1

Understanding the role of topographic relief in the sympatry of mammal species

1.1 Abstract

A sound understanding of the forces driving species-habitat relationships is critical to address ecological and biogeographical questions. The patterns of species distribution within a community are the result of the different habitat affinities, which every species has evolved within the landscape to adapt to their environment. A landscape can be defined as a portion of the Earth's surface, formed by a complex of biotic and abiotic systems, and made of spatially heterogeneous habitats. Both landscape and habitat should be viewed as species-specific concepts so that patterns of habitat-use can be interpreted as individualistic responses to spatial gradients in the environment. In this study, camera trap systems were used to record patterns of habitat-use among sympatric mammals of the Little Karoo in South Africa. A resource selection function was then used to quantify species' preferences along the ruggedness gradient, and multivariate statistics were applied to gain insight into spatial partitioning within the mammal community of the Little Karoo. The results show that heterogeneous topographic relief was likely to be an essential constituent of a species' niche and a crucial variable to predict species' habitat-use. The strength of affinities animals developed with specific terrain roughness varied between species; most of them strongly avoided highly-rugged terrain, whereas moderately- and slightly-rugged terrains were usually used in proportion to their availability. The Non-metric multidimensional scaling

15

plot spatially separated habitat-specialist from habitat-generalist species, as well as grouped species showing similar terrain affinities. The analysis enabled to recognise subtle and continuous nuances in the spectrum of habitat preferences, providing a novel tool to explore the forces driving species coexistence in local animal communities.

1.2 Introduction

Describing patterns of species distributions and habitat selection is a fundamental goal in ecology. A sound understanding of the forces driving species-habitat relationships is critical to address ecological and biogeographical questions, especially for species of conservation concern [130]. At the beginning of the 19th century, Alexander van Humboldt [350] showed interest in the spatial patterning and geographic distribution of organisms, as he described the latitudinal and altitudinal distribution of vegetation zones. His work triggered many more studies of the geographic distribution of various taxa throughout the rest of the century [78, 227, 228].

The patterns of species distribution in a community are the result of the varying habitat affinities, which every species has evolved to adapt to their environment [218]. The general assumption is that animals utilise the minimum economically defensible area (fitness maximization) [159, 206, 267], which is large enough to satisfy their metabolic needs [219, 276].

A landscape can be defined as a portion of the Earth's surface, formed by a complex of biotic and abiotic (geological, hydrological, meteorological, ecological and anthropological) systems [373]. It is made of spatially heterogeneous areas (habitats), which are characterised by structure, function and change (alteration through time) [343]. Habitat description consists of evaluating qualitatively and/or quantitatively landscape heterogeneity. Although much effort has been concentrated on developing vegetation indices (e.g. Ratio Vegetation Index, Vegetation Index Number, Normalised Difference Vegetation Index) [18], numerous landscape features (vegetation, soils, climate, geomorphology, land use) can be used to identify – in a discrete and/or continuous manner – different habitats over a surface [237]. Landscapes can be observed from many points of view and at different spatial and temporal scales [222, 229, 287, 344]. A 'landscape' for a large, mobile predator is a geographically larger area than that for a small rodent, therefore a landscape, just as habitats, should be viewed as species-specific concepts [237].

Gleason [119, 120] claimed that patterns of habitat-use are important and that they should be interpreted as individualistic responses to spatial gradients in the environment [153, 215, 225, 360]. Numerous studies have highlighted the fact that terrestrial mammal distribution and abundance vary along elevational gradients [214–216], especially in mountainous landscapes [48, 197, 282, 305]. For example, in 1971, at a study site close to that being used for this paper – in the Swartberg and Baviaanskloof Mountains – the Saasveld Forestry Research Station studied the ecology of the small mammal fauna, and showed that species composition as well as habitat variables (vegetation structure and cover) varied according to altitude [28]. Although elevation above sea level, like degree of latitude, is not itself of importance to organisms, the correlated environmental variables (both past and present, abiotic and biotic) drive patterns of abundance, distribution and diversity.

Nearly all mountainous areas are shaped by the erosion of exposed (due to uplift) and discontinuous geological substrates, to form ridges, valleys, stream networks and other geomorphological features, which makes for a heterogeneous topographic relief. Terrain heterogeneity is often an essential constituent of the niche of a species [50, 246, 361] and a crucial variable to predict species' habitat-use [101, 177]. Riley et al. (1999) developed the terrain ruggedness index (TRI) – a spatial gradient – which quantifies topographic heterogeneity [284].

Assessing habitat preferences in wild, free-ranging, elusive and often low-density species presents a number of challenges. Methods for defining animals' habitat preferences commonly use Resource Selection Functions (RSFs) that compare resource attributes in areas where animals are observed with those in areas that are considered available [37]. These methods traditionally depended on direct observations [178] and/or spoor transects [337] and/or tracking of radio-collared individuals [104, 165]. Observational studies can alter natural behaviour and activity patterns of the target animals, and can also be limited by sample sizes due to the secretive nature of the target species or to logistical constraints [42]. Spoor transects are feasible on malleable substrates only; they are time consuming and logistical constraining, especially due to habitat inaccessibility. Telemetry studies gather data remotely thereby preventing the biases that may result from observer presence, however the results remain reduced to those individuals that can be physically captured. Camera traps (also called remotely triggered cameras) are now commonly used worldwide in wildlife research, and are one of the newest tools in the ethologist's toolkit [42]. Remaining continuously active, each device is typically capable of generating large datasets and is particularly

useful for detecting elusive and low-density species. The disturbance caused by camera traps, despite some sounds and flashes [221], is minimal [3,41,128]. The non-selectivity of camera traps allows researchers to potentially sample a statistical population of the target and non-target species, which accurately reflect the members of the entire population. Several research teams have used camera traps with a single study design to collect information on habitat selection of sympatric species [36, 167], and sometimes at the larger community level [125].

In this study, camera trap systems were used to record patterns of habitat-use among sympatric mammals of the Little Karoo in South Africa. A resource selection function was then used to quantify species' preferences along the ruggedness gradient. Finally, multivariate statistics were applied to gain insight into spatial partitioning within the mammal community of the Little Karoo.

1.3   Material and methods

1.3.1   Study area

The Little Karoo is a semi-arid desert located at the southern tip of the African continent [Appendix 1A], within the Cape Fold Belt. It is hemmed in by the Langeberg Mountains in the south, the Swartberg Mountains in the north and the Outeniqua Mountains in the east. This desert is part of a unique biogeographic region because it belongs to one of the 36 internationally recognised biodiversity hotspots [230, 241] [Introduction]. It has a mean annual rainfall of 200 to 300 mm, falling primarily in winter [198]. The topography is a patchwork of mountains, valleys, rolling hills, rocky mesas, flat plains, and a network of small drainage lines. The average temperature varies from 23.7°C in January to 11.2°C in July, and the seasonality varies greatly due to the dry continental desert climate to the north, and the cool, moist oceanic climate to the south [198]. The land is sparsely populated and the landscape is a mosaic of farms and small protected areas: Anysberg Nature Reserve and Sanbona Wildlife Reserve being the two largest ones. The northern section of the Sanbona Wildlife Reserve represents 6% of the whole sampling area, and is delineated by a high voltage game fence with the objective of limiting the movements of medium to large animals [195]. The game fence enables the presence of species not found in the rest of the study area, lion *Panthera leo*, cheetah *Acynonyx jubatus*, African elephant *Loxondota africana*, African buffalo *Syncerus caffer*, Burchell's zebra *Equus quagga*

burchellii, giraffe *Giraffa camelopardalis*, and white rhinoceros *Ceratotherium simum*.

The Little Karoo can also be described as a mega-ecotone, where the succulent Karoo and the Cape Floristic Provinces intermingle. 41% of the study area falls into the succulent Karoo biome, in which the dominant plant life-form is dwarf shrubs (absence of trees and grasses). The remainder (59%) is part of the fynbos biome, with presence increasing with elevation [319]. Within those biomes, different vegetation types can be identified: fynbos (13.6%), thicket (29.3%), renoster (16.9%) and succulent Karoo (32.0%); the remaining 8.2% falling into the source and drainage vegetation categories. The vegetation and topographic maps (Fig. 1.1) suggest a strong association between terrain roughness and vegetation type; and the boxplots (Fig. 1.2) show that averaged ruggedness varies between all four different biomes.

