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Exploring habitat use by cheetahs using ecological niche factor analysis

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Abstract

Understanding the basis of habitat choice having important implications for explaining the distribution of organisms, as well as helping to differentiate between habitats of different quality for effective management. In this study, the effects of sex, age and reproductive status on habitat use patterns of cheetahs *Acinonyx jubatus* in the Serengeti plains were explored using Ecological Niche Factor Analysis (ENFA). Our results showed that gender and territoriality did not affect patterns of habitat use. However, females tended to be more specialized when they were young than when they were older, displaying a more restricted ecological niche. Likewise, older females without cubs were more specialized than the same adult females with young cubs. This result did not hold for younger females. Altogether, the ENFA approach allowed us to (1) use the large amount of incidental sighting data collected over 12 years on cheetah spatial distribution; (2) identify the importance of reproductive status and age on the relationship between animals and their habitat; (3) further demonstrate that ENFA is applicable in a wide range of situations, including for exploring individual variation in niche definition.

Introduction

Resource and habitat selection are central themes in ecology, as these selective processes may facilitate species coexistence as well as being important driving forces in evolution and speciation (Lack, 1933; McPeek, 1996; Morris, 2003). Understanding the basis of habitat choice has important implications for explaining the distribution of organisms, as well as helping to differentiate among habitats of different quality for effective management. Knowledge of those habitat characteristics essential for the viability of a species can also provide crucial information to wildlife managers dealing with reintroductions, translocations and the development of new protected areas (Araujo & Williams, 2000; Rotenberry, Preston & Knick, 2006; Stamps & Swaisgood, 2007).

Information on habitat use patterns by carnivores is relatively sparse and is mostly based on home range size evaluation or comparison. Using this approach, home range size varies according to gender, age or reproductive status. For example, males generally have larger home ranges than females in Eurasian lynx *Lynx lynx* (Herfindal *et al*., 2005), leopard *Panthera pardus* (Mizutani & Jewell, 1998), Ethiopian wolf *Canis simensis* (Sillero-Zubiri & Gottelli, 1995) and tiger *Panthera tigris* (Sunquist, 1981; see Nilsen, Herfindal & Linnell, 2005 for a review). In contrast, territorial male cheetahs *Acinonyx jubatus* in the Serengeti have territories which average 50 km^2, while males without territories and females range over an average of 800 km^2 in their lifetimes (Caro, 1994; Laver, 2005). Reproductive status can also strongly influence home range size: for example, female mountain lions *Puma concolor* with cubs have smaller home ranges than females without cubs (Grigione *et al*., 2002). No such difference was reported for cheetah females (Bissett & Bernard, 2007). Finally, home range size can be influenced by age: thus, younger leopards and subadult Ethiopian wolves have smaller home ranges than older ones (Sillero-Zubiri & Gottelli, 1995; Mizutani & Jewell, 1998).

Nevertheless, home range size is not a direct measure of habitat use, and an animal could increase or decrease its home range size while using the same habitat features in exactly the same way. In this regard, some studies have explored how animals are located relative to certain habitat features (such as roads or areas of human activity) according to age, sex or reproductive status (Bunnefeld *et al*., 2006; Reynolds-Hogland & Mitchell, 2007). However, this type of approach focuses on particular, targeted habitat features, with a concomitant reduction in information on how animals relate to their habitat as a whole.

In this study, we explore variation in habitat use by cheetahs according to sex, age and reproductive status. To characterize habitat use, we used Ecological Niche Factor Analysis (ENFA; Hirzel *et al*., 2002). Up to now, ENFA has mainly been used to build habitat suitability maps (Reutter *et al*.,

2003; Chefaoui, Hortal & Lobo, 2005; Santos *et al.*, 2006). However, the aim of the ENFA is to identify general patterns in habitat use based on marginality and specialization, and the method relies on presence-only data (Basille *et al.*, 2008). The method can, therefore, also be used to compare the habitat selectivity of groups of individuals within a species.

