

Intrinsic and extrinsic factors influencing large African herbivore movements

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Abstract

Understanding environmental as well as anthropogenic factors that influence large herbivore ecological patterns and processes should underpin their conservation and management. We assessed the influence of intrinsic, extrinsic environmental and extrinsic anthropogenic factors on movement behaviour of eight African large herbivore species. A cumulative odds ordinal logistic regression was used to determine the effect of season, feeding niche, number of vegetation types, home range size, and fences on the number of exponential distributions observed. When animals faced the trade-off between forage quality and quantity during the dry season, they moved further between forage areas and water sources in order to get to better forage, which added to the number of movement scales observed. Elephants had a lower number of movement scales, compared to all the other feeding types, which could be attributed to them being able to switch between browse and graze. The number of movement scales increased in more heterogeneous areas. Animals with larger home ranges, which are also larger species, and animals more restricted by fences, had fewer movement scales. In order for managers to effectively manage protected areas and associated biodiversity they need take cognisance of the different scales animals operate under, and the different factors that may be important for different species.

Key words: African elephant, African buffalo, Cape mountain zebra, blue wildebeest, red hartebeest, plains zebra, eland, Brownian motion, Mkambati Nature Reserve, Kruger National Park

1. Introduction

Environmental heterogeneity, such as in water or forage availability, species traits, and anthropogenic influences have a substantial effect on the ecological patterns and processes that shape the distribution of large herbivores (Boone and Hobbs, 2004; Cornélis et al., 2011; Loarie et al., 2009). Understanding how these factors influence the movement behaviour of large herbivores is important for protected area managers, as these could influence individual species' ability to persist, and have a negative effect on other species in an ecosystem (Fortin et al., 2005; Ripple and Beschta, 2007).

Large herbivores select resources at different scales (Bailey et al., 1996; Prins and Van Langevelde, 2008). In most cases, there is a proportional relationship between the time a large herbivore spends in an area, and the available quality and quantity of forage (Bailey et al., 1996; Owen-Smith et al., 2010). This relationship between herbivores and their environment can be detected in distinct movement scales (Frair et al., 2005), which takes place at several scale levels (Bartumeus et al., 2005; Prins and Van Langevelde, 2008).

There is considerable intraspecific variability in herbivore morphological traits (van Soest, 1996), and animals react to their environment in different ways, related to these traits (Bailey et al., 1996; Prins and Van Langevelde, 2008). Early studies have identified a variety of feeding patterns or feeding niche categories among large herbivores (Gagnon and Chew, 2000; Hofmann and Stewart, 1972). These feeding niches are normally driven by morphological traits such as body size, feeding type, digestive strategy and muzzle width (Shipley, 1999; van Soest, 1996). Broader feeding types categorise large herbivores into grazers, mixed feeders and browsers (Grunow, 1980; McNaughton and Georgiadis, 1986).

Abiotic factors, such as surface water, are one of the primary determinants of large-scale distribution patterns of large herbivores, and act as constraints within which they have to interact with biotic features such as forage resources (Redfern et al., 2003; Smit et al., 2007). In many cases, large herbivores select different habitats, and move differently, during times of low versus high resource availability (Birkett et al., 2012; Cornélis et al., 2011; Venter and Watson, 2008). This is because they become nutritionally stressed during the dry season

when both forage quality and quantity are reduced (Prins, 1996). Surface water sources can dry up, which influences the trade-off foragers face between nutritional requirements and surface-water constraints when forage quantity is reduced (Redfern et al., 2003). The trade-off between nutritional requirements and surface-water constraints that species face varies according to the species' water dependence, size, feeding type and digestive system (Redfern et al., 2003; Smit et al., 2007).

Animal movements consists of a discrete series of displacements (steps, varying in length) separated by successive re-orientation events (turning angles)(Bartumeus et al., 2005) and has been generally described using two different types of random movement behaviours, namely: random walks (Brownian motion) and Lévy walks (Bartumeus et al., 2005; Viswanathan et al., 1999). More recently the composite Brownian motion emerged as a strong alternative model to the Lévy walks (Benhamou, 2007; de Jager et al., 2011; Jansen et al., 2012; Reynolds, 2013), where animals switch between two or more Brownian walks (i.e. switch spatial scale), each characterised by an exponential step-length distribution representing a movement scale (Jansen et al., 2012; Reynolds, 2013).

