Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa

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Abstract

Landscape heterogeneity may influence ranging behaviour of mammals. Here we relate the home range size of elephants living in the Kruger National Park to the number of patches, proportion of each patch, spatial arrangement of patches, patch shape, and contrast between neighbouring patches. Home range sizes decreased exponentially with an increase in the number of patches per 100 km^2 and the home range sizes of bulls were in general more strongly related to measures of heterogeneity. This may reflect differences in perception of heterogeneity between the sexes.

Key words: FRAGSTATS, home range, landscape heterogeneity

Résumé

Il se peut que la hétérogénéité du paysage agisse sur le comportement des mammifères au pâturage. Dans cette étude nous associons la taille des domaines vitaux des éléphants résidant dans le Parc National de Kruger au nombre de parcelles et leurs dimensions, disposition spatiale et forme, ainsi que le contraste entre des parcelles avoisinantes. La taille des domaines vitaux diminua exponentiellement avec l'augmentation dans le nombre de parcelles par 100 km^2 alors que les domaines vitaux des mâles furent plus fortement associés aux mesures d'hétérogénéité en général. Cela est peut être dû aux différences au niveau de la perception d'hétérogénéité entre les sexes.

Introduction

The availability of resources including nutrients, food, cover (Tufto, Andersen & Linnell, 1996), and water (Stokke & du Toit, 2002) may account for the intra-specific

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variation in home range sizes of mammals. The age (Cederlund & Sand, 1994), sex (Relyea, Lawrence & Demarais, 2000) and reproductive status (Bertrand *et al.*, 1996) of individuals may also influence home range areas. Resource requirements underpin these factors and the distribution of resources across landscapes may therefore influence the size of home ranges. Resource distribution is rarely homogeneous, as the environment is made up of a mosaic of patches (Wiens, 1989). This patchiness at the landscape scale is referred to as landscape heterogeneity.

The use of landscape metrics to quantify landscape heterogeneity is currently open to misinterpretation (Fortin *et al.*, 2003). By considering landscape heterogeneity within the area of an individual's home range, the potential exists to become entwined in a circular argument (Kie *et al.*, 2002) – do animals select their home ranges for a certain level of heterogeneity, or is a certain level of heterogeneity caught within a home range size determined by another factor? This argument probably can only be fully resolved by observing relationships at different spatial scales.

Elephants roam across a wide range of landscapes over African savannas. Individual home ranges may include a variety of landscapes and vary, both within and between populations. For example in Etosha National Park home ranges may be as large as 7250 km^2 (Lindeque & Lindeque, 1991), but those in Lake Manyara National Park cover only 33 km^2 (Douglas-Hamilton, 1972). In this study we address this variability by investigating the contribution landscape heterogeneity may make to the variability in home range size of elephants in the Kruger National Park (KNP). Here home ranges varied from 45 to 1805 km^2 (Whyte, 2001). We are not aware of any earlier studies that have addressed the influence of landscape heterogeneity for home range in elephants. Landscape heterogeneity may explain variability in habitat selection (Crist *et al.*, 1992; Boyce *et al.*, 2003) and we therefore expect that measures of heterogeneity may explain variation in home range variables in elephants.

Materials and methods

Study area

The KNP is situated in the northeast of South Africa and extends over 18,992 km^2 (Whyte, van Aarde & Pimm, 2003). It lies between 22°20′ to 25°32′S and 30°53′ to 32°02′E. Gertenbach (1983) recognized 35 landscapes within the park based on plant communities, climate, soil type, and geology.

Home range analysis

We used data collected in two separate radiotelemetry studies on elephant movements within the KNP. Dr Anthony Hall-Martin collected data on elephant bulls from 1976 to 1992, and Dr Ian Whyte collected cow data from 1989 to 1996 (Whyte, 2001). These data were collected from 37 bulls and 50 cows. RANGES 6 (Anatrack Ltd., Wareham, UK) software was used to estimate home ranges using 95% minimum convex polygon estimator. This estimator has the ability to make better use of small amounts of data and is the only estimator that can be compared across studies (White & Garrott, 1990). Home ranges were separated by gender and season (wet season: September to April; dry season: May to August).