1.3.2   Data collection

Camera traps were deployed between March 2014 and August 2015 as part of a research project on large carnivores – brown hyenas *Hyaena brunnea* and leopards *Panthera pardus* – within a study area of 4,327 km^2 (minimum convex polygon). Digital automated cameras (Cuddeback Attack and Ambush, Cuddeback Inc., Green Bay, Wisconsin, USA) were set to take photos with a one-second delay between consecutive triggers, and with an incandescent flash at night [Chapter 1 section 1.3.3].

The sampling design was selected to estimate the population density of leopards and brown hyenas within the study site. Given the vastness of the study area, the camera trap study was undertaken as a series of six regional surveys (spatially and temporally separated). Using QGIS 2.10.1 software [268], a 7×7 km grid was designed and placed across the study site. The final camera trap positions were selected by identifying two locations in every grid square that were expected to maximise chances of photo-capturing medium to large-bodied animals. Grid size and camera spacing were selected in order to ensure relatively even sampling effort and to satisfy data collection protocols used to estimate population density using Spatially Explicit Capture-Recapture models (SECR) [163] [Chapter 4 section 4.3].

Camera trap stations consisted of a pair of camera traps facing each other (slightly off-set to avoid simultaneous flash triggers), positioned at a 90° angle with a linear channel such as gravel roads, animal paths and riverlines, and at an average height of 40 cm. Each sampling block (one per survey) ran for *c.* three months, and consisted of between 30 and 61 camera trap stations

with a mean inter-site distance of 3.5 km. The camera trap stations were checked once (*c.* 1.5 months, halfway through the survey) to change batteries. Data entry was facilitated by the software Camera Base [338], and the final database was exported into Excel and analysed in R Studio, using the R software 3.2.4 [269].

1.3.3 Analysis

Sampling with camera traps provided detection/non-detection information for all medium to large species that could be photo-captured. Using these data to make inferences about species occupancy at the sampling sites assumed that the species' detection probabilities were known. There was no uncertainty at locations where the species was photo-captured, but it became ambiguous at locations where the species was not detected. Imperfect observation made naïve estimates of occupancy (proportion of sites at which the species was detected) negatively biased [10]. However, assuming that a species detection probability did not vary from one habitat type to another, naïve estimates of occupancy offered a means to make inferences about the species' habitat preferences.

Datasets tend to be sparse for low density species and those with low detection probabilities. Species with at least 50 photo-captures and 10 capture sites, were included for this study. Small photo-capture rates can be explained in two ways: **1)** a small species detection probability (e.g. the camera setup is inadequate for small mammals such as mice) or **2)** a low species density (e.g. riverine rabbit *Bunolagus monticularis* [85]).

Social species moving in groups such as antelopes, generated a series of photographs when they encountered a camera trap station. Another example was with chacma baboon *Papio ursinus*, a primate which often took a curious interest in the cameras, leading the troop to play around the setup for several minutes, generating hundreds of photographs. This could considerably inflate the photo-capture counts per habitat type, which become no longer comparable between different species and between different locations. To work around this issue, every photo-capture was either defined as a capture-event or as a duplicate. When a species was photographed at the same location multiple times, the first photograph was considered to be the capture-event. Photo-events that occurred more than one hour apart were considered to be independent. All photographs of the same species collected within one hour after a capture-event, at the same location, were considered

to be duplicates; in other words, non-independent events. Duplicates were discarded for this study.

1.3.3.1 Active site detection

Every camera trap station operated for c. three months and collected detection/non-detection information in relation to spatial covariates such as the TRI. When species s was photo-captured at least once at a camera trap station, the latter was considered to be an active site for the species. Understanding the detection process of active sites is a first step in understanding the spatial dataset collected with camera traps.

In practice, the number of operating camera trap stations after the 85th camera trap night dropped rapidly, i.e. after 2.8 months (Fig. 1.3), which is why data collected from the 85th night were discarded. A camera trap night variable n could then be defined for all camera trap stations: $n \in [1 .. 85]$. Five camera trap stations failed (due to flooding, animal damage, technical malfunctioning) before the 30th camera trap night; the data from these cameras were discarded.

For every species s, and for every camera trap night n, the cumulative number of active sites $C_{n,s}$ (camera trap stations where species s was photo-captured from night 1 to n), weighted by the number of operating camera trap stations N_n, was calculated:

$$C'_{n,s} = \frac{C_{n,s}}{N_n} = \frac{C_{n-1,s} + S_{n,s}}{N_n} \quad \text{with} \quad C_{0,s} = 0 \tag{1.1}$$

In (1.1), $S_{n,s}$ is the number of new active sites registered on night n.

For every species s, the resulting cumulative curve was weighted by the total number of active sites ($C'_{85,s}$) revealed between the 1st and the 85th camera trap night:

$$C''_{n,s} = \frac{C'_{n,s}}{C'_{85,s}} \cdot 100 \tag{1.2}$$

Three capture-speed indexes $V^1_{,s}$, $V^2_{,s}$ and $V^{\text{end}}_{,s}$ were calculated for every species s:

$$\begin{aligned} V^1_{,s} &= C''_{28,s} \\ V^2_{,s} &= C''_{56,s} \\ V^{\text{end}}_{,s} &= C''_{85,s} - C''_{70,s} \end{aligned} \tag{1.3}$$

In (1.3), $V_{,s}^1$ and $V_{,s}^2$ give the percentage of active sites revealed after 28 and 56 camera trap nights (four and eight weeks), compared to the number revealed after 85 camera trap nights.

In (1.3), $V_{,s}^{\text{end}}$ gives the percentage of active sites revealed in the last two weeks of the study, compared to the number revealed at the end of the study (after 85 camera trap nights).

1.3.3.2 Effects of topography

Terrain data for the study area were downloaded as Digital Elevation Model (DEM) data files from Shuttle Radar Topography Mission (SRTM) [242] and analysed using QGIS 2.10.1 software [268]. The $30{\times}30\,\text{m}$ DEM data provide accurate information about the shape and features of the surface of the Earth. The change in elevation was measured using the Terrain Roughness (ruggedness) Index (TRI) [284]. TRI is calculated by summing change in elevation between a grid cell and its eight neighbours:

$$\text{TRI} = \left[\sum (x_{ij} - x_{00})^2\right]^{\frac{1}{2}}$$
$$\text{where } x_{ij} = \text{elevation of each neighbour cell and,}$$
$$x_{00} = \text{elevation in the central grid cell [284].}$$

TRI was then averaged over a 2-km radius circle around each camera trap station and used as a spatial covariate r in further analytical work (Fig. 1.4).

R_A is a vector storing the r value of each camera trap station within the study area. $R_{U,s}$ stores the r values associated with each photo-capture of species s, depending on the camera trap station where the photo-capture event took place. Applying a kernel density estimation to R_A and $R_{U,s}$, the ruggedness profile $r \mapsto A(r)$ of the study area (habitat available), as well as the ruggedness profile $r \mapsto U_{,s}(r)$ of the area used by species s (habitat used), were produced [309]. An example is provided for the leopard *Panthera pardus* in Fig. 1.5.

From each of the A and $U_{,s}$ kernel density functions, 512 points were extracted at regular intervals along the ruggedness r-axis. The species preference in terrain ruggedness was measured by the Jacob's preference index $r \mapsto D_{,s}(r)$ [155]:

For every value r along the ruggedness r-axis:

$$D_{,s} = \frac{A - U_{,s}}{U_{,s} + A - 2 \cdot U_{,s} \cdot A} \tag{1.4}$$

$U_{,s}$ being the proportion of habitat used, and A the proportion of habitat available.

The Jacob's index provides an adjustment for the relative abundance of each habitat available to the animals [155]. $D_{,s}$ lies between -1 (complete avoidance of a habitat) and $+1$ (complete preference for a single habitat). Values close to zero indicate that the habitat is used in proportion to its availability. Negative values indicate that the species is recorded in that habitat, but disproportionately few times considering the extent of that habitat which is available.

