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Multivariate analyses enable visualisation of temporal ressource partitioning in local mammal communities

3.1 Abstract

An important ecological goal is to understand the forces driving species co-existence in local animal communities, and ecologists have focused their attention on resource-partitioning to gain insights into the mechanisms driving sympatry. Interspecific competition takes place when resources are limiting, but coexistence can still be possible if sympatric species use different food sources and/or use them in different areas and/or at different times. Animals have evolved different diel activity rhythms to adapt to the time structure of the environment, which consists of 24-hour periodicity. The ecological implications that these diel activity rhythms have on the interactions and structure of ecological communities are still poorly understood. The nocturnal bottleneck hypothesis, that the majority of mammal species is nocturnal as a result of an ancestral characteristic of the group, has become commonplace in textbooks; nonetheless, behavioural differences among terrestrial mammals were documented, with species using different periods of the 24-hour sleep-wake cycle in complex and diverse ways. In this study, three multivariate statistical approaches were applied to camera trap data, to visually interpret a large multivariate ecological dataset. Each of these three methods is part of an exploratory data analysis philosophy aiming to produce graphical displays, which provide insights into, makes suggestions about, and even answer ques-

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tions dealing with temporal partitioning in animal communities. The three multivariate analyses provided similar two-dimensional graphical display explaining the essential structure of the data, which showed that the results are not sensitive to the choice of statistical method. These investigations enabled subtle nuances in the spectrum of diel activity rhythms to be visualised. The graphical outputs show a variety of temporal niche breadths and of activity onset/offset timings, which allowed diel activity rhythms to diversify and the mammal community to partition the temporal resources. By locating species along a continuum rather than in categories, these methods enable us to compare species in such a way that it leads to a better understanding of the forces driving species coexistence in local animal communities.

3.2   Introduction

An important ecological goal is to understand the forces driving species coexistence in local animal communities [133, 193, 357]. Ecologists have focused their attention on resource-partitioning to gain insights into the mechanisms driving sympatry [298]. The subdivision of food, space and time are the three essential means that facilitate species coexistence [160, 174, 176, 277, 298, 339].

Animals have evolved different diel activity rhythms to adapt to the time structure of the environment, which consists of 24-hour periodicity [73, 160, 370]. The ecological implications that these diel activity rhythms have on the interactions and structure of ecological communities are still poorly understood. However the main goal of resource-partitioning studies is to understand the limits that interspecific competition place on the number of species that can stably coexist [298]. Temporal partitioning of short time periods (e.g. diel) probably involves the interplay of competition and predation, in order to facilitate coexistence between competitors and between predators and their prey [58, 280, 298, 363]. Interspecific competition takes place when resources are limiting, but coexistence can still be possible if sympatric species differ in behaviour and morphology, and consequently if they use different food sources and/or use them in different areas and/or at different times [49, 75, 76, 298].

The nocturnal bottleneck hypothesis, that the majority of mammal species is nocturnal as a result of an ancestral characteristic of the group, has become commonplace in textbooks [116]. Early mammals of the Mesozoïc area, being subjected to predation pressure from ectothermic and diurnal reptiles (e.g. dinosaurs), evolved endothermic metabolisms, a major adaptation enabling them to restrict their activities to periods of darkness,

leading to considerable changes in photoreception [64, 71, 223, 354]. Although the ecology of diel time partitioning remains a grey area, many behavioural differences among terrestrial mammals were documented, with species converging their peak periods of activity to coincide with the periods of daylight, darkness or twilight, and with species using different periods of the 24-hour sleep-wake cycle in complex and diverse ways [26]. Among the many factors which can impact diel activity rhythms, the more influential one seems to be: daylength [26, 277], temperature [26], rainfall [24], competition [135] and human activities [173]. To unravel the underlying processes governing diel activity rhythms, it is crucial to collect basic quantitative data on these rhythms among sympatric mammal species. The use of remotely triggered cameras enables scientists to collect large datasets and information on diel activity rhythms of sympatric species [43, 80, 103, 135]. Most research in this area has been conducted on a restricted number of species, mainly carnivorous ones [77, 103, 352]. For example, Di Bitetti et al. (2009) [80] showed that temporal partitioning favours the coexistence of two competitors, one reducing its activity when that of the presumably dominant one is high. Harmsen et al. (2011) [135] also showed that predators have similar diel activity rhythms as their most important prey species, and have negligible overlap with less frequently consumed prey species.

In this study, three multivariate statistical approaches (non-metric multidimensional scaling, covariance biplot and correspondence analysis) were applied to camera trap data, in order to visually interpret a large multivariate ecological dataset, and to gain insights into the diel activity rhythms of the mammal community of the Little Karoo. Each of these three methods is part of an exploratory data analysis philosophy [217, 341], aiming to produce graphical displays, which provide insights into, makes suggestions about, and even answer questions dealing with temporal partitioning in animal communities.

3.3   Material and Methods

3.3.1   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 also described as a mega-ecotone, where the succulent Karoo and the Cape Floristic Provinces intermingle [Introduction, Chapter 1 section 1.3.1].

3.3.2 Data collection

Camera trap data were deployed between March 2014 and August 2015 [Chapter 1 section 1.3.2] as part of a research project on large carnivores – brown hyenas *Hyaena brunnea* and leopards *Panthera pardus* – within a study area of 4,327 km² (minimum convex polygon).

3.3.3 Analysis

3.3.3.1 Kernel density estimation

The times t recorded for every photo-capture i made throughout the 365-day cycle, provided information on the diel activity rhythm of species s, the later being displayed using a 24-hour kernel density function; a probability density function $A_{,s}$ of the species' activity [309]:

$$A_{,s} = \sum_{i=1}^{n} k(t_{i,s}) \quad \text{with} \quad \int_{0}^{24} A_{,s} \cdot dt = 1 \tag{3.1}$$

The probability density functions $A_{,s}$ are representations of circular distributions. Their graphical display was either noon- or midnight-centred, depending on the time period of the 24-hour cycle, in which most of the species daily activity is allocated.

Every photo-capture was either defined as a capture-event or as a duplicate [Chapter 1 section 1.3.3]. All duplicates were discarded for this study as they could significantly inflate the density function in certain areas of the curve, as well as the photo-capture counts per unit of time, which become no longer comparable between species. For this study, mammal species for which at least 50 photo-captures were collected, were included [Chapter 1 section 1.3.3].

3.3.3.2 Data heterogeneity

The northern section of Sanbona Wildlife Reserve differed from the rest of the study area due to its unique species diversity. It also constituted a biological system suspected to have evolved fairly independently, due to the high game fence delimitating its border [Chapter 1 section 1.3.1]. The northern section of Sanbona Wildlife Reserve was sampled in the middle of winter and the datasets were too small to run a bootstrap analysis [235] [Chapter 1 section 2.3.3.3] and search for any significant change in species' diel activity rhythm between Sanbona and the rest of the study site, in winter only. The data

collected within the northern section of the Sanbona Wildlife Reserve were consequently discarded for this study.

3.3.3.3 Data pre-processing

The diel activity rhythms of the mammals of the Little Karoo were not analysed using clock-time because sunrise and sunset times vary throughout the year and across study areas. The time variable t was transformed (t') so that daily sunrise and sunset times were standardised to the annual averages of sunrise and sunset times [Chapter 2 section 2.3.3.2]. Using t' as circular data, the probability density functions describing the diel activity rhythms $A'_{,s}$ of species s were computed.

3.3.3.4 Coefficient of overlap

Kernel density functions such as $A'_{,s}$ have an area under the curve equal to 1, which offers the opportunity to compare them against one another (e.g. species s_1 and s_2), by calculating their coefficient of overlap $O_{s_1}^{s_2}$ ranging from 0 (no overlap) to 1 (identical curves) [226, 283], with the *overlapEst* function from the *overlap* R-package [226]:

$$
\begin{aligned}
O_{s_1}^{s_2}{}' &= O_v(A'_{,s_1},\ A'_{,s_2}) \\
&= \int\limits_0^{24} \min(A'_{,s_1},\ A'_{,s_2}) \cdot dt'
\end{aligned}
\tag{3.2}
$$

3.3.3.5 Temporal partitioning

Non-metric Multi-Dimensional Scaling (NMDS) [32], covariance biplot [114] and correspondence analysis [27] are three statistical tools, each providing a means of displaying and summarising a set of data into a low-dimensional Euclidean space [126, 180, 181]. In two dimensions, the results are displayed in a plane (flat surface), which is the most visually intuitive and therefore most useful of all. They can, for example, be used as a first stage in the exploration of niche overlap in sympatric species. Temporal data collected for the 27 mammal species were analysed using the three approaches, by compiling all information into three matrixes: an Overlap Distance Matrix (ODM) which was used in the NMDS analysis, a Smoothed Community Matrix (SCM) used in the biplot analysis, and a Count Community Matrix (CCM) used in the correspondence analysis.

