

The spatial scaling of habitat selection by African elephants

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Summary

1. Understanding and accurately predicting the spatial patterns of habitat use by organisms is important for ecological research, biodiversity conservation and ecosystem management. However, this understanding is complicated by the effects of spatial scale, because the scale of analysis affects the quantification of species–environment relationships.
2. We therefore assessed the influence of environmental context (i.e. the characteristics of the landscape surrounding a site), varied over a large range of scales (i.e. ambit radii around focal sites), on the analysis and prediction of habitat selection by African elephants in Kruger National Park, South Africa.
3. We focused on the spatial scaling of the elephants' response to their main resources, forage and water, and found that the quantification of habitat selection strongly depended on the scales at which environmental context was considered. Moreover, the inclusion of environmental context at characteristic scales (i.e. those at which habitat selectivity was maximized) increased the predictive capacity of habitat suitability models.
4. The elephants responded to their environment in a scale-dependent and perhaps hierarchical manner, with forage characteristics driving habitat selection at coarse spatial scales, and surface water at fine spatial scales.
5. Furthermore, the elephants exhibited sexual habitat segregation, mainly in relation to vegetation characteristics. Male elephants preferred areas with high tree cover and low herbaceous biomass, whereas this pattern was reversed for female elephants.
6. We show that the spatial distribution of elephants can be better understood and predicted when scale-dependent species–environment relationships are explicitly considered. This demonstrates the importance of considering the influence of spatial scale on the analysis of spatial patterning in ecological phenomena.

Key-words: distribution, environmental context, habitat suitability, Kruger National Park, *Loxodonta africana*, model prediction, niche modelling, scale

Introduction

Ecology is fundamentally concerned with understanding the relationships between organisms and their environment.

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Because issues of spatial scale influence the quantification of these relationships, the influence of scale on habitat selection is currently highly debated (Levin 1992; Wheatley & Johnson 2009). Scale is usually expressed in terms of *resolution* (i.e. the detail of data; in rasters the grid cell size) and *extent* (i.e. the areal coverage of the data or study area), and no question in spatial ecology can be answered without referring explicitly to these components at which data are measured or analysed (Wiens 1989). Beyond these scale components, the importance of spatial context is increasingly being recognized (Guisan *et al.* 2006; Wheatley & Johnson 2009), because habitat selection may depend not only on site-specific characteristics, but also on the characteristics of the landscape surrounding a site, that is: *environmental context* (Holland, Bert & Fahrig 2004; Guisan *et al.* 2006). This raises a third-scale component: the *range* (i.e. the ambit radius) at which environmental context is considered.

Since we often have no *a priori* knowledge about the scales at which species respond to environmental heterogeneity, it is important to identify characteristic scales of this response to avoid a mismatch between the scale(s) used for analyses, and the one(s) at which habitat selection occurs (Wheatley & Johnson 2009; De Knegt *et al.* 2010). If different components of scale (resolution, extent or range) are changed simultaneously, one cannot decouple the importance of each if patterns change among scales (Wheatley & Johnson 2009). However, analysing how species–environment relationships depend on the range of environmental context, within the constraints set by the resolution and extent of the data, may provide the solution required to study the spatial scaling of species–environment relationships, as it may provide clues as to which scales are ecologically most relevant to the species of interest (Van Langevelde 2000; Holland, Bert & Fahrig 2004; De Knegt *et al.* 2010). Yet, the scales of analyses are often chosen arbitrarily with no biological connection to the system of study (Wheatley & Johnson 2009), and the number of ambit radii used, if any, is often limited (but see Pinto & Keitt 2008; Schmidt *et al.* 2008).

When better understanding the scale at which environmental context influences habitat selection, the predictive capacity of species distribution models can be increased. In recent years, such models have become an important tool to address issues in research, biodiversity conservation and management (Guisan *et al.* 2006). Such models are especially important for decisions regarding threatened species (e.g. black rhinoceros, *Diceros bicornis*) or those that play an important biotic role in the ecosystem (e.g. African elephants, *Loxodonta africana*). In this paper, we study the influence of the spatial scaling of environmental context on habitat selection by African elephants in Kruger National Park, South Africa. We focus specifically on the scaling of the elephants' response to food and water resources, because these are known to be key determinants of elephant distribution (Chamaille-Jammes, Valeix & Fritz 2007a,b; Smit, Grant & Devereux 2007a; Smit, Grant & Whyte 2007b; Van Aarde *et al.* 2008). We aimed at testing whether the explicit consideration of environmental context at appropriate scales

improves the understanding and predictability of habitat selection by elephants. We differentiate between dry and wet season habitat selection, since water is widely available during the wet season, whereas seasonal water sources dry up in the dry season (Van Aarde *et al.* 2008). Moreover, because several authors have observed sexual differences in foraging ecology of elephants (Stokke & Du Toit 2000; Smit, Grant & Whyte 2007b; Shannon *et al.* 2010), we analyse habitat selection by male and female elephants separately. By doing so, we aimed at increasing our understanding of the mechanisms behind elephant distribution and demonstrate methods to study the spatial scaling of habitat selection.

Materials and methods

STUDY AREA AND SPECIES

Kruger National Park (KNP) is South Africa's largest nature reserve, covering roughly 19 000 km² and harbouring close to 14 000 elephants. Besides linking habitat selection by the elephants in KNP to the distribution of food and water resources, we also included topographic and climatic variables in our analyses, as these have been shown to influence space usage by elephants (Nellemann, Stein & Rutina 2002; Wall, Douglas-Hamilton & Vollrath 2006). Below, we describe the environmental variables that we used in our analyses, which were all inserted into a geographic information system (GIS) and formatted to a regular grid with 1-km resolution for the entire KNP (Fig. 1). This resolution corresponded to the resolution of the coarsest input data and made ample analyses computationally feasible. The names of the environmental variables and corresponding abbreviations are listed in Table 1.

Vegetation characteristics

In our analyses, we used two structural components of vegetation; tree and herbaceous vegetation. The tree cover (TC; woody plants taller than 1.3 m) was estimated from combined optical (Landsat ETM+) and radar (JERS-1) imagery calibrated with field data, as described by Bucini *et al.* (2010). It resulted in a 90-m resolution woody cover map, which we averaged across the 1-km² grid cells. A 500-m resolution herbaceous biomass (HB) data layer was created through interpolating field records from various sites across the park (with $n = 533$ and the sites being proportionally representative of the different landscapes in the park). The methods for the field records are described in Trollope & Potgieter (1986), and the interpolation using co-kriging is described by Smit, Grant & Whyte (2007b). As vegetation heterogeneity (VH) has also been identified as a determinant of elephant distribution (Murwira & Skidmore 2005), we included the coefficient of variation of TC across each 1-km² grid cell in our analyses thereby being a proxy for the structural VH.