Using the Jacob's preference index, preferred habitat maps were built in QGIS 2.10.1 [268]. The ruggedness topographic indexes were averaged r_k within each square-polygon k of a $1.4 \times 1.4 \, \text{km}$ regular grid covering the whole study area. For every species s, the corresponding values of the Jacob's preference index $D_{,s}(r_k)$ were then georeferenced $D_{k,s}$ to produce chloropleth maps; these are graphical representations in which each geographical area (grid cell k) was shaded according to its associated $D_{k,s}$ value.

Two chloropleth maps, representing the same variable $D_{k,s}$, but using two different colour schemes, were built for every species s. The appearance of the map pattern could vary substantially between the two maps, further to the use of 1) different colour gradients and 2) different classification decisions (classification method and number of classes employed) for the variable of interest.

For the first chloropleth map, a species-specific colour scheme was used. The colour gradient ranges from white – matching the lowest value $\min(D_{k,s})$ of the georeferenced Jacob's index for species s – to dark red – matching the largest value $\max(D_{k,s})$ of the georeferenced Jacob's index for species s. The number of classes employed matched the number of distinctive values taken by $D_{k,s}$. All grid cells k having averaged ruggedness values r_k falling outside the spectrum of sampled ruggedness values ($3.54 \leq r \leq 33.08$), and for which inferences about habitat preferences could not be made, were shaded in black.

For the second chloropleth map, a colour scheme standardised across all species was used. The colour gradient is made of 100 classes ranging from white – matching the lowest possible values of the Jacob's index ($-1.00 \leq D_{k,s} \leq -0.98$) – to dark blue – matching the largest possible values of the georeferenced Jacob's index ($0.98 \leq D_{k,s} \leq 1.00$). All grid cells k having averaged ruggedness values r_k falling outside the spectrum of sampled ruggedness values ($3.54 \leq r \leq 33.08$), and for which inferences about habitat preferences could not be made, are shaded in black.

1.3.3.3   Spatial partitioning

Non-metric Multi-Dimensional Scaling (NMDS) is a statistical tool which provides a means of displaying and summarising a square symmetric matrix of dissimilarities into a low-dimensional Euclidean space [126, 180, 181]. The objective in NMDS is to find a configuration of points in Euclidean space so that the ordering of the interpoint distances matches, as closely as possible, the ordering of the dissimilarities in the matrix of dissimilarities. Summarising a set of data into a two-dimensional graph might not be feasible and a certain amount of distortion might be created. The measure of lack of fit in NMDS is known as the 'stress' of the configuration. Non-zero stress values occur with insufficient dimensionality, and as the number of dimensions increases, the stress value will either decrease or remain stable [32].

NMDS was applied to a matrix of dissimilarity data which estimated the dissimilarities of habitat preferences in relation to terrain ruggedness for each pair of species in the mammal community of the Little Karoo. The spatial information for the 27 mammal species was compiled into a matrix M with $n = 27$ rows (species) and $p = 512$ columns (ruggedness values selected at regular intervals between 3.54 and 33.08). Every element $M[s, r]$ gave the Jacob's preference index $D_{,s}(r)$ of species s for the ruggedness value r.

$$M[s,\ r] = D_{,s}(r)$$

Using the *dist* function from the *stats* R-package [22, 32, 209], M was computed to return a distance matrix with distances being measured between rows of M using the Manhattan method; the output distance matrix was a symmetric matrix with 27 rows and columns, and was referred to as the Ruggedness-preference Distance Matrix (RDM). Every element $\text{RDM}[s_1, s_2]$ quantified the dissimilarity between the Jacob's Indexes of species s_1 and s_2.

$$\text{RDM}[s_1,\ s_2] = \text{dist}(D_{,s_1}(r),\ D_{,s_2}(r))$$

An NMDS ordination was then performed on RDM, using the *isoMDS* function from the *MASS* R-package [285]. The objective of the ordination is to find the configuration with minimum 'stress' for a given number of dimensions. The operation was therefore repeated several times, each time with a different number of chosen dimensions k, and a screeplot (stress versus k) was plotted in order to identify the point beyond which additional dimensions do not substantially lower the stress value.

The output data information was then summarised into a two-dimensional graphical display, which maximised the rank correlation between the calculated species dissimilarities/distances and the plotted distances between species [32].

1.4 Results

The trapping effort of 17,631 camera trap nights resulted in 26,312 photo-captures (11,742 independent photo-capture events) of 91 wild species, including 51 mammals, 39 birds and 1 reptile. Of the 51 mammal species, 27 had more than 50 photo-captures and at least 10 active sites to father the analysis [Appendix 2A].

1.4.1 Active site detection

For the 27 mammal species, the cumulative percentages of active sites are illustrated in Fig. 1.6, and the daily detection rate of new active sites in Fig. 1.7. The capture-speed indexes are provided in Table 1.1.

The speed at which active sites were added decreased through time ($V_{,s}^1 > V_{,s}^2$). For the 27 species, the first month was most productive. For 21 species, it took 28 camera trap nights to discover at least 50% of all study-revealed active sites, and 56 nights to discover at least 75%.

$V_{,s}^{\text{end}}$, the percentage of active sites uncovered during the last two weeks of the camera operating time (70th to 85th camera trap nights) varied from 0 to 25%, according to species. For eleven of them, $V_{,s}^{\text{end}}$ was less than or equal to 5% – brown hyena *Hyaena brunnea*, Cape mountain zebra *Equus zebra zebra*, chacma baboon, grey duiker *Sylvicapra grimmia*, grysbok *Raphicerus melanotis*, steenbok *Raphicerus campestris*, African wildcat *Felis silvestris*, Cape hare *Lepus capensis*, klipspringer *Oreotragus oreotragus*, greater kudu *Tragelaphus strepsiceros* and Cape porcupine *Hystrix africaeaustralis* – suggesting that the asymptote of the cumulative curve was nearly reached by the 85th camera trap night.

1.4.2 Ruggedness preferences

The patterns of ruggedness preferences vary significantly among the 27 mammal species, and are displayed in Fig. 1.8.

The ruggedness values r, ranging from 3.54 (smooth, level ground) to 33.08 (rough ground), were categorised into three groups of equal length:

Slightly-rugged terrain:	$3.54 \le r_l \le 13.39$
Moderately-rugged terrain:	$13.39 < r_m \le 23.24$
Highly-rugged terrain:	$23.24 < r_h \le 33.08$

Table 1.2 shows that although 23 of the 27 species strongly avoided certain types of rugged terrain, 5 strongly favoured some.

$$\text{Strong avoidance:} \quad \exists\, r,\; D_{,s}(r) < -0.5$$
$$\text{Strong preference:} \quad \exists\, r,\; D_{,s}(r) > +0.5$$

Highly-rugged terrain: 18 of the 27 species strongly avoided highly-rugged terrain. Indeed, four species – brown hyena, steenbok, springbok *Antidorcas marsupialis* and Cape hare – strictly avoided highly-rugged terrain: $\forall\, r_h,\; D_{,s}(r_h) < -0.5$. Honey badger *Mellivora capensis*, grysbok and rock hyrax *Procavia capensis*, were the three species that strongly favoured highly-rugged terrain.

Moderately-rugged terrain: 23 of the 27 species used moderately-rugged terrain in proportion to its availability (no preference or avoidance); however, the remaining four species – steenbok, springbok, Cape hare and rock hyrax – strongly avoided it.

Slightly-rugged terrain: Two species – springbok and Cape hare – strongly preferred slightly-rugged terrain, whereas seven others – Cape gray mongoose *Galerella pulverulenta*, grysbok, Cape mountain zebra, Hewitt's red rock rabbit *Pronolagus saundersia*, klipspringer, leopard and rock hyrax – strongly avoided it. The 18 remaining species used slightly-rugged terrain in proportion to its availability.

Most species showed strong preference and/or avoidance for certain types of rugged terrain, except three – chacma baboon, African wildcat and Cape porcupine – for which the Jacob's index curve lay almost along the horizontal line $y = 0$ (Fig. fig. 1.6(c), 1.6(i) and 1.6(k)), meaning that $\forall\, r,\; D_{,s}(r) \simeq 0$. The range of values taken by the Jacob's index $[\max(D_{,s}),\, \min(D_{,s})]$, for those three species, was therefore small (respectively 0.13, 0.14 and 0.35), whereas it was large for species showing both strong preference and strong avoidance for different terrain roughness, which was the case for springbok, Cape hare and rock hyrax (respectively 1.58, 1.68 and 1.87) (Fig. 1.2).

