψ*(habitat), *p*(.)	96.58	0.00	0.74	0.74
	ψ(.), *p*(.)	99.87	3.29	0.14	0.88
	ψ(habitat), *p*(habitat)	100.58	4.00	0.10	0.98
	ψ(.), *p*(habitat)	103.92	7.34	0.02	1.00
Black-backed jackal	*ψ*(.), *p*(habitat)	188.06	0.00	0.77	0.77
	ψ(habitat), *p*(.)	191.29	3.23	0.15	0.92
	ψ(habitat), *p*(habitat)	192.64	4.58	0.08	1.00
	ψ(.), *p*(.)	201.54	13.48	0.00	1.00
Cape fox	*ψ*(.), *p*(habitat)	436.10	0.00	0.88	0.88
	ψ(habitat), *p*(habitat)	440.08	3.98	0.12	1.00
	ψ(.), *p*(.)	485.39	49.29	0.00	1.00
	ψ(habitat), *p*(.)	485.83	49.73	0.00	1.00
Cape grey mongoose	*ψ*(habitat), *p*(.)	569.05	0.00	0.47	0.47
	ψ(.), *p*(.)	569.46	0.41	0.38	0.85
	ψ(habitat), *p*(habitat)	572.49	3.44	0.08	0.94
	ψ(.), *p*(habitat)	572.97	3.92	0.07	1.00
Small-spotted genet	*ψ*(.), *p*(.)	137.27	0.00	0.41	0.41
	ψ(.), *p*(habitat)	137.77	0.50	0.32	0.73
	ψ(habitat), *p*(.)	138.67	1.40	0.20	0.94
	ψ(habitat), *p*(habitat)	141.01	3.73	0.06	1.00
Zorilla	*ψ*(.), *p*(.)	122.99	0.00	0.68	0.68
	ψ(.), *p*(habitat)	125.72	2.73	0.18	0.86
	ψ(habitat), *p*(.)	126.66	3.67	0.11	0.97
	ψ(habitat), *p*(habitat)	129.13	6.14	0.03	1.00

The models selected for each species as the best, or those that despite being insufficient showed a higher relative weight than the rest, were represented in graphs to visualise the distribution of the occupancy and detectability estimates along the habitats (Figure 10, a to h). In these, the models ψ(.), *p*(habitat) and ψ(habitat), *p*(.) were chosen 3 times each as the ones that would best represent the species detection data. In the case of the small spotted genet (Figure10g) and the zorilla (Figure 10h), the estimates obtained in the null model (ψ(habitat), *p*(.)) were represented for all habitats since this model has a constant value of estimates for all cameras no matter the habitat they were located.





Figures 10(a-h). Graphs representing the estimates of occupancy and detection probabilities obtained for the model that best fit the distribution of each species of small carnivore. Red circles represent the values for Rocky Mountain (RM), green squares for Milky Shrubland (MS) and yellow triangles for Sandy plain (SP).

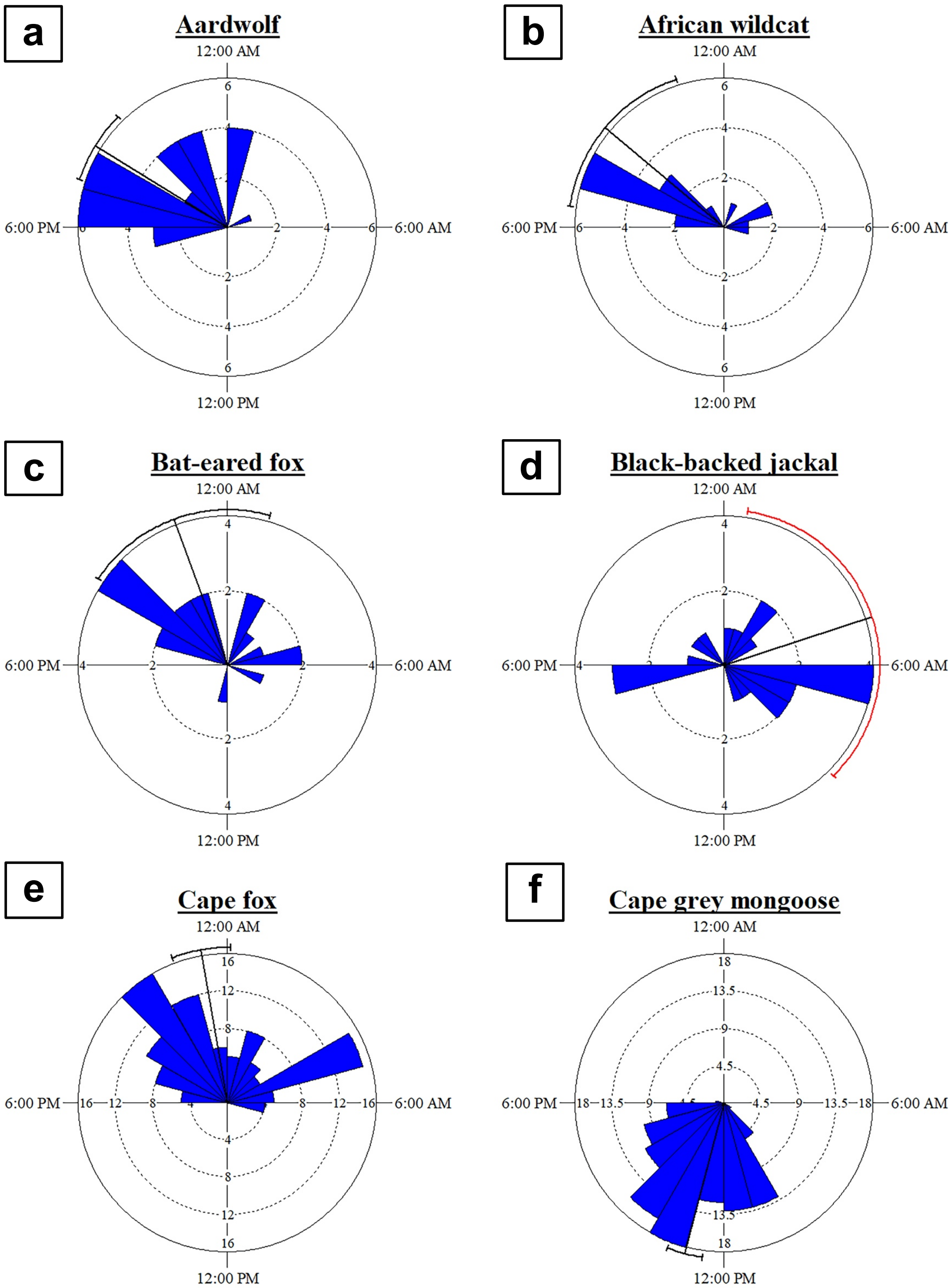
In general, the occupancy estimates for the ψ(habitat), p(.) model, matched with the Naïve occupancy results (Figure 9 and 10, Table 5), showing that the chosen model had a good quality of fit. For all species, the probability of detection was low, below 20 %, only exceeded in the case of Cape fox in the sandy plain habitat (p(habitat) = 0. 276 ± 0.03). Occupancy values are maintained in all habitats above 50 % for the black-backed jackal (ψ(.) = 1.0), Cape fox (ψ(.) = 0.691 ± 0.114), Cape grey mongoose (ψ(habitat) = 0.508 ± 0.161for sandy plain; 0.812 ± 0.129 for milky shrubland; and 0.912 ± 0.096 for rocky mountain) and zorilla (ψ(.) = 0.532 ± 0.258). The African wildcat was the only species having a higher estimated occupancy in milky shrubland habitat, reaching the 0.599 value.

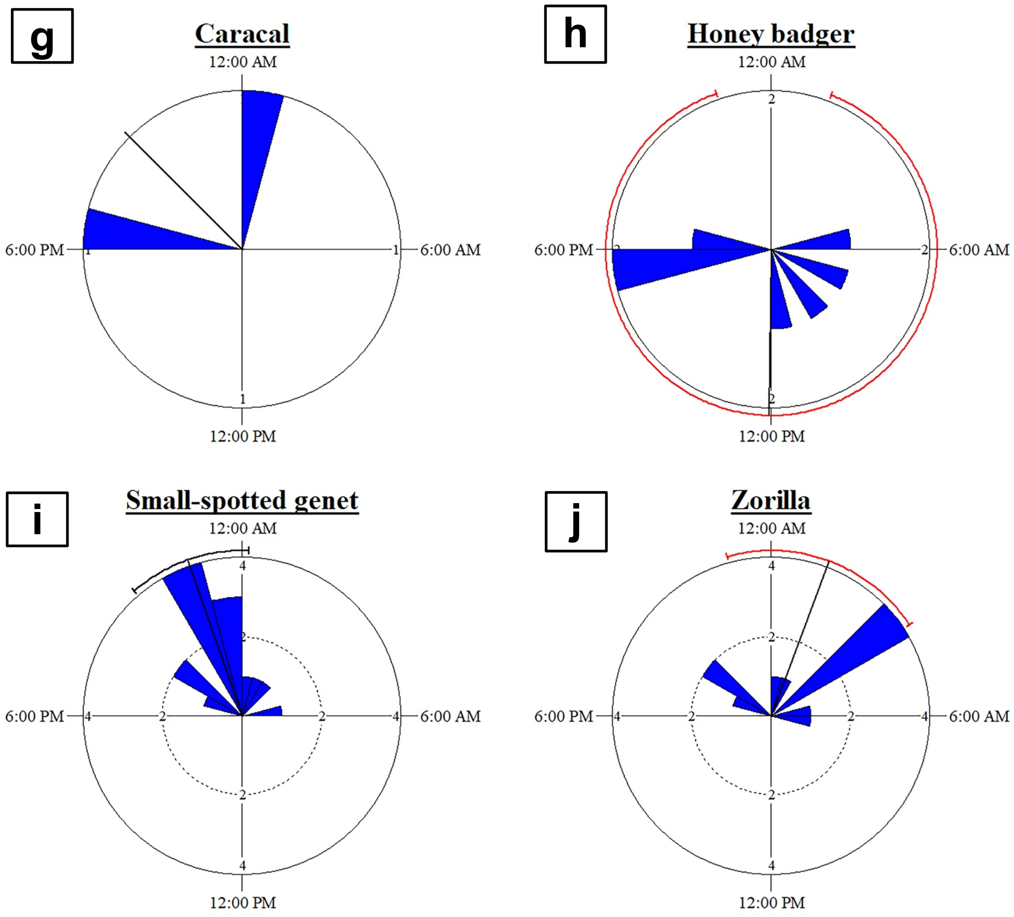
Table 5. Occupancy and detection probability values estimated (± SE) for the model with the best fit. Numbers in brackets below the species show the interval for the home ranges for the species. This table complements the information showed in Table 4 and Figure 10.