Surface-water availability

Six perennial rivers cross the park from west to east, while 14 ephemeral rivers only contain surface water during a large part of the wet season (Smit, Grant & Whyte 2007b). In addition, KNP contains around 300 water points (pans and artificial boreholes). Using data on rivers and water points, dry and wet season distance-to-water layers were created, calculated as the Euclidean

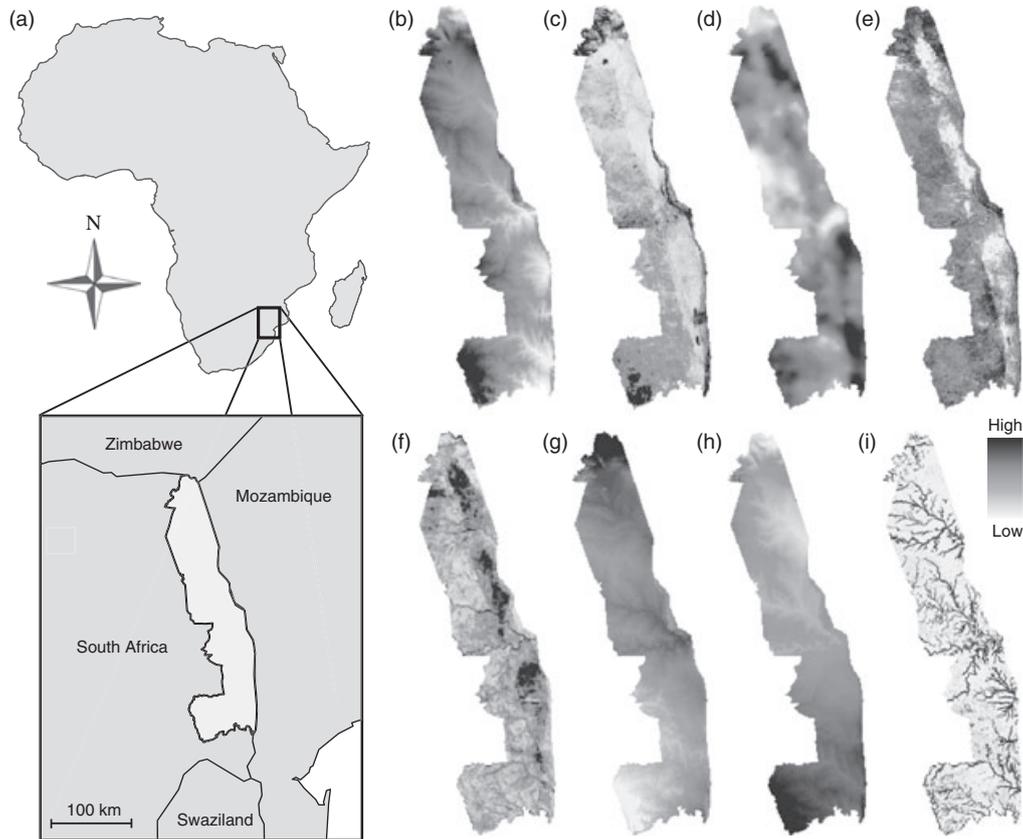


Fig. 1. (a) The location of the study area and maps of the environmental variables: (b) elevation, (c) slope, (d) herbaceous biomass, (e) tree cover, (f) vegetation heterogeneity, (g) mean annual temperature, (h) mean annual rainfall and (i) water occurrence. The variables are mapped at a resolution of 1 km².

Table 1. Correlation between the environmental variables used in our analyses. Values depict the Pearson correlation coefficients

| Environmental variable | Abbreviation | Temp | Prec | dWP | dR | Slope | Elev | VH | WO | TC |
|--------------------------|--------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Herbaceous biomass | HB | -0.39 | 0.56 | -0.03 | 0.33 | 0.07 | -0.01 | 0.27 | 0.03 | -0.31 |
| Tree cover | TC | -0.25 | 0.19 | 0.07 | -0.11 | 0.32 | 0.18 | -0.69 | -0.04 | |
| Water occurrence | WO | 0.15 | -0.04 | 0.04 | -0.07 | 0.03 | -0.22 | 0.21 | | |
| Vegetation heterogeneity | VH | 0.25 | -0.15 | -0.07 | 0.08 | -0.15 | -0.28 | | | |
| Elevation | Elev | -0.58 | 0.19 | -0.17 | 0.08 | 0.23 | | | | |
| Slope | Slope | -0.38 | 0.47 | 0.17 | -0.15 | | | | | |
| Distance to river | dR | -0.23 | 0.16 | -0.25 | | | | | | |
| Distance to water point | dWP | 0.15 | 0.02 | | | | | | | |
| Precipitation | Prec | -0.85 | | | | | | | | |
| Temperature | Temp | | | | | | | | | |

distance of the centroid of each grid cell to the nearest water source. The artificial water points and perennial rivers were assumed to carry water year-round, whereas the ephemeral rivers and pans were assumed to have water only during the wet season. As other studies found elephants in the study area to be more attracted to the river system than to artificial water points (Smit, Grant & Whyte 2007b; Grant *et al.* 2008), we differentiated between distance to the nearest water-carrying river (dR), distance to the nearest water point (dWP) or distance to the nearest source of water regardless of which type (dW). Furthermore, we used aerial census data of surface-water sightings in each 1 km² grid cell over a 17-year period. These data resulted in a water occurrence

(WO) data layer, representing the number of surface-water sightings per km² over the 17-year period.

Topography and weather conditions

A 90-m resolution Shuttle Radar Topography Mission (SRTM) elevation model (Jarvis *et al.* 2008) was used to represent the surface elevation across KNP, which ranges from 100 to 840 m a.s.l. The mean elevation (Elev) and slope (Slope) in each 1-km² grid cell were used in the analyses. Furthermore, we used the WorldClim data set (Hijmans, Cameron & Parra 2007) to represent the weather conditions in the study area. Mean annual rainfall (Prec) varied from 400 to

940 mm, and mean annual temperature (Temp) varied from 19.5 to 24.5 °C.

Correlations between environmental variables

To explore the correlation structure between the environmental variables used in our analyses, we calculated Spearman correlation coefficients between each pair of environmental variables (Table 1). The correlations between the environmental variables were generally low, except for the correlation between temperature and precipitation (−0.85), temperature and elevation (−0.58), precipitation and HB (0.56), and TC and VH (−0.69). The latter correlation means that areas with high TC in the study area are relatively homogenous regarding the structure of vegetation.

Elephant occurrence data

Data on elephant habitat use were obtained from 33 elephants (19 females and 14 males; Appendix S1, Supporting information) deployed with global positioning system (GPS) collars (Hawk105 collars, Africa Wildlife Tracking cc., South Africa). To acquire a robust estimate of habitat usage while minimizing battery drainage, we recorded the elephants' locations at hourly intervals. Over a three-year period (2005–2008), this resulted in 218 065 recorded locations. Although the collar data provided locations of individual elephants, we analysed the data on a population level thereby corresponding to a commonly used type II design as described by Manly, McDonald & Thomas (1993). For the female elephants, which live in family herds, only one individual was collared per herd, minimizing the influence of non-independence between individuals.

The precision of the GPS fixes was assessed using points ($n = 11\,244$) recorded when the collars were located at known stationary locations: the Skukuza and Tanda Tula research stations. The deviations from these known locations followed a bivariate normal distribution (x -directional normality: $P = 0.300$, y -directional normality: $P = 0.279$, x - y correlation: Pearson's $r = 0.08$), with 95% of the points situated within 27.8 m from the sites' geometric centroids. The maximum deviation from these centroids was 151.9 m, which is still small relative to the resolution of our analyses. Although mountainous terrain and high canopy cover can lead to biased GPS fix-rates (D'Eon *et al.* 2002; Frair *et al.* 2004), the terrain in our study area is relatively level, and the vegetation is generally open (low TC), such that we could not find an indication that these factors influenced the fix-rates of the GPS collars (no correlation was found between Slope, TC and the temporal interval between recorded GPS fixes).

GENERAL APPROACH

We analysed habitat selection by comparing the environmental variables of used sites (i.e. those at the recorded GPS locations) to the reference conditions in the study area. This parallels the Grinnellian concept of *ecological niche*, defined here as the subspace of species occurrences within the hyperspace defined by the environmental variables (both abiotic and biotic) of the area considered to be available to the species of interest (the *ecological space*; Hirzel *et al.* 2002; Hirzel & Le Lay 2008). Following Loarie, van Aarde & Pimm (2009), we considered the area within a distance of one day of travel (10 km) around all recorded locations to be available to the elephants. This conservative extent avoids spurious analyses with artificially inflated test statistics when data are drawn from too large an area (Anderson

& Raza 2010) and corresponds to the within-home range habitat selection as defined by Johnson (1980). Furthermore, it avoids linking the environmental characteristics of the geologically distinctive northern part of KNP to the patterns of habitat selection by the collared elephants, which were collared in the southern and central part of KNP.