Overlap Distance Matrix: a symmetric matrix with $n_1 = 27$ rows and $p_1 = 27$ columns (total number of species). Every ODM element ODM$[s_1, s_2]$ quantifies the dissimilarity between the diel activity rhythms of species s_1 and s_2:

$$\text{ODM}[s_1, s_2] = 1 - O_{s_1}^{s_2}{}' \tag{3.3}$$

Smoothed Community Matrix: for every species s, 128 points were extracted at regular time intervals from the kernel density function $A'_{,s}$. SCM consisted of $n_2 = 27$ rows of species and $p_2 = 128$ columns of time variables. Because the probability density functions are smooth, the choice of alternative values of p_2 makes no difference in the results.

Count Community Matrix: counts of photo-captures were extracted for every x-minutes time slots of the day. CCM consisted of $n_3 = 27$ rows of species and $p_3 = 24 \cdot \frac{60}{x}$ columns of time variables. Three CCMs were built using respectively 15, 30 and 60 as x values.

3.3.3.6 Non-metric Multi-Dimensional Scaling (NMDS)

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 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, 180, 181].

Using the *isoMDS* function from the *MASS* R-package [285], an NMDS ordination was performed on ODM, a matrix of dissimilarity data which estimated the dissimilarities of diel activity rhythms between each pair of species in the mammal community of the Little Karoo. 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 cal-

culated species dissimilarities/distances and the plotted distances between species [32].

3.3.3.7   Covariance biplot

A biplot is a multivariate technique proposed by Gabriel (1971) [114], which summarises into a low-dimensional graph the relationships between two continuous and/or categorical variables that are defined within a data matrix, using the singular value decomposition [123].

The covariance biplot analysis was applied to SCM in statistical software Genstat [351]. The term 'bi' refers to the simultaneous display of both rows and columns, not to a two-dimensionality of the plot. The data were collapsed into a two-variable scatterplot, where both species and time information were displayed simultaneously, in the same plane. It showed the relations and interrelations among the rows (species) and columns (time) in the two dimensions, which accounted for the maximum amount of variation in SCM [114].

Summarising a set of data into a two-dimensional graph might not be feasible and a certain amount of distortion might be created. An increase of the number of dimensions will increase the amount of variation in the data matrix, which is accounted for.

3.3.3.8   Correspondence analysis

The correspondence analysis is a multivariate technique developed by Benzécri (1973) [27] after being proposed by Hirschfeld, in 1935 [143]. Similarly to the covariance biplot analysis, it aims to summarise the data into a graphical display of the rows and columns of the CCM contingency table. It is an extension of a chi-square test, where the null hypothesis being tested is whether rows (species) and columns (time) are independent. In other words, whereas the chi-square test answers the question "is the type of species photocaptured independent to the time of capture?", the correspondence analysis aims to provide insights into the nature of the dependence between species and time. The correspondence analysis was performed on CCM (also called a contingency table), using the *ca* function from the *ca* R-package [245].

Summarising a set of multidimensional data into a two-dimensional graph might not be feasible and a certain amount of distortion is inevitably created. An increase of the number of dimensions will increase the amount of variation in the data matrix, which is accounted for.

3.4   Results

The trapping effort of 16,409 camera trap nights resulted in 25,211 photo-captures (10,991 independent photo-capture events) of 86 wild species: including 46 mammals, 39 birds and 1 reptile. Twenty-seven of the 46 mammal species had more than 50 photo-captures to enable the analysis to be conducted [Appendix 2A].

3.4.1   Kernel density functions $A^{'}_{,s}$

The midnight-centred diel activity rhythms $A^{'}_{,s}$ of the 27 mammal species s – calculated using camera trap data collected throughout two consecutive years – are provided in Fig. 3.1; $\overline{SS}$ and $\overline{SR}$ being the annual average times of sunrise and sunset, $\overline{MD}$ and $\overline{MN}$ being true midday and midnight in the study area, given the inclination angle of the rotation axis of the Earth (as compared to its orbital plane). The time periods shaded in light grey represent the daily hours of twilight (one hour before and after sunrise and sunset), while the time period shaded in dark grey represents the daily hours of darkness (from one hour after sunset until one hour before sunrise), according to previous studies [151].

The kernel density functions showed that while some species seemed to constrain their peak periods of activity to concur with the periods of daylight (e.g. rock hyrax *Procavia capensis*), darkness (e.g. Cape hare *Lepus capensis*) or twilight (e.g. grey duiker *Sylvicapra grimmia*), other species used different periods of the 24-hour sleep-wake cycle in complex and diverse ways (e.g. springbok). Species' diel activity rhythms also differed according to the species' temporal niche breadth (variety of temporal resources used by a given species). While certain species displayed a wide temporal niche breadth (e.g. caracal *Caracal caracal*), others exploited a short temporal window (e.g. *aardvark Orycteropus afer*) of the 24-hour cycle.

3.4.2   Non-metric Multi-Dimensional Scaling (NMDS)

The NMDS iterative algorithm captured, in two dimensions, the essential structure of the dissimilarity matrix data (Table 3.1). It produced the NMDS plot (Fig. 3.3), which represents, as closely as possible, the dissimilarity between species' diel activity rhythms in a two-dimensional space. For example, leopards had closer diel activity rhythms to African wildcats than they had to caracals, although the graph does not quantify this difference.

The NMDS screeplot, provided in Fig. 3.6(a), showed a decrease in ordination stress with an increase in the number of ordination dimensions allowed, which revealed that attempting an ordination with one NMDS axis yielded reasonably high stress (0.061), however two dimensions was more suitable. The stress value equaled 0.032 in two dimensions and, like all stress values equal to or below 0.05, it indicated good fit. The NMDS plot showed a clear and gradual left-right transition along the first (horizontal) axis, from species with strictly nocturnal diel activity rhythms to species with strictly diurnal diel activity rhythms. Cathemeral species – active throughout the 24-hour cycle – were found in the centre of the graph, although the timing of their activity peaks might have differed.

The second (vertical) axis explained less of the data structure and might have also picked up noise in the data. This was to be expected given the small decrease in stress between an ordination with one and an ordination with two NMDS axis.

3.4.3   Correspondence analysis

The correspondence analysis, applied to the three CCMs, built with the time slots $x = 15$, 30 and 60 minutes respectively, summarised the data and produced graphical displays of the cross tabulations. The two-dimensional ordinations respectively explained 66.5%, 77.2% and 86.1% of variance in the data of the three CCMs. These percentages increased by 3% (Fig. 3.6(b)) after adding a third dimension, suggesting that the CA graphical display in two dimensions was adequate, especially because the first axis always explained most of the variance in the data (respectively 58.9%, 69.2% and 77.0%). Fig. 3.7 provides for the 27 mammal species a quality value, a percentage of reliability of the data structure displayed in two dimensions. Greater kudu *Tragelaphus strepsiceros* and grysbok *Raphicerus melanotis* were the two species with the lowest quality values (respectively 31% and 33%), indicating that a substantial part of their data structure was explained in higher dimensions (≥ 3). The next lowest quality value (48%) were that of springbok *Antidorcas marsupialis* and Cape mountain zebra *Equus zebra zebra*. The 15.9% of variance in the data, explained in dimensions higher than 2, was not evenly spread over all 27 species, but mainly over greater kudu and grysbok.

The graphical results of the correspondence analysis were very similar for the three different CCMs. The 60-minute correspondence analysis was the selected version because of the reduced number of time points which facilitated the readability of the output plot. The latter, a two-dimensional plot (Fig. 3.4), represented both variables, species and time, in the same plane. The

species points formed an arch along which, a gradual left-right transition from strictly nocturnal species to strictly diurnal species, was observed. Species displaying similar temporal preferences and therefore similar diel activity rhythms were plotted side-by-side (e.g. Cape porcupine *Hystrix africaeaustralis* and small spotted genet *Genetta genetta*). For each 60-minute time slot of the 24-hour cycle, a time-profile summarising the activity level of the 27 species within the mammal community was defined and then plotted in blue in Fig. 3.4 (the details of the 24 time-profiles of the daily cycle are provided in Fig. 3.2). Forming also an arch, the time points followed the same trend as the species points. Species concentrating their activity to the night were found close to the time-profiles of the darkest hours of the 24-hour cycle, whereas species concentrating their activity to the day, were close to the time-profiles of the brightest hours. Species with larger temporal niche breadth – and therefore exploiting a wider range of temporal resources – were found along the lower section of the arch, close to the time-profiles matching hours with rapid changes in light intensities. 60-minute time slots with similar time-profiles (similar composition of diel activity rhythms among the 27 mammal species of the community) were plotted side-by-side (e.g. 04:00 and 05:00).

Following the chronological order of the hours within the 24-hour cycle, two clusters of time points were observed; one gathering the time-profiles of the dark hours starting 1h20 after sunset and ending 1h38 before sunrise ($20{:}00 < t^{'} < 05{:}00$), the second one gathering the time-profiles of the bright hours starting 3h22 after sunrise and ending 2h38 before sunset ($10{:}00 < t^{'} < 16{:}00$). Within each of these two time periods, the time-profile remained stable, indicating that – within the mammal community – little variation of species activity occurred during the darkest and brightest hours of the daily cycle. On the contrary, during the remaining hours of the daily cycle, the activity of the species in the mammal community underwent high-amplitude variations. The imaginary curves connecting the morning ($05{:}00 < t^{'} < 10{:}00$) and evening ($16{:}00 < t^{'} < 20{:}00$) hours overlapped, indicating that the variations undergone by the time-profiles of the morning hours followed a pattern which was conversely reproduced by the time-profiles of the evening hours. Consequently, the activity of the 27 species within the mammal community minutes after sunrise ($t^{'} = 07{:}00$) and minutes before sunset ($t^{'} = 18{:}00$) were nearly identical, so as that roughly two hours after sunrise ($t^{'} = 09{:}00$) and two hours before sunset ($t^{'} = 17{:}00$).