Important environmental features that are expected to influence the presence of cheetahs include vegetation cover, roads, geographical features such as rocky outcrops (kopjes), the presence of predators and the availability of water and prey (Caro, 1994; Broomhall, Mills & du Toit, 2003; Muntifering *et al.*, 2006; Bissett & Bernard, 2007). Dense vegetation is believed to provide essential cover as a refuge from predators, as well as camouflage when stalking prey (Durant, 1998; Muntifering *et al.*, 2006). Based on this, cheetahs are expected to select areas where bushland and thickets are readily available (Hypothesis 1, H1). Roads have been demonstrated previously to affect the behaviour and performance of large carnivores (Corsi, Dupre & Boitani, 1999; Kerley *et al.*, 2002). Cheetahs are thought to avoid roads, as these tend to be used by tourists and predators such as lions *Panthera leo* and hyenas *Crocuta crocuta* [S. Durant, pers. comm.; (H2)]. Water is important, not only for consumption, but as a feature around which prey species tend to congregate (Durant *et al.*, 1988). However, for this very same reason other predators are also attracted to water features (Hopcraft, Sinclair & Packer, 2005); hence, cheetahs may tend to avoid major water features (H3). Kopjes provide important vantage points and are often located in male territories (Caro & Collins, 1987; Hopcraft *et al.*, 2005), so cheetahs are expected to actively select for kopjes (H4). Humans are generally the most common cause of death among carnivores (Cardillo *et al.*, 2004), both inside and outside protected areas (Woodroffe & Ginsberg, 1998): cheetahs are therefore expected to avoid human settlements (H5). Sex differences in space use have been suggested for cheetahs (Bissett & Bernard, 2007) and therefore were also expected in this analysis (H6). Territorial cheetah males occupy far smaller areas than non-territorial males (Caro, 1994): we therefore expect an effect of territoriality on space use in males (H7). Age and reproductive status are also expected to influence habitat use by females (Durant, 1998; Bunnefeld *et al.*, 2006). Reproductive success is lower among younger than older females (Pettorelli & Durant, 2007), and variation in reproductive success might, therefore, be linked to differences in habitat use across females. In particular, experience could increase females' selectivity, so that older females might better know their environment and have a more narrow ecological niche than younger females (H8). Similarly, females with young cubs can be expected to be particularly prudent and selective compared with females without cubs (Durant, 1998; Bunnefeld *et al.*, 2006; H9).

Materials and methods

Study site and cheetah data

Cheetahs of the south-eastern plains of the Serengeti National Park, Tanzania, have been studied continuously since 1969 (Caro, 1994). The region is characterized by an extensive grassland plain surrounded by *Acacia* and *Commiphora* woodland, irregularly interspersed with kopjes of granite and gneiss (Sinclair & Arcese, 1995; Durant *et al.*, 2007). Although cheetahs in the Serengeti are not radio-collared, large amounts of spatial information have been gathered on the population. Animals in the study area are located by scanning through binoculars from high vantage points. Once located, they are individually identified according to unique spot patterns on their pelage (Caro & Durant, 1991). Details of their GPS location, reproductive status (e.g. lactating or not) and the presence of dependent cubs are noted (Durant, Kelly & Caro, 2004). We considered 2153 female locations, 387 non-territorial male locations and 429 territorial male locations, all collected between 1993 and 2005. A male was considered to be territorial if it was observed scent marking in generally the same area. All the individuals considered were at least 2 years old (Caro, 1994). Because reproductive success is lower among younger (<4 years) females than among older ones (Pettorelli & Durant, 2007), we distinguished young females from the other females. We also distinguished mothers with young cubs (i.e. females accompanied with <5 months cubs or lactating females) from mothers without cubs.

Habitat variables

The choice of maps was based on features believed to be essential components of cheetah habitat, such as vegetation cover, landform, kopjes, roads, water features (rivers, lakes, larger water bodies) and human settlements (see Appendix S1). The main vegetation characteristics are represented by ecoregions, vegetation cover maps and average annual primary productivity from 1993 to 2003, as indexed by satellite data (see Appendix S1). The ecoregions occurring in the study area are the Serengeti volcanic grassland and the Southern *Acacia–Commiphora* bushlands, with a small patch of montane forest in both the north-eastern and south-eastern parts of the study area. Vegetation cover for the study site was categorized into six classes, depending on the type of vegetation and the amount of cover, as a percentage (Appendix S1). The study site is dominated by plains, with other landforms only making a minor contribution. The roads are a combination of main roads together with seasonal and administrative roads. Hills are randomly scattered within the study area, whereas kopjes occur more centrally and towards the north. Only one settlement occurs in the Park, with the remainder established outside the park boundaries. The main rivers and a dense network of tributaries occur mainly in the north and in a small area in the south-east. Two large water features (i.e. waterbody layer in our analysis) occur in the south of the area, while smaller lakes (i.e. the lake layer in our analysis) are mainly in the north. The common resolution of the maps that were used for the analysis was set at 30 m. This resolution represented a trade-off between accuracy and computation time (Chefaoui *et al.*, 2005).