The mobility of the elephants, the conservative extent that we used, and the long time frame over which GPS locations were recorded, suggests that the entire area we considered available to the elephants was indeed likely to be 'available' to them. Moreover, the long-term (spatial) memory of elephants (e.g. McComb *et al.* 2001; Van Aarde *et al.* 2008) suggests that the area we considered to be available was also 'known' to the elephants. In the following, we refer to this area as the available area.

We used the Mahalanobis distance statistic (D^2 ; Rotenberry, Preston & Knick 2006), the frequently used ecological-niche factor analysis (ENFA; Hirzel *et al.* 2002), and the related Mahalanobis distance factor analysis (MADIFA; Calenge *et al.* 2008) to study the patterns of habitat selection by elephants. We first used a series of univariate Mahalanobis D^2 analyses to quantify the response of the elephants to food and water resources as function of the range of environmental context. We then included all environmental variables into the ENFA and tested whether the explicit consideration of environmental context at appropriate scales regarding food and water resources increased the quantified level of habitat selectivity. Lastly, we predicted habitat suitability (HS) within the available area using a MADIFA on all environmental variables and tested whether the inclusion of environmental context at appropriate scales increased the predictability of habitat selection.

Mahalanobis D^2 , ENFA and MADIFA assume that the distributions of the environmental variables are symmetric and unimodal (Hirzel *et al.* 2002; Calenge & Basille 2008). Hence, we normalized the distributions when needed, using Box-Cox and logarithmic transformations. Furthermore, we normalized all environmental variables (also those for which the scale of analysis was varied, see below) to zero mean and unit variance, so that the distributions of the environmental variables are comparable.

Throughout, we analysed the patterns of habitat selection separately for male and female elephants and differentiated between patterns in the dry season (Jun–Aug) and wet season (Dec–Feb). We assumed an equal available area for both sexes and seasons, justified by the fact that no large-scale migration takes place for elephants in KNP (Venter, Scholes & Eckhardt 2003) so that availability does not change over the seasons. As our methods can only be used to compare different data sets provided that the same area is used as reference area (Hirzel *et al.* 2002), the assumption of equal available area makes comparisons between the seasons and sexes possible. All the analyses were carried out using the software R (R Development Core Team 2007) and the package Adehabitat (V1.7.3; Calenge 2006). The analyses are further discussed elsewhere.

SPATIAL SCALING OF ENVIRONMENTAL CONTEXT

Mahalanobis D^2 quantifies the standardized difference between locations in the ecological space and the centroid of the ecological niche, taking into account the structure of the ecological niche. The more similar in environmental conditions a location is to the centroid of the ecological niche (the species' mean), the smaller is D^2 , and the more suitable the habitat at that location (Rotenberry, Preston & Knick 2006; Calenge *et al.* 2008). Conversely, a larger D^2 indicates a greater dissimilarity to the species' mean. Hence, we used the mean D^2 over the available area ($\overline{D^2}$) as measure of the level of habitat

selectivity regarding an environmental variable and analysed the relationship between $\overline{D^2}$ and the range of environmental context considered.

We varied the range of environmental context by averaging the environmental predictor variables HB, TC and WO within circular focal neighbourhoods, centred on each site, while varying the ambit radius (Holland, Bert & Fahrig 2004; De Knecht *et al.* 2010). We varied the ambit radius from 0 km (thus essentially no environmental context and hence only site-specific information) up to 40 km, with 1-km increments (*viz.* the resolution of the data). For each of the environmental variables ($n = 3$) and each of the buffer sizes ($n = 41$), we quantified $\overline{D^2}$ in a series of univariate Mahalanobis D^2 analyses. We did this for 1000 bootstrap analyses (all with 1000 randomly selected locations) to acquire a mean scaling pattern as well as its confidence limit (which we assessed using the 2.5% and 97.5% percentiles of the bootstrap estimates). Following Holland, Bert & Fahrig (2004), we refer to the buffer size that yields the highest $\overline{D^2}$ as the *characteristic scale* of the elephants' response to the environmental variable considered (denoted by a subscript: HB_s , TC_s and WO_s).

If such characteristic scales are found, the elephants might respond to their environment at these specific scales, or it might represent the spatial scales of environmental heterogeneity with which the elephants are forced to cope (Wheatley & Johnson 2009). To distinguish between the two, we quantified the environmental heterogeneity regarding HB, TC and WO using variograms that plot the degree of spatial variation as function of separation distance between paired observations (Fig. 2a). The distance where the variogram levels off (the 'range' of the variogram) is of interest here, because it gives information regarding the dominant scale of spatial variation (Murwira & Skidmore 2005; De Knecht *et al.* 2008). Through comparing the dominant scales of environmental heterogeneity to the characteristic scales of the elephants' response, we can draw conclusions about the elephants following spatial patterns in the landscape, or the elephants selecting environmental variables at biologically meaningful scales, in which case the dominant scales of the landscape and the characteristic scales of habitat selection differ.

ECOLOGICAL-NICHE FACTOR ANALYSIS

We included all environmental variables in subsequent ENFA, with HB, TC and WO at their characteristic scales (which we will refer to as 'spatial' analyses). All other environmental variables were included as their mean values within each 1-km² grid cell. We compared the results of ENFA including these variables, with those from ENFA where the influence of environmental context was not considered regarding HB, TC and WO (which we refer to as the 'non-spatial' analyses, as no information regarding environmental context is considered beyond the grid cell). ENFA quantifies the dissimilarity between ecological niche and ecological space in terms of marginality and specialization, where marginality is defined as the standardized difference between the centroids of the ecological space and the ecological niche, whereas specialization is defined as the narrowness of the ecological niche relative to the ecological space (Hirzel *et al.* 2002; Basille *et al.* 2008). Marginality itself expresses some specialization: the higher the marginality, the higher is the specialization (Hirzel *et al.* 2002; Basille *et al.* 2008). ENFA complements analyses based on Mahalanobis D^2 , as it allows identification of the part of the Mahalanobis D^2 corresponding to specialization and marginality (Calenge *et al.* 2008).

ENFA extracts information regarding the ecological niche by computing new, uncorrelated factors: one marginality axis and several axes of specialization (Hirzel *et al.* 2002). All environmental variables

are scored for their contribution to each axis, with scores ranging from -1 to $+1$. A positive marginality score for an environmental variable indicates that the centroid of the ecological niche is in value higher (for negative scores lower) than the average value in the study area. Only the absolute value of the specialization scores is meaningful: a high value indicates a narrow niche breadth in comparison with the ecological space (Hirzel *et al.* 2002). The eigenvalue associated with any axis expresses the amount of specialization it accounts for (Hirzel *et al.* 2002).

Besides scores per environmental variable, an overall value of marginality (M) and specialization (S) can be calculated, providing general clues about the degree of niche restriction (Hirzel *et al.* 2002). M indicates how far the ecological niche is from the average conditions in the available area, with higher values indicating a higher marginality, whereas S indicates the breadth of the niche, with high values indicating narrow niches. Following Basille *et al.* (2008), we used bi-plots projecting both the ecological niche and the environmental variables on the subspace defined by the first two axes of the ENFA to interpret the results. We used a Monte-Carlo randomization procedure with 1000 permutations, randomizing the locations of the elephants within the available area, to test the significance of M and S. Because such randomization tests are sensitive to spatial autocorrelation in the data, we also computed randomizations on a rarefied data set using only one GPS location per elephant per day.