3.4.4 Covariance biplot

The covariance biplot, applied to SDM, summarised the data into a scatter-plot representing the two sets of variables – species and time – in the same plane (Fig. 3.5). The two-dimensional ordination explained 88.6% of variance in the data of the SDM, most of which was explained by the first axis (82%). The percentage of variance explained, increased by 5% (Fig. 3.6(c)) after adding a third dimension, suggesting that the biplot in two dimensions was adequate. Fig. 3.8 provides for the 27 species a quality value, a percentage of reliability of the data structure displayed in two dimensions. Grysbok was the species with the lowest quality value (27%), indicating that a substantial part of its data structure was explained in higher dimensions (≥ 3). The 11.4% of variance in the data, explained in dimensions higher than 2, was not evenly spread over all 27 mammal species, but mainly over grysbok. This indicated that within the multidimensional space, grysbok was the farthest from the plane, among all other species.

Similarly to the CA graphical display, the species points formed an arch along which a gradual left-right transition from strictly nocturnal species to strictly diurnal species was observed. The cosin of the angle between two vectors extending from the origin to a species point estimated the correlation between the diel activity rhythms of the two species in question. In other words, species displaying similar temporal preferences (e.g. diel activity rhythms) were plotted in such a way that their respective position vectors pointed nearly to the same direction (e.g. brown hyena *Hyeana brunnea* and aardwolf *Proteles cristatus*). On the contrary, species with divergent temporal preferences displayed position vectors pointing to opposite directions (e.g. chacma baboon *Papio ursinus* and leopard *Panthera pardus*). The length of the species vector gave insights into the variability of the diel activity rhythm. The longer it was, the more variability was found within the data.

The time-profile – summary of the activity level of all species in the community at time $t^{'}$ – represented by time points (in blue in Fig. 3.5), goes through a periodic cycle within 24-hours, which pattern is built around four specific times: $\overline{MD}$, $\overline{MN}$, $\overline{SR}$ and $\overline{SS}$. Time points plotted side-by-side in Fig. 3.5 indicate that, at those different times, the time-profiles of the mammal community were similar (e.g. 15h45 and 09h45). Two clusters of time points were observed; one gathering the time-profiles of the dark hours starting 3h20 after sunset and ending 1h38 before sunrise ($22{:}00 < t' < 05{:}00$), the second one gathering the time-profiles of the bright hours starting 3h22 after sunrise and ending 2h38 before sunset ($10{:}00 < t' < 16{:}00$). Within each of these two time periods, the time-profile remained stable, indicating that –

within the mammal community – little variation of species activity occurred during the darkest and brightest hours of the daily cycle. On the contrary, during the remaining hours of the daily cycle, the activity of the species in the mammal community underwent high-amplitude variations. The imaginary curves connecting the morning ($05{:}00 < t' < 10{:}00$) and evening ($16{:}00 < t' < 22{:}00$) hours overlapped, indicating that the variations undergone by the time-profiles of the morning hours followed a pattern which was conversely reproduced by the time-profiles of the evening hours. Consequently, the activity of the 27 mammal species within the mammal community minutes after sunrise ($t' = 07{:}00$) and minutes before sunset ($t' = 18{:}00$) were nearly identical, so as that roughly two hours after sunrise ($t' = 09{:}00$) and two hours before sunset ($t' = 16{:}30$). These results were remarkably similar to those of the CA analysis.

The relative positioning of species points to time points depended on the species' temporal preferences. For example, strictly diurnal species tended to be plotted in the same direction from the origin as that of the $\overline{MD}$ time point (e.g. rock hyrax). The length of $\overrightarrow{ij}$, linking species point i and time point j, was calculated as follow: $z_{ij} = \lVert i \rVert \cdot \lVert j \rVert \cdot \cos(\theta_{ij})$

3.5 Discussion

Each of the three multivariate analyses provided a two-dimensional graphical display which explained most of the data structure. The collapse and summary of the complex initial data table allowed for an intuitive and visual exploration of the data. Although not identical, the relative spatial positioning of all 27 mammal species within the plane was similar in the three analyses. From this it can be inferred that the data are robust in relation to statistical method. In other words, the results are not sensitive to the choice of method. These investigations did not only enable to classify species as diurnal, nocturnal, crepuscular, or cathemeral but also to grasp subtle nuances in the spectrum of diel activity rhythms. The species were located along a continuum rather than simply categorised. These methods enable us to compare species in such a way that it leads to a better understanding of the forces driving species coexistence in local animal communities.

A variety of temporal niche breadths and of activity onset/offset timings allowed diel activity rhythms to diversify and the mammal community to partition the temporal resources. Both phylogenetic and environmental factors are crucial to elucidate the biological principles underlying the diversity of diel activity rhythms [116, 122, 175, 223, 224, 317, 345]. Several studies indicated

that while a circadian clock – an endogenous timing mechanism built on the foundation of an oscillator providing a time tracking system – can regulate diel activity rhythm in organisms, the latter are not slaves to the physiological and biochemical processes of their circadian clock [65, 73, 169, 170, 291, 365]. The niche occupied by an animal within the community results from the interactions this animal may have with the biological and physical factors which contribute to its survival and reproduction [147]. The Earth's daily rotation prevents the influence of these factors to be uniform throughout the day-night cycle, which is why the diel structure of a niche is as fundamental as its spatial, chemical, energetic and social structures in order to understand the segregation of the activities of individuals to specific times of day, as well as the diversity of species that inhabit a community [147, 298].

There is evidence for light-entrained activity (synchronisation of activities with the light-dark cycle) [263, 346], due to genetic [266, 301], latitudinal [262] and seasonal [65, 170] differences in the responsiveness of the circadian system to light. Entrainment is then defined by a stable relationship between determined environmental occurrences (e.g. sunrise or sunset) and specific behaviour (e.g. the onset or offset of activity). In Fig. 3.4, it is observed that within the 24-hour cycle, the time-profile (summary of the activity level of all species in the community at time t') goes through a periodic cycle characterised by four periods. Two stable ones, matching the darkest and brightest hours of the cycle. Outside those hours, the time-profile goes through two transitional periods during which it varies rapidly to get from one stable state to another. The transitional periods are considered to be the crepuscular hours of the daily cycle (periods of rapidly changing light intensities). The synchronisation of the community activity cycle with the light-dark cycle, supports the assumption of light-entrained activity within the mammal community of the Little Karoo.

There is also evidence for non-photic influences on circadian rhythms, resulting into the partition of the temporal environment within a community, to maximise species energy intake while minimizing species exposure to predation and/or to other stressors (e.g. competitors) [168, 179, 239]. Kotler et al. (1993) [179] conducted research studies on granivorous gerbils in the Israeli desert, and showed that the smaller species (*Gerbillus allenbyi*) emerges from underground to forage after the retreat of the larger species (*Gerbillus pyramidum*), which had by then reduced the seed densities to suboptimal levels. Without *G. pyramidum* within the community, *G. allenbyi* shifts its activity to an earlier time, supporting the hypothesis that the temporal feeding partitioning between these species of gerbils is maintained by agressive encounters. Species positioned close to one another in the plane of multi-

variate analysis (e.g. caracal and black-backed jackal *Canis mesomelas*) in Fig. 3.3, 3.4, and 3.5, belonged to the same temporal niche, and coexistence was either possible because resources were abundant and the resource competition was weak, or facilitated by the partitioning of resources in different niches (e.g. space and/or food).

3.6 Table

Table 3.1: Overlap Distance Matrix ODM (%)

This ODM was built for 27 mammal species in the Little Karoo. Every ODM element ODM$[s_1, s_2]$ quantifies the dissimilarity between the diel activity rhythms of species s_1 and s_2: $1 - O_{s_1}^{s_2'}$. ODM$[s_1, s_2] < 20\%$ are showing in bold.