Chloropleth maps: The preferred habitat maps for the 27 mammal species are provided in appendix 3A.
Chloropleth maps built with a species-specific colour scheme, have the two extreme colours found at the opposite ends of the gradient matching the extreme **observed** values of the Jacob's index. Therefore, these maps always displayed the full colour spectrum of the applied gradient (white to dark red), and emphasised the contrast between preferred and avoided terrain, independently of the range of values taken by the Jacob's index. However,

grid cells with the same colour value between two different chloropleth maps (from two different species) might not indicate the same Jacob's index value.

Chloropleth maps built with a standardised colour scheme, have the two extreme colours found at the opposite ends of the gradient matching the extreme **possible** values of the Jacob's index (-1 and 1). Therefore, these maps did not necessarily display the full colour spectrum of the applied gradient (white to dark blue). The map's colour spectrum broadened with the range of values taken by the Jacob's index, and grid cells with the same colour values between two different chloropleth maps (from two different species) indicated the same Jacob's index values.

When the range of values taken by the Jacob's index $[\max(D_{k,s}),$ $\min(D_{k,s})]$ gets close to the range of **possible** values $[-1, 1]$, the two choloropleth maps become nearly identical (e.g. rock hyrax, Fig. 3A.23). On the contrary, their appearances vary greatly as the range of values taken by the Jacob's index shrinks (e.g. African wildcat, Fig. 3A.3).

1.4.3   Habitat partitioning

The NMDS iterative algorithm captured, in two dimensions, the essential structure of the dissimilarity data. It also produced the graph shown in Fig. 1.9, which represents, as closely as possible, the dissimilarity between species' ruggedness preferences in a two-dimensional Euclidean space. In other words, points close together represent species that favoured more similar terrain (in terms of ruggedness) than species represented by points farther apart; however, the graph does not provide quantitative information regarding this difference. Whenever possible, the species' ruggedness preferences were illustrated with the Jacob's index curve (thin black line in Fig. 1.9).

A screeplot (Fig. 1.10) shows the decrease in ordination stress with an increase in the number of ordination dimensions allowed – revealed that attempting an ordination with one NMDS axis yielded high stress (0.108) whereas two or three dimensions was adequate. The stress value equaled 0.047 in two dimensions and, like all stress values equal to or below 0.050, it indicated good fit. Allowing the algorithm to use more than two dimensions reduced the stress slightly (e.g. 0.032 in three dimensions) suggesting that the NMDS plot in two dimensions was adequate.

In the NMDS plot, the 27 species were spatially placed along a convex arch showing a clear and gradual left-right transition along the arch, from species favouring slightly-rugged terrain (e.g. Cape hare) to species favouring highly-

rugged terrain (e.g. rock hyrax). In the middle part of the arch there was a gradual bottom-top transition along the second axis from species favouring moderately-rugged terrain (e.g. Hewitt's red rock rabbit), to species showing no particular preferences for any type of terrain (e.g. African wildcat). The honey badger was the species showing a slightly convex Jacob's index curve, which explains its isolation in the plot.

1.5   Discussion

Examining habitat preferences among 27 terrestrial mammals of the Little Karoo in South Africa, I found that heterogeneous topographic relief was likely to be an essential constituent of the niche of a species and a crucial variable to predict species' habitat-use. The distribution of most species showed a continuum of variations along the ruggedness gradient; this has already been observed with numerous terrestrial mammals [7, 106, 107, 118, 295, 333, 359]. The analysis revealed that most species strongly avoided highly-rugged terrain, whereas moderately-rugged terrain was usually used in proportion to its availability. Although slightly-rugged terrain was also mainly used in proportion to its availability by most species, the trend was not as clear with a third of them strongly avoiding or favouring this habitat.

The strength of affinities animals developed with specific terrain roughness varied between species and can be quantified with the range of values taken by the Jacob's preference index $[\max(D_{,s}), \min(D_{,s})]$; species were positioned along a transitional gradient of habitat specialisation. Habitat-generalist species – chacma baboon and African wildcat – were at the lower end, and habitat-specialist species – rock hyrax and Cape hare – at the upper end.

The study showed that chloropleth maps are useful tools to geographically visualise species' habitat-use. The choice of two different colour schemes resulting from two different classification rules, enabled to produce, for every species, two maps providing complementary insights into space-use and space partitioning. The standardised chloropleth maps (blue) provide a quick visual interpretation of the intensity of habitat specialisation and how it varies between species of the same community; habitat-generalist species will tend to have homogeneous monochrome maps, whereas habitat-specialist species will tend to have kaleidoscopic and contrasted maps. The standardised colour scaling failed to distinguish nuanced variations in habitat preferences. A second chloropleth map, built with a stretched colour scaling (red), emphasised those nuances, which is especially insightful for habitat-generalist species.

The selected method for studying habitat preference among the mammal community of the Little Karoo, relied on data collected throughout the year (series of three-month long surveys) and was therefore less sensitive to seasonal variations. Although the detection rate of new active sites decreased substantially for most species after 56 sampling nights, it remained non-negligible for some species even after completion of the three-month sampling period. Inferences about habitat preferences could however still be made because it is the relative frequency of habitat-use which is of importance, assuming that species detection probability does not vary from one habitat type to another.

Space-partitioning could be a mechanism by which sympatric species co-exist in a stable manner. Interspecific competition takes place when resources are limiting, but coexistence can still be achieved if sympatric species evolved different behaviours and morphologies, allowing them to use different food sources and/or to use them in different areas and/or at different times [49, 75, 76, 298].

The analysis of the dissimilarity of habitat-use patterns among the mammal community of the Little Karoo, led to a collapse and summary of a complex ecological database, allowing an intuitive and visual exploration of the data. The NMDS plot spatially separated habitat-specialist from habitat-generalist species, as well as grouped species showing similar terrain affinities. This method does not only allow one to classify species as habitat-specific or generalist but to also recognise nuances in the spectrum of preferences, have a more continuous approach and be able to compare species to one another for a better understanding of the forces driving species coexistence in local animal communities.

It would be precarious to extrapolate these results and findings to a broader landscape. However, if similar studies were conducted on habitat-use patterns within mammal communities inhabiting variant study sites in the Western, Eastern and Northern Cape Provinces, it should be possible to build a distribution map with suitable habitat for each species, based on ruggedness preferences. Additional camera trap studies would then need to be implemented in order to ground truth projections but it ought to be feasible to delimit the area in which there is a probability greater than zero that a species, e.g. leopard, occurs.

1.6 Tables

Table 1.1: Capture-speed indexes

For 27 mammal species in the Little Karoo: CE is the total number of photo-captures; AS, the total number of active sites (where species s was photo-captured); $V_{,s}^1$, the percentage of active sites revealed after 28 camera trap nights; $V_{,s}^2$, the percentage of active sites revealed after 56 camera trap nights; $V_{,s}^{\mathrm{end}}$, the percentage of active sites revealed during the last two weeks of the study. r gives the ranking position and Δr gives the ranking change between $V_{,s}^1$ and $V_{,s}^2$.