Statistical analysis

We used an exploratory factor analysis technique (ENFA; Hirzel *et al.*, 2002) that does not require absence data to identify the environmental factors that best relate to the distribution of cheetahs in the study area. The principle of ENFA is to compare the distributions of ecogeographical variables (hereafter EGVs) between the presence dataset and the whole study area: it searches for directions in the ecological space so that (1) the difference between the conditions used on average by the species and the conditions available in the study area (termed the marginality) is maximized and (2) the ratio between the variance of available conditions and the variance of conditions used by the species (termed specialization) is maximized (Basille *et al.*, 2008). Marginality and specialization are uncorrelated factors, with the major information contained within the first factors (Hirzel *et al.*, 2002). A low marginality value (close to 0) indicates that the species tends to live in average conditions throughout the study area, whereas a higher value indicates a tendency to live in marginal habitats. Specialization on the other hand ranges from 1 to infinity and measures the choosiness of the species regarding the available range of EGVs. Tolerance is defined as the inverse of specialization (Hirzel *et al.*, 2002). A randomly chosen set of cells is expected to have a tolerance of 1, that is, any value below 1 indicates some form of specialization.

Three general ENFAs were carried out on (1) all the female observations made in the study area; (2) all the observations made on territorial males; (3) all the observations made on non-territorial males. The study area considered corresponds to the area known to be actively searched and where most sightings were made. The ENFA was performed using Biomapper 3.1 (Hirzel, Hausser & Perrin, 2004), following the procedures outlined by Hirzel *et al.* (2002). Before carrying out the analysis, all the EGV maps were normalized using the Box–Cox algorithm. The coefficients of each EGV that were computed by the ENFA should be interpreted with care: with distance maps, a high negative marginality value indicates the species' preference for the EGV considered (Appendix S1).

We evaluated the accuracy of the reported patterns by means of *k*-fold cross-validation (Sattler *et al.*, 2007), and *k* was determined using Huberty's rule (Fielding & Bell, 1997). We computed three presence-only evaluation measures, the Absolute Validation Index (AVI), the Contrast Validation Index (CVI; Sattler *et al.*, 2007) and the continuous Boyce's Index (BI; Hirzel *et al.*, 2006). AVI indicates how well the model discriminates high-suitability from low-suitability areas and varies from 0 to 1, while CVI indicates how much the AVI differs from what would have been obtained with a random model and varies from 0 to AVI. BI varies from −1 to 1, with 0 indicating a random model. Four classes of habitat suitability were determined in order to estimate AVI and CVI (Sattler *et al.,* 2007). A window width of 20 was considered to estimate BI (Hirzel *et al.*, 2006). For all these measures (AVI, CVI and BI), high mean values indicate a high consistency with evaluation datasets, while lower standard deviations indicate more robust predictions.

To explore the effect of age and reproductive status on habitat use by females, we compared the outcomes of the ENFA based on young females with or without cubs, and on adult females with or without cubs. The same females were used in each of the four comparisons. To determine whether tolerance significantly differed between groups, we performed 100 spatial bootstraps for each of the eight groups. We then performed an ENFA on each of the 800 spatial samples obtained. This allowed us to generate a distribution for each tolerance value associated with each of the eight groups. We subsequently compared these distributions using *t* tests (Sokal & Rohlf, 1995).