|	aardvark	aardwolf	African wildcat	black backed jackal	brown hyena	Cape gray mongoose	Cape hare	Cape mountain zebra	Cape porcupine	caracal	chacma baboon	eland	gemsbok	greater kudu	grey duiker	grey rhebuck	grysbok	Hewitts red rock rabbit	honey badger	klipspringer	leopard	red hartebeest	rock hyrax	scrub hare	small spotted genet	springbok	steenbok
aardvark	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
aardwolf	**11**	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
African wildcat	31	22	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
black backed jackal	52	44	23	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
brown hyena	24	**15**	24	41	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cape gray mongoose	99	95	79	60	93	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cape hare	**16**	**18**	27	46	30	94	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cape mountain zebra	52	42	31	28	41	56	51	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cape porcupine	**15**	**10**	22	**17**	96	**14**	44		100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
caracal	47	39	**18**	**10**	37	62	41	24	40	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chacma baboon	97	91	74	53	89	**16**	92	49	93	55	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
eland	70	62	41	21	57	49	64	34	63	23	38	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
gemsbok	75	67	48	27	63	39	69	36	69	29	27	**12**	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-
greater kudu	71	64	44	24	59	44	66	35	65	26	32	**11**	**8**	100	-	-	-	-	-	-	-	-	-	-	-	-	-
grey duiker	56	48	26	**7**	45	60	50	31	48	**15**	53	21	26	24	100	-	-	-	-	-	-	-	-	-	-	-	-
grey rhebuck	93	86	67	45	83	27	87	46	88	49	**14**	31	25	26	43	100	-	-	-	-	-	-	-	-	-	-	-
grysbok	54	46	27	**15**	43	58	47	32	48	**12**	49	**19**	24	**20**	**18**	44	100	-	-	-	-	-	-	-	-	-	-
Hewitts red rock rabbit	26	26	28	46	35	97	**16**	51	20	42	94	64	71	68	50	89	50	100	-	-	-	-	-	-	-	-	-
honey badger	57	49	30	**17**	46	60	51	27	50	**15**	47	**20**	26	23	21	42	20	52	100	-	-	-	-	-	-	-	-
klipspringer	94	90	74	55	87	**11**	90	48	91	56	**9**	41	31	36	55	**18**	51	92	50	100	-	-	-	-	-	-	-
leopard	26	**16**	**8**	31	**18**	87	23	36	**15**	26	82	48	55	51	34	75	33	25	38	82	100	-	-	-	-	-	-
red hartebeest	87	80	61	40	77	28	82	46	83	43	**19**	26	**16**	**19**	37	**13**	37	84	40	23	69	100	-	-	-	-	-
rock hyrax	96	91	74	53	88	**11**	91	53	92	55	**12**	43	32	35	52	**20**	52	94	56	**10**	82	21	100	-	-	-	-
scrub hare	28	21	**15**	33	25	91	23	41	**18**	30	86	50	60	56	34	76	39	**20**	42	87	**12**	72	85	100	-	-	-
small spotted genet	23	**16**	**15**	37	**20**	95	**18**	41	**12**	34	90	55	63	60	40	83	41	**17**	45	90	**9**	77	89	**9**	100	-	-
springbok	92	87	68	46	84	28	86	53	88	50	26	37	29	32	43	**20**	47	88	52	26	76	**15**	22	76	84	100	-
steenbok	89	83	66	46	80	22	84	53	85	47	22	37	25	29	45	23	43	86	49	21	74	**15**	**19**	79	82	**18**	100

3.7 Figures
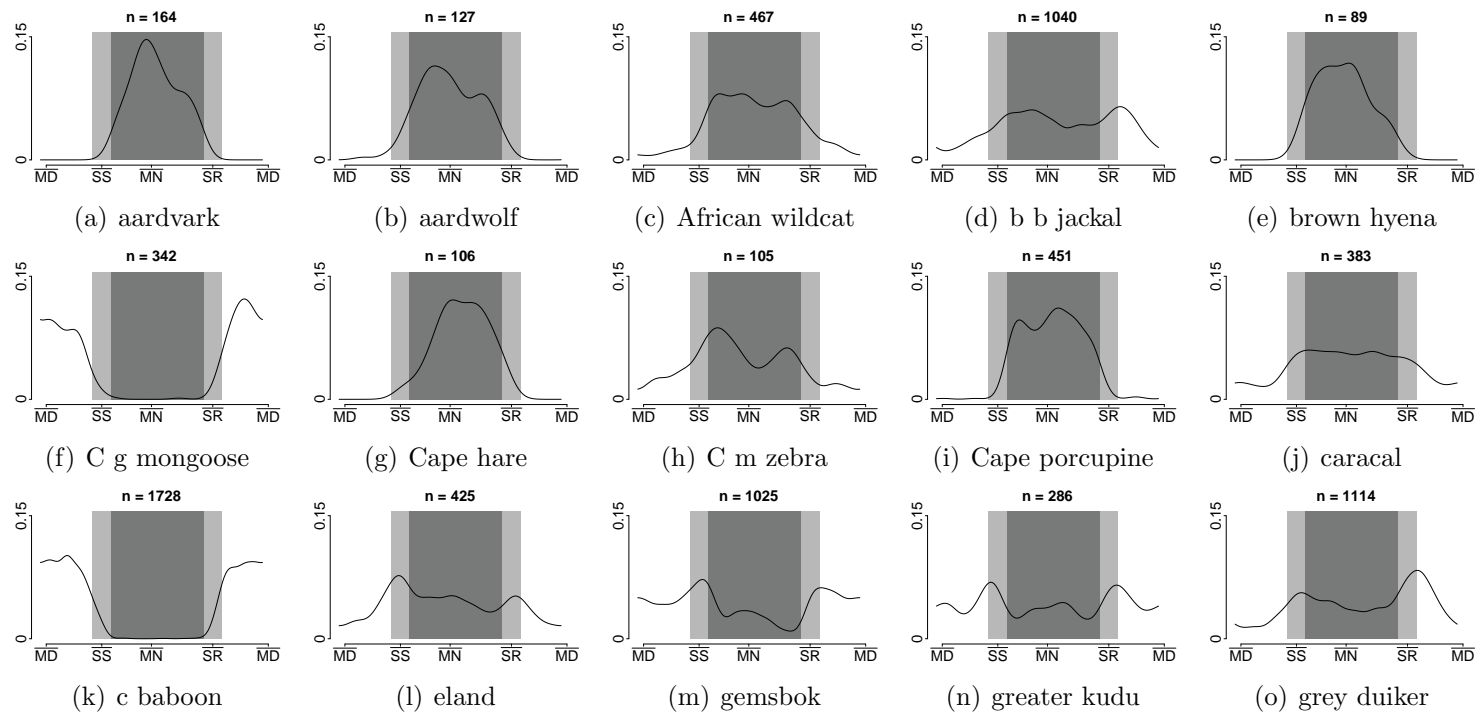
Figure 3.1: Diel activity rhythm of the 27 mammal species in the Little Karoo, throughout the year.
Kernel density functions were midnight-centred. $\overline{SS}$ and $\overline{SR}$ represent the annual average times of sunrise and sunset. $\overline{MD}$ and $\overline{MN}$ are true midday and midnight in the study area. The time periods shaded in light grey represent the daily hours of twilight (one hour before and after sunrise and sunset), while the time period shaded in dark grey represents the daily hours of darkness (from one hour after sunset until one hour before sunrise); these were defined in previous studies [151]. The number of photo-captures on which each kernel density function is based is provided at the top of each plot.
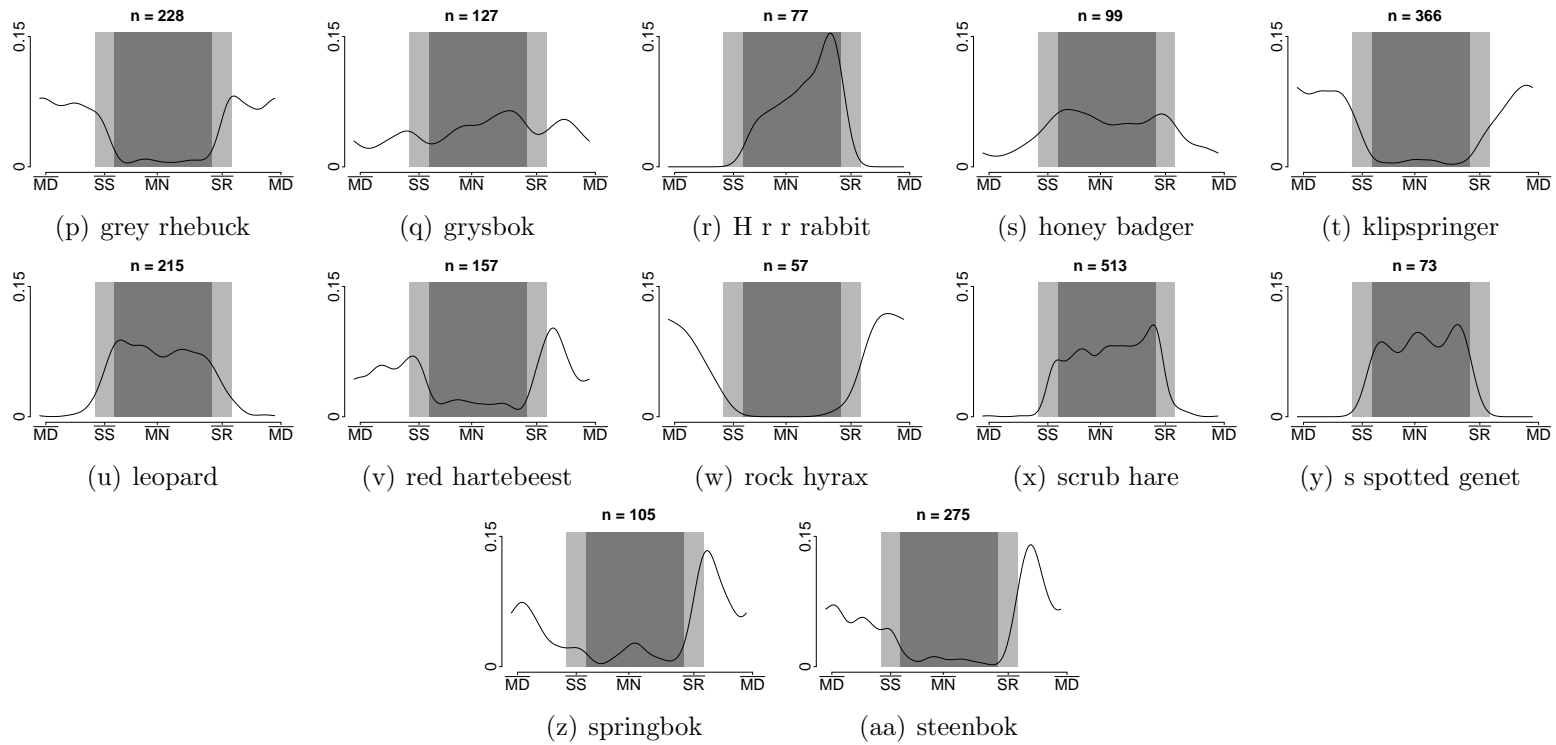
(p) grey rhebuck   (q) grysbok   (r) H r r rabbit   (s) honey badger   (t) klipspringer