To determine how many fixes were needed to reach an asymptotic home range size, we plotted the percentage of the total home range size against the number of fixes. For illustrative purposes a one-phase exponential association curve was fitted to these data using GraphPad Prism Version 3.00 (Graph Pad Software Inc., San Diego, California, USA). To determine the starting point of asymptote we used a two-phase linear regression model (see Fox et al., 1997). Differences in home range between sexes were tested using a Mann–Whitney U-test.

We superimposed home ranges on to a landscape map of the Park and on maps depicting the distribution of natural water sources (rivers, springs, and pans) across the Park (available from SANParks) using the facilities of ArcView Version 3.3. (Environmental Systems Research Institute Inc., Redlands, California, USA).

Landscape heterogeneity analysis

Within home ranges we measured eight landscape variables using the raster version of FRAGSTATS (Version 3.3, McGarigal & Marks, 1995). FRAGSTATS expresses metrics as both absolute and relative measures. We used relative measures to compare heterogeneity across different home range sizes. For example, patch richness (the number of patches in a landscape or map) is of no use when comparing home ranges of different sizes and consequently we used patch richness density (the number of patches in a landscape or map per square kilometre). Those metrics that best described at least one facet of Li & Reynolds (1994) five descriptive variables of landscape heterogeneity were chosen (Table 1). In this study a patch was defined as an area of one landscape type surrounded by other landscape types or delimited by the home range boundary.

Table 1 Summary of the metrics used to quantify landscape heterogeneity, adapted from McGarigal & Marks (1995)

Descriptor of landscape heterogeneity	Landscape metrics	Description of measurement
Number of patches	Patch richness density	Measures the number of patches in a landscape map but accounts for overall area. Expressed as number of patches per 100 km^2
Proportion of each patch	Largest patch index	Measures the percentage of the total area comprised by the largest patch
Spatial arrangement of patches	Cohesion	Measures the spatial distribution of patch types. Expressed as percentage
	Contagion	Measures the intermixing of different patch types in a landscape map. Expressed as a percentage
	Euclidean nearest neighbour distance	Measures in km the distance to the next patch of the same type as the focal patch
Patch shape	Mean shape index	Compares the complexity of the patch shape with a simple shape (circle). Expressed as a ratio between number of cells in the patch and the number of cells needed to create a circle
	Edge density	Measures the total edge between patches divided by total area. Expressed as km per 100 km^2
Contrast between neighbouring patches	Mean edge contrast	Measures the degree of user-defined contrast between patches. Expressed as percentage contrast

For the mean edge contrast metric FRAGSTATS allows the user to specify contrast between landscape types. Contrast is scored on a scale of 0–1, with 0 being the minimum and 1 being the maximum contrast. A contrast score was assigned to each landscape type after Gertenbach's (1983) landscapes were reclassified into mountainous landscapes, thicket landscapes, woody vegetation landscapes and open tree savannah landscapes. The highest level of contrast was considered to be between mountain landscapes and the other landscapes and assigned a level of 0.9. Less contrast was considered between thicket and woody vegetation landscapes and assigned a score of 0.4 (Table 2). The relationship between home range size and each metric was tested using either linear or nonlinear regression analyses.

Results

Elephant home range

Bulls had clearly defined home ranges (i.e. the areas reached an asymptote) after 30 location fixes in the dry season (n = 37) and 40 location fixes in the wet season (n = 34). Data for 33 bulls in the dry season and 27 bulls in the wet season were excluded from further analyses because of insufficient data. Cows had clearly defined home ranges after eighteen locations in the dry season (n = 49) and 40 locations in the wet season (n = 50). Data for 38 cows in the dry season and 42 cows in the wet season were not analysed because of insufficient data.

