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Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas?

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ABSTRACT

Elephants live in heterogeneous landscapes where their search for resources may increase individual survival. The uneven distribution of such resources may be linked to landscape heterogeneity. We therefore hypothesized that landscape heterogeneity determines elephant home range location and size in Etosha National Park, Khaudum Game Reserve and Ngamiland District 11. We used landscape maps to quantify landscape heterogeneity based on five metrics calculated using FRAGSTATS and compared these for elephant and randomly located ranges within the study areas. We further related elephant range size to the landscape metrics and water point density. The elephants located their home ranges in areas with relatively high Patch density, Landscape shape index and Shannon diversity index, and relatively low Largest patch index and Contagion. Elephants therefore seem to locate their home ranges in areas of the landscape where higher levels of heterogeneity occur during wet and dry seasons. Home range size decreased with increasing water point density and heterogeneity and water distribution influence elephant space utilisation. Management of elephants should therefore be directed at ensuring the inclusion of heterogeneous landscapes in conservation areas and at reconsidering water management policies that may influence home range sizes and landscape selection.

1. Introduction

Elephants roam across heterogeneous landscapes where they search for resources that may enhance their individual survival. Within the landscape, vegetation patches (homogenously vegetated areas that differ from the surrounding landscape) vary in their composition and spatial arrangement and this complexity represents landscape heterogeneity (Turner et al., 2001). Aspects of landscape heterogeneity can be measured through an assessment of patch characteristics. Hierarchy theory predicts that resource selection at smaller scales (i.e. plant parts or species) will cause an aggregate selection response at larger scales (O'Neill et al., 1986). The combination of preferred plant resources within vegetation patches may consequently elicit a selection response at the landscape level. Landscape heterogeneity may therefore benefit large herbivores through an increased stability of food resources (Illius and O'Connor, 1999). This may enhance their opportunities to achieve nutritional balance and to avoid toxin accumulation (Jachmann, 1989; Owen-Smith, 1988).

As large-bodied mixed feeders, elephants include low-quality plant matter in their diets (Owen-Smith, 1988). However, to maximise their energy intake there should be a trade-off between selection for scarce, high-quality resources and the

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utilisation of lower quality resources that are presumably more abundant (Illius, 2006). Spatial and temporal variability in habitat quality can therefore influence individual fitness which, at the population level, shows up in demographic responses such as age-specific fecundity and survival (Sibly and Hone, 2003; Wang et al., 2006). During critical periods, such as the dry season, elephants may rely on 'key-resources' (e.g. Gaylard et al., 2003; Smit et al., 2007) that are sought after regardless of the spatial distribution of other resources (Illius, 2006). Water may be such a key-resource (see Harris et al., 2008).

The home range is expected to reflect the elephant's nutritional requirements (e.g. Schoener, 1981), especially for cows that are less restricted by social interactions than bulls (Owen-Smith, 1988). For elephants, nutritional constraints should be more pronounced as the dry season progresses. In theory, elephants are therefore expected to increase the size of their home ranges during the dry season to include the resources otherwise available during the wet season within smaller areas. Contradictory to this, elephants tend to concentrate their foraging activities in areas close to water during the dry season (Chamaillé-Jammes et al., 2007; de Beer et al., 2006; Gaylard et al., 2003; Leggett, 2006; Osborn and Parker, 2003; Redfern et al., 2003; Smit et al., 2007) and they then conceivably depend on lower quality food (Owen-Smith, 1988). The restriction imposed by the distribution of water as a 'key-resource' (see Illius, 2006) may therefore coincide with selection for areas with higher food resource availability within the landscape, which may consequently determine the location of elephant home ranges.

In our study, we hypothesized that landscape heterogeneity and water distribution are determinants of the location and size of elephant home ranges in arid savannas. The apparent selection for variables that are encapsulated by landscape heterogeneity metrics may explain the uneven distribution of elephants across landscapes as an outcome of their preferences for certain habitats. Moreover, by identifying how landscape heterogeneity and water distribution affects the spatial dynamics of elephants we may be able to predict how elephants will respond to areas in which they do not occur at present. This may facilitate initiatives to improve conservation management plans that incorporate aspects of landscape ecology (see Damschen et al., 2006; van Aarde and Jackson, 2007).