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

(z) springbok   (aa) steenbok

Figure 3.1: Diel activity rhythm of the 27 mammal species in the Little Karoo, throughout the year (continued).
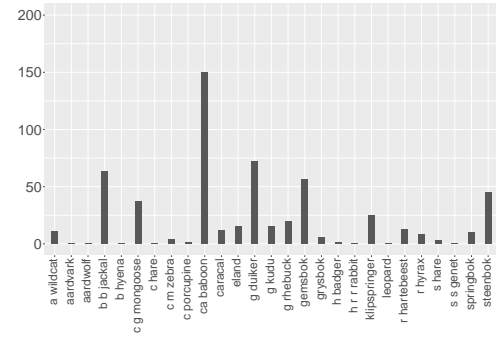A full caption is provided on p144

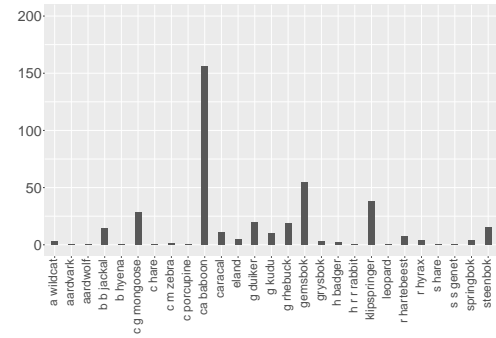(a) $\overline{MD}$

(b) $\overline{MD} + 1$h

(c) $\overline{MD} + 2$h

(d) $\overline{MD} + 3$h

(e) $\overline{SS} - 2$h

(f) $\overline{SS} - 1$h
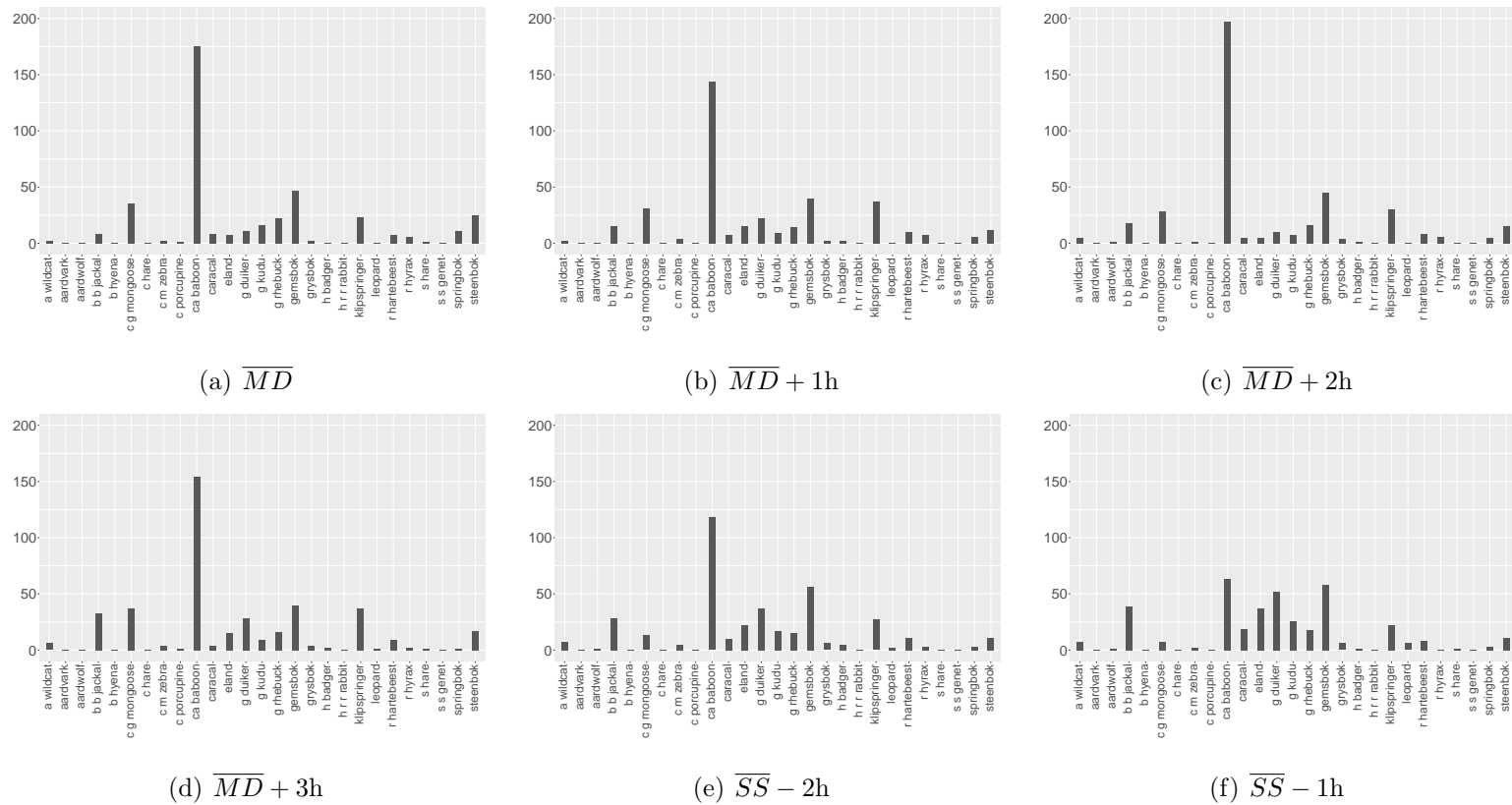
Figure 3.2: Time-profile of mammal activity throughout the 24-hour cycle.

A time-profile is a snapshot of the activity level of the 27 mammal species in the community at time t. The 24 hourly time-profiles provided, for the 27 mammal species, the number of photo-captures recorded during hour H, throughout the study conducted in the Little Karoo.
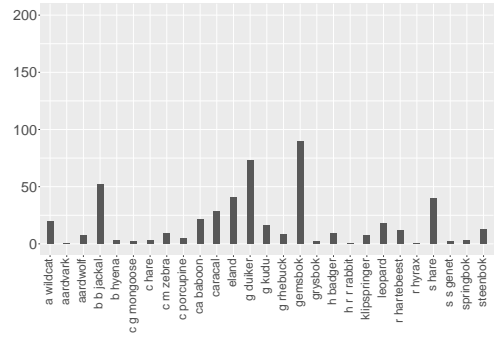
(g) $\overline{SS}$
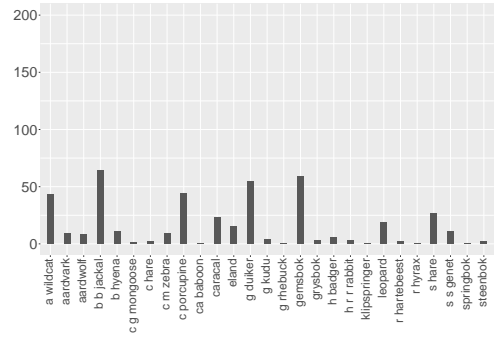
(h) $\overline{SS} + 1\text{h}$
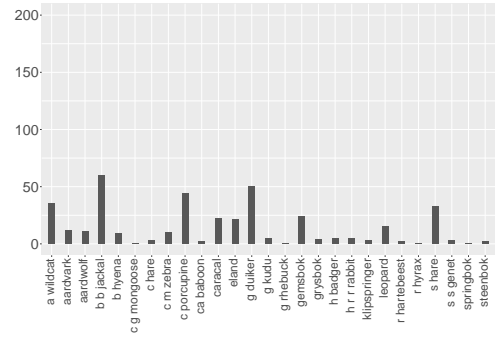
(i) $\overline{SS} + 2\text{h}$
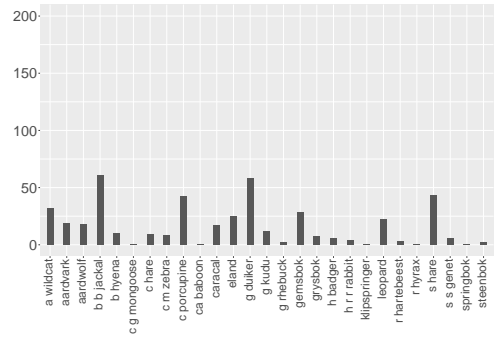
(j) $\overline{SS} + 3\text{h}$
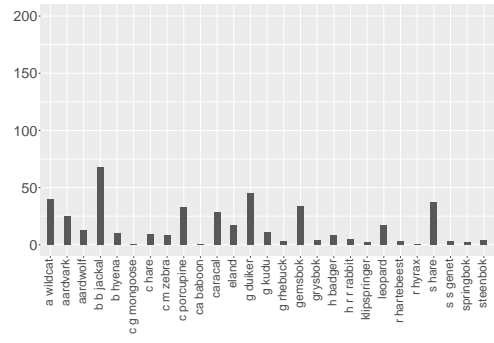
(k) $\overline{MN} - 2\text{h}$
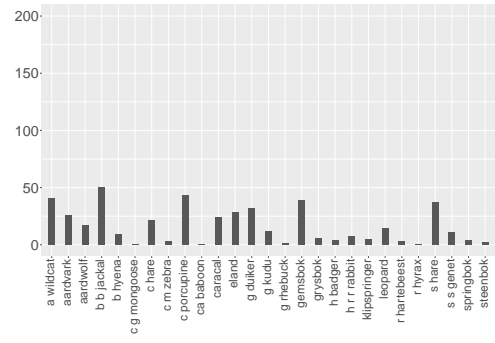
(l) $\overline{MN} - 1\text{h}$