MODEL PREDICTION AND EVALUATION

To test whether the explicit consideration of environmental context at appropriate scales improves the predictability of elephant distribution, we compared the predictability of the spatial and non-spatial models, using the same variables as used in the ENFA. While the ENFA is often used to create HS maps, it is not recommended to combine the ENFA axes into a single measure of HS, because they do not all have the same mathematical status: the marginality axis extracts the difference between the mean available habitat and the centroid of the ecological niche, whereas the specialization axes maximize the ratio in variances between the available area and ecological niche (Calenge & Basille 2008). We therefore used the MADIFA to compute HS maps, because Mahalanobis D^2 combines marginality and specialization into one single measure of habitat selection while its factorial decomposition allows the computation of reduced-rank Mahalanobis distances (Rotenberry, Preston & Knick 2006; Calenge & Basille 2008). Because of their high contribution to explained variation ($> 85\%$), we only used the first 5 MADIFA axes, because not all available n axes define ecologically relevant measures of HS but reflect the *a priori* decision by the investigator to include n environmental variables (Rotenberry, Preston & Knick 2006). This avoids overfitting while retaining most information regarding habitat selection (Calenge *et al.* 2008).

We evaluated the HS models using a k -fold cross-validation procedure (with $k = 10$). We used $k-1$ parts to calibrate the model while computing the evaluation on the left-out partition. This procedure was repeated k times, each time leaving out another partition. The evaluation was carried out using the method described by Boyce *et al.* (2002): the ratio (O/E) of the observed number of evaluation points within a HS class relative to the expected number of evaluation points in case of random habitat use is plotted against the midpoint HS value. As binning and classification issues become problematic, Hirzel *et al.* (2006) developed a continuous version of this method, with the O/E ratio computed within a moving window (with size w) along the HS gradient. We used $w = 0.2$ for a gradient of HS values ranging from 0 (highly unsuitable) to 1 (highly suitable).

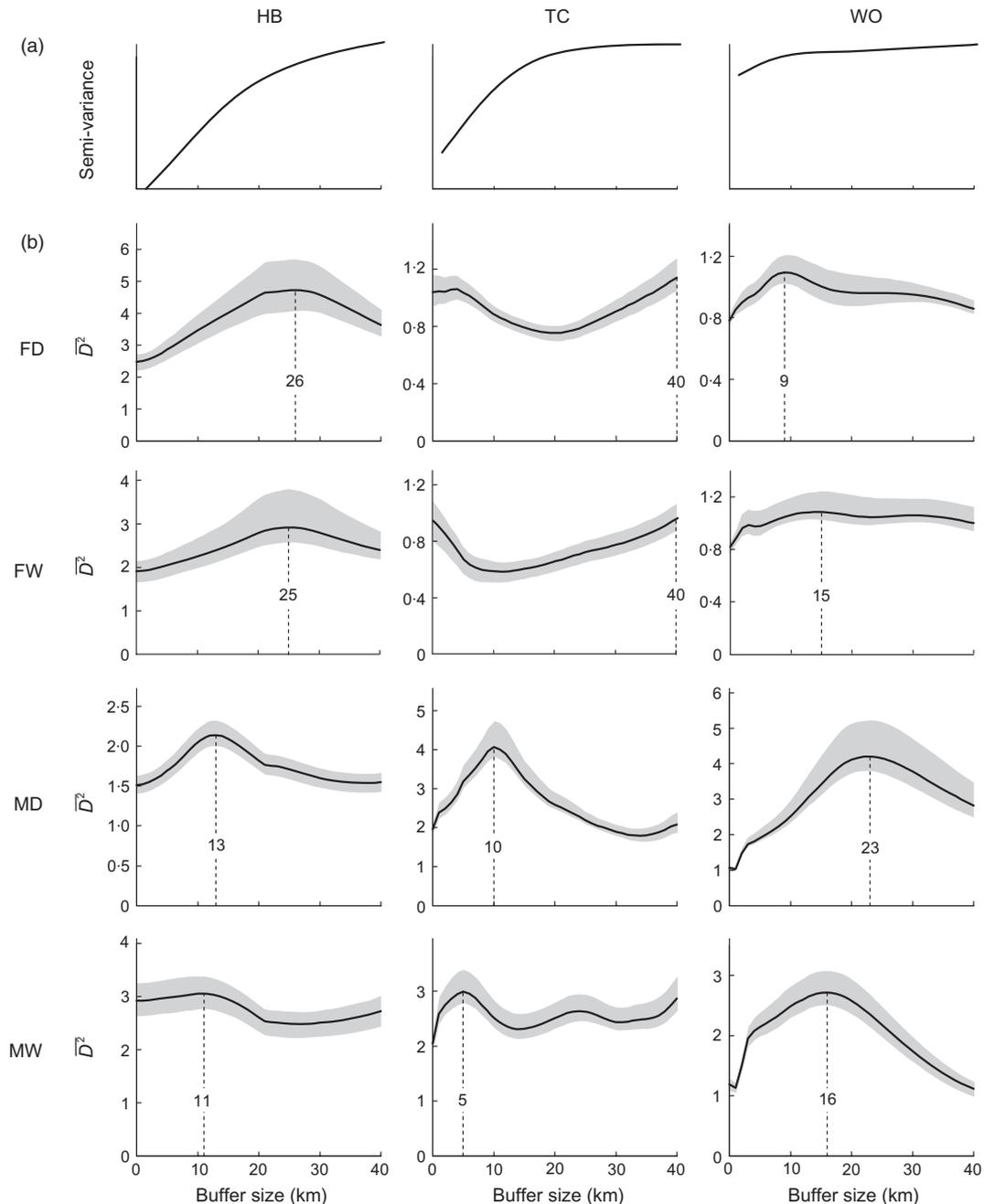


Fig. 2. (a) Variograms expressing the spatial structure of the environmental variables herbaceous biomass (HB), tree cover (TC) and water occurrence (WO). The scales for the y-axes are omitted because of differences in measurement scales; however, they all start at zero. (b) The mean Mahalanobis distance (\bar{D}^2) over the available area for the environmental variables, measured at different buffer sizes. FD, female elephants in the dry season; FW, female elephants in the wet season; MD, male elephants in the dry season; and MW, male elephants in the wet season. The vertical dotted lines indicate the characteristic scales, i.e. the buffer size where \bar{D}^2 is maximized, with the corresponding buffer sizes indicated. The spatial analyses were conducted using these buffer sizes. The grey area depicts the 95% confidence interval of 1000 random bootstraps with each 1000 locations.

This procedure produces k curves of O/E vs. HS, providing three levels of information regarding the predictability of HS. First, the variance among the curves gives information about model robustness along the HS range. Second, if the O/E ratio increases with increasing HS, the model has a good predictive ability (Hirzel *et al.* 2006). We used the Spearman rank correlation coefficient (ρ) of the mean O/E ratio with HS to quantify the consistency of the HS model, with high values of ρ in case

of a monotonically increasing O/E curve, indicating a good model (Hirzel *et al.* 2006). Although an ideal model would have a linear O/E curve, meaning that HS is proportional to the probability of use (Manly, McDonald & Thomas 1993), real curves may exhibit nonlinear (e.g. exponential) or stepwise shapes (Hirzel *et al.* 2006). Third, the maximum value of the O/E curve reflects how much the model differs from chance expectation (i.e. O/E = 1) thereby reflecting the model's ability

to differentiate the characteristics of the species' niche from those of the studied area (Hirzel *et al.* 2006).