Total home range size ranged between 72 and 4451 km^2 (mean ± SD = 988 ± 991 km^2, n = 26) and was not affected by sex ($P > 0.05$; Mann–Whitney U-test). Season also had no influence on the range sizes of bulls and cows ($P > 0.05$ Mann–Whitney U-test).

Landscape heterogeneity

Home range sizes for both sexes and in both seasons (bulls: n = 10, $r^2 = 0.84$; cows: n = 16, $r^2 = 0.82$; Fig. 1; bulls: dry season, n = 4, $r^2 = 0.99$, wet season, n = 7, $r^2 = 0.96$; cows: dry season, n = 11, $r^2 = 0.74$, wet season, n = 8, $r^2 = 0.61$; Fig. 2) declined exponentially with an increase in landscape patch richness density (number of landscape patches per 100 km^2).

Home range size also declined exponentially as a function of natural water source richness for the bulls in the wet season (n = 7, $r^2 = 0.99$), cows in the dry season (n = 11, $r^2 = 0.59$) and cows in the wet season (n = 8, $r^2 = 0.69$). Ranges for bulls in the dry season showed no relationship with natural water source richness.

Landscape patch index was significantly negatively related to home range size in cows and to cows in the wet season. Percentage contagion was significantly positively related to home range size for bulls, and to bull ranges in the dry and wet season. Bull ranges in the wet season were also significantly positively related to percentage cohesion. Cow home range and bull range in the wet season showed a significant positive relationship to mean shape index. Edge density was significantly negatively related to home range for bulls and to bulls in the wet season. There was a significant positive relationship to mean edge contrast for bulls (see Table 3 for summary of results).

Discussion

Home range sizes vary within mammal species (Franklin *et al.*, 1999; Whyte, 2001; Kie *et al.*, 2002). For elephants the home ranges of bulls tends to be larger than those of cows (Viljoen, 1989; Stokke & du Toit, 2002). This may partly be attributed to sexually mature bulls roaming large distances in search of oestrous cows. Another factor may be the restriction juvenile elephants place on the ability of
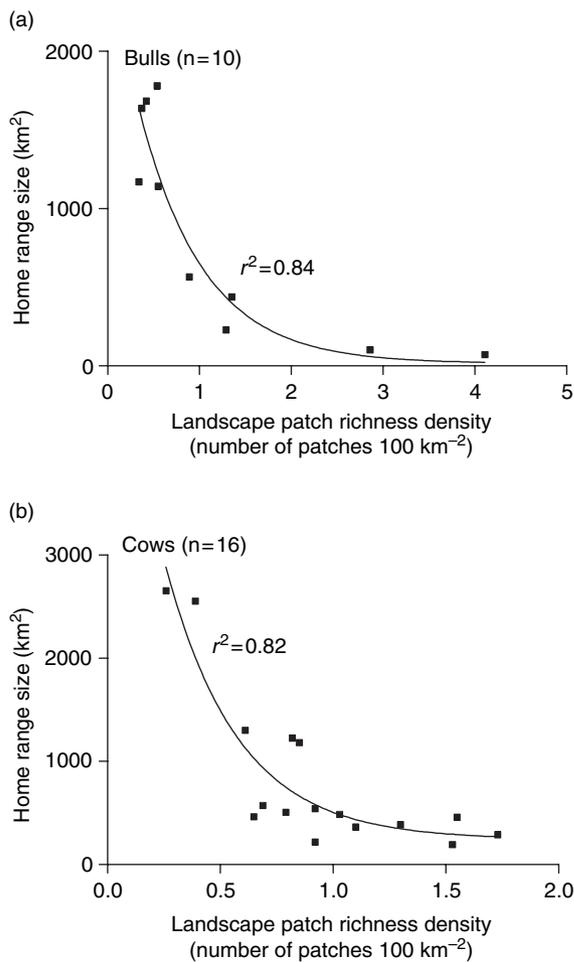
Table 2 Edge contrast weights between landscapes. Contrast was scored between 0 and 1, with 1 being the maximum contrast