2. Materials and methods

2.1. Study region

The Etosha National Park, Khaudum Game Reserve and Ngamiland District 11 (henceforth, referred to as Etosha, Khaudum and NG11, respectively), occur within the arid to semi-arid savanna regions of southern Africa (see Sankaran et al., 2005). At the time of the study, Etosha was a fenced off conservation area that stretched over 22,270 km^2 in north-central Namibia. Khaudum extended over 3841 km^2 in north-eastern Namibia along part of the international border between Namibia and Botswana. The NG11 lay along the Okavango Panhandle in north-western Botswana and stretched over 4704 km^2 within a controlled hunting concession.

Situated along the 19°S latitude, annual rainfall generally increased from ~200 mm in the west (Etosha) to ~650 mm in the east (NG11). Rainfall in the region was erratic and annual rain fell mostly between November and April (Data provided by the Ministry of Environment and Tourism, Namibia; Meteorological Services, Botswana).

Mopane (*Colophospermum mopane*) woodlands dominated in Etosha (Lindeque, 1988). In Khaudum, *Burkea africana* and *Baikiaea plurijuga* woodlands on the sand dunes and *Terminalia sericea*, *Acacia* species and *Combretum* species in the inter-dune valleys characterised the patchy vegetation of the reserve (Weaver and Skyer, 2005). In NG11, mopane woodlands dominated along the panhandle but *Burkea africana* and *Baikiaea plurijuga* woodlands were also prominent within the area (Mendelsohn and el Obeid, 2004).

Elephant numbers in Etosha have remained relatively stable (~2000 elephants) since the 1980s (Etosha Ecological Institute, unpublished data). Since the provisioning of water in Khaudum, elephant numbers in the reserve increased rapidly from a guestimated 80 in 1976 to the present population in excess of 3000 (Weaver and Skyer, 2005). In NG11, 3579 elephants occurred during the 2003 dry season and 1060 during the 2004 wet season (Jackson et al., 2008).

2.2. Elephant home ranges

Home ranges were estimated from location data obtained from satellite GPS units that were fitted to adult cows living in different breeding herds in Etosha ($n = 6$), Khaudum ($n = 6$) and NG11 ($n = 4$). The GPS units (model AWT SM2000E) provided accuracy within 15 m (Ott, 2007) and GPS error was reduced by using kernel density estimates instead of the locations as individual points (Dussault et al., 1999).

Elephant home ranges were calculated for two dry (May–October) and two wet seasons (November–April) in each of the study areas using the Animal Movement extension (Hooge and Eichenlaub, 1997) of ArcView GIS 3.3 (ESRI, Inc. 2002). We used the 95% fixed kernel density estimate with least square cross validation (LSCV) smoothing (Börger et al., 2006; Seaman and Powell, 1996; Seaman et al., 1999). The minimum and maximum sample size for an elephant in this study was 49 and 178 locations, respectively.

2.3. Randomly located ranges

Randomly located ranges were simulated as independent random samples that represented the landscapes of the study areas (see Potvin et al., 2001). This enabled us to quantify landscape metrics for the study areas and to compare them with those calculated for the elephant ranges.

Locations placed randomly in each of the study areas served as centroids for the positions of the randomly located ranges (ArcView GIS 3.3). Additional locations (mean number recorded during each season for the elephants) were then generated at area intervals around the centroids to create different sizes of randomly located ranges that were similar in size than elephant home ranges in a given study area. Area intervals were at 500 km^2 circles within which the locations were randomly generated and the number of intervals ranged between the minimum and maximum size of elephant ranges. The locations were then used to estimate the areas of the ranges using the 95% fixed kernel density estimate. The shapes and sizes of the randomly located ranges relied on the distribution of the randomly generated locations within the circles at 500 km^2 size intervals. Initially, ten repeats of each size interval were simulated to create enough variation in random range sizes between the upper and lower limits set by the elephant range sizes for a given study area. However, the logarithmic transformation of the data used for further analyses caused clumping towards the larger ranges. We therefore added more of the smaller ranges and excluded some of the larger ranges through a random selection function in Microsoft® Office Excel, 2003 (Copyright©1985–2003, Microsoft Corporation).