Results

According to the ENFA analyses (Tables 1–3), habitat use did not differ between the sexes or between territorial and non-territorial males in the study area. Based on broken-stick heuristics (Jackson, 1993), the 18 environmental variables were reduced to three factors in all cases, totalling 77% of overall information for females, 92% for non-territorial males and 82% for territorial males. The same patterns of habitat use were observed in all cases: the presence of cheetahs was positively associated with roads, kopjes, medium vegetation cover (i.e. high selection for 40% of shrubs, slight selection for 60% of shrubs), rivers and lakes, and negatively associated with montane forest, hills, settlements, large water bodies and densely vegetated areas. Marginality reached 1.04 for females, 1.13 for non-territorial males and 1.08 for territorial males. Tolerance was estimated as 0.56 for females ($N = 2153$ locations), 0.31 for non-territorial males ($N = 387$ locations) and 0.44 for territorial males ($N = 429$ locations), suggesting that cheetahs were relatively specialized and selected for relatively marginal habitats. The accuracy of the reported patterns was high, as all indices pointed to the generated model being different from random (females: AVI = 0.45 ± 0.15; CVI = 0.30 ± 0.15; BI = 0.80 ± 0.10; for $k = 5$; non-territorial males: AVI = 0.46 ± 0.15; CVI = 0.31 ± 0.11; BI = 0.72 ± 0.16; for $k = 5$; territorial males: AVI = 0.50 ± 0.16; CVI = 0.35 ± 0.14; BI = 0.80 ± 0.31; for $k = 5$).

Age and reproductive status had effects on habitat use patterns of female cheetahs (Table 4). The same females were generally more specialized when they were young (<4 year of age) than when they were adult, whether they had young cubs (<5 months) or not (both $P < 0.001$). Contrary to our predictions, adult females without cubs were also more specialized than the same adult females with young cubs ($P < 0.001$). This result did not hold for young females ($P > 0.05$).

Discussion

The results regarding habitat use by cheetahs are mostly in accordance with initial hypotheses (H1–H5). Cheetahs were first found to select for vegetation cover, in line with results obtained in other ecosystems (Broomhall *et al.*, 2003; Muntifering *et al.*, 2006; Bissett & Bernard, 2007), and

Table 1 Scores extracted from the general ENFA performed on all the female locations (*N*=2153)

Ecogeographical variables	Factor 1 marginality	Factor 2 specialization	Factor 3 specialization
Distance to the East African montane forest	0.33	0.77	0.27
Distance to hills	0.22	−0.07	−0.11
Integrated Normalized Difference Vegetation Index	0.006	−0.002	−0.72
Distance to kopjes	−0.48	0.04	0.09
Distance to lakes	−0.36	0.19	−0.02
Distance to valley	0.08	−0.07	0.03
Distance to waterbody	0.27	−0.30	−0.05
Distance to alluvial plain	−0.02	0.10	0.36
Distance to hills and montane footridge	0.08	−0.25	0.03
Distance to rivers	−0.06	−0.02	0.03
Distance to roads	−0.45	0.10	−0.10
Distance to human settlement	0.18	0.19	0.16
Distance to trees (cover around 100%)	0.30	−0.10	−0.38
Distance to trees (with a cover averaging 60%)	0.02	0.36	−0.004
Frequency of shrubs(cover around 100%)	−0.16	−0.02	−0.008
Distance to shrubs (with a cover averaging 60%)	−0.08	−0.03	−0.21
Frequency of shrubs (with a cover averaging 40%)	0.16	−0.02	0.16
Distance to grassland (cover around 100%)	−0.08	0.10	0.10
% variance explained	22	22	10

Marginality was estimated as 1.04, tolerance as 0.56. Three factors were retained using the broken-stick heuristics, explaining 77% of the information.
ENFA, Ecological-Niche Factor Analysis.

Table 2 Scores extracted from the general ENFA performed on non-territorial male locations (*N*=387)

Ecogeographical variables	Factor 1 marginality	Factor 2 specialization	Factor 3 specialization
Distance to the East African montane forest	0.29	0.81	−0.71
Distance to hills	0.10	−0.05	0.15
Integrated Normalized Difference Vegetation Index	0.01	0.02	−0.11
Distance to kopjes	−0.49	0.05	−0.07
Distance to lakes	−0.33	0.12	−0.03
Distance to valley	0.12	0.01	−0.03
Distance to waterbody	0.24	−0.28	0.29
Distance to alluvial plain	−0.03	0.15	−0.05
Distance to hills and montane footridge	0.04	−0.09	−0.4
Distance to rivers	0.005	−0.006	−0.02
Distance to roads	−0.48	0.10	0.02
Distance to human settlement	0.15	0.09	0.30
Distance to trees (cover around 100%)	0.32	−0.24	0.26
Distance to trees (with a cover averaging 60%)	0.06	0.36	−0.09
Frequency of shrubs (cover around 100%)	−0.21	−0.05	−0.05
Distance to shrubs (with a cover averaging 60%)	−0.14	0.03	−0.03
Frequency of shrubs (with a cover averaging 40%)	0.18	−0.04	−0.02
Distance to grassland (cover around 100%)	−0.11	0.03	0.18
% variance explained	68.4	10.4	4.5