	Best Model	Habitat	ψ	SE	p	SE
Aardwolf (*1-6 km²*)	ψ(.), p(habitat)	Rocky Mountain	0.301	0.093	0.031	0.018
		Milky Shrubland	0.301	0.093	0.102	0.041
		Sandy Plain	0.301	0.093	0.189	0.041
African wildcat (*3.5-13 km²*)	ψ(habitat), p(.)	Rocky Mountain	0.119	0.114	0.175	0.016
		Milky Shrubland	0.599	0.200	0.175	0.016
		Sandy Plain	0.241	0.155	0.175	0.016
Bat-eared fox (*0.3-3.5 km²*)	ψ(habitat), p(.)	Rocky Mountain	0.000	0.003	0.133	0.035
		Milky Shrubland	0.000	0.001	0.133	0.035
		Sandy Plain	0.304	0.147	0.133	0.035
Black-backed jackal (*1-24.9 km²*)	ψ(.), p(habitat)	Rocky Mountain	1.000	0.000	0.000	0.000
		Milky Shrubland	1.000	0.000	0.019	0.008
		Sandy Plain	1.000	0.000	0.047	0.012
Cape fox (*1-32.1 km²*)	ψ(.), p(habitat)	Rocky Mountain	0.691	0.114	0.018	0.010
		Milky Shrubland	0.691	0.114	0.063	0.019
		Sandy Plain	0.691	0.114	0.276	0.030
Cape grey mongoose (*0.3-0.92 km²*)	ψ(habitat), p(.)	Rocky Mountain	0.912	0.096	0.193	0.013
		Milky Shrubland	0.812	0.129	0.193	0.013
		Sandy Plain	0.508	0.161	0.193	0.013
Small-spotted genet (*0.33-12 km²*)	ψ(.), p(.)		0.400	0.152	0.034	0.014
Zorilla *Unknown*	ψ(.), p(.)		0.532	0.258	0.021	0.012

4.3. Activity pattern

The results for the activity patterns of the different species were plotted in the Figures 11(a to j). During the study period the hours of light were distributed between 7:00-7:12 and 18:25-18:50 hours (The Time and Place 2020), so it can be seen that most species except black-backed jackal, Cape grey mongoose and honey badger had mostly nocturnal or crepuscular habits. The Cape grey mongoose showed a pattern of daytime activity while black-backed jackal appears to be active during both day and night.





Figures 11(a-j). Circular plots representing the circadian activity pattern of the small carnivore species. Black line represents Mean vector (μ) and its 95 % Confidence Intervals (red CI lines show unreliable results). Internal axes represent the frequency of events/hour.

This last affirmation was confirmed by the results of the Rao's spacing test (Table 6), whose differences were not significant in the case of the black-backed jackal (U = 1.516; P = 0.22) and the honey badger (U = 0.686; P < 0.5). All other species have an uneven distribution throughout the day (P < 0.05), most of them having clustered distribution, as shown by the p-value results for the Rayleight index (P < 0.05). The lack of a higher number of events for the caracal provides null results for the Rao test and non-significant results for the Rayleight test (U = 1; P = 0.427).

Table 6. Summary table of circular descriptive statistics, showing the values for the mean vector and its circular standard deviation ($\mu \pm$ CSD) and the results and p-values for the uniformity tests.

Species	$\mu \pm$ CSD	Rayleight's test (p-value)	Rao's spacing test (p-value)
Aardwolf	20:06 ± 02:33	19.12 (<0.01)	264 (<0.01)
African Wildcat	20:39:00 ± 4:11	5.11 (<0.05)	221.47 (<0.01)
Bat-eared fox	22:39 ± 04:25	4.264 ((<0.05)	185 (<0.01)
Black-backed jackal	4:47:00 ± 6:11	1.516 (**0.22**)	156.43(<**0.1**)
Cape fox	23:20 ± 3:42	40.25 (<0.01)	314.56 (<0.01)
Cape grey mongoose	12:59 ± 02:20	73.39 (<0.01)	322.99 (<0.01)
Caracal	21:00 ± 03:10	1 (**0.427**)	****
Honey badger	12:03 ± 05:49	0.686 (**0.02**)	152.14 (<**0.5**)
Small-spotted genet	22:42 ± 3:46	9,2 (<0.01)	207.86 (<0.01)
Zorilla	1:21 ± 3:46	4.13 (<0.05)	189.55 (<0.05)

The results for Watson's U^2 Test (Table 7) showed similar results to those observed above. The high levels of significance ($P < 0.05$) between clearly nocturnal species (Cape fox, small-spotted genet, zorilla) and clearly diurnal species (Cape grey moongose) allowed the observation of some gradients in the rest of the species. The absence of significant differences between the honey badger and the bat-eared fox (U^2 test = 0.15; $P > 0.1$), and the closeness to the level of significance of honey badger with African wildcat ($U^2 = 0.19$; $P < 0.1$), suggested certain level of overlap. Other species, such as the aardwolf (U^2 test = 0.21; $P < 0.05$) and the zorilla (U^2 test = 0.20; $P < 0.05$) presented significant differences with the honey badger. The broad activity pattern of black-backed jackal was again proven in the paired comparison, as this species only showed significant differences with the Cape grey mongoose (U^2 test = 0.36; $P < 0.002$), overlapping its circadian activity with that of all the other species. The caracal was excluded from the comparison as the test could not run with only 2 events.

Table 7. Temporal overlap of the small carnivores in the area of study. Results for the paired Watson's U^2 Test are shown. The number of asterisks represents the p-vale: *** for values < 0.05, ** for values = 0.05, and * for values < 0.1.

	African wildcat	Bat-eared fox	Black-backed jackal	Cape fox	Cape grey mongoose	Honey badger	Small-spotted genet	Zorilla
Aardwolf	0.03	0.07	0.13	0.05	0.31***	0.21**	0.05	0.06
African wildcat		0.01	0.04	0.04	0.37***	0.19*	0.08	0.02
Bat-eared fox			0.02	0.03	0.36***	0.15	0.07	0.02
Black-backed jackal				0.09	0.35***	0.08	0.14	0.05
Cape fox					0.49***	0.27***	0.027	0.02
Cape grey mongoose						0.10	0.4***	0.37***
Honey badger							0.26***	0.20**
Small-spotted genet								0.041

5. Discussion

According to the results, the sampling period was sufficient to detect 10 of the 14 (71.4 %) species expected in the study area (Table 1). Among the undetected species there are some of them linked to aquatic habitats (marsh mongoose and African clawless otter) and rare (black-footed cat) and common species (meerkat and yellow mongoose) that have not been detected in the reserve previously. The yellow mongoose is a particular case, since it was a species seen and detected on several occasions during the data collection period by camera traps installed in the farms adjacent to the reserve, used for a complementary study conducted by Clara Koch Jiménez for her Master's thesis (unpublished).

The results obtained for diversity and richness of small carnivores in the study area show that the distribution of species is quite uniform in terms of presence in the area, with more than 80 % of species detected in all habitats (Table 2) and an absence of significant differences between the effective number of species across the habitats. The value of Jackknife estimators and bibliographic data on detected species provided by field guides and encyclopaedias of African fauna (see Appendix 2) allow the inference of the fact that all detected species may be potentially present in two or more habitats, results that could be verified by increasing the sampling effort.

Hierarchical analysis of occupancy models showed that for 6 of the 8 species studied, habitat played an important role in their detection or distribution. These results are largely supported by those obtained for CTR values, indicating that there are significant differences in the number of detections of each species between habitats. In both analyses, sandy plain habitat was observed to have higher values than the rest of habitats in terms of occupancy, detection probability and CTR for a greater number of species.

The graphic representation of the activity patterns and the analysis of temporal overlap (Table 7) showed two clear and defined activity patterns, with a temporal partition among diurnal and nocturnal species, only excluded by the black-backed jackal.

In order to interpret the results as concisely and efficiently as possible, the discussion that frames the description of the diversity of small carnivores in the area is presented by species. The patterns of abundance, distribution, detection and different activity must be explained within the vital context of each species, which is generally species-specific. These descriptive aspects of each species can be observed together with their results for this survey in the Appendix 2.

Aardwolf

During the study period the species was found almost uniformly in all habitats despite the fact that the probability of detection of this species and its photographic rate were higher in the habitat of sandy plain. These results are consistent with the description of the species presented in the Appendix 2(a), since the habitat of predilection for the species is the semi-desert or rocky plains, highly influenced by the presence of burrows or a high abundance of termites (Kingdon et al. 2013), making their presence possible in those areas that meet these characteristics. The period of activity was mainly nocturnal, with a certain level of activity in the late afternoon, a pattern which coincides with that observed for the species during the winter, seeing its activity compromised by low temperatures and the presence of active termites on the surface (Kingdon et al. 2013). The lack of competition for resources is reflected in the absence of temporal and possibly spatial partitioning with the rest of the nocturnal small carnivores, which are smaller in size and have a much wider food spectrum.