2.4. Preparation of landscape maps

Elephant and randomly located ranges were superimposed onto landscape maps for each of the study areas. The landscape maps were based on the dominant tree species and growth structure (trees or shrubs) and were prepared by classifying satellite TM images using the ERDAS protocol (Leica Geosystems GIS and Mapping, Illinois). The Etosha map (Harris et al., 2008), yielded an overall accuracy of 76% and the Khaudum map an overall accuracy of 56% based on the Kappa statistical procedure (Congalton, 1991). Statistical information was not available for the NG11 map (Conservation International, University of Botswana—HOORC, 2005).

Patch mosaic classifications that divide landscapes into homogeneous units may be biased and may lead to a loss of information (see Murwira and Skidmore, 2005) depending on the scale and grain (resolution) of the patch mosaic (Gustafson, 1998; Turner et al., 2001). However, the relatively high resolution (minimum mapping unit: 30×30 m pixels) of the maps we used made it possible to retain the differences in the patch type characteristics and therefore landscape heterogeneity, which may have been lost at lower resolutions (see Boyce, 2006). We were not interested in finer-scale information that may explain diet selection and therefore all three of the maps were considered to be fine-grained for the purpose of the study.

2.5. Landscape heterogeneity as a determinant of elephant home range location and size

We used FRAGSTATS v. 3.3 (McGarical and Marks, 1995) to quantify five area-corrected landscape metrics (see Table 1) as indices of heterogeneity (also see Li and Reynolds, 1994; Riitters et al., 1995) and compared these for elephant ranges during wet and dry seasons with those of randomly located ranges. Indices of landscape heterogeneity should vary across landscapes (Turner et al., 2001; Wiens et al., 1993) and we therefore treated the three study areas that are situated on different substrates and along a rainfall gradient, separately.

To address our hypothesis on the location of home ranges, we used a macro in Microsoft® Office Excel to randomly select the same number of randomly located ranges as the number of collared elephants for each season within a study area. The procedure was repeated 10,000 times with replacement (Legendre and Legendre, 1998), and for each repeat the macro returned the mean values and variances for each of the landscape metrics and seasons.

For each landscape metric, we calculated the class width required to produce 20 classes (or 'bins') of equal range by using the minimum and maximum of the 10,000 values. We then constructed a frequency distribution for each landscape metric and season by assigning the values of the randomly located ranges for each metric in the relevant 'bins'. We fitted a Normal and Gamma distribution (Microsoft® Office Excel) to the frequency distributions of the means and variances, respectively.

The observed mean and variance values of the elephant ranges for each of the metrics within each season and study area were marked on the frequency distributions for the means and the variances, respectively. Selection for landscape heterogeneity as suggested by the mean values of the elephant ranges outside the two-tailed 95% confidence limits were confirmed when the variance values of the elephant ranges were also outside the two-tailed 95% confidence limit. However, when the variance values were within the 95% confidence limits, but the mean values were outside, selection was implied but not confirmed. By the nature of the metrics (see Table 1), higher values for Patch density, Landscape shape index and Shannon diversity index and lower values of Largest patch index and Contagion for elephant ranges than for randomly located ranges implied selection for greater landscape heterogeneity. Avoidance was implied when values of the elephant ranges were lower for Patch density, Landscape shape index and Shannon diversity index and higher for Largest patch index and Contagion.

Table 1
A summary of the landscape metrics that were used to compare heterogeneity among the randomly located ranges and elephant ranges within study areas

Landscape metrics	Metric description	Units	Range
Patch density	Measures the number of all patches per unit area and *increases with increasing heterogeneity*	#/km^2	Patch density >0, constrained by cell size. Maximum Patch density is attained when every cell is a separate patch
Largest patch index	Measures the percentage of the total area comprised by the largest patch. The *metric decreases with increasing heterogeneity*	%	0<Largest patch index⩽100. Largest patch index approaches 0 when the largest patch in the landscape is increasingly small. Largest patch index = 100 when the entire landscape consists of a single patch
Landscape shape index	Measures the total edge or edge density while adjusting for the size of an area. The *metric increases with increasing heterogeneity*	n/a	Landscape shape index⩾1, without limit. Landscape shape index = 1 when the landscape consists of a single square patch; Landscape shape index increases as landscape shape becomes more irregular and as the length of edge within the landscape increases
Contagion	Measures aggregation and interspersion of patches in an area and *decreases with increasing heterogeneity*	%	0<Contagion⩽100. Contagion approaches 0 when the patch types are maximally disaggregated and interspersed. Contagion = 100 when all patch types are maximally aggregated; i.e., when the landscape consists of a single patch
Shannon diversity index	Measures the proportional distribution of area among patch types and *increases with increasing heterogeneity*	n/a	Shannon diversity index⩾0, without limit. The index increases as the number of different patch types (i.e., patch richness) increases and/or the proportional distribution of area among patch types becomes more equal

These are based on the descriptions provided by McGarical and Marks (1995).