Species	CE	AS	$V_{,s}^1(r)$	$V_{,s}^2(\Delta r)$	$V_{,s}^{\mathrm{end}}$
brown hyena	89	33	86 (01)	96 (-1)	4
scrub hare	508	60	77 (02)	89 (-8)	7
gemsbok	1006	96	75 (03)	91 (-2)	7
Cape mountain zebra	105	24	75 (04)	89 (-5)	0
chacma baboon	1696	172	71 (05)	93 (1)	3
grey duiker	1109	108	70 (06)	91 (0)	3
black backed jackal	1034	113	70 (07)	86 (-6)	6
grysbok	127	14	69 (08)	91 (1)	0
red hartebeest	150	22	68 (09)	94 (6)	6
steenbok	275	37	68 (10)	86 (-4)	4
African wildcat	465	119	66 (11)	87 (0)	2
Cape hare	106	18	64 (12)	100 (11)	0
klipspringer	365	75	64 (13)	90 (5)	2
eland	417	68	63 (14)	79 (-4)	10
greater kudu	283	57	62 (15)	84 (0)	5
Cape porcupine	445	115	60 (16)	87 (4)	4
rock hyrax	57	14	60 (17)	82 (1)	10
aardwolf	127	34	59 (18)	80 (1)	16
grey rhebuck	228	57	56 (19)	76 (-4)	9
leopard	215	78	52 (20)	78 (-1)	7
springbok	105	16	51 (21)	69 (-5)	16
aardvark	162	62	47 (22)	78 (2)	11
caracal	381	98	47 (23)	76 (1)	8
Cape gray mongoose	341	68	47 (24)	65 (-3)	16
small spotted genet	73	26	46 (25)	70 (0)	25
Hewitts red rock rabbit	77	20	45 (26)	79 (7)	7
honey badger	99	54	38 (27)	70 (3)	12

Table 1.2: Ruggedness preferences

For 27 mammal species in the Little Karoo: *range* is the range of Jacob's index values $\max(D_{,s}) - \min(D_{,s})$; + indicates a strong preference; − indicates a strong avoidance; −− indicates a strict avoidance. r_l, r_m and r_h consist of slightly-, moderately- and highly-rugged terrain.

| Species	*range*	r_l	r_m	r_h
chacma baboon	0.13			
African wildcat	0.14			
Cape porcupine	0.35			
caracal	0.78			−
honey badger	0.79			+
Cape gray mongoose	0.85	−		
aardvark	1.05			−
grey rhebuck	1.05			−
greater kudu	1.11			−
scrub hare	1.11			−
aardwolf	1.12			−
grey duiker	1.14			−
gemsbok	1.16			−
small spotted genet	1.16			−
black backed jackal	1.20			−
eland	1.20			−
grysbok	1.23	−		+
red hartebeest	1.23			−
Cape mountain zebra	1.24	−		−
Hewitts red rock rabbit	1.28	−		−
brown hyena	1.33			− −
steenbok	1.43		−	− −
klipspringer	1.44	−		
leopard	1.45	−		
springbok	1.58	+	−	− −
Cape hare	1.68	+	−	− −
rock hyrax	1.87	−	−	+

1.7   Figures
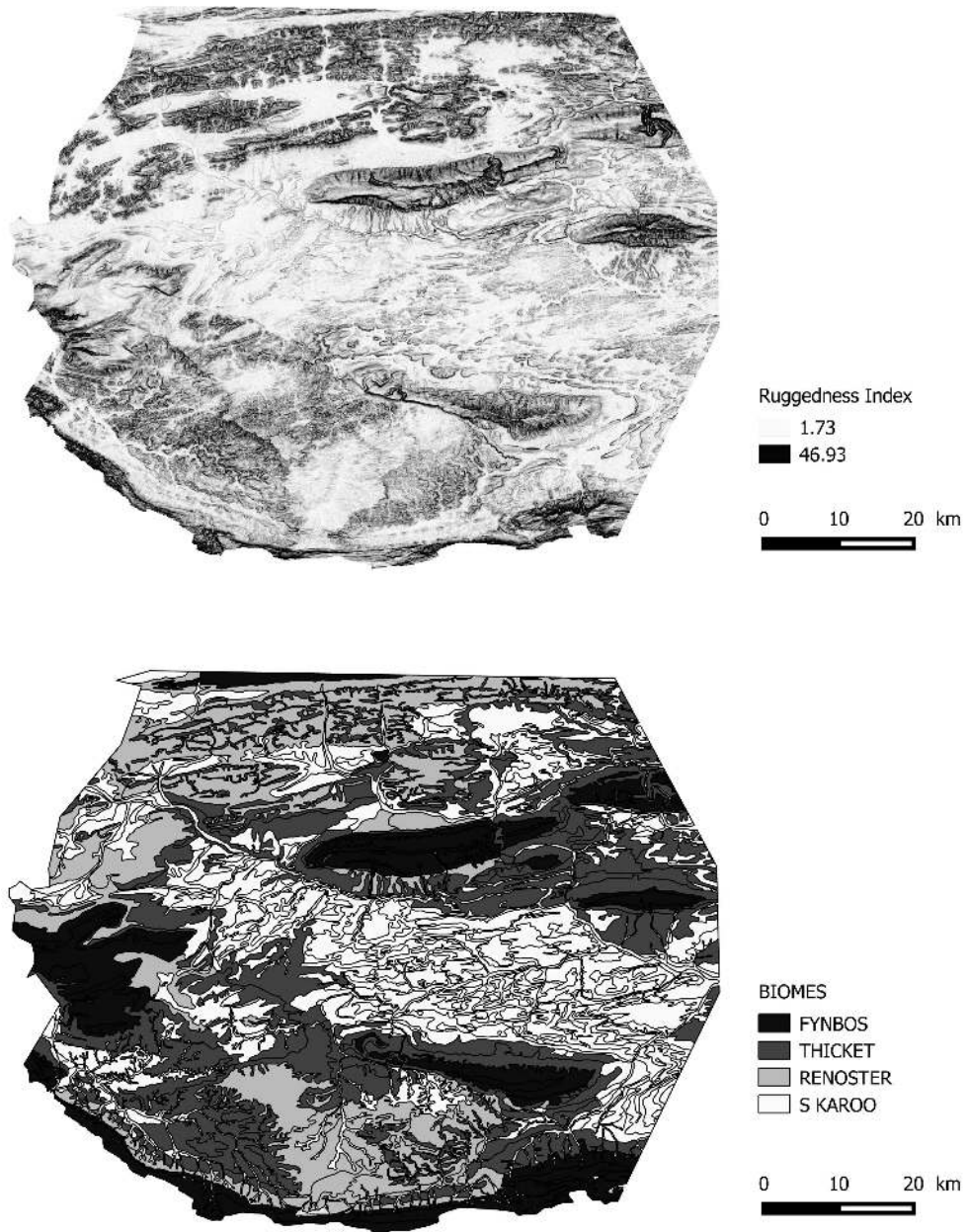
Figure 1.1: Topographic and vegetation maps of the study area

Four main vegetation types can be identified within the study area located in the Little Karoo: fynbos (13.6%), thicket (29.3%), renoster (16.9%) and succulent Karoo (32.0%). The two maps suggest a strong association between terrain roughness and vegetation.
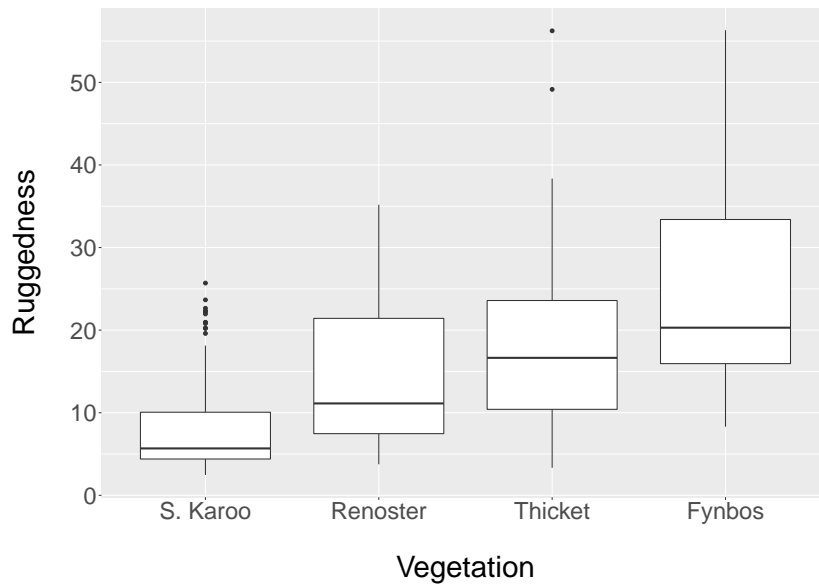
Figure 1.2: Ruggedness Index in each vegetation patch
Using QGIS 2.10.1 software [268], the ruggedness index was averaged in each vegetation polygon, before being displayed with boxplots, in order to illustrate the strong association between terrain roughness and vegetation.
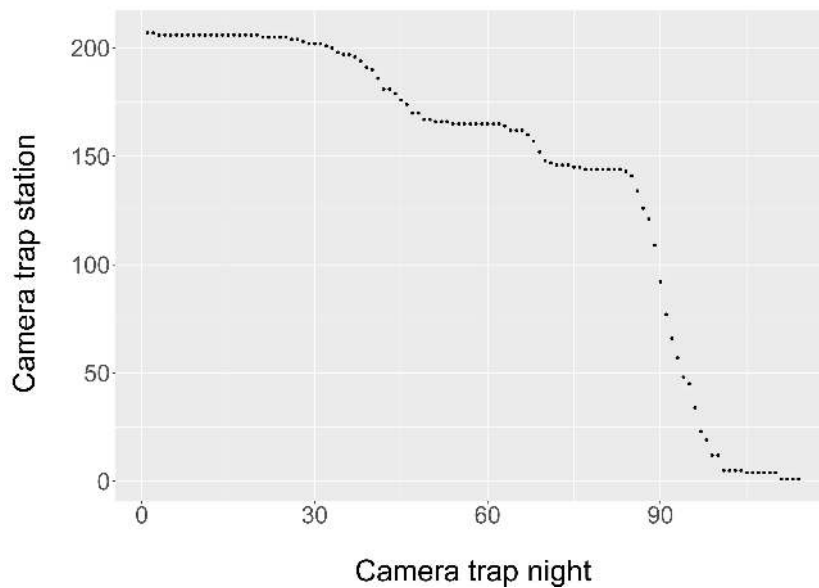