We tested whether eight African large herbivore species, with a variety of morphological traits, coming from landscapes of varying vegetation heterogeneity, showed a difference in step length distributions and movement scale complexity. In addition, we also tested a number of hypotheses related to factors that could affect movement scale complexity: a) we expected that large herbivores would show more movement scales during the dry season versus the wet season because they have to move further to find adequate forage resources; b) we predicted that animals with different morphological traits, specifically feeding type and digestive strategy, would differ in their number of movement scales; c) we expected more movement scales in areas with higher heterogeneity; d) we expected species with larger home ranges, which are normally larger bodied species (which we confirm with our data), to have fewer movement scales because they feed at a courser grain scale; and e) we expected species that are more constrained by fences to have fewer movement scales due to large migratory movements and their “natural” ranging behaviour being restricted.

2. Study area

The species data originated from eight different reserves in South Africa representing various levels of seasonal variability, heterogeneity, area size, and large herbivore assemblages (Table 1).

Table 1: The species and reserves investigated during this study. Biomes were classified according to (Rutherford et al., 2006)

Study area and biome	Species studied with number of data subsets	Geographical location	Size (ha)
Mkambati Nature Reserve – Grassland	Eland (<i>Tragelaphus oryx</i>) (n = 5) Plains zebra (<i>Equus burchelli</i>) (n = 5) Red hartebeest (<i>Alcelaphus buselaphus</i>) (n = 9)	31°13' - 31°20' S and 29°55' - 30°04' E	7720
Baviaanskloof Nature Reserve - Fynbos	Cape mountain zebra (<i>Equus zebra</i>) (n = 6) African buffalo (<i>Syncerus caffer</i>) (n = 4)	33°26' - 33°53' S and 23° 35' - 24° 59' E	211476
Kruger National Park - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 17)	22°20' - 25°32' S and 30°53' - 32°02' E	2300000
Pilanesberg National Park - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 4)	25°08' - 25°22' S and 26°57' - 27°13' E	55000
Mkhuze Game Reserve - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 1)	27°33' - 27°48' S and 32°08' - 32°25' E	45291
Mapungubwe National Park - Savanna	Impala (<i>Aepyceros melampus</i>) (n = 5) Eland (<i>Tragelaphus oryx</i>) (n = 5) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 9)	22°10' - 22°17' S and 29°08' - 29°32' E	28168

Welgevonden Private Game Reserve - Savanna	Plains zebra (<i>Equus burchelli</i>) (n = 14) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 13)	24°10' - 24°25' S and 27°45' - 27°56' E	33000
Asante Sana Private Game Reserve - Nama-Karoo	Impala (<i>Aepyceros melampus</i>) (n = 3) Eland (<i>Tragelaphus oryx</i>) (n = 6) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 8)	32°15' - 32°21' S and 24°52' - 25°04' E	10700

3. Methods

The collars were set to take a coordinate reading every 2 hours. Step lengths were calculated for each animal's data set using Geospatial Modelling Environment (Beyer, 2012) and ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). All step lengths < 6 m were excluded during the analysis in order to remove non-movements and false movements due to GPS-error. Two subsets of data were extracted from each animal's data set with one representing two dry season months and one representing two wet season months.

In order to test our hypotheses we identified a number of explanatory variables, i.e. season, feeding niche, number of vegetation types, home range size and level of space use. Feeding niche represented a combination of the feeding niche and digestive system of each species and was grouped into ruminant grazers, non-ruminant grazers, ruminant mixed feeders and non-ruminant mixed feeders. Number of vegetation types represented the number of categories, as classified by (Mucina and Rutherford, 2006), that were visited by the animals over that period determined by the location (GPS) points. Vegetation types visited were grouped into three categories: ≤ 2 vegetation types, 3 vegetation types and ≥ 4 vegetation types. We used space use index that gave a relative value of how much of the space available to an individual animal was used. The closer to 1 this index was the more the animal used all the available space within the reserve.