Landscape classification	Mountain landscape	Thicket landscape	Woody vegetation landscape	Open tree savannah landscape
Mountain landscape	0	0.9	0.9	0.9
Thicket landscape	0.9	0	0.4	0.6
Woody vegetation landscape	0.9	0.4	0	0.4
Open tree savannah landscape	0.9	0.6	0.4	0

Fig 1 The relationship between 95% minimum convex polygon home range size (km^2) and landscape patch richness density for (a) bulls and (b) cows. For illustrative purposes a one-phase exponential association curve has been fitted to these data

breeding herds to travel away from water, because of mortality (Barnes, 1983).

In our study, we did not find a significant gender difference in the home range size. The complete fencing of the KNP may prevent bulls from moving the large distances that are seen in unfenced populations. Water sources within Kruger are positioned less than 10 km apart (Thrash, 1998) so water may not limit the movement of breeding herds (Barnes, 1983; Viljoen, 1989).

Home range in elephants generally increases in the wet season, possibly as water availability increases (Stokke & du Toit, 2002). This was not, however, the case in the

KNP. Here the availability of artificially maintained perennial water sources might negate these differences. Unfortunately, the lack of chronological information on the history of these sources did not allow us to assess their impact on ranging behaviour.

Variation in home range size is perhaps best related to the resource requirements of individual animals (Harestad & Bunnell, 1979). The spatial distribution of resources will therefore influence home range. Theoretically we would expect an animal foraging in a patchy environment to decrease its home range size with an increase in resource availability (Ford, 1983).

Elephants in the Kruger may reduce their home range size in response to increasing landscape patch richness density. The variability this factor explains in cow range size is, however, less than for bulls. We argue this may be ascribed to cows being affected by processes that operate at different scales than bulls, as spatial and temporal scales affect movement decisions of animals (Ims, 1995). This is because of different life processes (that lead to movement) being manifested at different scales (Ims, 1995). As female reproductive success may be closely linked to resources (Gehrt & Fritzell, 1998), cow elephants may be selecting at a scale that is more directly related to resource acquisition.

The availability of water sources is a major determinant of home range size for water-dependent mammals (Viljoen, 1989; Ordway & Krausman, 1986). Stokke & du Toit (2002) showed that elephant family groups in Chobe National Park, Botswana, did not move further than 3.5 km from rivers in the dry season and 5 km in the wet season. Bull and cow home range size in our study declined exponentially with an increase in water source patch richness density. This indicates that elephants in areas of high water point richness density have smaller home ranges than those in areas with low water point richness density. This has implications for conservation managers, as an increased density of water sources could reduce home range area and increase the intensity of patch use within a home range.