Figure 1.3: Operating camera trap stations
Most of the camera trap stations ran for c. three months, which explains why the number of operating camera trap stations after the 85th camera trap night drops significantly.
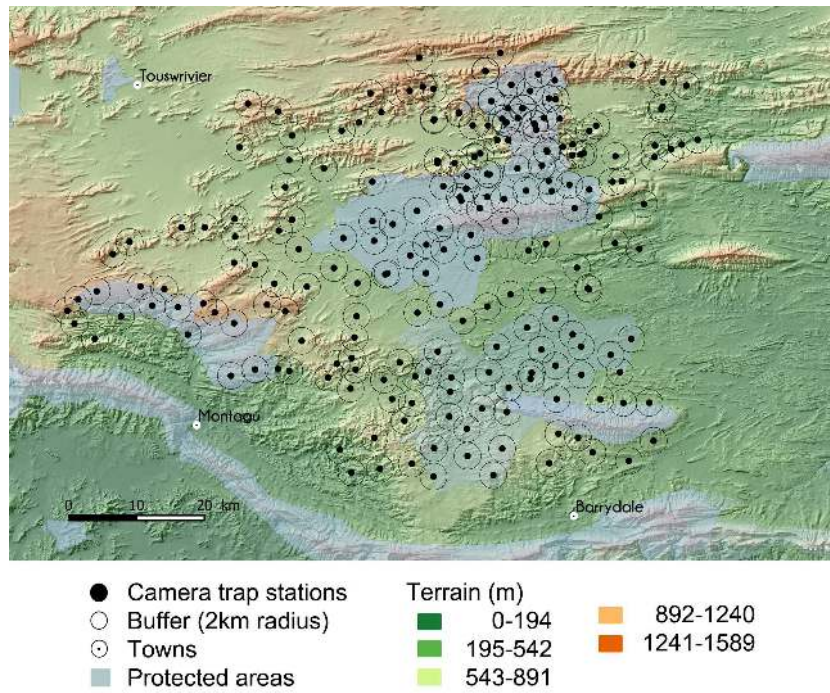
Figure 1.4: Study area
30×30 m Digital Elevation Model (DEM) data provide accurate information about the shape and features of the surface of the study area in the Little Karoo. The change in elevation was measured using the Terrain Roughness (ruggedness) Index (TRI) in QGIS 2.10.1 software [268]. The latter was averaged throughout a 2-km radius circle around every camera trap station and used as a spatial covariate.
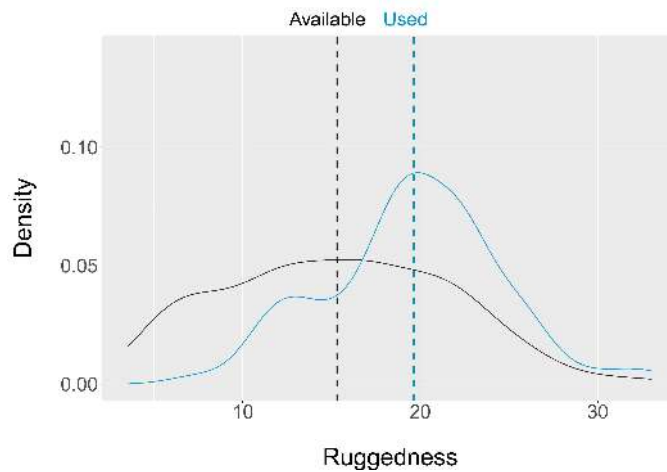

Figure 1.5: Ruggedness profiles: available and used by leopards
The ruggedness profile A (black line) of the study area describes the habitat available to all species s, whereas the ruggedness profile $U_{,leopard}$ (blue line) describes the habitat used by leopards.

(a) aardvark (b) aardwolf (c) African wildcat (d) b b jackal

(e) brown hyena (f) C g mongoose (g) Cape hare (h) C m zebra

(i) Cape porcupine (j) caracal (k) c baboon (l) eland

(m) gemsbok (n) greater kudu (o) grey duiker (p) grey rhebuck

(q) grysbok (r) H r r rabbit (s) honey badger (t) klipspringer

(u) leopard (v) red hartebeest (w) rock hyrax (x) scrub hare
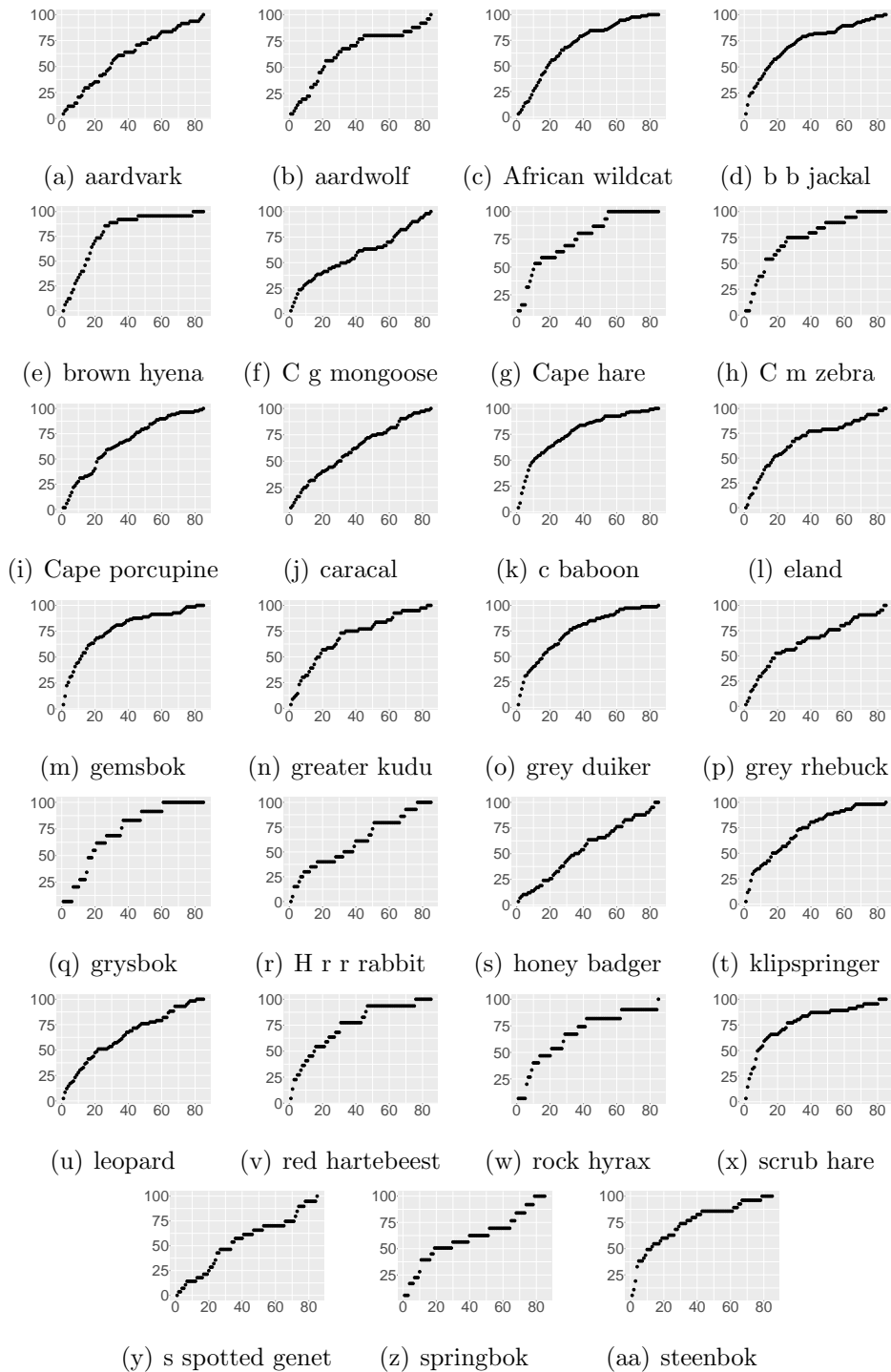
(y) s spotted genet (z) springbok (aa) steenbok