Results

SPATIAL SCALING OF ENVIRONMENTAL CONTEXT

The strength of habitat selection as quantified by $\overline{D^2}$ was highly dependent on the range of environmental context considered regarding HB, TC and WO (Fig. 2). For all gradients, $\overline{D^2}$ was lower at a buffer size of 0 km (i.e. without environmental context) than when including environmental context at most scales considered. All gradients (except for TC for female elephants) showed a distinct single maximum $\overline{D^2}$ for a buffer size > 0 and < 40 km, i.e. the characteristic scales. The gradients for TC regarding female elephants showed a clear minimum $\overline{D^2}$ at a buffer size of *ca.* 10 km during the dry season and *ca.* 20 km during the wet season (Fig. 2). Male and female elephants differed regarding their maximum $\overline{D^2}$ values and characteristic scales for the different gradients (Fig. 2). The dominant scales of spatial variation regarding the examined environmental variables (Fig. 2a) did not match the characteristic scales of the elephants' response to these environmental variables (Fig. 2b), suggesting that the scale at which the elephants responded to the environment predictors examined here did not follow the scales at which environmental heterogeneity was most dominant.

ECOLOGICAL-NICHE FACTOR ANALYSIS

The Monte-Carlo randomization tests showed that the ENFA axes, for both spatial and non-spatial analyses, were highly significant (all $P < 0.001$, for both the full data sets and rarefied data sets). Thus, the habitat occupied by the elephants differed unequivocally from the conditions in the study area, or, in other words, the elephants exhibited pronounced habitat selection. The spatial models that explicitly considered environmental context had higher values of M and S than the non-spatial models, for both male and female elephants (Table 2).

The first 4 axes of the spatial ENFA explained *ca.* 80% of all the information regarding the niche structure, that is

Table 2. Comparing the overall ecological-niche factor analysis (ENFA) statistics for a non-spatial (i.e. environmental context is not considered) and spatial (i.e. environmental context is explicitly considered; see Fig. 2) models in terms of overall marginality (M) and specialization (S). Higher values of both M and S indicate a higher level of habitat selectivity as measured by ENFA

| | Non-spatial | | Spatial | |
|-------------|-------------|------|---------|-------|
| | M | S | M | S |
| Females dry | 2.25 | 8.76 | 2.67 | 10.95 |
| Females wet | 1.38 | 9.75 | 1.70 | 12.20 |
| Males dry | 1.45 | 8.13 | 2.27 | 9.36 |
| Males wet | 0.82 | 6.95 | 1.85 | 8.33 |

100% of the marginality and *ca.* 60% of the specialization. The marginality axes explained only little of the specialization ($< 5\%$), meaning that the niche breadth of the elephants was not particularly narrow for the variables for which their optimum was the furthest from the average conditions. The eigenvalues attributed to the first specialization axes (females: 8.8 and 12.8 for the dry and wet season, respectively; males: 17.2 and 11.1, respectively) indicated that the variance in the environmental variables in KNP was much higher than the variance in environmental conditions experienced by the elephants; in other words, the elephants had a relatively narrow ecological niche compared to the available area.

The magnitude of the marginality and specialization scores for HB, TC and WO increased in most analyses when explicitly considering environmental context at appropriate spatial scales: the length of the vectors in Fig. 3 mostly increased when considering environmental context (cf. HB vs. HB_s, TC vs. TC_s and WO vs. WO_s; Fig. 3, Appendix S2, Supporting information). For HB and TC, including environmental context resulted in larger marginality scores, of the same sign, relative to non-spatial analyses. For WO, however, the inclusion of environmental context resulted in smaller marginality scores for the female elephants, but larger scores for the male elephants, yet of the opposite sign. For most analysed scenarios, the inclusion of environmental context increased the contribution of the corresponding environmental variables to the specialization axes.

The ENFA (Fig. 3, Appendix S2, Supporting information) showed that the female elephants were primarily associated with areas with high WO, HB and VH, areas close to water points or water in general (dWP and dW) and areas with low TC and gentle terrain (i.e. low slope). Furthermore, the niche of the female elephants was most restricted in the dimension associated with precipitation and HB. In contrast, the male elephants avoided areas with high HB, but preferred areas with high TC. Moreover, the male elephants avoided areas associated with much surface water at a large scale (WOs). The niche of the male elephants was mostly restricted in those dimensions associated with elevation and slope. Both male and female elephants were on average far from perennial rivers in the dry season (dR), although they preferred to be close to water points, or water regardless of the source (dW and dWP, respectively). The effect of seasonality was small compared to the effect of sexual segregation.

MODEL PREDICTABILITY

The spatial models predicted HS very well for all scenarios (Fig. 4); all evaluation graphs increased monotonically (all $\rho > 0.95$), albeit in a nonlinear fashion. The HS models were very robust, as the different cross-validation graphs exhibited low variance: the 95% confidence intervals were within 3% of the mean. Furthermore, the spatial models were able to differentiate HS for female elephants even at low HS values (< 0.4), whereas the non-spatial models were rather non-discriminatory at low HS values (Fig. 4). Moreover, the spatial models yielded higher O/E values for all scenarios than the