The ecological importance of edges has been widely studied because of the increased fragmentation of habitats. Tufto *et al.* (1996) suggest that edges are one of the most important landscape attributes influencing home range size. If complementary resources are adjacent to each other, animals should spend more time on the edge of resource patches in order to maximize the availability of these neighbouring resources, and subsequently increase
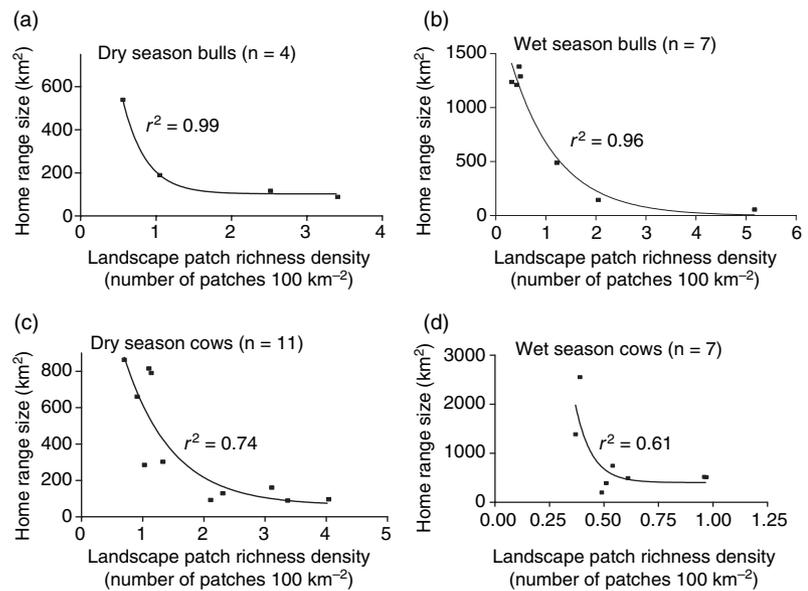
Fig 2 The relationship between 95% minimum convex polygon home range size (km^2) and landscape patch richness density for bulls in the (a) dry season, (b) wet season and cows in the (c) dry season and (d) wet season. For illustrative purposes a one-phase exponential association curve has been fitted to these data

habitat heterogeneity (Tufto *et al.*, 1996). Therefore, as more edges become available we would expect home range size to decrease (Tufto *et al.*, 1996; Kie *et al.*, 2002). During the wet season elephant bull ranges decreased with increasing edge density, while those of cows increased with increasing edge density. This is difficult to interpret.

Patch shape is also a measure of edge as an irregular patch has more edge. Elephants in the KNP did not appear to select for irregular shaped patches; there was a weak positive relationship for cows and a stronger positive relationship for bull ranges and patch shape in the wet season. The fact that these two relationships are positive suggests that this is not an ecologically significant relationship.

Our measures of edge may be affected by the boundaries that Gertenbach (1983) produced when delineating the Park's landscape types. At the landscape scale landscape types may not represent complementary resources for cow elephants. Cows may be selecting home range variables at a finer scale of heterogeneity than the landscape maps we used allows, given that this is the scale at which foraging decisions take place (Ims, 1995). It appears that, to some extent, bull elephants do select home range size in relation to edge at the landscape scale. Thus, the two sexes may perceive landscape heterogeneity differently.

The percentage edge contrast was only significantly related to range size in bull elephants. This relationship was positive whereas we would expect it to be negative. The more contrast between patches that are close together, the more resources that are available (Dunning, Danielson & Pulliam, 1992). The lack of any relationship for cows, and for bulls in the dry season suggests that elephants do not perceive contrast between landscape patches in the same way that we assessed them.

None of the metrics we considered reacted in the same way to all conditions (bull, cow, wet season, dry season), which suggests that the metrics were not merely displaying an area relationship, increasing or decreasing as home range size increased. This has been a concern in other studies of this nature (Kie *et al.*, 2002).

We have shown that home range size in elephants, more particularly bulls, is related to certain measures of landscape heterogeneity. Furthermore, we showed that the availability and distribution of natural water sources is a strong determinant of home range size of elephants. The artificial manipulation of water sources in Kruger may influence home range size, influencing the effects of elephants on vegetation within their ranges.

Acknowledgements

Table 3 Linear regression variables (b) between home range size (km^2) and selected landscape metrics for bull elephants (n = 10), cows (n = 16), and bulls in the dry (n = 4) and wet season (n = 7), and cows in the dry (n = 11) and wet season (n = 8) in the Kruger National Park. N/A: Not Available