Table 2
A summary of the comparison of landscape metrics for elephant and randomly located ranges for two wet and two dry seasons in Etosha, Khaudum and NG11

Study area	Season[a]	Patch density	Largest patch index	Landscape shape index	Contagion	Shannon diversity index
Etosha	Dry 1	ns	Confirmed +	Confirmed +	Confirmed +	ns
	Dry 2	Implied +	ns	Confirmed +	ns	ns
	Wet 1	Confirmed +	Confirmed +	Confirmed +	ns	ns
	Wet 2	Confirmed +	ns	Confirmed +	ns	ns
Khaudum	Dry 1	Confirmed +	ns	Confirmed +	ns	ns
	Dry 2	Confirmed +	ns	Implied −	Implied +	Implied −
	Wet 1	Implied −	ns	Confirmed +	Confirmed +	ns
	Wet 2		Confirmed +	Confirmed −	Confirmed +	Implied −
NG11	Dry 1	Implied +	ns	ns	Confirmed +	Implied +
	Dry 2	Implied +	ns	Implied +	Implied +	Implied +
	Wet 1	Confirmed +	Implied +	Implied +	ns	ns
	Wet 2	ns	Implied +	Confirmed +	ns	ns

"Implied" refers to instances where the position of the elephant range mean was outside the two-tailed 95% confidence limit, but the corresponding variance was not. "Confirmed" refers to instances where both the mean and variance fell outside the two-tailed confidence limit. Selection and avoidance are indicated by + and − signs, respectively. "ns" indicates no selection.

[a] Dry seasons were from May to October and wet seasons from November to April.

To test the hypothesis that home range size decreases with an increase in landscape heterogeneity we plotted home range size as a function of each of the five landscape metrics for the wet and the dry seasons to search for possible relationships using linear and non-linear regression analyses (GraphPad Prism v. 3.00, GraphPad Software Inc., 1999). We also related home range size to water point density (number of water points per home range area) using linear and non-linear regression.

3. Results

3.1. A comparison of landscape metrics for elephant home ranges and randomly located ranges

In Etosha, we confirmed selection for Patch density in both wet seasons and implied during one of the dry seasons. Patch density was selected for both during dry seasons by elephants in Khaudum, while avoidance was implied for one wet season. Selection was confirmed only for one wet season and implied for both dry seasons in NG11 (see Table 2).

Elephants selected for the lower values of Largest patch index in one wet and one dry season of Etosha and one wet season of Khaudum. In NG11, selection for Largest patch index was implied but not confirmed during both wet seasons. Selection for Landscape shape index occurred during both wet and dry seasons in Etosha. For Khaudum, results were inconsistent, with selection confirmed during one dry and one wet season, but avoidance during the other wet and dry season confirmed and implied, respectively. In NG11, selection for Landscape shape index was implied during one dry and one wet season while selection for the other wet season was confirmed (see Table 2).

Selection for Contagion was confirmed for one dry season of Etosha. During the wet seasons and one of the dry seasons in Khaudum, elephants apparently avoided areas where lower values of Contagion occurred. In NG11, selection for Contagion was confirmed and implied for the two dry seasons, respectively. Elephants in Etosha showed no preferences for Shannon diversity index and in Khaudum avoidance for the metric was noted during one dry and one wet season. In NG11, however, selection for the Shannon diversity index was implied during both dry seasons (see Table 2).