African wildcat

It was a species detected in all habitats, showing preference for the milky shrubland in terms of CTR and Occupancy, meaning a greater abundance of individuals in this habitat, assuming uniform detection probabilities and home range size smaller than the spacing of the cameras it was detected (Appendix 2(b)). These results agreed with the description of the preferred habitats, areas with vegetation cover, rich in refuges and prey (Kingdon et al. 2013; Hunter 2018). The activity pattern was nocturnal, with a peak during the first hours of the night, showing no significant differences with any of the other nocturnal species, same results observed by Satgé et al. (2017) regarding the absence of temporal division between wildcats, zorillas and small-spotted genets.

Bat-eared fox

This species was found only in 3 camera traps, located exclusively in the wide sandy plains of Pelgrimsrust (Appendix 2(c)), denoting a high preference for this habitat. These results coincide with those of Mackie & Nel (1989), which establish that habitat selection criteria for bat-eared foxes depend on the ease of termites foraging and the potential burrows (own or upcycled) for reproduction. Several individuals per event were detected in all the camera stations, showing that the family groups forage together. In addition, the small size of their home ranges would indicate that the groups observed in each location belonged to different families. The active period was mainly nocturnal, overlapping with the rest of the nocturnal species, which do not present major threats either at a competitive or predatory level.

Black-backed jackal

It was difficult to interpret the results for this species. When trying to analyse the occupancy model, it was observed that the model tries to explain all the detections based on practically null detection probability values. These conclusions are implausible in the real world, since black-backed jackal is a species with territories small enough to accommodate several breeding pairs in the area, which if present in 100 % of the area as modelled, should be detected with a certain value of probability of detection higher than the estimated, according to the observations collected in this study. Leaving behind the occupancy model, the presence of black-backed jackal in the study area was distributed between the sandy plain and milky shrubland habitats, with average detection values for these above the values obtained for many other species, as well as a high distribution of detections throughout the study area, being found in 40 % of the cameras. These results would allow us to infer that the species is relatively well distributed throughout the reserve, preferring open and flat areas. The activity pattern of this species was also inconclusive, showing events distributed throughout the day except for the period between noon and sunset. However, in general this pattern of activity is similar to that observed by Satterfield (2014), showing a less crepuscular and more nocturnal pattern, provided by a higher number of detections (n = 811).

Cape fox

It was the second species with the highest number of detections in terms of individuals sampled and number of camera traps occupied (53.3 %). The estimated values of detection probability according to the highest fitting model, ψ(.), p(habitat), would explain the higher number of detections in the Sandy plain for this species, which would be uniformly distributed over 69.1 % of the study area. The territorial range of this species is quite variable, between 1-32.1 km^2, which makes it difficult to infer whether the correlation between the estimated values of occupancy and the relative abundance of the species was reliable enough to indicate a high abundance of individuals in the area. The period of activity of this species was extended throughout the night, with no temporal avoidance with species that share the same trophic niche (de Satgé et al. 2017), nor with those that consider Cape fox as prey, contradicting the results obtained by Kamler et al. (2012) in which a clear space-time difference is shown between Cape fox and its main predator, the black-backed jackal.

Cape grey mongoose

The most abundant species in terms of number of individuals and sites detected (22 camera traps, 77.3 % of the total), indicating its wide distribution in the area, mainly encountered in rocky mountain and milky shrubland, habitats that offer them multiple refuge sites where they can escape from their predators, being the only species with a clear predilection for this rocky area. Its uniform detection values in all habitats (predicted by the first two occupancy models) and its small home ranges, indicate that this species is very abundant in the study area. Its pattern of activity is unique in comparison with the rest of the species of small carnivores, being exclusively diurnal, active from noon until dusk. The behaviour of this species could be influenced by the avoidance of possible predators such as black-backed jackal (Bagniewska & Kamler 2014) or caracal (Avenant et al. 2016), observable in the temporal and in the spatial range; increasing its ocurrence in mountainous areas and decreasing in sandy plain areas where black-backed jackal seems more frequent and Cape grey mongoose has less places to hide.

Caracal

This species was only detected on two occasions in two different habitats, so it is not possible to draw any major inferences. Although the territories of the species are quite large, the separation between the camera traps (Appendix 2(g)) would allow to infer that the individuals detected in both locations were different ones. Both detections occurred at night, but the number of events is too small to predict that the activity pattern was exclusively nocturnal.

Honey badger

The honey badger also counted with a limited number of detections. However, each one of them was taken in a different location, leading to the observation that this species was mainly distributed in the mountain habitat and the sandy plain areas nearby (Appendix 2(h)). The wide home range of this species can reach more than the entire study area and may overlap with other conspecifics (Kingdon et al. 2013), making it impossible to deduce the abundance of the species in the area without an individual identification. The temporal activity pattern for the 7 detections in the study indicates a diurnal-crepuscular activity, observable in the figure and the results of Watson's U^2 test, showing little or no significant differences with both diurnal (Cape grey mongoose) and nocturnal species (Table 7), coinciding with the activity patterns of the species for the winter season.

Small-spotted genet

This species was observed in all habitats with very limited occupancy values. No single occupancy model was sufficient to rule out the influence of habitat on its distribution, and the observed occupancy results do appear to reflect certain differences between rocky mountain and milky shrubland habitats with sandy plain, coinciding with the preferred habitats reviewed in the literature (Appendix 2(i)). The results for the pattern of activity were exclusively nocturnal, showing overlap with the rest of species in the same trophic niche (African wildcat, small spotted genet), coinciding with the results of de Satgé (2017), which infer that possible competition linked to the same period of activity is solved by spatial partitioning, not analysed in this study.

Zorilla

Detection for this species was also low, counting only one detection per camera during the whole data collection. However, it was distributed in 11 of the 30 cameras (36.67 %), being present in all habitats with a more or less uniform distribution and detection probability in all of them. The relative abundance of this species would be moderate considering the estimated occupancy values, being present in 53.2 % of the study area, assuming that the unknown home ranges of this species were small enough to fit inside the spacing among cameras. This species is one of the exclusively nocturnal species analysed by de Satgé (2017), presenting the same results presented above. Even though the distribution of the species in the area was not analysed or compared for this study, it is easy to observe the absence of spatial-temporal division of this species with one of its major predators, the caracal (Avenant et al. 2016), being present in the two locations where the caracal was detected. Similar results were obtained for the black-backed jackal, another of its top predators (Bagniewska & Kamler 2014).

The interpretation of the results for each of the species allowed to perceive some of the limitations of this study, which had a greater influence on some species than others. One of the most frequent limitations was observed during the description of species abundance, being the inability to correlate this with the estimated occupancy value. This was due to a lack of knowledge of the home ranges of the different species in the area, followed by an elaboration of the design based on those species with smaller home ranges. Another limitation observed was the time of data collection, which limited the number of events sufficient for some species to produce significant results in terms of abundance, distribution and activity pattern.

In general aspects, it can be concluded that the main objective of this thesis, "identify and describe the diversity of small carnivores in the area, studying their distribution, abundance and activity over the space and time" was fulfilled, since it was possible to identify the diversity and richness of species, the abundance of some of them, as well as their activity patterns, fulfilling in turn all the proposed objectives.

6. Conclusions

The findings provided in this study offered pioneering information on the species diversity of small carnivores in an atypical region of the Nama Karoo biome. Within the reserve, 10 species of small carnivores were observed, all of them common and non-endangered in Southern Africa.

These species were distributed throughout the study area, some of them exhibiting clear preferences for those habitats that best suited their life traits. At the activity level, the vast majority of the species studied showed a nocturnal pattern, without observing different intervals of activity that could indicate a temporal division that would reduce the possible encounters between the species, important for those that share a trophic niche or may prey on each other.

The sampling effort appeared to be insufficient for the optimal detection of some species, which would have needed a larger number of cameras or an extension of the sampling period to reach sufficiently robust levels of detection enough to draw reliable conclusions.

Despite this limitation, this thesis sheds light on some species that have received little attention from the scientific community. Species that can perform very complex functions in the ecosystems where they live. Furthermore, at the local level, knowledge of these species can be decisive for their conservation, since several of the species detected in the area are potential predators of sheep, being persecuted and exterminated on the surrounding farms, finding in the reserve a safe place to settle.

This inventory presented a first approximation to the study of small carnivores in the area, creating a basis for the subsequent study of species at both individual and multispecies levels. These lines of work could have an impact not only at the local level but could also provide general information on those species, especially for those with large gaps in knowledge of their biology and ecology.

7. References

Agnarsson I, Kuntner M, May-Collado LJ. 2010. Dogs, cats, and kin: a molecular species-level phylogeny of Carnivora. Molecular phylogenetics and evolution **54**(3): 726-745.

Alves RRN, Pinto LCL, Barboza RRD, Souto WMS, Oliveira REMCC, Vieira WLS. 2013. A global overview of carnivores used in traditional medicines. Pages 171-206 in Alves RRN, Rosa IL, editors. Animals in traditional folk medicine. Springer, Berlin.

Amin R, Davey K, Wacher T. 2017. Camera trap data management and analysis package - user guide. ZSL.

ASCaRIs. 2020. African Small Carnivore Research Initiatives. ukit. Available from https://ascaris.org/ (Accessed April 2020).

Avenant N. 2011. The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South African grasslands. Wildlife Research, **38**(7): 626-639.

Avenant NL, Drouilly M, Power RJ, Thorn M, Martins Q, Neils A, du Plessis J, Do Linh San E. 2016. A conservation assessment of *Caracal caracal*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Bagniewska JM, Kamler JF. 2014. Do black-backed jackals affect numbers of smaller carnivores and prey?. African Journal of Ecology **52**(4): 564-567.

Barea-Azcón JM, Virgós E, Ballesteros-Duperon E, Moleón M, Chirosa M. 2006. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Vertebrate Conservation and Biodiversity **16**: 1213-1230.

Bateman PW, Fleming PA. 2012. Big city life: carnivores in urban environments. Journal of Zoology **287**(1): 1-23.