4. Data analysis

Regarding the space use index, we were not able to use body size as an explanatory variable in the analysis because, with it included, the assumption of proportional odds was not met, as assessed by a full likelihood ratio test ($X^2 = 26.377, p = 0.091$). Larger bodied species however, normally have larger home ranges (Lindstedt et al., 1986), so we regressed the natural logarithm of species body mass against the natural logarithm of home range size, which indicated a significant positive correlation ($r(100)=0.920, p<0.001$) when two outliers were removed (identified using box-plots) (Figure 1). We were therefore able to use home range size as a proxy for body size because it was intrinsically connected. Home range size (H) was calculated as the minimum convex polygon in hectares using the 'bounding containers' tool in ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) and divided into quartiles using IBM-SPSS Statistics 21 (SPSS Inc., Chicago IL).

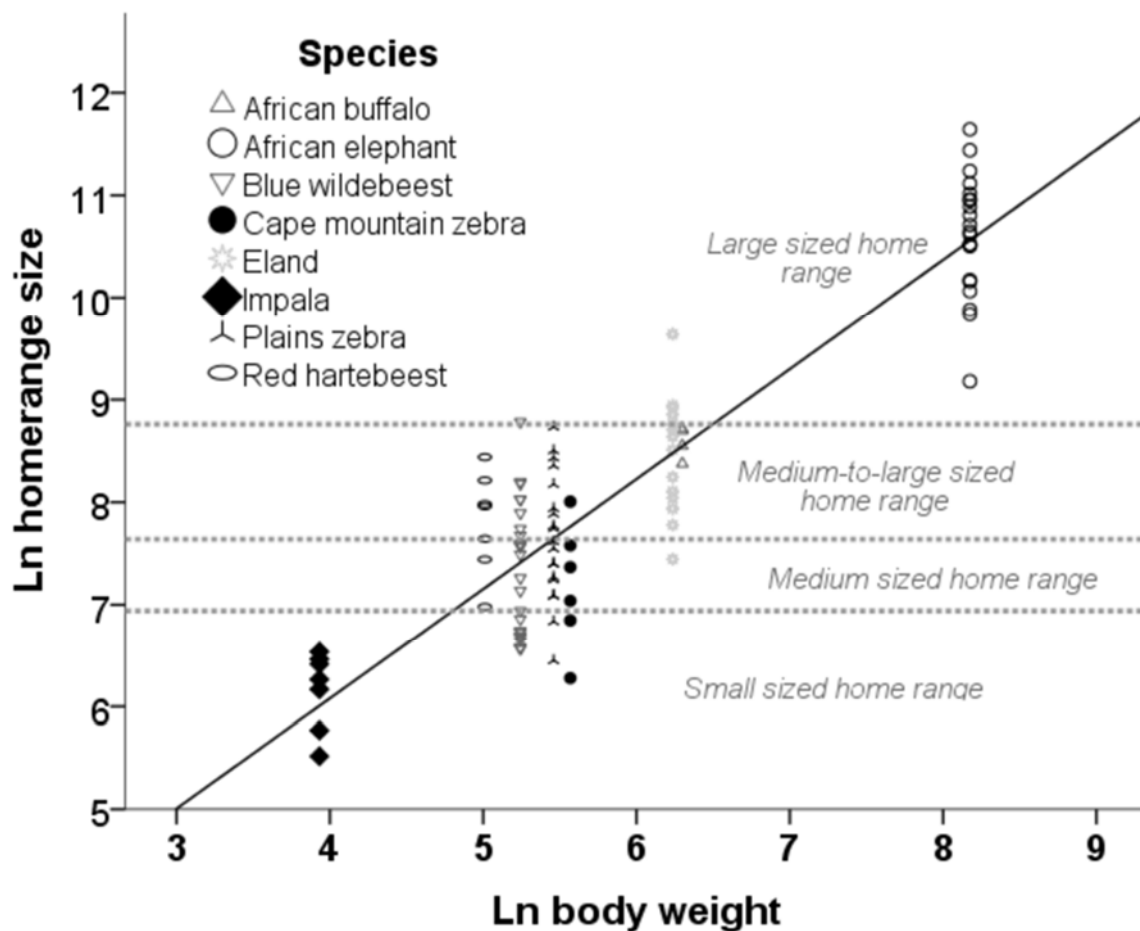


Figure 1: The regression line indicates a linear relationship between the natural logarithm of species body weight (kg) plotted against home range size (ha) for the species studied ($R^2 =$

$0.827; y = 1.79 + 1.07 * x$). The reference lines separate the different home range size groupings used in our analysis. The level of space use variable was divided into quartiles using IBM-SPSS Statistics 21 (Armonk, NY: IBM Corp.). The resultant four space use groupings was ≤ 0.028 (low); $0.029-0.060$ (medium); $0.061-0.181$ (medium-to-high); and ≥ 0.182 (high).