	Bulls	Cows	Dry season bulls	Wet season bulls	Dry season cows	Wet season cows
Largest patch index	b = −0.002 ± 22.91; $F_{1,9}$ = 0; r^2 = 0	b = −17.67 ± 6.583; $F_{1,14}$ = 7.203; r^2 = 0.34*	b = 8.036 ± 2.099; $F_{1,2}$ = 14.65; r^2 = 0.88	b = 17.11 ± 18.62; $F_{1,5}$ = 0.844; r^2 = 0.14	b = −6.530 ± 4.061; $F_{1,9}$ = 2.586; r^2 = 0.22	b = −19.99 ± 7.543; $F_{1,6}$ = 7.025; r^2 = 0.54*
Percentage contagion	b = 53.21 ± 22.88; $F_{1,9}$ = 5.409; r^2 = 0.38*	b = −15.84 ± 13.77; $F_{1,14}$ = 1.323; r^2 = 0.09	b = 7.291 ± 1.345; $F_{1,2}$ = 29.38; r^2 = 0.94*	b = 36.39 ± 7.977; $F_{1,5}$ = 20.81; r^2 = 0.81*	b = 3.822 ± 5.894; $F_{1,9}$ = 0.420; r^2 = 0.04	b = −18.62 ± 13.75; $F_{1,6}$ = 1.832; r^2 = 0.23
Percentage cohesion	b = 124.4 ± 44.03; $F_{1,9}$ = 7.980; r^2 = 0.50*	b = −206.8 ± 105.2; $F_{1,14}$ = 3.864; r^2 = 0.27	b = 35.77 ± 22.26; $F_{1,2}$ = 2.582; r^2 = 0.56	b = 128.9 ± 34.11; $F_{1,5}$ = 14.28; r^2 = 0.74*	b = 17.68 ± 29.48; $F_{1,9}$ = 0.359; r^2 = 0.04	b = −277.8 ± 126.4; $F_{1,6}$ = 4.834; r^2 = 0.45
Mean shape index	b = 2963 ± 6958; $F_{1,9}$ = 0.1814; r^2 = 0.02	b = 1977 ± 747.2; $F_{1,14}$ = 7.002; r^2 = 0.33*	b = 1065 ± 801.8; $F_{1,2}$ = 1.763; r^2 = 0.47	b = 3034 ± 1115; $F_{1,5}$ = 7.404; r^2 = 0.60*	b = 1221 ± 666.2; $F_{1,9}$ = 3.360; r^2 = 0.27	b = 2106 ± 1287; $F_{1,6}$ = 2.678; r^2 = 0.31
Edge density	b = −35530 ± 13010; $F_{1,9}$ = 7.463; r^2 = 0.45*	b = 22690 ± 19460; $F_{1,14}$ = 1.360; r^2 = 0.09.	b = −6954 ± 5559; $F_{1,2}$ = 1.565; r^2 = 0.44	b = −32430 ± 10220; $F_{1,5}$ = 10.07; r^2 = 0.67*	b = −17130 ± 23830; $F_{1,9}$ = 0.1371; r^2 = 0.02	b = 75400 ± 23300; $F_{1,6}$ = 10.47; r^2 = 0.64
Mean edge contrast	b = 44.07 ± 8.969; $F_{1,9}$ = 24.14; r^2 = 0.75*	b = 23.95 ± 23.47; $F_{1,14}$ = 1.041; r^2 = 0.07	b = 6.793 ± 19.85; $F_{1,2}$ = 0.117; r^2 = 0.05	b = 38.22 ± 26.15; $F_{1,5}$ = 2.136; r^2 = 0.30	b = 12.67 ± 17.74; $F_{1,9}$ = 0.510; r^2 = 0.05	b = 43.52 ± 25.99; $F_{1,6}$ = 2.803; r^2 = 0.32
Natural water source ENN	N/A	N/A	b = −0.005 ± 0.017; $F_{1,2}$ = 0.08; r^2 = 0.04	b = −379.6 ± 374.2; $F_{1,5}$ = 1.029; r^2 = 0.17	b = 10.86 ± 9.394; $F_{1,8}$ = 1.337; r^2 = 0.14	b = −3.767 ± 272.6; $F_{1,6}$ = 0; r^2 = 0

*Significant at $P < 0.05$.

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