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data **5** (180214) DOI: 10.1038/sdata.2018.214.

Begg CM, Begg KS, Power RJ, van der Merwe D, Camacho G, Cowell C, Do Linh San E. 2016. A conservation assessment of *Mellivora capensis*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Bengsen A. 2014. Analysis of camera trap surveys to detect effects of population management. Pages 325-330 in Meek P, Fleming P, Ballard G, Claridge A, Sanderson J, Swann D, editors. Camera Trapping Wildlife Management and Research. CSIRO Publishing, Melbourne.

Brooke ZM, Bielby J, Nambiar K, Carbone C. 2014. Correlates of research effort in carnivores: body size, range size and diet matter. PloS one **9**(4) (e93195) DOI: 10.1371/journal.pone.0093195.

Burnham KP, Anderson DR. 2002. Model selection and multi-model inference. A practical information–theoretic approach. Springer-Verlag, New York.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**(3): 675-685.

Buskirk SW, Zielinski WJ. 2003. Small and mid-sized carnivores. Pages 207- 249 in Zabel CJ, Anthony RG, editors. Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America. Cambridge University Press, Cambridge.

Caravaggi A, Banks PB, Burton AC, Finlay CM, Haswell PM, Hayward MW, Rowcliffe MJ, Wood MD. 2017. A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation **3**(3), 109-122.

Carbone C, et al. 2002. The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle et al. Animal Conservation **5**(2): 121-123.

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology **2**(7): 909-914.

Carvalho F, Matolengwe T, Camps D, Gaubert P, Do Linh San E. 2016. A conservation assessment of *Genetta genetta*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Cowling RM. 1986. Description of the Karoo Biome project. South African National Scientific Programmes Report 122, Pretoria.

Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**: 563-566.

Crooks KR. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation biology **16**(2): 488-502.

Dalerum F, Le Roux A, de Vries JL, Kamler JF, Page-Nicholson S, Stuart C, Stuart M, Wilson B, Do Linh San E. 2016. A conservation assessment of *Otocyon megalotis*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

de Satgé J, Teichman K, Cristescu B. 2017. Competition and coexistence in a small carnivore guild. Oecologia **184**(4): 873-884.

de Vries JL, Marneweck D, Dalerum F, Page-Nicholson S, Mills MGL, Yarnell RW, Sliwa A, Do Linh San E. 2016. A conservation assessment of *Proteles cristata*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Do Linh San E, Ferguson AW, Belant JL, Schipper J, Hoffmann M, Gaubert P, Angelici FM, Somers MJ. 2013. Conservation status, distribution and species richness of small carnivores in Africa. Small Carnivore Conservation **48**: 4-18.

Do Linh San E, Mbatyoti OA, Palmer G, Stuart C, Stuart M, Avenant NL, Cavallini P. 2016. A conservation assessment of *Herpestes pulverulentus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Edelman AJ. 2019. Carnivora. In Vonk J, Shackelford T, editors. Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

Escribano-Avila G. 2019. Non-specialized frugivores as key seed dispersers in dry disturbed environments: an example with a generalist neotropical mesocarnivore. Journal of arid environments **167**:18-25.

Ferreira-Rodríguez N, Pombal MA. 2019. Bait effectiveness in camera trap studies in the Iberian Peninsula. Mammal Research **64**(2): 155-164.

Fiske I, Chandler R. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of statistical software **43**(10): 1-23.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin **34**(4): 1142-1151.

González-Maya JF, Ramírez-Chaves H. 2017. Global Small Carnivore Conservation: geographical distribution of small carnivore research. Small Carnivore Conservation. **55**: 1-3.

González-Varo JP, Laffitte, JMF, Guitián, J, López-Bao JV, Suárez-Esteban A. 2015. Frugivoría y dispersión de semillas por mamíferos carnívoros: rasgos funcionales. Revista Ecosistemas **24**(3): 43-50.

Gorman ML, Trowbridge BJ. 1989. The role of odor in the social lives of carnivores. Pages 55-88 in Gittleman JL, editor. Carnivore behavior, ecology, and evolution. Springer US, Boston, MA.

Goswami A. 2010. Introduction to Carnivora. Pages 1-24 in Goswami A, Friscia A, editors. Carnivoran Evolution: New Views on Phylogeny, Form and Function. Cambridge University Press, Cambridge.

Grilo C, Bissonette JA, Santos-Reis M. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological conservation **142** (2): 301-313.

Hämäläinen A, Broadley K, Droghini A, Haines JA, Lamb CT, Boutin S, Gilbert S. 2017. The ecological significance of secondary seed dispersal by carnivores. Ecosphere, **8**(2), e01685 DOI: 10.1002/ecs2.1685.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1-9.

Hanke PU, Dickman CR. 2013. Sniffing out the stakes: hair-snares for wild cats in arid environments. Wildlife Research **40**(1): 45-51.

Herbst M, Foxcroft L, Le Roux J, Bloomer P, Do Linh San E. 2016. A conservation assessment of *Felis silvestris*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Herrera CM. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos **55**(2): 250-262.

Humphries BD, Ramesh T, Hill TR, Downs CT. 2016. Habitat use and home range of black-backed jackals (*Canis mesomelas*) on farmlands in the Midlands of KwaZulu-Natal, South Africa. African Zoology **51**(1): 37-45.

Hunter L. 2018. Field Guide to Carnivores of the World. Bloomsbury Publishing Plc, London.

IUCN. 2020a. IUCN, SSC Groups: directory of Specialist Groups, Red List Authorities, Task Forces of the Species Survival Commission (SSC). Available from https://www.iucn.org/ssc-groups/disciplinary-groups (accessed April 2020).

IUCN. 2020b. The IUCN Red List of Threatened Species. Version 2020-1. Available from https://www.iucnredlist.org (accessed March 2020).

IUCN/SSC. 2020. Small Carnivore Conservation: The journal of the IUCN Small Carnivore Specialist Group. Available from http://www.smallcarnivoreconservation.org/about.html (accessed April 2020).

Jackson RM, Roe JD, Wangchuk R, Hunter DO. 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildlife Society Bulletin **34**(3): 772-781.

Johnson A, Vongkhamheng C, Saithongdam T. 2009. The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. Oryx, **43**(4):626-633.

Jost L, González-Oreja J. 2012. Midiendo la diversidad biológica: más allá del índice de Shannon. Acta zoológica lilloana **56**(1-2): 3-14.

Jost, L. 2006. Entropy and diversity. Oikos **113**(2): 363-375.

Jürgens N, Desmet PG, Rutherford MC, Mucina L, Ward RA. 2006. Desert Biome. Pages 301- 323 in Mucina L, Rutherford MC editors. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia19, Pretoria.

Kamler J, Palmer G, Cowell C, Mills MGL, Stuart C, Stuart M, Do Linh San E. 2016. A conservation assessment of *Vulpes chama*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Kamler JF, Stenkewitz U, Klare U, Jacobsen NF, Macdonald DW. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. The Journal of Wildlife Management **76**(6), 1241-1253.

Kays RW, Slauson KM. 2008. Remote cameras. Pages 110-140 in Long RA, MacKay P, Ray J, Zielinski E, editors. Noninvasive survey methods for carnivores. Island Press, Washington, DC.

Kingdon J, Hoffmann M. 2013. Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsbury Publishing, London.

Kingdon J. 2015. The Kingdon field guide to African mammals. Bloomsbury Publishing, London.

Kiros W, Kibrom F, Raman PV, Teferi M, Solomon K, Meheretu Y. 2016. Vehicle–wild vertebrate collision mortality on the highways of Tigray, Ethiopia, implications for conservation. African Journal of Ecology **54**(4): 442-449.

Kitchener AC, Meloro C, Williams T. 2017. Form and function of the musteloids. Pages 98-135 in Macdonald DW, Newman C, Harrington LA, editors. Biology and Conservation of Musteloids. Oxford University Press, Oxford.

Kovach Computing Services. 2011. Oriana: users' manual: Version 4.0. Kovach Computing Services, Pentraeth.

Kruuk H. 2002. Hunter and hunted: relationships between carnivores and people. Cambridge University Press, New York.

Leuchtenberger C, de Oliveira ÊS, Cariolatto LP, Kasper CB. 2018. Activity pattern of medium and large sized mammals and density estimates of *Cuniculus paca* (Rodentia: Cuniculidae) in the Brazilian Pampa. Brazilian Journal of Biology **78**(4): 697-705.

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS. 2007. Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. The Journal of Wildlife Management **71**(6): 2018-2025.

Long RA, Zielinski WJ. 2008. Designing effective noninvasive carnivore surveys. Pages 8-44 in Long RA, MacKay P, Ray J, Zielinski E, editors. Noninvasive survey methods for carnivores. Island Press, Washington, DC.

Łopucki R, Klich D, Kitowski I. 2019. Are small carnivores urban avoiders or adapters: Can they be used as indicators of well-planned green areas?. Ecological indicators **101**: 1026-1031.

Lyra-Jorge MC, Ciocheti G, Pivello VR, Meirelles ST. 2008. Comparing methods for sampling large-and medium-sized mammals: camera traps and track plots. European Journal of Wildlife Research, **54**(4): 739-744.

Macdonald DW, Kays RW. 2005. Carnivores of the world: an introduction. Pages 1-67. in Nowak RM, editor. Walker's carnivores of the world. The Johns Hopkins University Press, London, Baltimore.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. 2002. Estimating site occupancy when detection probabilities are less than one. Ecology **83**(8):2248-2255.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, London.

Mackie AJ, Nel JAJ. 1989. Habitat selection, home range use, and group size of bat-eared foxes in the Orange Free State. South African Journal of Wildlife Research **19**(4): 135-139.

Magurran AE. 2004. Measuring biological diversity. Blackwell-Science Ltd, Oxford.