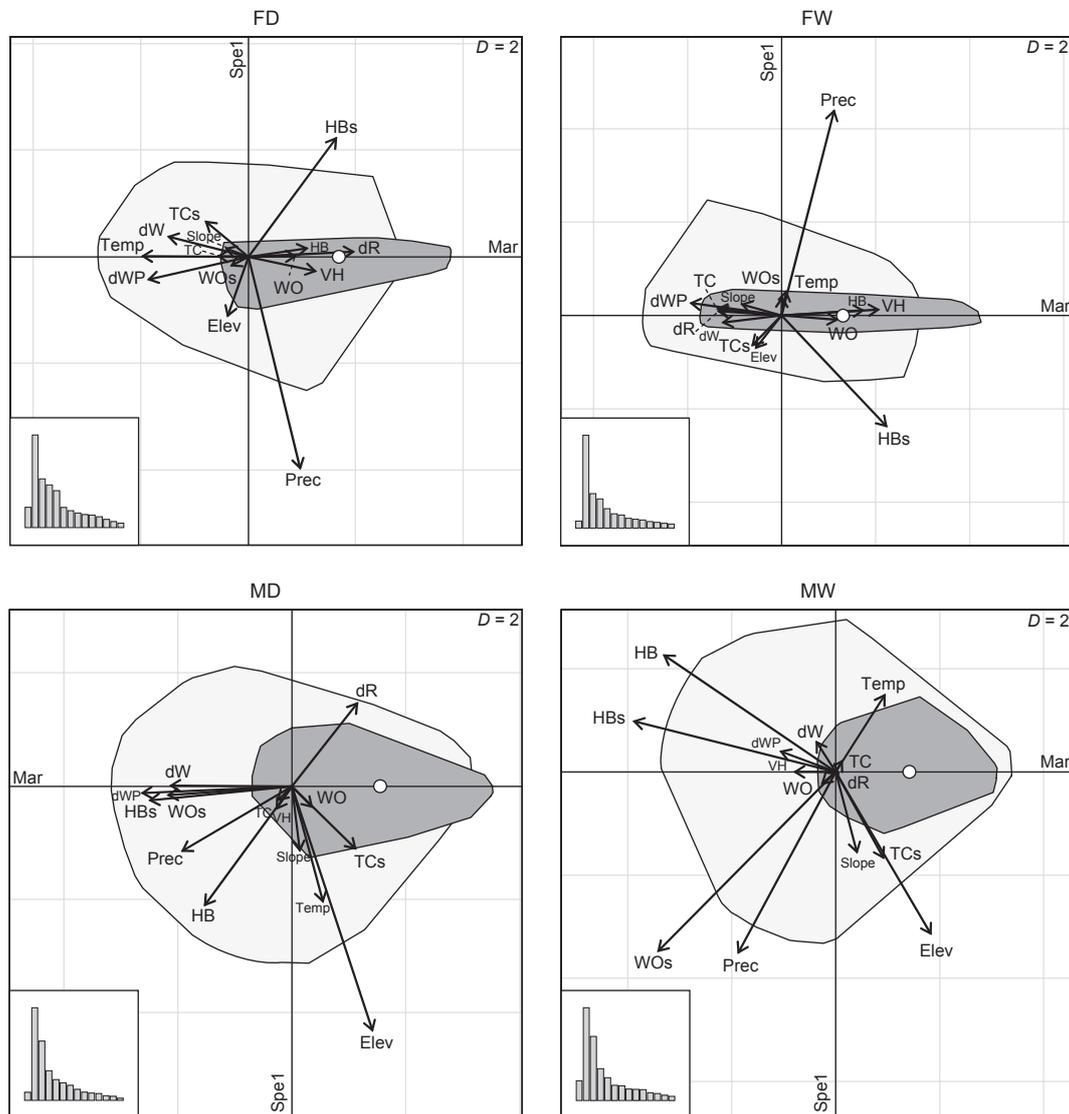


Fig. 3. Ecological-niche factor analysis (ENFA) bi-plots of female elephants in the dry season (FD), female elephants in the wet season (FW), male elephants in the dry season (MD) and male elephants in the wet season (MW). The plots display factorial maps of the used and available sites: the light grey area depicts the 95% minimum convex polygon (MCP) of the projection of the available sites in the subspace extracted by the ENFA, whereas the dark grey area depicts the 95% MCP of the projection of sites used by the elephants. The horizontal axis displays the first axis of the ENFA, i.e. the marginality axis, whereas the vertical axis represents the second axis of the ENFA, thus the first axis of specialization. The inset bar-plots show the contribution of each axis to the overall specialization. The vectors depict the scores of the environmental variables with the two axes. For abbreviations of the environmental variables see Table 1 (the subscript *s* denotes the variables for which environmental context was considered at characteristic scales, see Fig. 2). The white dot represents the centroid of the sites used by the elephants, while the origin of the plot is the centroid of the available sites.

non-spatial models and thus were better able to differentiate between HS and randomness.

Discussion

Although the importance of spatial scale and spatial context when studying species distributions is increasingly being recognized (Wheatley & Johnson 2009), little is still known about the relative influence of localized and contextual environmental factors on the distribution of animals. We have therefore analysed the influence of environmental context,

measured over a large range of scales (i.e. ambit radii), on habitat selection by African elephants.

THE SCALING OF ENVIRONMENTAL CONTEXT

Our analyses showed that explicitly considering environmental context increased the quantified level of habitat selection by elephants relative to analyses where this was not considered. We measured habitat selectivity using the average Mahalanobis distance D^2 ($\overline{D^2}$), overall marginality (M) and specialization (S), as well as the scores of the environmental

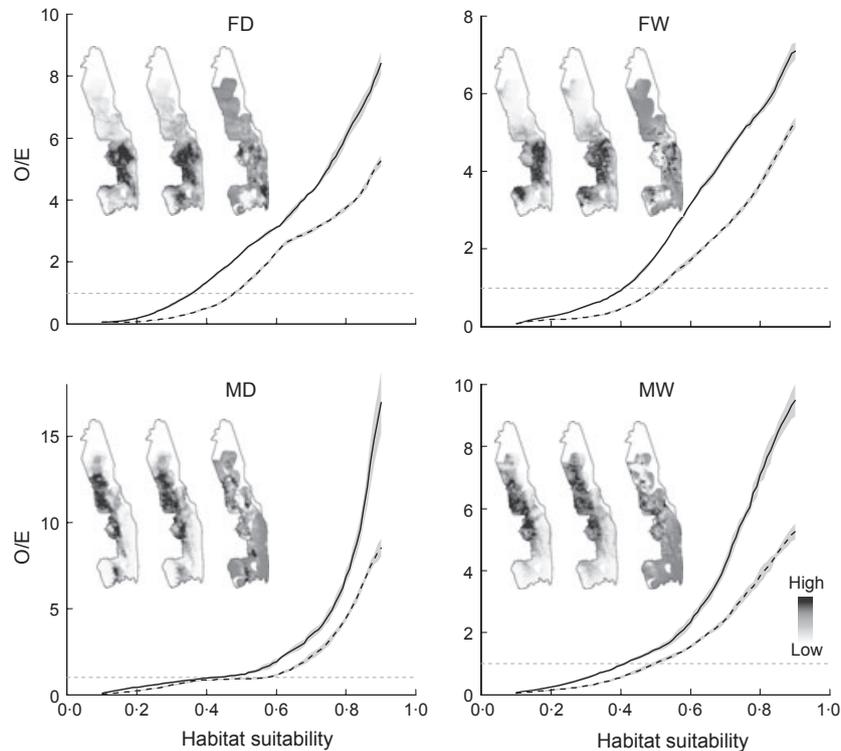


Fig. 4. Tenfold cross-validation graphs, showing the ratio between the observed number of evaluation points in each habitat suitability (HS) class (a moving window of size 0.2 centred around each value on the *x*-axis) relative to the expected number of evaluation points based on random chance (*O/E*), for female elephants in the dry season (FD), female elephants in the wet season (FW), male elephants in the dry season (MD) and male elephants in the wet season (MW). The solid and dashed lines depict the mean *O/E* of the 10 folds for the spatial models and non-spatial models, respectively. The grey area depicts the 95% confidence interval of the mean. The dotted line at *O/E* = 1 indicates habitat use based on chance alone. The inset maps display the predicted HS using the spatial model (left map) and non-spatial model (middle map) and the difference between the two (right map). Note that the models do not predict HS across the entire Kruger National Park, as only the area within 10 km from the recorded elephant locations was defined to be available to the elephants, and hence HS was predicted within this available area.

variables on the axes of the ENFA, where higher values regarding these statistics indicate higher levels of habitat selectivity.

Characteristic scales could be indicated for most analysed gradients, as nearly all gradients showed a distinct hump-shaped response with increasing buffer size. This corresponds to other studies on the influence of environmental context, which generally find that the correlation between species abundance is highest when environmental context is considered at characteristic scales (e.g. Holland, Bert & Fahrig 2004; Drapela *et al.* 2008). Our analyses support the view that the scaling of elephant-habitat relationships arises from the elephants' scale-dependent response to habitat, instead of being determined by the spatial structure of the environment itself. Namely, the dominant scales of spatial variation regarding the examined environmental variables did not match the characteristic scales of the elephants' response to these environmental variables.

We believe that these characteristic scales are not because of the perceptual range of the elephants, which could define an informational window to base decisions on (Olden *et al.* 2004), because it is impossible to visually assess the characteristics of the environment over all the scales that we considered. However, elephants have long-term, extensive spatial

and temporal memory of acquired knowledge regarding their environment (McComb *et al.* 2001; Van Aarde *et al.* 2008; Van Langevelde & Prins 2008), and this could lead to informed decisions with regard to habitat selection. The influence of memory on decision-making by organisms is implicated for a wide variety of species (e.g. Wolf *et al.* 2009).

THE PATTERNS OF HABITAT SELECTION

The male elephants avoided areas with high WO at large scales, whereas the females did not show a distinct selection or avoidance of areas associated with high WO at large scales. Some caution is needed when explaining these findings. Instead of avoiding WO at large spatial scales, it could be that the elephants were in fact not limited by water at larger scales. As Grant *et al.* (2008) argue, surface water is expected to have a relatively small and localized effect in KNP, because it is usually widely available here. Because elephants drink on average every two days (Van Aarde *et al.* 2008), they need not always be in areas with a high WO, as long as they are effectively within walking distance from a source of water. Our analyses suggest that this could be any source of water, regardless of its origin (e.g. natural or artificial water sources). Namely, while the elephants were

predominantly located far from perennial rivers in the dry season, they preferred areas close to artificial water points or areas close to water regardless of the source. This may indicate that the influence of artificial water points is overriding the usual biological pattern that elephants are found predominantly close to rivers (Smit, Grant & Whyte 2007b; Grant *et al.* 2008). Thus, it is likely that the distance to the nearest water source, rather than WO at a large scale, is determining elephant movements in KNP.