Marginality was estimated as 1.13, tolerance as 0.31. Three factors were retained using the broken-stick heuristics, explaining 92% of the information.
ENFA, Ecological-Niche Factor Analysis.

consistent with Durant's (1998) suggestion that the availability of vegetation cover could be the key to cheetah survival in the Serengeti. Cover indeed provides safe denning sites for cubs (Laurenson, 1995*a*) and is required for stalking (Fitzgibbon, 1990; Caro, 1994), concealment from other predators and resting (Paulson, 1985; Caro, 1994; Mills, Broomhall & du Toit, 2004). According to our results however, cheetahs tended to avoid the most densely

Table 3 Scores extracted from the general ENFA performed on territorial male locations ($N = 429$)

Ecogeographical variables	Factor 1 marginality	Factor 2 specialization	Factor 3 specialization
Distance to the East African montane forest	0.26	0.84	0.15
Distance to hills	0.26	−0.16	0.03
Integrated Normalized Difference Vegetation Index	−0.04	0.01	−0.51
Distance to kopjes	−0.53	0.05	−0.09
Distance to lakes	−0.33	0.12	−0.03
Distance to valley	0.06	−0.07	−0.16
Distance to waterbody	0.17	−0.29	−0.29
Distance to alluvial plain	−0.04	0.08	0.39
Distance to hills and montane footridge	0.15	0.004	−0.33
Distance to rivers	−0.04	−0.02	0.003
Distance to roads	−0.39	0.06	0.006
Distance to human settlement	0.16	0.05	0.37
Distance to trees (cover around 100%)	0.31	−0.19	−0.31
Distance to trees (with a cover averaging 60%)	0.11	0.32	−0.17
Frequency of shrubs (cover around 100%)	−0.22	0.02	−0.08
Distance to shrubs (with a cover averaging 60%)	−0.18	0.04	−0.17
Frequency of shrubs (with a cover averaging 40%)	0.15	0.02	0.16
Distance to grassland (cover around 100%)	−0.14	0.05	0.07
% variance explained	27	27	10

Marginality was estimated as 1.08, tolerance as 0.44. Three factors were retained using the broken-stick heuristics, explaining 82% of the information.
ENFA, Ecological-Niche Factor Analysis.

Table 4 Results of the ENFAs performed for each subgroup of females

Category	N_f	N_{obs}	T	Mean (T)	Test	P
Young females without cubs	34	173	0.22	0.19	$T = 9.63$	< 0.001
Adult females without cubs	34	236	0.24	0.23		
Adult females with young cubs	41	193	0.23	0.22	$T = 7.13$	< 0.001
Adult females without cubs	41	294	0.20	0.20		
Young females with young cubs	23	63	0.12	0.09	$T = 31.74$	< 0.001
Adult females with young cubs	23	104	0.16	0.14		
Young females with young cubs	38	95	0.28	0.21	$T = 0.97$	> 0.05
Young females without cubs	38	173	0.21	0.20		

N_f, number of females considered; N_{obs}, number of observations considered; T, tolerance estimated by performing the ENFA on all the data available (Tolerance = 1/Specialization); mean (T), mean tolerance from the boostraps; Test, t-test value comparing the two tolerance estimates; P, probability associated with the t-test performed; ENFA, Ecological-Niche Factor Analysis.

vegetated areas. However, a negative association between cheetah sightings and these areas might also be generated by a decrease in visibility with increased vegetation density (a factor we could not correct for in these analyses). Kopjes, a feature actively selected for by cheetahs in this study, were previously described by Caro & Collins (1987) as an important component of male territories in the Serengeti plains. Our study demonstrates that both sexes select for those rocky outcrops in the study area. As expected, cheetahs avoided large water features as well as human settlements. The avoidance of human settlements by large carnivores is not always the rule, with frequent reports of cheetahs killing livestock in Namibian farmlands (Marker *et al.*, 2003). In our study area, however, high concentrations of prey are found in the park (Durant *et al.*, 1988; Caro, 1994).