Mann G. 2014. Aspects of the ecology of leopards (*Panthera pardus*) in the Little Karoo, South Africa [PhD Dissertation]. Rhodes University, Grahamstown.

McComb B, Zuckerberg B, Vesely D, Jordan C. 2010. Monitoring animal populations and their habitats: a practitioner's guide. CRC Press, Taylor and Francis Group, Boca Raton.

Meek PD, et al. 2014. Recommended guiding principles for reporting on camera trapping research. Biodiversity and conservation **23**(9): 2321-2343.

Meek PD, Ballard GA, Fleming PJ. 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. Australian Mammalogy **37**(1): 13-22.

Mendelsohn J, Jarvis A, Roberts C, Robertson T. 2003. Atlas of Namibia: a portrait of the land and its people. New Africa Books (Pty) Ltd, Cape Town.

Mikslová K. 2019. Spatio-temporal overlap between leopard and potential prey [MSc.Thesis]. Czech University of Life Sciences Prague, Prague.

Minnie L, Avenant NL, Kamler J, Butler H, Parker D, Drouilly M, du Plessis J, Do Linh San E. 2016. A conservation assessment of *Canis mesomelas*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Moore AC. 1981. The Tantalite Valley shear zone—a major locus for igneous activity in Southern Namibia (South West Africa)?. Journal of Volcanology and Geothermal Research **10**(4): 383-393.

Morrison ML, Block WM, Strickland MD, Collier BA, Peterson MJ. 2001. Wildlife study design. Springer-Verlag, New York.

Msuha MJ. 2009. Human impacts on carnivore biodiversity inside and outside protected areas in Tanzania [PhD Dissertation]. University College London, London.

Mucina et al. 2006. Nama-Karoo Biome. Pages 324- 347 in Mucina L, Rutherford MC editors. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia19, Pretoria.

Mudappa D, Noon BR, Kumar A, Chellam R. 2007. Responses of small carnivores to rainforest fragmentation in the southern Western Ghats, India. Small Carnivore Conservation **36**: 18-26.

Niedballa J, Sollmann R, bin Mohamed A, Bender J, Wilting A. 2015. Defining habitat covariates in camera-trap based occupancy studies. Scientific reports **5** (17041) DOI: 10.1038/srep17041.

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

O'Connell AF, Nichols JD, Karanth KU. 2011. Camera traps in animal ecology: methods and analyses. Springer Japan, Tokyo.

Palomares F, Caro TM. 1999. Interspecific killing among mammalian carnivores. The American Naturalist **153**(5): 492-508.

Pérez-Irineo G, Santos-Moreno A. 2013. Trends in research on terrestrial species of the order carnivora. Mastozoología Neotropical **20**(1): 113-121.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings: Biological Sciences **267**(1456): 1947-1952.

Ramachandran P, Devarajan K. 2018. ViXeN: An open-source package for managing multimedia data. Methods in Ecology and Evolution **9**(3): 785-792.

Rich LN. 2016. Monitoring and Conserving Wildlife Communities across Northern Botswana [PhD Dissertation]. Virginia Tech, Blacksburg.

Roemer GW, Gompper ME, Van Valkenburgh B. 2009. The ecological role of the mammalian mesocarnivore. BioScience **59**(2): 165-173.

Rovero F, Martin E, Rosa M, Ahumada JA, Spitale D. 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PloS one **9** (e103300) DOI: 10.1371/journal.pone.0103300.

Rovero F, Tobler M, Sanderson, J. 2010. Camera trapping for inventorying terrestrial vertebrates. Pages 100-128 in Eymann J, Degreef J, Häuser C, Monje JC, Samyn Y, VandenSpiegel D, editors. Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring. Abc Taxa, Brussels.

Rowcliffe JM, Carbone C. 2008. Surveys using camera traps: are we looking to a brighter future?. Animal Conservation **11**(3): 185-186.

Rowe-Rowe D, Stuart C, Stuart M, Do Linh San E. 2016. A conservation assessment of *Ictonyx striatus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Satterfield LC, Thompson JJ, Snyman A, Candelario L, Rode B, Carroll JP. 2017. Estimating occurrence and detectability of a carnivore community in eastern Botswana using baited camera traps. African Journal of Wildlife Research **47**(1): 32-46.

Satterfield LC. 2014. Use of baited camera traps to sample carnivore communities in eastern Botswana [PhD Dissertation] University of Georgia, Athens.

Schipper J, Hoffmann M, Duckworth JW, Conroy J. 2008. The 2008 IUCN red listings of the world’s small carnivores. Small Carnivore Conservation **39**: 29-34.

Schlexer FV. 2008. Attracting animals to detection devices. Pages 263-292 in Long RA, MacKay P, Ray J, Zielinski E, editors. Noninvasive survey methods for carnivores. Island Press, Washington, DC.

Sechrest WW, Brooks TM. 2002. Biodiversity–threats. eLS. John Wiley & Sons Ltd, Chichester. DOI: 10.1038/npg.els.0003257.

Silveira L, Jacomo AT, Diniz-Filho JAF. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological conservation **114**(3): 351-355.

Stuart C, Stuart M. 2015. Stuarts' field guide to mammals of southern Africa: including Angola, Zambia & Malawi. Struik Nature, Cape Town.

Sunarto, Sollmann R, Mohamed A, Kelly MJ. 2013. Camera trapping for the study and conservation of tropical carnivores. The Raffles Bulletin of Zoology **28**: 21-42.

Sunquist M, Sunquist F. 2002. Wild Cats of the World. University of Chicago Press, Chicago.

Terborgh J, et al. 2001. Ecological meltdown in predator-free forest fragments. Science **294**: 1923-1926.

The Time and Place. 2020. Sunrise and Sunset times for Warmbad, Namibia. The Time and Place. Good Stuff. Available from https://www.thetimeandplace.info/global/warmbad-karas-namibia/2019-08-16#.Xq1NMRMzY1I (accessed May 2020).

Tobler MW, Carrillo-Percastegui SE, Pitman RL, Mares R, Powell G. 2008. An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. Animal Conservation **11**(3): 169-178.

Trolle M, Kéry M. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. Journal of mammalogy **84**(2): 607-614.

Watkeys MK. 1999. Soils of the arid south-western zone of Africa. Pages 17-26 in Dean WRJ, Milton S, editors. The Karoo: ecological patterns and processes. Cambridge University Press, Cambridge.

Wilson GJ, Delahay RJ. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildlife Research **28**(2): 151-164.

World Weather Online 2020. Tantalite Valley Monthly Climate Averages. Available from https://www.worldweatheronline.com/tantalite-valley-weather-averages/karas/na.aspx (accessed April 2020).

Zar JH. 2010. Biostatistical analysis; 5th edition. Prentice Hall, New Jersey.

Appendices

List of the Appendices:

Appendix 1: Wild mammal species detected by camera traps in the study area **............ II**

Appendix 2: Small carnivore's information summary **...III**

a. Aardwolf (*Proteles cristata*).. III
b. African wildcat (*Felis silvestris lybica*) IV
c. Bat-eared fox (*Otocyon megalotis*)...V
d. Black-backed jackal (*Canis mesomelas*) VI
e. Cape fox (*Vulpex chama*) VII
f. Cape grey mongoose (*Herpestes pulverulentus*) VIII
g. Caracal (*Caracal caracal*)... IX
h. Honey badger (*Mellivora capensis*) X
i. Small-spotted genet (*Genetta genetta*) XI
j. Zorilla (*Ictonyx striatus*)...XII

Appendix 1: Wild mammal species detected by camera traps in the study area [a].

	Species	Status (IUCN 2020)
Carnivores	Aardwolf (*Proteles cristata*)	LC
	African wildcat (*Felis silvestris*)	LC
	Bat-eared fox (*Otocyon megalotis*)	LC
	Black-backed jackal (*Canis mesomelas)*	LC
	Brown Hyaena (*Hyaena brunnea*)	NT
	Cape fox (*Vulpes chama*)	LC
	Cape grey mongoose (*Herpestes pulverulentus*)	LC
	Caracal (*Caracal caracal*)	LC
	Honey badger (*Mellivora capensis*)	LC
	Leopard (*Panthera pardus*)	VU
	Small-spotted genet (*Genetta genetta*)	LC
	Zorilla (*Ictonyx capensis*)	LC
Ungulates	Common eland (*Tragelaphus oryx*)	LC
	Gemsbok (*Oryx gazella*)	LC
	Greater kudu (*Tragelaphus strepsiceros*)	LC
	Klipspringer (*Oreotragus oreotragus*)	LC
	Mountain zebra (*Equus zebra*)	VU
	Red hartebeest (*Alcelaphus buselaphus caama*)	LC
	Rock Hyrax (*Procavia capensis*)	LC
	Springbok (*Antidorcas marsupialis*)	LC
	Steenbok (*Raphicerus campestris*)	LC
Small mammals	Cape crested porcupine (*Hystrix africaeaustralis*)	LC
	Cape ground squirrel (*Xerus inauris*)	LC
	Cape hare (*Lepus capensis*)	LC
	Smith's red rock hare (*Pronolagus rupestris*)	LC
	Southern African springhare (*Pedetes capensis*)	LC
Other	Aardvark (*Orycteropus afer*)	LC

[a.] Micromammals such as small murids, gerbils, elephant shrews and bats were excluded from this list due to inability of identification through photographs.