The resultant four home range groupings was ≤ 954 ha (small); $955-2524$ ha (medium); $2525-6348$ ha (medium-to-large); and ≥ 6349 ha (large). The level of space use, or space use index (SUI), independent variable was calculated as:

$$SUI = H/s$$

where s is nature reserve size in hectares. The space use index gives a relative value of how much of the space available to an individual animal was used (i.e how much the animals is contained/bounded by the boundaries/fences of the reserve relative to their home range).

Regarding step length, two frequency distributions were used to express this distribution for the data subsets: (a) exponential (Brownian motion); (b) hyper exponential functions (composite Brownian walk) following the methodology of (Jansen et al., 2012) (Table 2 and Figure 2). A model selection procedure based on the Akaike Information Criterion (AIC) was applied to compare the step length distributions (Jansen et al., 2012) (Figure 2 and Table 2). We used Kolmogorov-Smirnov (KS) goodness-of-fit tests and R^2 values to test if the models were consistent with the data. This statistical test were conducted using R (R-Development-Core-Team, 2011). R-codes for step length analysis are available from <http://mathbio.bl.rhul.ac.uk/People/alla/r-code>.

A cumulative odds ordinal logistic regression with proportional odds was used to determine the effect of season, feeding niche, number of vegetation types, home range size, and fences on the number of movement using IBM-SPSS Statistics 21 (Armonk, NY: IBM Corp.). For the movement scales the ordinal dependent variable was number of exponential step-length distributions, i.e. movement scales derived from the step length distribution model which produced the best fit according to the Akaike weights and Kolmogorov-Smirnov goodness-

of-fit tests. Individual datasets with one and two movement scales was combined due to the low number of movements with only one scale (only $n=6$ from $N=114$).

Table 2: Probability density function, inverse cumulative, Maximum Likelihood Estimate (MLE) and log-likelihood functions for exponential and hyper-exponential (mix of exponentials) distributions of (Jansen et al., 2012) was used to model the movement data.

Models	Probability density function	Inverse cumulative	MLE or log-likelihood
Exponential (Brownian motion)	$P(x) = \lambda e^{-\lambda(x-x_{\min})}$	$P(X \geq x) = e^{-\lambda(x-x_{\min})}$	$\lambda_{best} = \frac{1}{\frac{1}{n} \sum_{i=1}^n x_i - x_{\min}}$
Mix of k exponentials (Composite Brownian walk)	$P(x) = \sum_{j=1}^k p_j \lambda_j e^{-\lambda_j(x-x_{\min})}$ with $\sum_{j=1}^k p_j = 1$	$P(X \geq x) = \sum_{j=1}^k p_j e^{-\lambda_j(x-x_{\min})}$	$L = \sum_{j=1}^k \log P(x_j)$