Given the ample supply of water in KNP, the elephants could thus select habitat based on other resources, e.g. forage, but nevertheless be constrained by the distance to the nearest water source. The male elephants selected areas with high TC while avoiding areas with high HB, and increasingly did so at larger spatial scales. Conversely, the female elephants avoided areas with high TC while preferring areas with ample HB, also showing more distinctive patterns of selection (or avoidance) when environmental context was explicitly considered. These contrasting patterns between the sexes suggest sexual habitat segregation and are in line with other studies on sexual differences in foraging ecology of African elephants (e.g. Stokke & Du Toit 2000; Smit, Grant & Whyte 2007b; Shannon *et al.* 2010), providing further support for the notion that male and female elephants can effectively be seen as two distinct 'ecological' species (but note that there remains quite some individual variation; see Appendix S3, Supporting information).

Besides their diverging response to vegetation, the male and female elephants also responded differently to terrain ruggedness. The female elephants preferred areas associated with gentle terrain, which is in line with the conclusion of Wall, Douglas-Hamilton & Vollrath (2006) that elephants avoid costly mountaineering. However, the male elephants were mainly found in areas with intermediate slope, avoiding very flat or very steep areas. This may be because of the establishment of nutrient hotspots in a more undulating terrain (Nellemann, Stein & Rutina 2002; Grant & Scholes 2006), whereas the female elephants may be more limited in their mobility, amplified by youngsters at foot and therefore prefer more gentle terrain. However, because slope and TC are positively associated (Table 1), the elephants' response to terrain ruggedness may also relate to their response to TC.

THE SPATIAL SCALING OF HABITAT SELECTION

Our analyses showed what is often termed the 'modifiable areal unit problem' or 'change of support problem': relationships among variables at coarse scales are not necessarily of the same strength, or even direction, as those at fine scales (Openshaw & Taylor 1981). The change in marginality scores when including the contextual influence of HB and TC showed a different pattern than when including spatial context regarding WO. While including environmental context mostly increased the magnitude of the scores regarding HB and TC, it led to a reduction in the scores for WO, or even to scores of the opposite sign. As suggested earlier, it could be that the elephants responded to their environment in a

scale-dependent and hierarchical manner, with different environmental variables driving habitat selection at different spatial scales (Senft *et al.* 1987). We suggest that the elephants first select areas in relation to vegetation characteristics at large spatial scales (albeit constrained by the distance to water), and subsequently exhibit preferential habitat use regarding vegetation characteristics and surface-water availability at finer scales. However, because our analyses were set up in a scale-dependent, yet not hierarchical, manner, we leave this as an untested hypothesis.

The rapidly advancing field of movement ecology increasingly recognizes that processes that act across multiple spatial and temporal scales drive the movements of organisms and thereby their distribution (e.g. Fryxell *et al.* 2008; Nathan *et al.* 2008). The daily movements of elephants relate predominantly to foraging, the activity they do most during a day, although these movements become extended by the distance traversed to water sources and back (Owen-Smith, Fryxell & Merrill 2010). When foraging, animals often slow their movements and move more tortuously when entering profitable areas (De Knegt *et al.* 2007). This behaviour concentrates their activity in profitable areas, but allows them to move rapidly through less profitable areas (Walsh 1996; De Knegt *et al.* 2007). The interaction between the elephants' movement response (and especially time-lags therein) to forage density and the spatial structure of the environment may produce the observed scale dependence in the elephant-habitat relationships (Walsh 1996). Hence, we suggest that the elephants concentrated their foraging within areas of high forage availability that were sufficiently close to water and sufficiently large so as to optimize the efficiency of movement and foraging.

Note that our study deviates from many others in that our study species is not severely affected by predation. Hence, the spatial patterns of habitat selection by the elephants are not severely influenced by a 'landscape of fear' (e.g. Brown & Kotler 2007). For many species, however, the risk of predation affects individuals in many ways and influences their patterns of habitat use via a site's position with respect to refuges and ambush sites, escape substrata, site lines and possibly other landscape properties that influence the risk of predation (Brown & Kotler 2007). As such, the risk of predation will influence the scaling patterns of habitat selection for many other species, next to the influences that foraging and drinking exert on habitat selection, probably by increasing the importance of more fine-scale environmental information, as the distance to landscape features associated with predation risk becomes important. Several studies observed shifts in the spatial patterns of habitat selection by prey species after predator species had been reintroduced (e.g. Ripple & Beschta 2007, 2008).

ECOLOGICAL IMPLICATIONS AND CONCLUSIONS

Besides being better able to describe the patterns of habitat selection, our analyses showed that explicitly incorporating environmental context at appropriate spatial scales could

also lead to a major increase in the predictive ability of habitat suitability (HS) models. The inclusion of environmental context resulted in more significant and consistent HS models than non-spatial models that ignored the influence of environmental context. Namely, they yielded higher O/E scores, thereby being better able to discriminate between HS and randomness, and yielded more consistent monotonically increasing cross-validation curves, meaning that they were able to predict HS in more detail (Hirzel *et al.* 2006). Furthermore, these models had a high stability, as they exhibited little cross-validation variance.

Being able to accurately assess or predict the relationships between organisms and their environment is paramount to the effective management and conservation of natural systems (Guisan *et al.* 2006). However, the effects of spatial scale on model performance and predictability are among some of the most prominent challenges to habitat selection analysis and species distribution modelling (Araújo & Guisan 2006). Here, we have shown the importance of explicitly considering environmental context in habitat selection, and especially the spatial scale at which environmental context exerts influence on the patterns of habitat use by organisms, and demonstrated a method to assess the importance of environmental context measured along a wide range of scales.

As advances in satellite imagery and remote sensing permit scientists to access spatial data at increasingly higher resolutions, the relative influence of environmental context in the analyses of species distributions may become increasingly important. However, ignoring the effects of spatial context may then increasingly result in scale mismatches, which affect the rigor of statistical analyses and thereby the ability to understand ecological processes (De Knecht *et al.* 2010). We thus conclude that ecologists should explicitly consider the influence of environmental context, at appropriate spatial scales, as this is paramount to understanding the processes behind the distribution of organisms and therefore required for successful ecosystem management.

Acknowledgements

We thank Sandra MacFadyen and Izak Smit for their assistance with the data. We are also greatly indebted to two anonymous referees who gave excellent comments on earlier versions of this paper, and thereby helped to improve its content. This study was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) of the Netherlands Organization for Scientific Research (NWO). We also thank Amarula (Distell), the National Research Foundation of South Africa, and Save The Elephants for financially and logistically supporting the collaring of elephants.

References

Anderson, R.P. & Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, **37**, 1378–1393.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.

Basille, M., Calenge, C., Marboutin, E., Andersen, R. & Gaillard, J.M. (2008) Assessing habitat selection using multivariate statistics: some refinements of the ecological-niche factor analysis. *Ecological Modelling*, **211**, 233–240.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Brown, J.S. & Kotler, B.P. (2007) Foraging and the ecology of fear. *Foraging: Behaviour and Ecology* (eds D.W. Stephens, J.S. Brown & R.C. Ydenbert), pp. 437–480. The University of Chicago Press, Chicago, IL.