Appendix 2: Small carnivores' information summary[i]

a. Aardwolf (*Proteles cristata*)

Description:

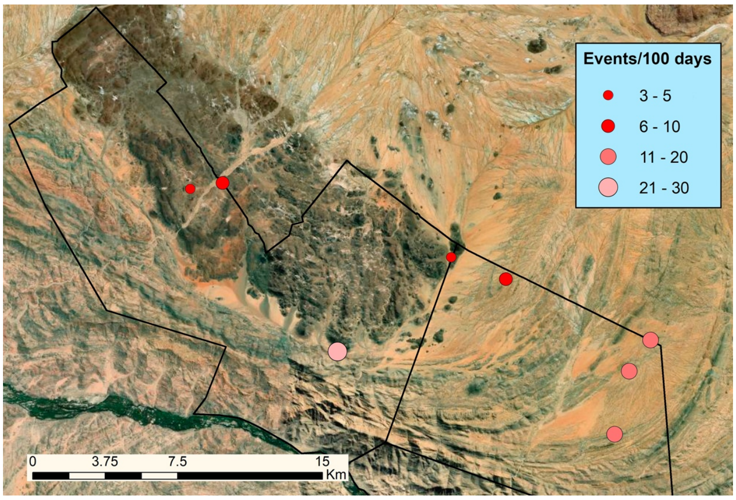
Aardwolf in camera CT9

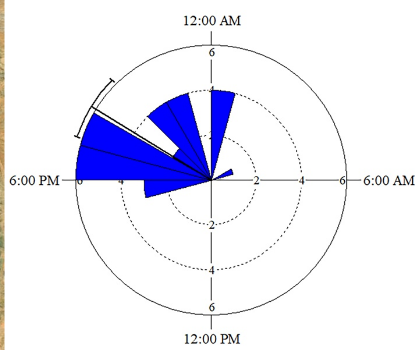
- Home Range: 1 – 6 km^2.
- SH: 50 cm. Long erectile mane hairs, cheekteeth reduced. Sticky saliva for trapping insects.
- Habitat: semi-deserts, grasslands mainly, also savanna woodlands and gravel plains.
- Live in dens excavated by other mammals.
- Diet: insectivore, mainly termites (*Trinervitermes* sp)
- Monogamous and territorial.
- Breeding season: June-July.
- Activity pattern: nocturnal, late afternoon (winter)
- Main predator: Black-backed jackal.
- Global Conservation status: LC.
- Research needed: genetic population studies, population trends, ecological impact in ecosystems, distribution studies (de Vries et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	8	3	2	3
Nº of Events	30	4	10	19
CTR ± SD	3.49 ± 3.94	1.48 ± 5.34	1.85 ± 3.96	7.15 ± 8.68
Naïve Occupancy	0.267	0.3	0.3	0.3
Occupancy (ψ ± SE)		0.301 ± 0.093	0.301 ± 0.093	0.301 ± 0.093
Detection Probability (p ± SE)		0.031 ± 0.18	0.102 ± 0.041	0.189 ± 0.041

Spatial distribution and circadian activity pattern:





b. African wildcat (*Felis silvestris lybica*)

Description:

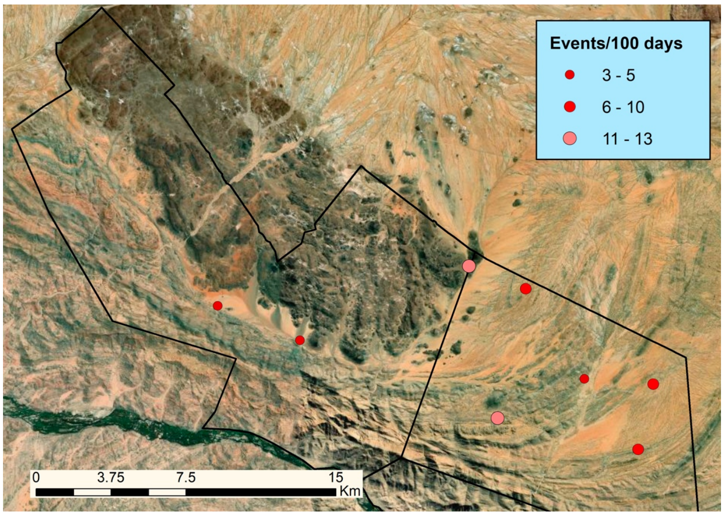
African wildcat in camera CT31

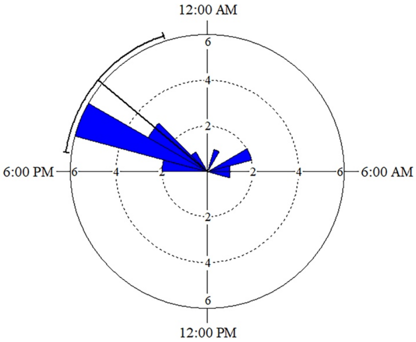
- Home Range: 3.5-13 km^2.
- Similar to domestic cat but heavier.
- Habitat: broad habitat tolerance, some cover needed avoiding very open areas.
- Rest in rocky hillsides, trees, shrubs, tall grasses, or abandoned burrows.
- Diet: small rodents, birds, lagomorphs, squirrels, springhares, reptiles. Very opportunistic.
- Solitary, ♂ ranges overlap with ♀♀.
- Breeding season: all over the year.
- Activity pattern: mainly nocturnal, dependent in season and food availability.
- Predators: large carnivores, honey badgers and raptors.
- Global Conservation status: LC.
- Research needed: hybridisation with domestic cats, assess possible subspecies, monitor current interventions protecting wildcats against hybridisation (Herbst et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	8	1	5	2
Nº of Events	17	4	10	3
CTR ± SD	1.76 ± 1.96	1.11 ± 3.20	2.96 ± 4.65	1.11 ± 3.20
Naïve Occupancy	0.267	0.1	0.5	0.2
Occupancy (ψ ± SE)		0.119 ± 0.114	0.599 ± 0.200	0.241 ± 0.155
Detection Probability (p ± SE)		0.175 ± 0.016	0.175 ± 0.016	0.175 ± 0.016

Spatial distribution and circadian activity pattern:





c. Bat-eared fox (*Otocyon megalotis*)

Description:

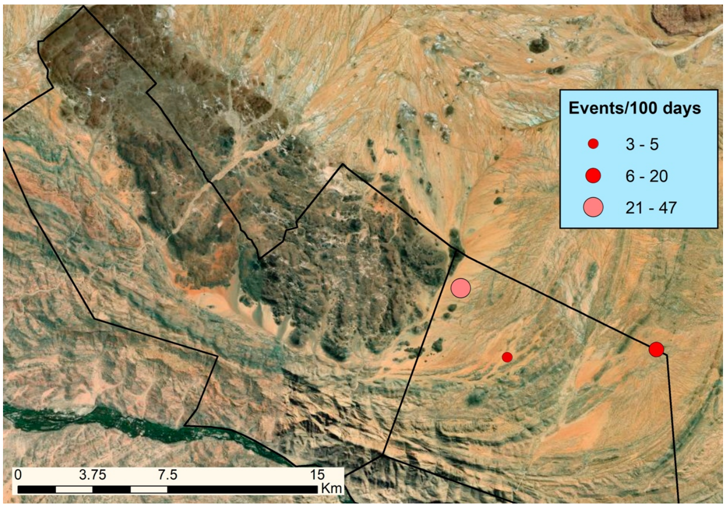
Family of bat-eared foxes in camera CT28

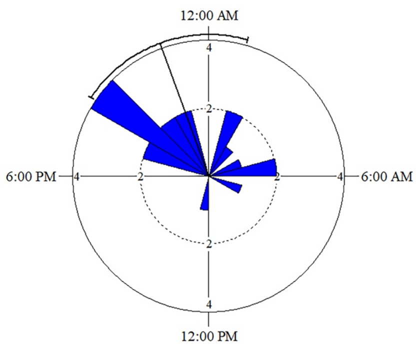
- Home Range: 0.3-3.5 km^2.
- Small with slender legs and fluffy pelage with long bushy tail, large ears and short muzzle.
- Habitat: mainly open grasslands with short vegetation and bare patches, open scrub and arid or semi-arid shrublands.
- Adapted to insectivorous lifestyle: big ears to locate insects underground.
- Diet: insectivorous (termites, beetles). sometimes small vertebrates and fruits
- Live in family groups in excavated dens.
- Breeding season: July – September.
- Activity pattern: nocturnal or early morning foragers.
- Main predator: raptors, large carnivores, honey badgers and black backed jackals.
- Global Conservation status: LC.
- Research needed: population trends, effects of disease, road mortalities, formation of breeding pairs and how food availability affects the ecology (Dalerum et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	3	0	0	3
Nº of Events	18	0	0	18
CTR ± SD	2.14 ± 3.81	0.00	0.00	6.68 ± 12.1
Naïve Occupancy	0.1	0	0	0.3
Occupancy (ψ ± SE)		0.000 ± 0.003	0.000 ± 0.001	0.304 ± 0.147
Detection Probability (p ± SE)		0.133 ± 0.035	0.133 ± 0.035	0.133 ± 0.035

Spatial distribution and circadian activity pattern:





d. Black-backed jackal (*Canis mesomelas*)

Description:

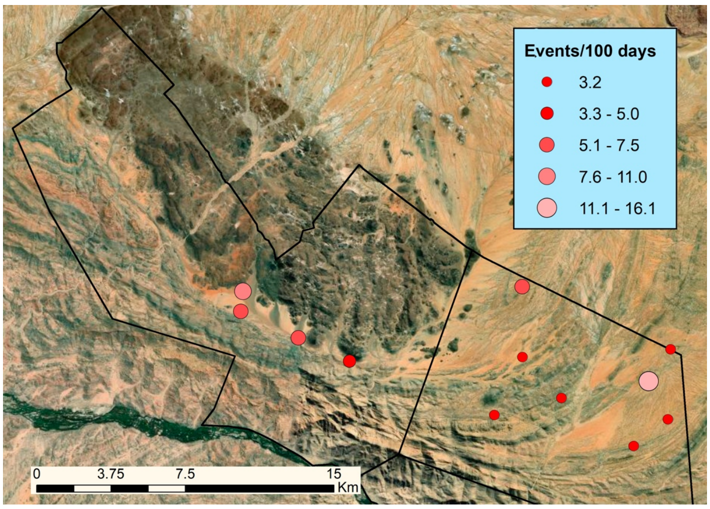
Pair of black-backed jackals in camera CT9