Figure 1.6: Cumulative number of active sites

The plots show the cumulative number of active sites for 27 mammal species in the Little Karoo. The discrete first axis ranges from 0 to 85 camera trap nights; and the second axis gives the percentage of active sites revealed after x camera trap nights, in relation to the total number revealed after three months.

(a) aardvark (b) aardwolf (c) African wildcat (d) b b jackal

(e) brown hyena (f) C g mongoose (g) Cape hare (h) C m zebra

(i) Cape porcupine (j) caracal (k) c baboon (l) eland

(m) gemsbok (n) greater kudu (o) grey duiker (p) grey rhebuck

(q) grysbok (r) H r r rabbit (s) honey badger (t) klipspringer

(u) leopard (v) red hartebeest (w) rock hyrax (x) scrub hare
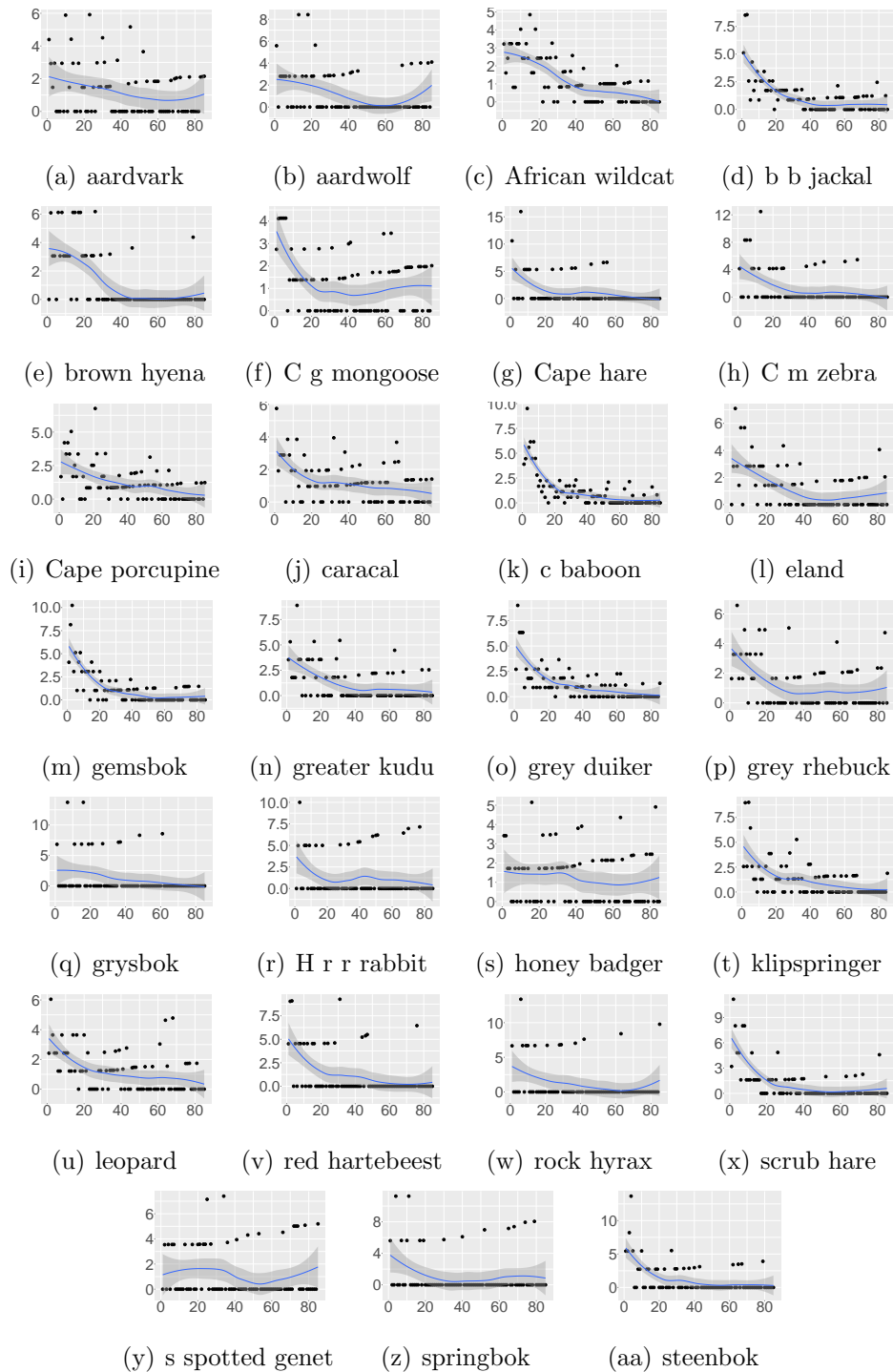
(y) s spotted genet (z) springbok (aa) steenbok