Figure 3.2: Time-profile of mammal activity throughout the 24-hour cycle (continued).
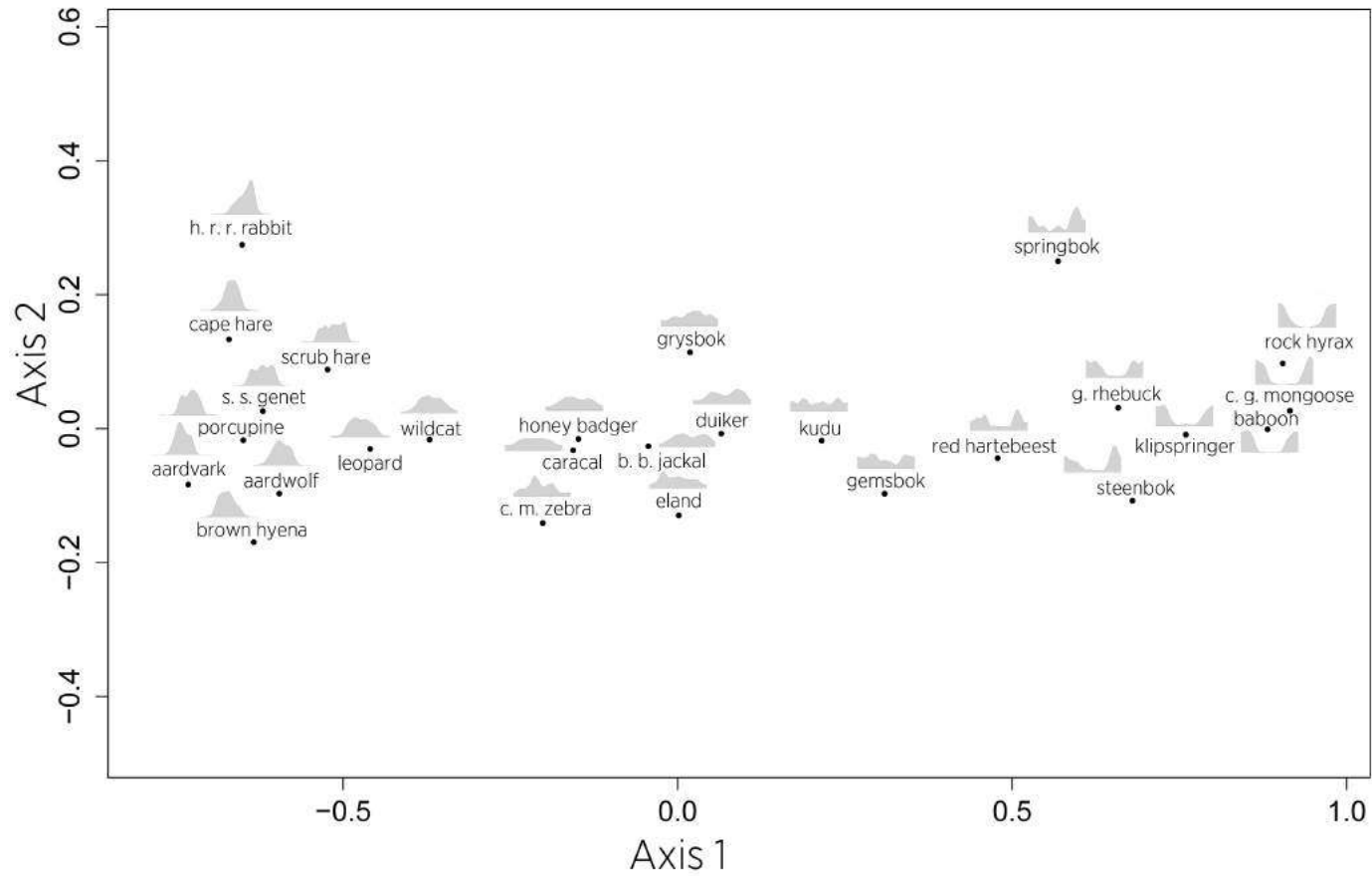A full caption is provided on p146.

(m) $\overline{MN}$

(n) $\overline{MN} + 1h$

(o) $\overline{MN} + 2h$

(p) $\overline{MN} + 3h$

(q) $\overline{SR} - 2h$

(r) $\overline{SR} - 1h$
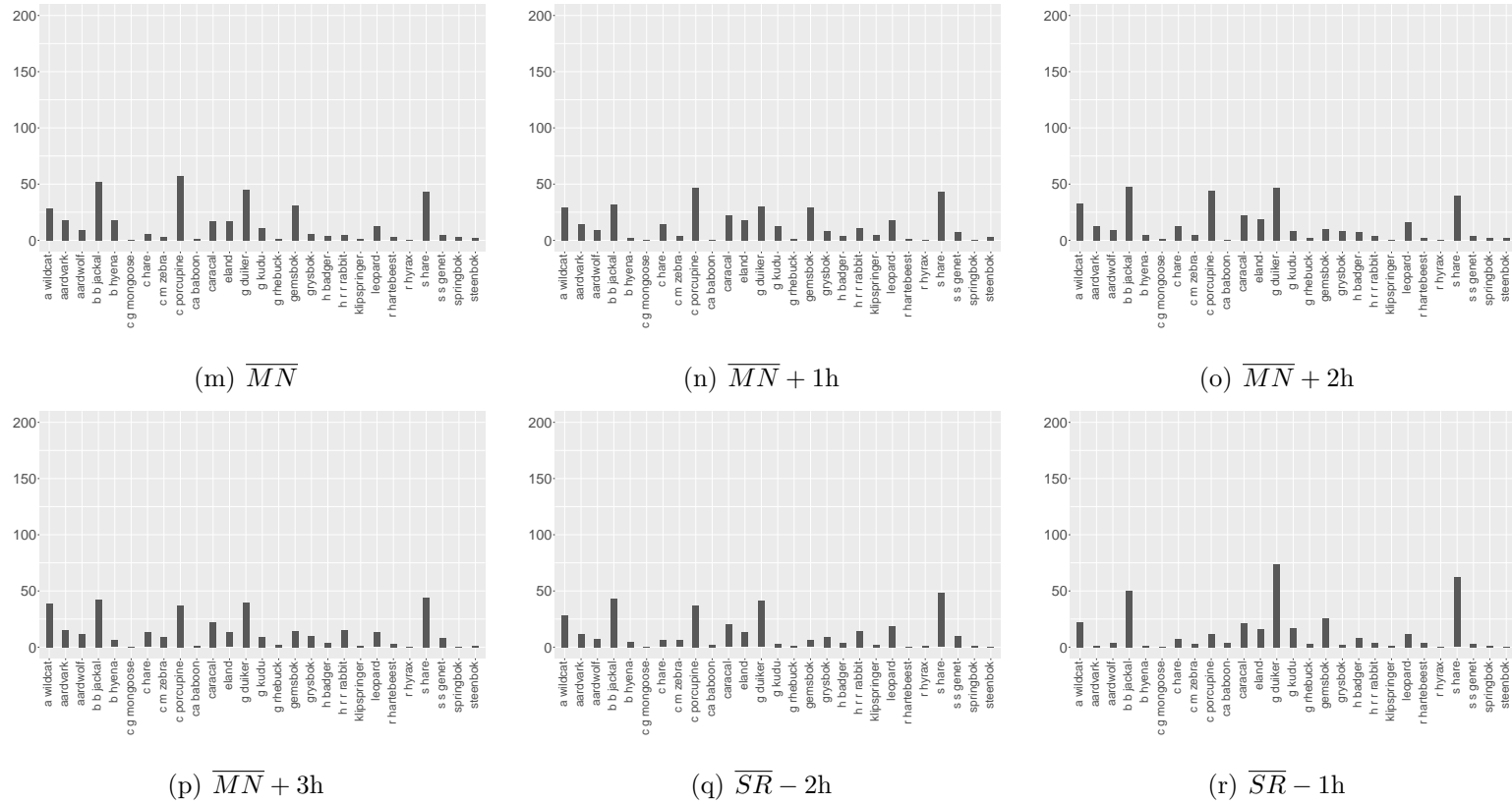
Figure 3.2: Time-profile of mammal activity throughout the 24-hour cycle (continued).
A full caption is provided on p146.