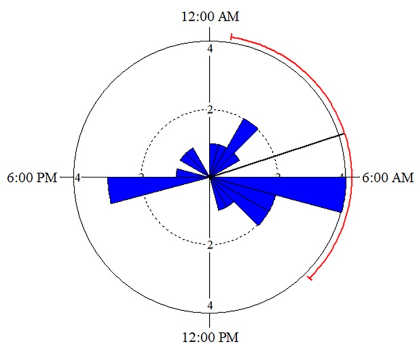
- Home Range: 1-24.9 km^2.
- SH: 38-48 cm. Fox-like appearance, dark saddle, bushy tail and reddish head, flanks and limbs, large ears and very mobile.
- Habitat: huge variety: from coast to mountains, from arid to humid areas, preference for open habitats.
- Diet: Generalist omnivore, bigger and smaller mammals, birds, reptiles, eggs.
- Use abandoned dens from other mammals.
- Forages alone or in pairs, monogamous and territorial.
- Breeding season: May – August.
- Activity pattern: mainly nocturnal when persecuted, crepuscular/diurnal where protected.
- Main predator: Leopards, hyaenas, wild dogs, caracals and honey badgers.
- Global Conservation status: LC.
- Research needed: HWC regarding livestock predation, ecology and behaviour, compensatory reproduction studies, ecological role in communities (Minnie et al 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	12	0	5	7
Nº of Events	21	0	6	15
CTR ± SD	2.21 ± 3.16	0.00	1.85 ± 3.96	5.63 ± 7.98
Naïve Occupancy	0.4	0	0.5	0.7
Occupancy (ψ ± SE)		1	1	1
Detection Probability (p ± SE)		0	0.019 ± 0.008	0.047 ± 0.012

Spatial distribution and circadian activity pattern:





e. Cape fox (*Vulpex chama*)

Description:

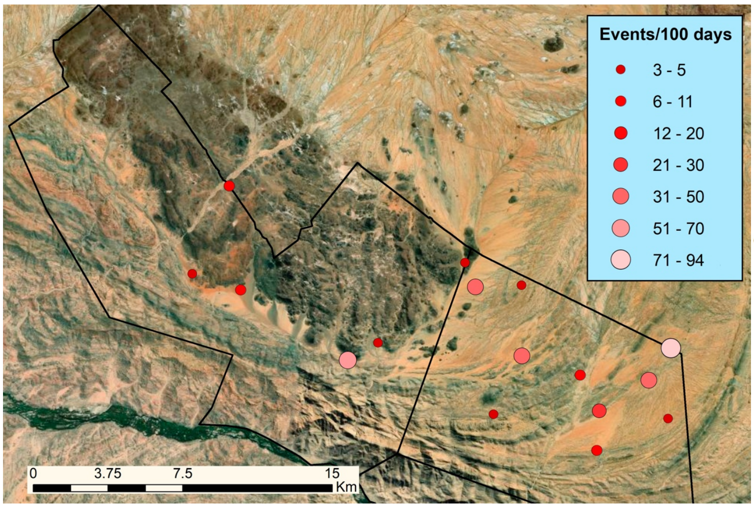
Cape fox in camera CT9

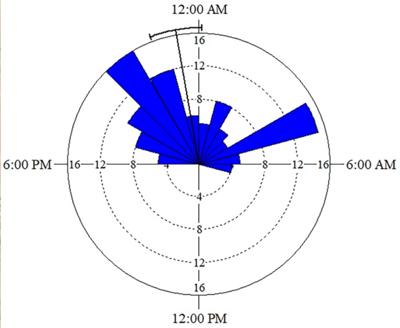
- Home Range: 1-32.1 km^2.
- The only light-coloured (silver-grey) fox of southern Africa. Long bushy tail with characteristic black tip.
- Habitat: semiarid/arid habitats, open country.
- Diet: mice and gerbils, invertebrates, small birds, reptiles and fruits.
- Solitary and monogamous. Pairs share the range.
- Breeding season: winter, from June.
- Activity pattern: nocturnal
- Main predator: Black-backed jackal, sometimes raptors and large carnivores.
- Global Conservation status: LC.
- Research needed: range, impacts of human persecution, their role in disease transmission, population numbers and trends and intraguild predation by black-backed jackals and other carnivores (Kamler et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	16	3	6	7
Nº of Events	103	4	16	83
CTR ± SD	11.16 ± 6.11	1.36 ± 4.06	5.19 ±7.53	27.39 ± 17.5
Naïve Occupancy	0.533	0.3	0.6	0.7
Occupancy (ψ ± SE)		0.691 ± 0.114	0.691 ± 0.114	0.691 ± 0.114
Detection Probability (p ± SE)		0.018 ± 0.010	0.063 ± 0.019	0.276 ± 0.030

Spatial distribution and circadian activity pattern:





f. Cape grey mongoose (*Herpestes pulverulentus*)

Cape grey mongoose hunting a scorpion in camera CT30

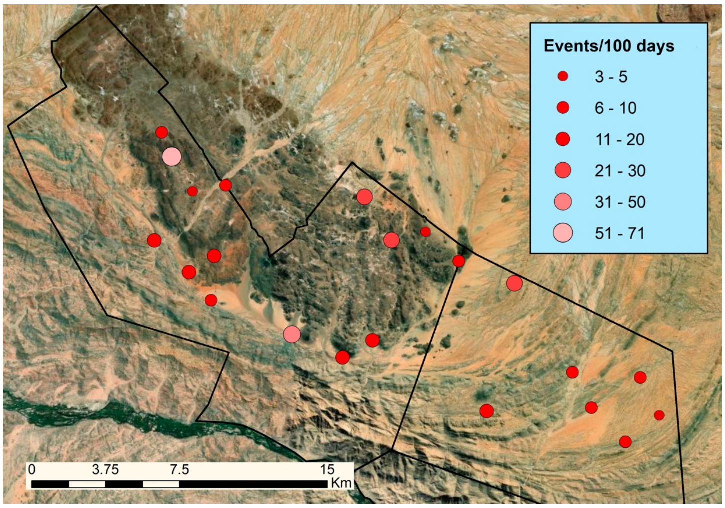
Description:

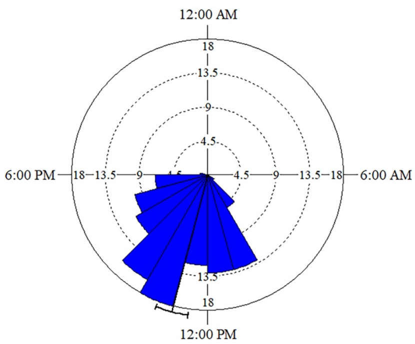
- Home Range: 0.25-1 km^2.
- Small mongoose, grizzle grey pelage, bushy tail, black nose, tip of the tail inconspicuously dark.
- Habitat: mostly in habitats with cover, absent in very open areas.
- Rest in holes or under rocks.
- Diet: small vertebrates and invertebrates.
- Solitary, male pairs occasional.
- Breeding season: winter.
- Activity pattern: diurnal.
- Main predator: larger predators, mainly raptors.
- Global Conservation status: LC.
- Research needed: monitoring of subpopulations, general biology and ecology in different habitats (Do Linh San et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	22	9	8	5
Nº of Events	107	52	31	24
CTR ± SD	9.70 ± 6.32	14.81 ± 11.37	8.52 ± 10.27	6.83 ± 8.13
Naïve Occupancy	0.733	0.9	0.8	0.5
Occupancy (ψ ± SE)		0.912 ± 0.096	0.812 ± 0.129	0.508 ± 0.161
Detection Probability (p ± SE)		0.193 ± 0.013	0.193 ± 0.013	0.193 ± 0.013

Spatial distribution and circadian activity pattern:





g. Caracal (*Caracal caracal*)

Description:

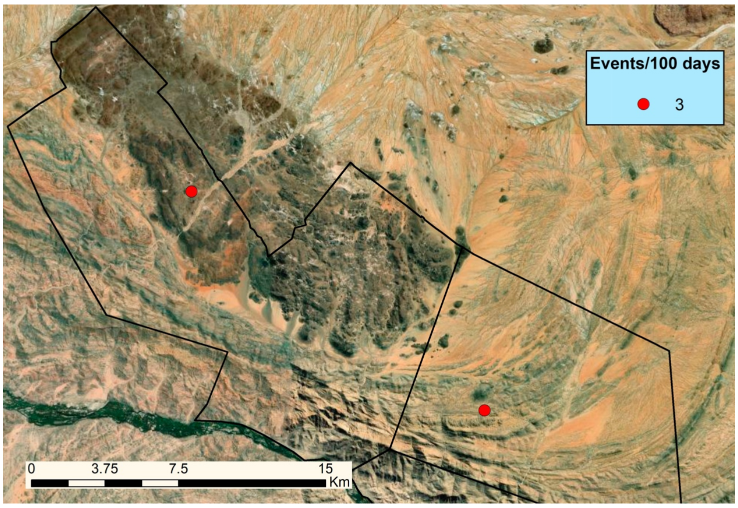
- Home Range: 3.9-65 km^2.
- Medium size. Uniformly coloured, pale sandy brown to red, long black tufts in ears.
- Habitat: dry woodland savannah, dry forest, grassland, semi-desert and arid mountainous habitat. In Karoo plains related to rugged mountain and hill ranges.
- Diet:mostly small prey as birds, rodents, hyraxes, hares and springhares, but also antelopes up to 50 kg.
- Solitary and territorial.
- Breeding season: all-year round.
- Main predator: larger predators, Black-backed jackal kills kittens.
- Global Conservation status: LC.
- Research needed: management strategies and their effects, population sizes and trends, impact of livestock in their ecology, HWC (Avenant et al. 2016).