Figure 1.7: Detection rate of new active sites
The plots show the detection rate of new active sites for 27 mammal species in the Little Karoo. The discrete first axis ranges from 0 to 85 camera trap nights; and the second axis gives the percentage of active sites revealed on each camera trap night x, in relation to the total number revealed after three months. The area shaded in blue is the confidence interval of the detection rate function.
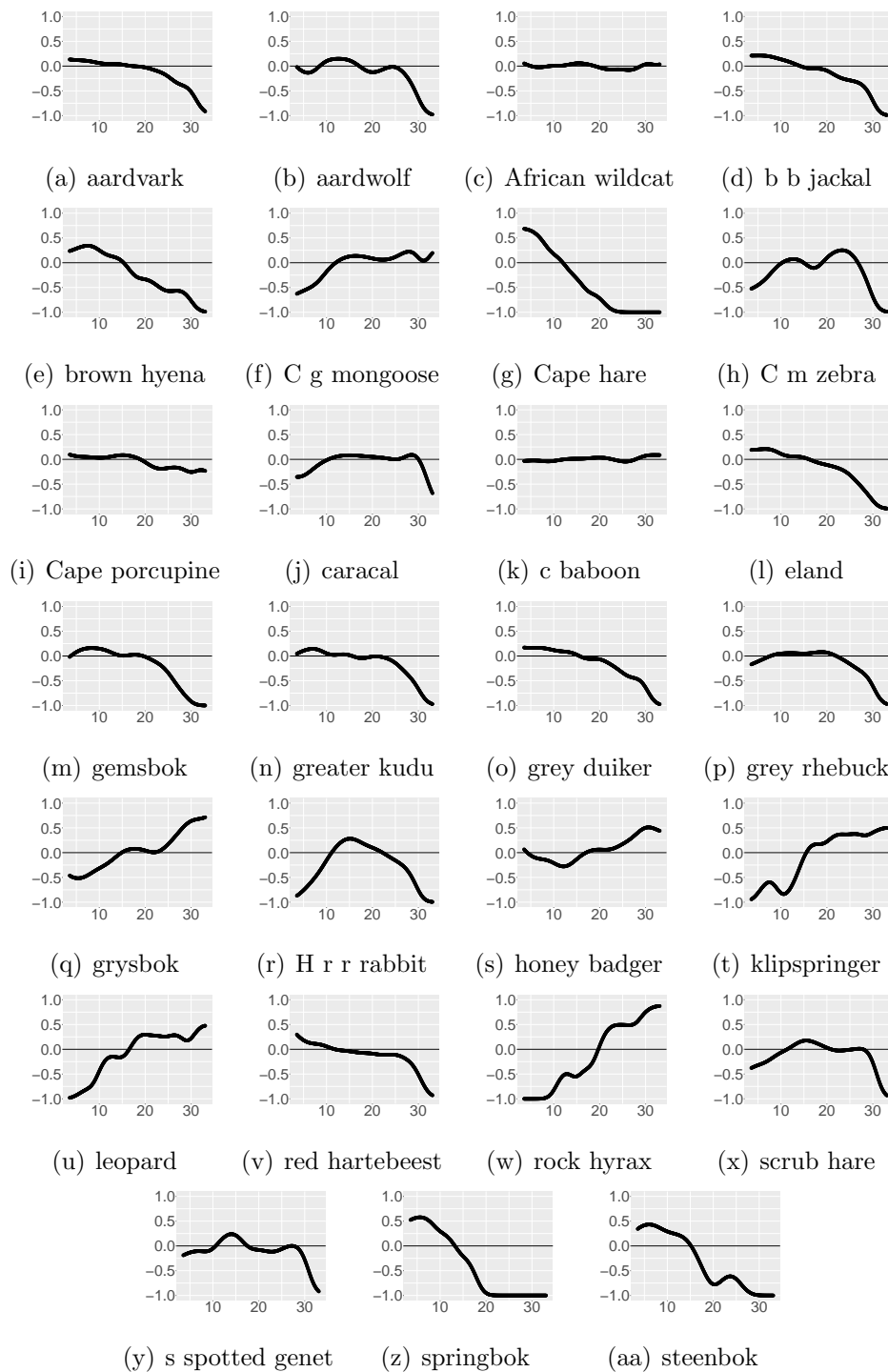
(a) aardvark   (b) aardwolf   (c) African wildcat   (d) b b jackal

(e) brown hyena   (f) C g mongoose   (g) Cape hare   (h) C m zebra

(i) Cape porcupine   (j) caracal   (k) c baboon   (l) eland

(m) gemsbok   (n) greater kudu   (o) grey duiker   (p) grey rhebuck

(q) grysbok   (r) H r r rabbit   (s) honey badger   (t) klipspringer

(u) leopard   (v) red hartebeest   (w) rock hyrax   (x) scrub hare

(y) s spotted genet   (z) springbok   (aa) steenbok

Figure 1.8: Jacob's Index curve

The plots show the Jacob's Index curve for 27 mammal species in the Little Karoo. The Jacob's preference index is independent of the relative abundance of each habitat available to the animals [155]. It varies from −1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that the habitat is used in proportion to its availability.
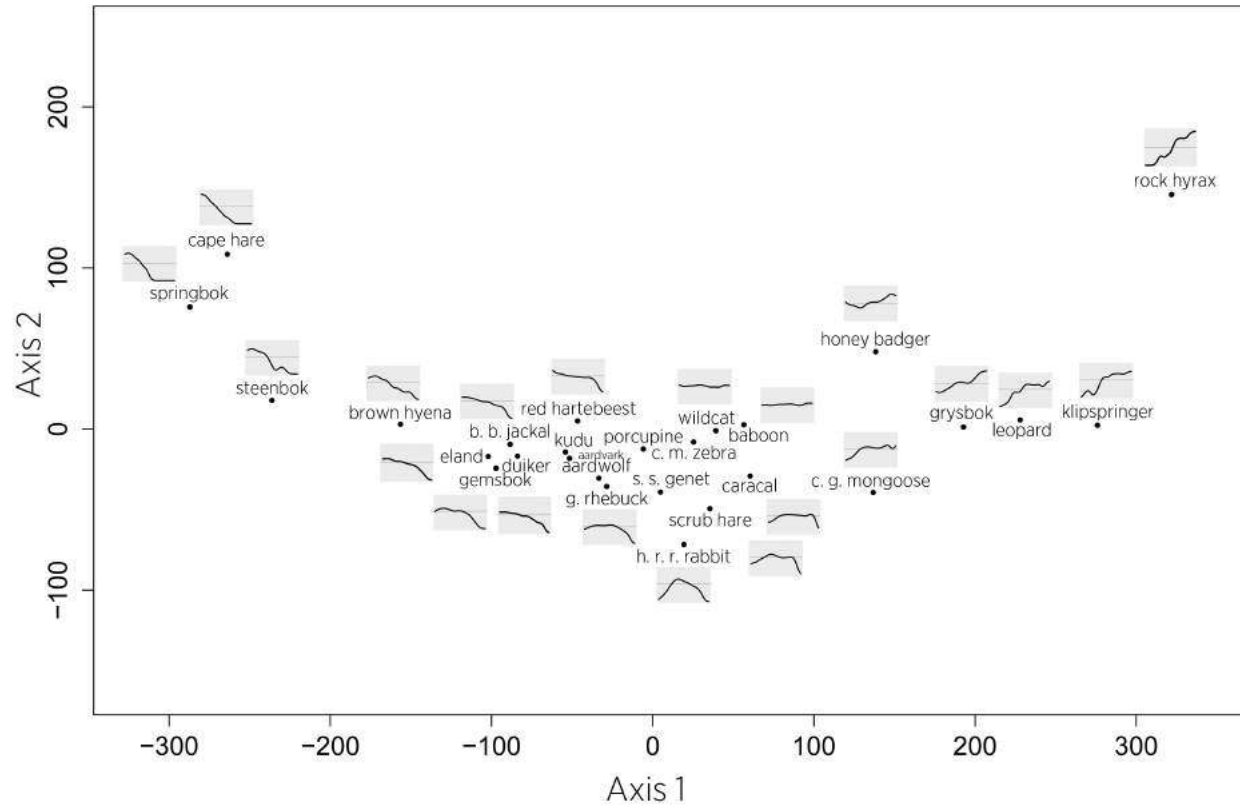
Figure 1.9: Non-metric multidimentional scaling (NMDS) of the Ruggedness-preference Distance Matrix (RDM)
The NMDS analysis includes 27 mammal species of the Little Karoo. Axis one is interpreted as a left-right gradient from species favouring slightly-rugged terrain to species favouring highly-rugged terrain. Axis two is interpreted as a bottom-top gradient from species favouring moderately rugged terrain to species showing no particular preferences, and finally to the three strictly habitat-specialised species (either for slightly- or highly-rugged terrain).
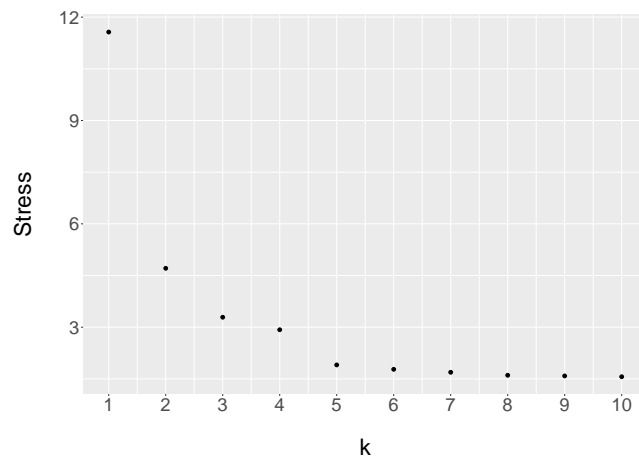
Figure 1.10: Stress values in relation to the number of dimensions k

The measure of lack of fit in NMDS is known as the 'stress' of the configuration. Non-zero stress values occur with insufficient dimensionality, and as the number of dimensions increases, the stress value will either decrease or remain stable.