(s) $\overline{SR}$

(t) $\overline{SR} + 1\mathrm{h}$

(u) $\overline{SR} + 2\mathrm{h}$
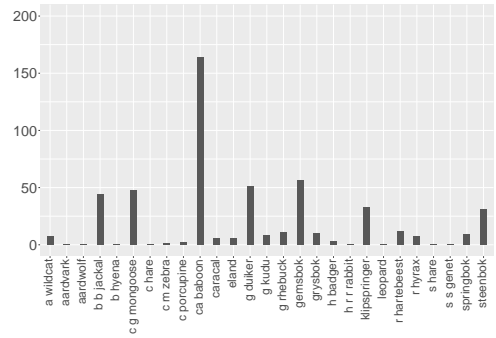
(v) $\overline{SR} + 3\mathrm{h}$
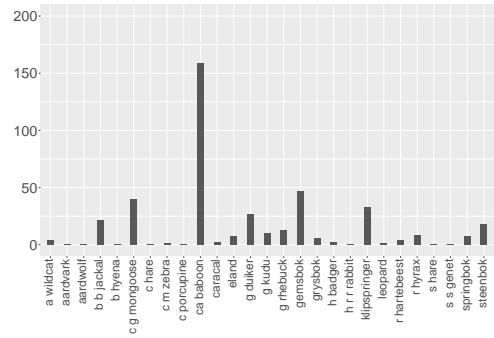
(w) $\overline{MD} - 2\mathrm{h}$

(x) $\overline{MD} - 1\mathrm{h}$

Figure 3.2: Time-profile of mammal activity throughout the 24-hour cycle (continued).
A full caption is provided on p146.

Figure 3.3: Non-metric Multi-Dimensional Scaling.
Dissimilarity study of the 27 mammals' diel activity rhythms in the Little Karoo. The stress value (0.032) indicated good fit. The kernel density functions of the diel activity rhythm of each species have been added to the NMDS display.
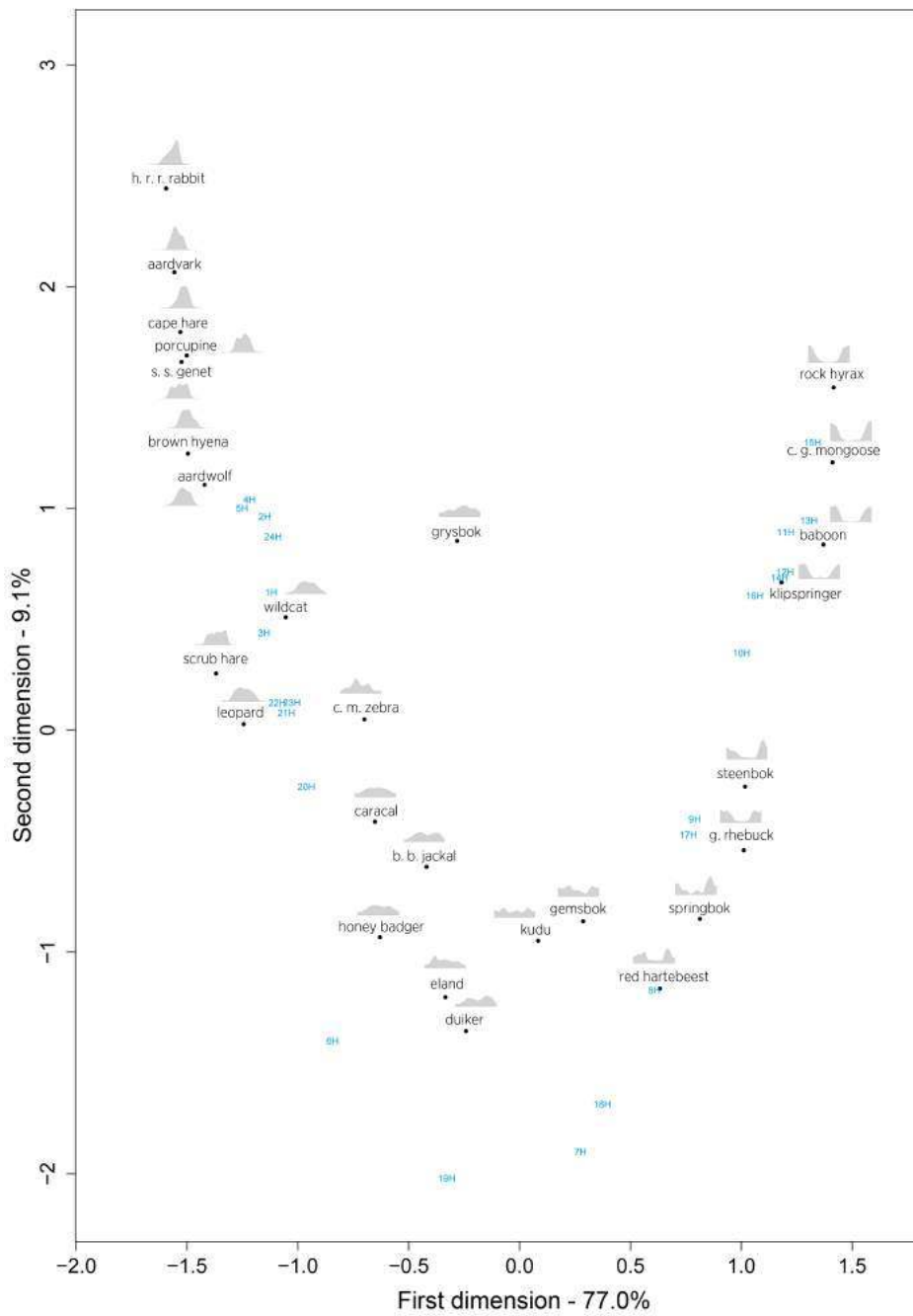
Figure 3.4: Correspondence analysis.

The kernel density functions of the diel activity rhythm of 27 mammal species in the Little Karoo, have been added onto the plot. For each 60-minute time period of the 24-hour cycle of time t', a time-profile (e.g. Fig. 3.2 p146) summarising the activity level of all species in the community, was plotted in blue. $\overline{SR}$ and $\overline{SS}$ represent the annual average of sunrise and sunset times; $\overline{MD}$ and $\overline{MN}$ represent true midday and midnight for the study area.
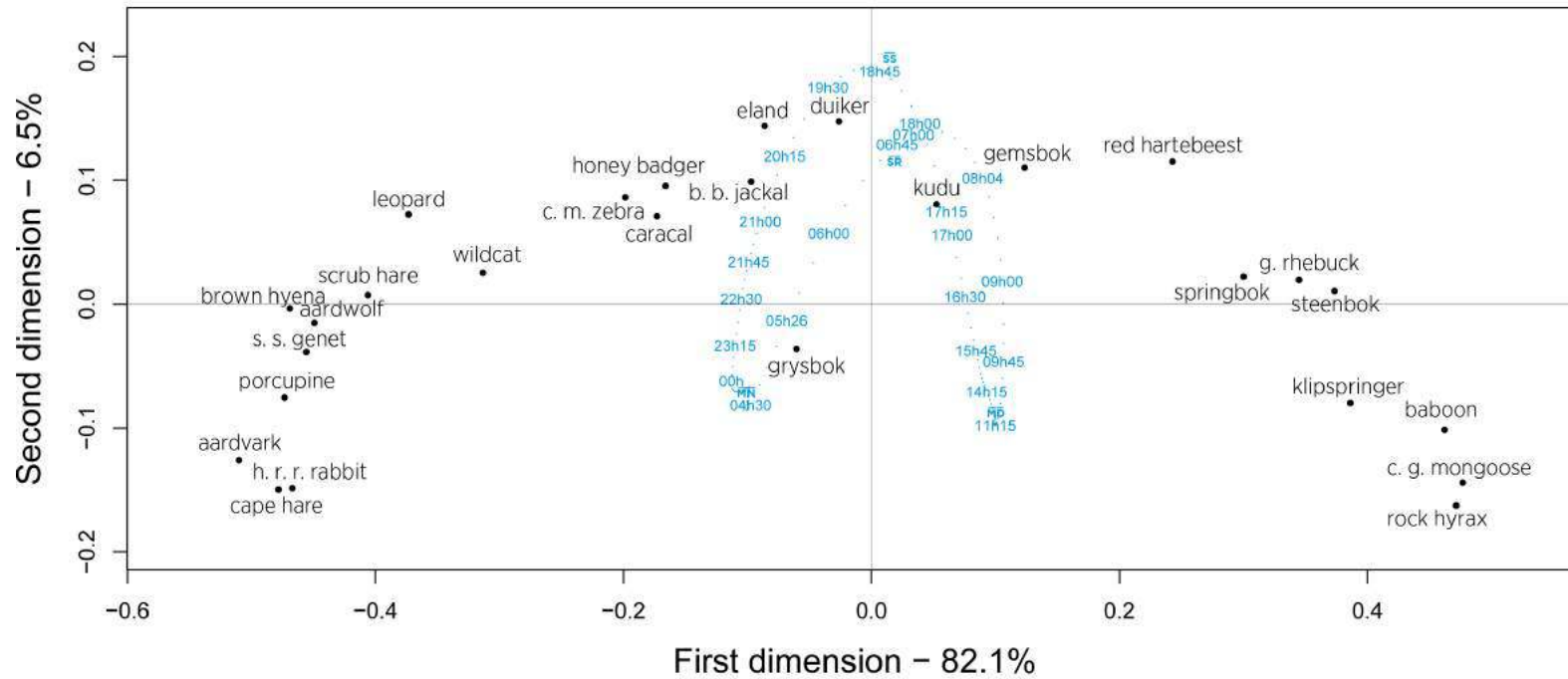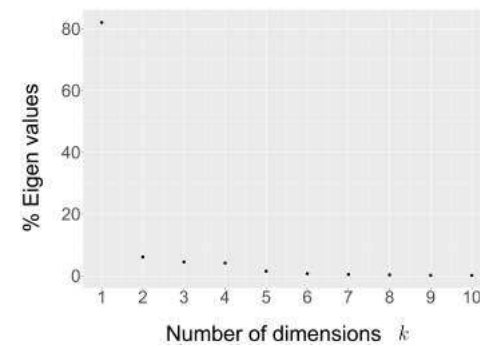
Figure 3.5: Covariance biplot.