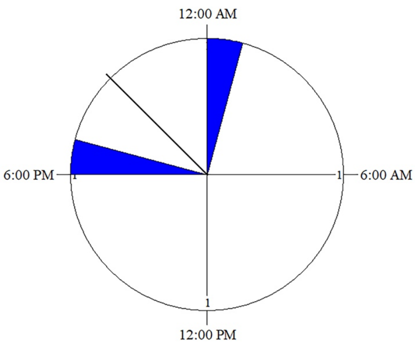
Caracal in camera CT32

Survey results:

	Whole Study Area	**Rocky Mountain**	**Milky Shrubland**	**Sandy plain**
Nº of cameras (present)	2	1	1	0
Nº of Events	2	1	1	0
CTR ± SD	0.12 ± 0.64	0.00	0.37 ± 1.93	0.00
Naïve Occupancy	0.067	0.1	0.1	0
Occupancy (ψ ± SE)		-	-	-
Detection Probability (p ± SE)		-	-	-

Spatial distribution and circadian activity pattern:





h. Honey badger (*Mellivora capensis*)

Description:

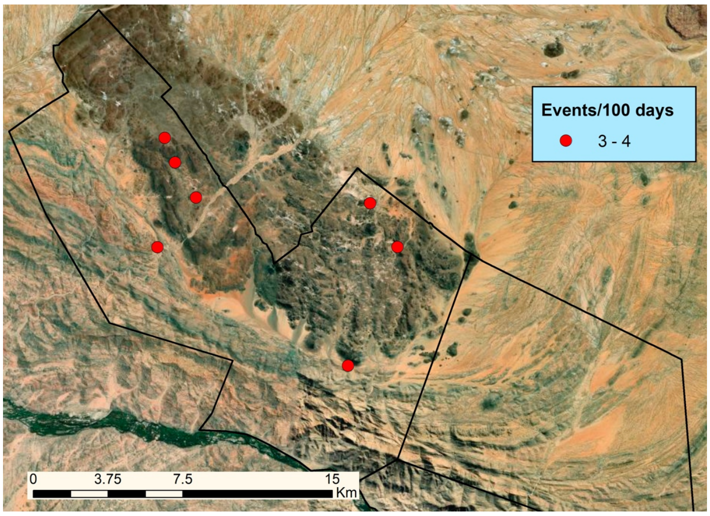
Honey badger in camera CT 30

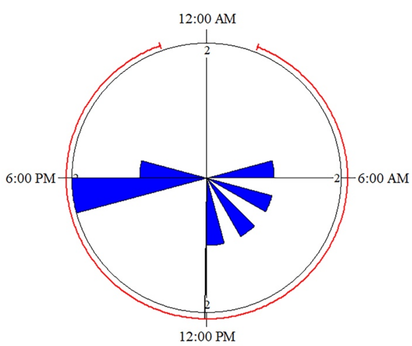
- Home Range: 126-541 km^2.
- Powerfully built and black and grey (warning coloration). Skin very loose and thick, preventing attacks from large predators and snake bites. Anal gland secretions used as deterrent.
- Habitat: all kinds of habitats.
- Diet: omnivorous and highly opportunistic, mainly small mammals and reptiles including venomous snakes, birds, bees and honeycombs.
- Solitary, ♂ ranges overlap with ♀♀ (up to 13).
- Breeding season: Aseasonal.
- Activity pattern: nocturno-crepuscular, diurnal during winter.
- Main predator: large cats and hyaenas, infanticide reported.
- Global Conservation status: LC.
- Research needed: distribution, abundance, trends and ranges (Begg et al. 2016).

Survey results:

	Whole Study Area	**Rocky Mountain**	**Milky Shrubland**	**Sandy plain**
Nº of cameras (present)	7	5	0	2
Nº of Events	7	5	0	2
CTR ± SD	0.89 ± 1.80	1.85 ± 3.96	0.00	0.78 ± 2.82
Naïve Occupancy	0.233	0.5	0	0.2
Occupancy (ψ ± SE)		-	-	-
Detection Probability (p ± SE)		-	-	-

Spatial distribution and circadian activity pattern:





i. Small-spotted genet (*Genetta genetta*)

Description:

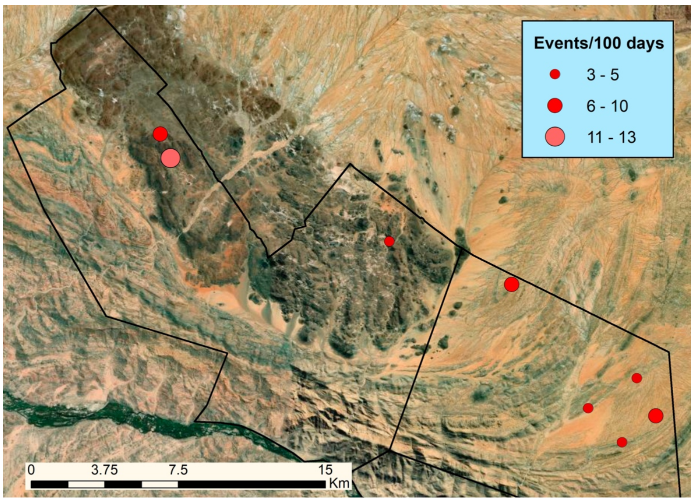
Small-spotted genet in camera CT37

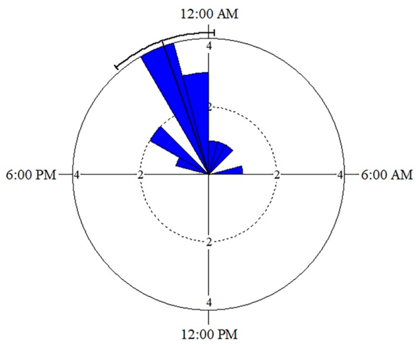
- Home Range: 0.33-12 km^2.
- Mid-size genet, grey with black dots, erectile dorsal crest, white tip in the tail. Southern Africa subspecies with dark limbs.
- Habitat: forest, scrubland, woody grassland and rocky habitats.
- Use woody or rocky shelters, or abandoned dens of other mammals.
- Diet: small rodents and insectivores, birds, reptiles and invertebrates and fruits.
- Solitary, ♂ ranges overlap with ♀♀.
- Breeding season: winter.
- Activity pattern: nocturnal.
- Predator: Larger carnivores.
- Global Conservation status: LC.
- Research needed: update distribution range, DNA analysis (southern population may be *G. felina*) (Carvalho et al. 20016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	8	3	4	1
Nº of Events	14	7	6	1
CTR ± SD	0.88 ± 1.78	0.74 ± 2.67	0.74 ± 2.67	0.37 ± 1.92
Naïve Occupancy	0.267	0.3	0.4	0.1
Occupancy (ψ ± SE)		0.400 ± 0.152	0.400 ± 0.153	0.400 ± 0.154
Detection Probability (p ± SE)		0.034 ± 0.014	0.034 ± 0.015	0.034 ± 0.016

Spatial distribution and circadian activity pattern:





j. Zorilla (*Ictonyx striatus*)

Zorilla in camera CT35

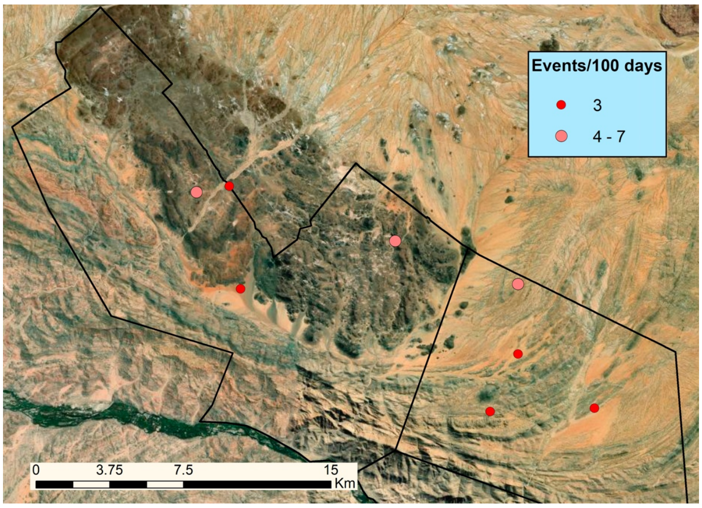
Description:

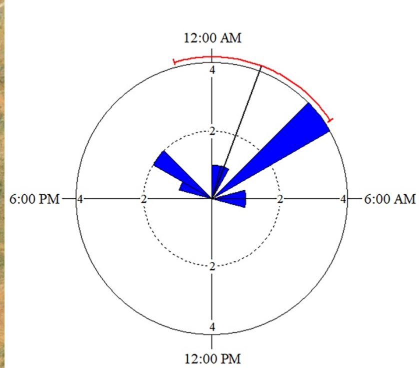
- Home Range: Unknown.
- Black with 4 white stripes, bushy tail. Ejects anal secretions when threatened.
- Habitat: wide variety of habitats, in arid areas related to drainage lines.
- Diet: small rodents and insects, reptiles, birds.
- Solitary and territorial, rather unknown.
- Breeding season: unknown.
- Activity patter: nocturnal.
- Main predator: poorly known, large raptors, caracals, black-backed jackals and leopards confirmed.
- Global Conservation status: LC.
- Research needed: general biology and ecology aspects (Rowe-Rowe et al. 2016).

Survey results:

	Whole Study Area	Rocky Mountain	Milky Shrubland	Sandy plain
Nº of cameras (present)	8	3	3	2
Nº of Events	11	5	4	2
CTR ± SD	1.16 ± 1.67	1.48 ± 3.62	1.11 ± 3.21	0.74 ± 2.67
Naïve Occupancy	0.267	0.3	0.3	0.2
Occupancy (ψ ± SE)		0.532 ± 0.258	0.532 ± 0.259	0.532 ± 0.260
Detection Probability (p ± SE)		0.021 ± 0.012	0.021 ± 0.013	0.021 ± 0.014

Spatial distribution and circadian activity pattern:





[i] Sources for all species: Kingdon & Hoffmann (2013), and Hunter (2018).