3.2. Relationships between home range size and landscape heterogeneity metrics

Home range sizes of elephants in the three study areas did not decrease with increasing Landscape shape index (Fig. 1c i–iv) or Shannon diversity index (Fig. 1e i–iv). Elephant home range sizes also did not decrease with decreasing Largest patch index (Fig. 1b i–iv) or Contagion (Fig. 1d i–iv). Within the three study areas, home range size variability could not be explained by Patch density during the wet seasons (Fig. 1a i–ii), however, we noted that home range size decreased

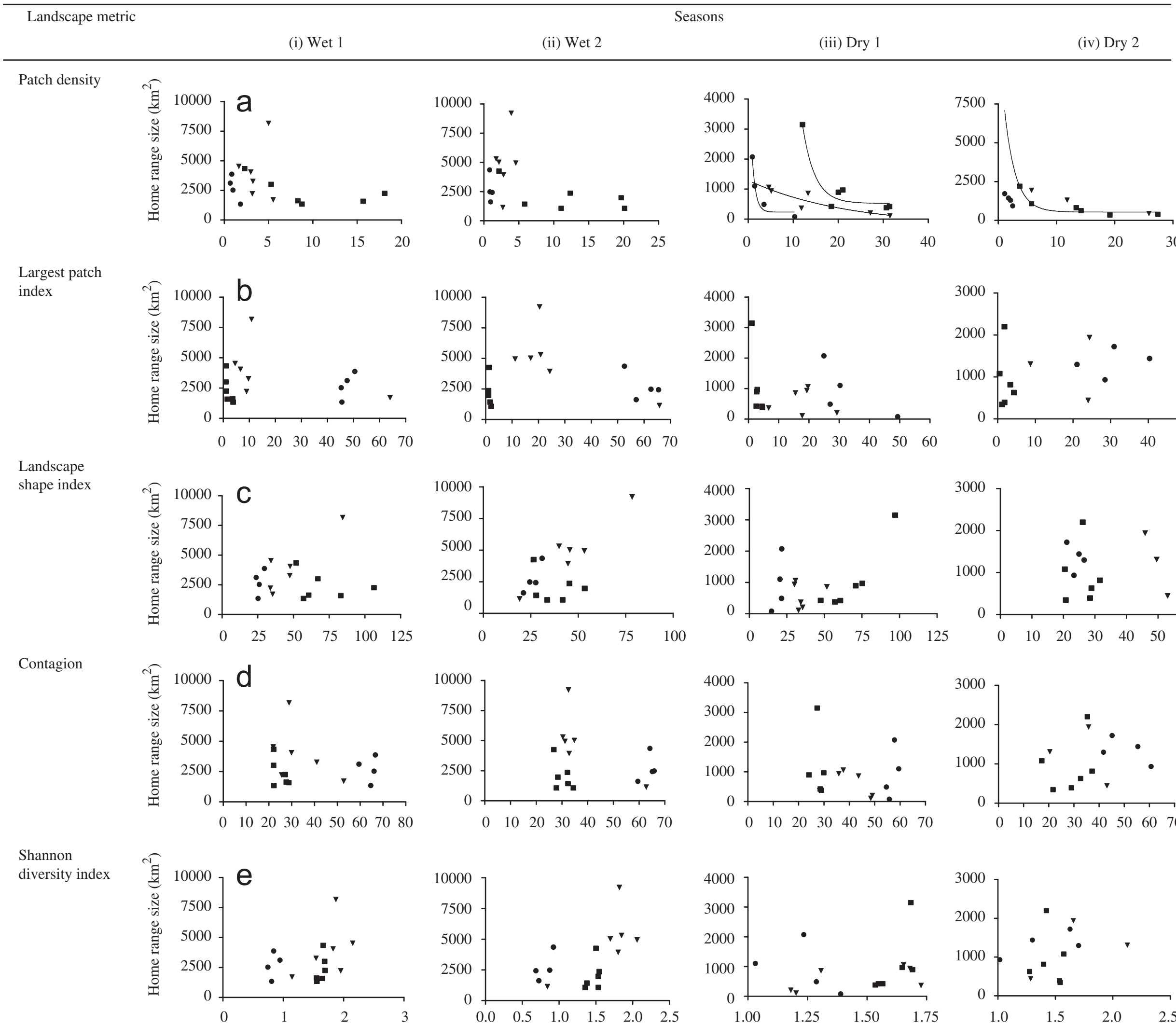

Fig. 1. Home range size as a function of Patch density, Largest patch index, Landscape shape index, Contagion and Shannon diversity index for elephants living in Etosha (▼), Khaudum (■) and NG11 (●) for two wet and two dry seasons. Curves were fitted only in cases where a significant relationship between home ranges size and a metric were identified.