The only result that deviates from the original hypotheses is the positive association between cheetah sightings and roads. This unlikely result might be explained by several mechanisms. First, it could be an artefact reflecting higher search effort near roads, since the plains are searched using vehicles. An underlying assumption in the ENFA is that the different habitats considered have been searched with equal effort. Habitats that are searched more intensively will have higher detection frequencies and might be interpreted by the ENFA as being favourable cheetah habitats (Brotons *et al.*, 2004). We do not have relevant data to completely exclude this hypothesis. However, to the best of our knowledge, all habitat types are searched relatively equally, and roads are not strongly favoured while searching for cheetahs. We therefore believe that the reported correlation is more likely to be driven by a strong spatial correlation between the

occurrence of roads, the occurrence of lakes and the occurrence of kopjes (Appendix S1). To explore these issues further, radio-collared animals would be needed.

Surprisingly, gender and territoriality did not affect the patterns of habitat use and all animals selected for or avoided the same habitat features. Contrary to our hypothesis, females were more specialized regarding the use of their habitat when they were young than when they were older, whether these females were accompanied by young cubs or not. At least two mechanisms could explain this result: first, Laurenson (1995*b*) reported that young females hunted more often than older females. If habitat selection is linked to activity as suggested by previous habitat selection analyses on cheetahs (Broomhall *et al.*, 2003), and if cheetahs favour certain type of landscape features to hunt, then young females could appear to be more habitat-specialist than older females. Second, females confidence in exploring different habitat types may increase with age. Predation by lions and hyenas on cheetahs focuses on cubs (Laurenson, 1994), so that individuals might learn that predators pose a lesser threat to their own survival as they age. Also, females might become more experienced at spotting and avoiding predators as they age. Young females might therefore tend to select known features and habitats that they associate with safer environments, while the same females might have gained sufficient confidence as adults to use a greater diversity of habitats. This mechanism could explain the findings of several studies that show that younger carnivores have smaller home ranges than older ones (Sillero-Zubiri & Gottelli, 1995; Mizutani & Jewell, 1998).

Also surprising was the finding that adult females without cubs were reported to be more specialized than the same adult females with young cubs. The explanation might lie in mobility differences. Mobility has been suggested to be the key to the coexistence of cheetahs with hyenas and lions (Durant, 1998). By constantly moving, cheetahs may be able to increase spatial avoidance of their main competitors, allowing coexistence. Females with young cubs, however, have reduced mobility as cubs are confined to a den during their first 2 months (Laurenson, 1994) and have reduced mobility in the initial months after the cubs have emerged from the den. Adult females with young cubs might therefore be less selective than the same females without cubs and be forced to exploit all habitats surrounding the den. This decrease in selectivity echos a previous result which showed that lactating females were more likely to be found near lions, and were thus more likely to risk predation than free ranging individuals (Durant, 1998).

Understanding how organisms explore and exploit their environment is a central topic in ecology, and the assessment of factors affecting their habitat use is of great value for conservation. Altogether, the ENFA approach has allowed us to use the large amount of information collected over the years on cheetah spatial distribution in the Serengeti plains to explore habitat use in this species, and to identify the importance of reproductive status and age on the relationship between cheetah females and their habitat. Previous attempts to characterize habitat selection patterns by cheetahs relied on small numbers of radio-collared animals [Kruger National Park: $n = 7$ (Broomhall *et al.*, 2003); Eastern Cape province, South Africa: $n = 10$ (Bissett & Bernard, 2007)], whereas we were able to consider more than 100 individuals of known-age. Our analyses also demonstrate the relevance of ENFA in habitat use studies, giving a full picture of how the ecological niche of an individual might vary according to its condition. We believe such an approach could be easily undertaken in various situations where presence data only are available, given that spatial information on habitat characteristics exists at the relevant scale. Moreover, Biomapper is a well-detailed, highly accessible and user-friendly free software (http://www2.unil.ch/biomapper/). Such an approach can shed insights on the relationship between animals and their habitat, especially when radio-collaring is not an option.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Primary productivity

Figure S1. Locations of the cheetahs and study area. The locations are represented using black circles, red spot represent the kopjes, light blue spots the small lakes (their size have been enhanced for readability) and the dark blue lines represent the roads. The black polygon represents the study area.

Table S1. Habitat features used in the ENFA analysis.

Table S2. Effect of age on the marginality factor. N: number of females considered.

Table S3. Effect of reproductive status on the marginality factor. N: number of females considered.

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