Bucini, G., Hanan, N.P., Boone, R.B., Smit, I.P.J., Saatchi, S., Lefsky, M.A. & Asner, G.P. (2010) Woody fractional cover in Kruger National Park, South Africa: remote-sensing-based maps and ecological insights. *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales* (eds M.J. Hill & N.P. Hanan), pp. 219–238. CRC/Taylor and Francis, Boca Raton, FL.

Calenge, C. (2006) The package ‘‘Adehabitat’’ for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Calenge, C. & Basille, M. (2008) A general framework for the statistical exploration of the ecological niche. *Journal of Theoretical Biology*, **252**, 674–685.

Calenge, C., Darmon, G., Basille, M., Loison, A. & Jullien, J.M. (2008) The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology*, **89**, 555–566.

Chamaille-Jammes, S., Valeix, M. & Fritz, H. (2007a) Elephant management: why can't we throw out the babies with the artificial bathwater? *Diversity and Distributions*, **13**, 663–665.

Chamaille-Jammes, S., Valeix, M. & Fritz, H. (2007b) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, **44**, 625–633.

De Knecht, H.J., Hengeveld, G.M., Van Langevelde, F., De Boer, W.F. & Kirkman, K.P. (2007) Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology*, **18**, 1065–1072.

De Knecht, H.J., Groen, T.A., Van de Vijver, C.A.D.M., Prins, H.H.T. & Van Langevelde, F. (2008) Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos*, **117**, 543–554.

De Knecht, H.J., Van Langevelde, F., Coughenour, M.B., Skidmore, A.K., De Boer, W.F., Heitkönig, I.M.A., Knox, N., Slotow, R., Van der Waal, C. & Prins, H.H.T. (2010) Spatial autocorrelation and the scaling of species-environment relationships. *Ecology*, **91**, 2455–2465.

D'Eon, R.G., Serrouya, R., Smith, G. & Kochanny, C.O. (2002) GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, **30**, 430–439.

Drapela, T., Moser, D., Zaller, G. & Frank, T. (2008) Spider assemblages in winter oilseed rape affected by landscape and site factors. *Ecography*, **31**, 254–262.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004) Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, **41**, 201–212.

Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T. & Rosatte, R.C. (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences*, **105**, 19114–19119.

Grant, C.C. & Scholes, M.C. (2006) The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, **130**, 426–437.

Grant, C.C., Bengis, R., Balfour, D. & Peel, M. (2008) Controlling the distribution of elephants. *Elephant Management: A Scientific Assessment of South Africa* (eds R.J. Scholes & K. Mennell), pp. 329–369. Witwatersrand University Press, Johannesburg, South Africa.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.M.C., Aspinall, R. & Hastie, T. (2006) Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, **43**, 386–392.

Hijmans, R.J., Cameron, S. & Parra, J. (2007) *WorldClim*, Version 1.4. University of California, Berkeley, <http://www.worldclim.org>.

Hirzel, A.H. & Le Lay, G. (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372–1381.

Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*, **83**, 2027–2036.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142–152.

Holland, J.D., Bert, D.G. & Fahrig, L. (2004) Determining the spatial scale of species' response to habitat. *BioScience*, **54**, 227–233.

Jarvis, A., Reuter, H., Nelson, A. & Guevara, E. (2008) Hole-filled seamless SRTM data V4, Consortium for Spatial Information, International Centre for Tropical Agriculture, <http://srtm.csi.cgiar.org>.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Loarie, S.R., van Aarde, R.J. & Pimm, S.L. (2009) Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, **142**, 3099–3107.
- Manly, B.F.J., McDonald, L.L. & Thomas, D.L. (1993) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman and Hall, London.
- McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001) Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**, 491–494.
- Murwira, A. & Skidmore, A.K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a southern African agricultural landscape. *Landscape Ecology*, **20**, 217–234.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**, 19052–19059.
- Nellemann, C., Stein, R.M. & Rutina, L.P. (2002) Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology*, **18**, 835–844.
- Olden, J.D., Schooley, R.L., Monroe, J.B. & Poff, N.L. (2004) Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*, **73**, 1190–1194.
- Openshaw, S. & Taylor, P.J. (1981) The modifiable areal unit problem. *Quantitative Geography: A British View* (eds N. Wrigley & R.J. Bennett), pp. 60–69. Routledge and Kegan Paul, London.
- Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010) Foraging theory up-scaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B*, **365**, 2267–2278.
- Pinto, N. & Keitt, T.H. (2008) Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, **117**, 1725–1731.
- R Development Core Team (2007) R: a language and environment for statistical computing. Version 2.8.1. *R Foundation for Statistical Computing*, Vienna, Austria, <http://www.R-project.org>.
- Ripple, W.J. & Beschta, R.L. (2007) Restoring Yellowstone's aspen with wolves. *Biological Conservation*, **138**, 514–519.
- Ripple, W.J. & Beschta, R.L. (2008) Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation*, **141**, 1249–1256.
- Rotenberry, J.T., Preston, K.L. & Knick, S.T. (2006) GIS-based niche modeling for mapping species' habitat. *Ecology*, **87**, 1458–1464.
- Schmidt, M.H., Thies, C., Nentwig, W. & Tschamntke, T. (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, **35**, 157–166.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *BioScience*, **37**, 789–799.
- Shannon, G., Page, B.R., Duffy, K.J. & Slotow, R. (2010) The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation. *Austral Ecology*, in press.
- Smit, I.P.J., Grant, C.C. & Devereux, B.J. (2007a) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, **136**, 85–99.
- Smit, I.P.J., Grant, C.C. & Whyte, I.J. (2007b) Landscape-scale sexual segregation in the dry season distribution and resource utilization of elephants in Kruger National Park, South Africa. *Diversity and Distributions*, **13**, 225–236.
- Stokke, S. & Du Toit, J.T. (2000) Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, **23**, 70–80.
- Trollope, W.S.W. & Potgieter, A.L.F. (1986) Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa*, **3**, 148–152.
- Van Aarde, R., Ferreira, S., Jackson, T., Page, B., De Beer, Y., Gough, K., Guldemond, R., Junker, J., Olivier, P., Ott, T. & Trimble, M. (2008) Elephant population biology and ecology. *Elephant Management: A Scientific Assessment of South Africa* (eds R.J. Scholes & K. Mennell), pp. 84–145. Witwatersrand University Press, Johannesburg, South Africa.
- Van Langevelde, F. (2000) Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography*, **23**, 614–622.
- Van Langevelde, F. & Prins, H.H.T. (2008) *Resource Ecology – Spatial and Temporal Dynamics of Foraging*. Springer, Dordrecht, the Netherlands.
- Venter, F.J., Scholes, R.J. & Eckhardt, H.C. (2003) The abiotic template and its associated vegetation pattern. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds J.T. Du Toit, H.C. Biggs & K. Rogers), pp. 83–129. Island Press, Washington, DC.
- Wall, J., Douglas-Hamilton, I. & Vollrath, F. (2006) Elephants avoid costly mountaineering. *Current Biology*, **16**, R527–R529.
- Walsh, P.D. (1996) Area-restricted search and the scale dependence of patch quality discrimination. *Journal of Theoretical Biology*, **183**, 351–361.
- Wheatley, M. & Johnson, C. (2009) Factors limiting our understanding of ecological scale. *Ecological Complexity*, **6**, 150–159.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Wolf, M., Frair, J., Merrill, E. & Turchin, P. (2009) The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography*, **32**, 401–410.

Received 26 February 2010; accepted 18 September 2010

Handling Editor: Atle Mysterud

Supporting Information

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

Appendix S1. Metadata per collared elephant.

Appendix S2. Scores for the environmental variables on the first axes of the ENFA.

Appendix S3. Exploring individual variation and sexual segregation.

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