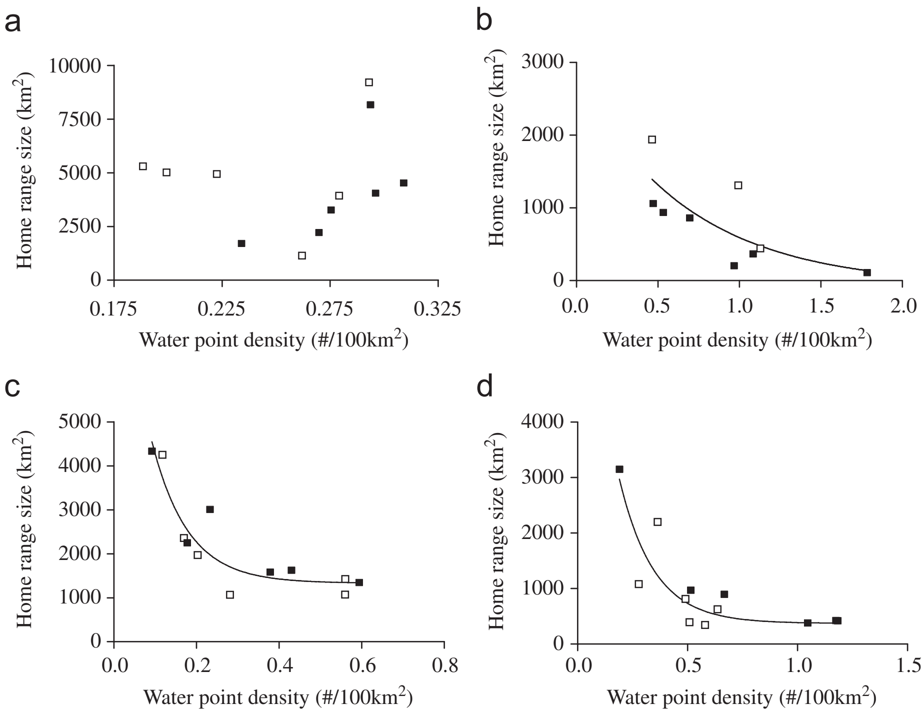

Fig. 2. The sizes of the elephant home ranges as a function of water point density during two wet and two dry seasons for Etosha National Park (a and b) and Khaudum Game Reserve (c & d). Curves were fitted only in cases where a significant relationship between home ranges size and water point density were identified. Open and closed symbols represent wet and dry seasons of different years.

exponentially with increasing Patch density during the first dry season of Etosha (df = 3; $R^2 = 0.81$), Khaudum (df = 3; $R^2 = 0.94$) and NG11 (df = 1; $R^2 = 0.81$) (Fig. 1a iii) and during the second dry season of Khaudum (df = 3; $R^2 = 0.94$) (Fig. 1a iv).

3.3. *Relationship between home range size and water point density*

In Etosha, the sizes of the elephant home ranges decreased exponentially with an increase in water point density during the dry seasons (Fig. 2b—df = 6, $R^2 = 0.57$). During both the wet seasons there was no relationship between water point density and elephant home range sizes (Fig. 2a). In Khaudum, elephant home range size decreased exponentially with increasing water point density during the wet seasons (Fig. 2c df = 9, $R^2 = 0.84$) and the dry seasons (Fig. 2d—df = 9, $R^2 = 0.77$).

4. Discussion

Landscape heterogeneity influenced elephant home range use. The locations of elephant home ranges in all three study areas could be explained by selection for some of the landscape metrics. Patch density, a measure of the amount and distribution of vegetation and the integration of resources that occur at different scales (Johnson et al., 2004), was selected for during the wet seasons in Etosha and NG11 and in the dry seasons in Khaudum. This suggests that elephants preferred areas where the number of patches per unit area was greater than that typical for each of the study areas, probably because resources were more aggregated here than elsewhere.

Largest patch index measures the percentage of the total area made up by the largest homogenous patch (or structural class). Elephants in all three study areas avoided areas with large homogenous patches and therefore seemed to locate their home ranges in relatively more heterogeneous parts of the landscape.