The kernel density functions of the diel activity rhythm of 27 mammal species in the Little Karoo, have been added onto the plot. For each time interval (about 11 minutes) of the 24-hour cycle of time t', a time-profile (e.g. Fig. 3.2 p146) summarising the activity level of all species in the community, was plotted in blue. $\overline{SR}$ and $\overline{SS}$ represent the annual average of sunrise and sunset times; $\overline{MD}$ and $\overline{MN}$ represent true midday and midnight for the study area.
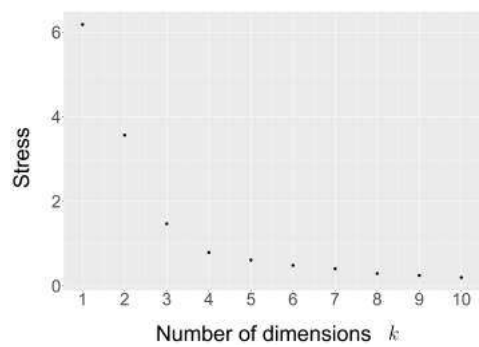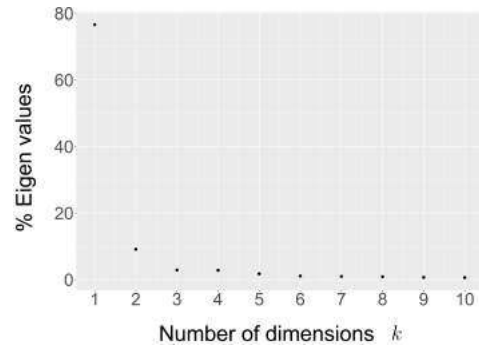
(a) NMDS   (b) CA   (c) Covariance biplot

Figure 3.6: Screeplots.

Screeplots show, in descending order of magnitude, the eigenvalues of a correlation matrix (or the stress value of an NMDS analysis); they help to visualise the relative importance of the factors and to decide on the adequate number of dimensions used in the analysis.
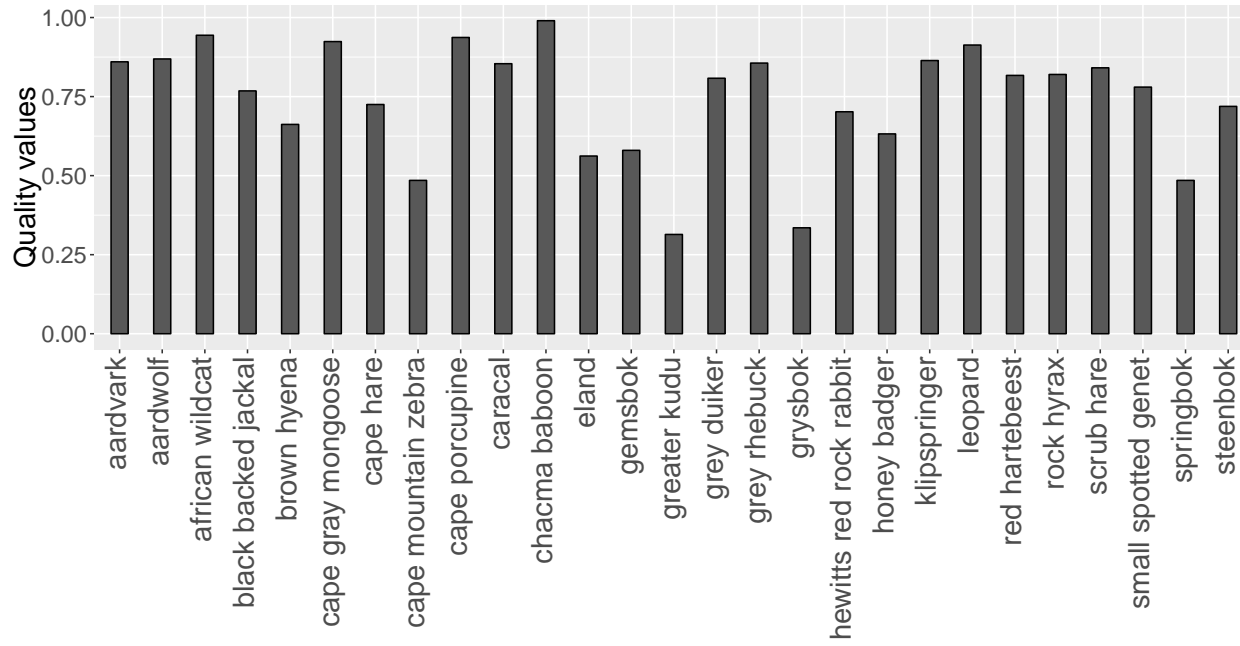
Figure 3.7: Quality values from the correspondence analysis, for the 27 mammal species of the Little Karoo.
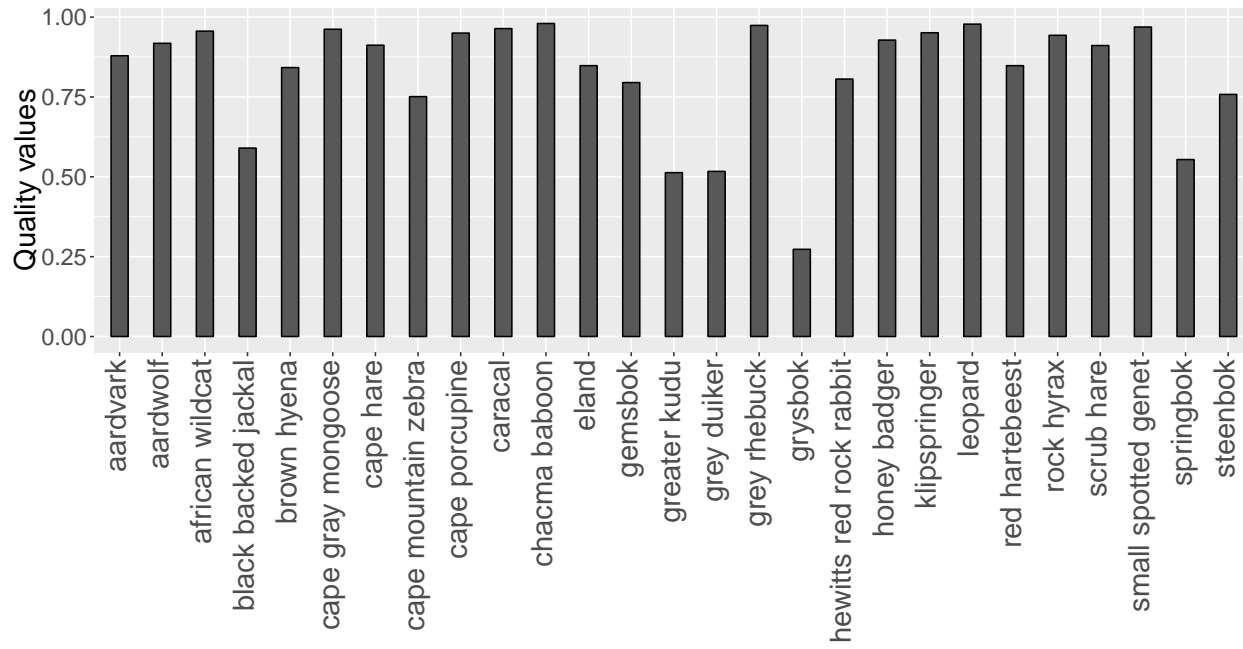
Figure 3.8: Quality values from the covariance biplot analysis, for the 27 mammal species of the Little Karoo.