During all seasons, elephants in Etosha consistently selected for relatively high values of Landscape shape index, a measure of patch edges within an area. This was also the case during both wet seasons and one dry season in NG11 and during the first wet and dry season in Khaudum. Edges are transition zones where resource diversity increases as a result of more than one habitat patch type adjoining each other (Ries and Sisk, 2004). Conceivably, foraging by elephants may be more efficient in these transition zones than in non-edges (patch interiors) (see Fagan et al., 1999; Ries and Sisk, 2004; Ries et al., 2004).

Contagion is a measure of the interspersion and aggregation of patches within the landscape. The patterns observed for Contagion were not consistent for the three study areas. For instance, elephants in Etosha and NG11 preferred higher interspersion and less aggregation of patches than were represented by the surrounding landscape during one and both of the dry seasons, respectively. In Khaudum, however, the location of elephant home ranges could not be explained by this metric.

The Shannon diversity index measures the proportional distribution of area among different patch types. Conceivably, elephants would select for areas within the landscape where the equal distribution of a larger number of different patch types implies greater opportunity to encounter a greater diversity of resources (see Honnay et al., 2003; Ortega et al., 2004). In the dry seasons, the elephants of NG11 selected for such resource diversity. In Khaudum and Etosha, this measure of heterogeneity apparently was not important for the elephant home range location.

The selection for metrics during both wet and/or dry seasons by elephants therefore suggests that landscape heterogeneity plays some role in the location of home ranges within the landscape.

Elephants tend to be more selective during the wet season when water availability poses less restriction on their movements (e.g. de Beer et al., 2006; Ntumi et al., 2005; Osborn, 2004; Western and Lindsay, 1984). However, seasonal differences in landscape heterogeneity within elephant home ranges did not agree with our expectation that selection for higher levels of heterogeneity would be accentuated in the wet season when the distribution of water may not restrict roaming. Indeed, Harris et al. (2008) suggest that selection for habitat by elephants is not consistent and differs between individuals and seasons. Verlinden and Gavor (1998) also found no large differences between wet and dry season selection for habitats in northern Botswana. Here, migratory herds moved large distances to locate nutrient-rich habitats, while resident herds used the less nutritious habitats close to water sources throughout the year (Verlinden and Gavor, 1998).

We expected areas with relatively high heterogeneity to support smaller home ranges than less heterogeneous areas based on the premise that resource abundance should increase with increased landscape heterogeneity (Kie et al., 2002; Saïd and Servanty, 2005; Tufto et al., 1996).

Across our study region elephant home range sizes were inversely related to Patch density only during one dry season in Etosha and NG11 and both dry seasons in Khaudum. This result was inconsistent and we could not draw any specific conclusions. The Largest patch index, Landscape shape index, Contagion and Shannon diversity index did not explain variability in home range sizes. This finding differs from that of Kie et al. (2002) who showed that variation in home range size of mule deer is related to metrics of heterogeneity.

Home range size for elephants in both Etosha and Khaudum decreased with increasing water point density during the dry seasons and the wet seasons in Khaudum. This suggests that water is a strong determinant of elephant spatial use and may take precedence over the role that landscape heterogeneity may play in determining the size of elephant home ranges (also see Grainger et al., 2005). In NG11, the Okavango River provides the only permanent source of water and here one would expect that heterogeneity would play a larger role in determining home range size than in areas where management provides water. However, this expectation did not hold for NG11 and suggests that even in unmanaged situations, the need for water may still be more important in determining home range size than the benefits that may be achieved by selecting for landscape heterogeneity. The reduction in home range size with an increase in water point density suggests that water management has implications for impact since the utilisation density of small home ranges could be expected to be higher than for large home ranges. Such artificial reduction in home range areas may be counterproductive when management is directed at ameliorating impact (see van Aarde et al., 2006).

5. Conclusion

We have demonstrated that the elephants we studied locate their home ranges in areas where aspects of landscape heterogeneity were higher than elsewhere. However, in our study, landscape metrics could not explain variability in home range size of elephants. In this case, selection for water apparently plays a larger role than landscape heterogeneity.

These findings may have implications for the conservation and management of elephants across southern Africa. Ideally the management of elephants may have to be directed at managing heterogeneity and a reconsideration of water management policies (Chamaillé-Jammes et al., 2007; van Aarde et al., 2006). The landscape metrics we used to measure heterogeneity are relatively easy to apply and may provide a tool to identify areas that elephants may prefer. This may further facilitate initiatives to improve conservation management plans for elephants (see van Aarde and Jackson, 2007).

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