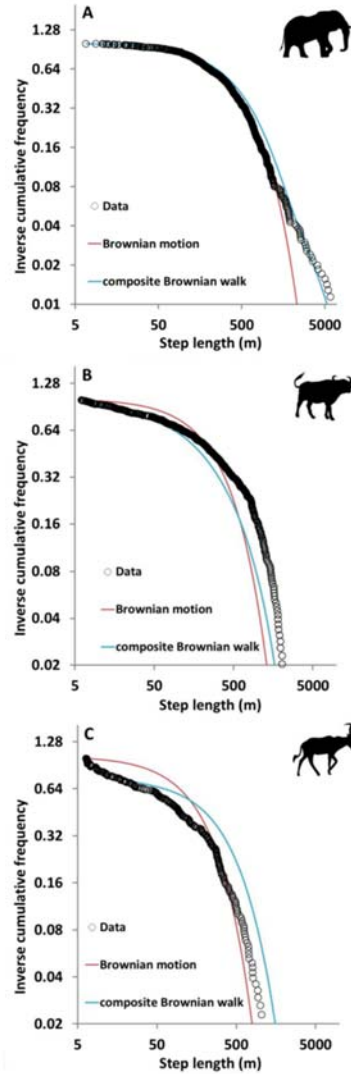


Figure 1: Examples indicating the step length distributions with the two frequency distributions used to model step length distribution. The circles represent the inverse cumulative frequency of step length data. The curves represent Brownian motion and a composite Brownian walk consisting of a mixture of two, three or four exponentials depending on which model was favoured. Models favoured in these examples are (A) Brownian walk with 2 exponential distributions ($p_1 = 0.917$, $\lambda_1 = 0.002$, $\lambda_2 = 0.0004$); (B) Brownian walk with 3 exponential distributions ($p_1 = 0.137$, $p_2 = 0.325$, $p_3 = 0.538$, $\lambda_1 = 0.123$, $\lambda_2 = 0.007$, $\lambda_3 = 0.002$); (C) Brownian walk with 4 exponential distributions ($p_1 = 0.678$, $p_2 = 0.179$, $p_3 = 0.086$, $p_4 = 0.057$, $\lambda_1 = 0.008$, $\lambda_2 = 0.061$, $\lambda_3 = 0.297$, $\lambda_4 = 0.002$). An individual result of an elephant, buffalo and red hartebeest are displayed in these examples.

5. Results

We tested a total of 114 animal data subsets from eight species in eight reserves. For impala, red hartebeest, blue wildebeest and Cape mountain zebra, the resulting Akaike weights most supported the composite Brownian motion step length distributions with three or four movement scales; for eland, three or four movement scales in the dry season, but two and three movement scales in the wet season; for African buffalo, three movement scales; for plains zebra, three or four movement scales in the wet season but two and three movement scales in the dry season; and for African elephant, three movement scales in the dry season and two in the wet season.

The cumulative odds ordinal logistic regression with proportional odds test the final model statistically significantly predicted the dependent variable over and above the intercept-only model, ($X^2(12) = 53.728, p < 0.001$). Overall, there was a lower number of movement scales for wet versus dry season (Table 3 and Figure 4). In general, the feeding type (Wald $X^2(3) = 14.875, p = 0.002$) had a significant effect on the number of movement scales, but there was no significant effect on the number of vegetation types (Wald $X^2(2) = 5.682, p = 0.058$), home range size (Wald $X^2(3) = 6.572, p = 0.087$), or space use index (Wald $X^2(3) = 5.108, p = 0.164$) on the number of movement scales (Figure 3). For pairwise contrasts, we detected significantly more movement scales for non-ruminant grazers, ruminant grazers, and ruminant mixed feeders versus non-ruminant mixed feeders (Table 3). There were fewer movement scales detected for ≤ 2 vegetation types versus ≥ 4 vegetation types (Table 3). A lower number of movement scales for medium-to-large home ranges versus the medium sized home range were also observed (Table 3). There were more movement scales for medium-to-high space use indices versus the high space use indices (Table 3).

Table.3: The result of the cumulative odds ordinal logistic regression with pairwise comparisons indicating the effect of season, feeding type, home range size, and level of space use on the number of movement scales (p – values in bold indicate significant effects).

Pairwise comparison	B	Std. Error	Wald	df	p-value	Lower Bound	Upper Bound	Exp B	Lower	Upper
Wet season versus Dry season	-1.121	0.409	7.501	1	0.006	-1.924	-0.319	0.326	0.146	0.727
Non-ruminant grazer versus Non-ruminant mixed feeder	4.008	1.274	9.895	1	0.002	1.511	6.505	55.016	4.529	668.266
Non-ruminant grazer versus Ruminant mixed feeder	-0.237	0.656	0.13	1	0.718	-1.522	1.049	0.789	0.218	2.856
Nonruminant grazer versus Ruminant grazer	-0.7	0.544	1.656	1	0.198	-1.766	0.366	0.497	0.171	1.442
Ruminant grazer versus Non-ruminant mixed feeder	4.708	1.26	13.951	1	<0.001	2.237	7.178	110.776	9.368	1309.959
Ruminant grazer versus Ruminant mixed feeder	0.463	0.568	0.666	1	0.414	-0.649	1.576	1.589	0.522	4.835
Ruminant mixed feeder versus Non-ruminant mixed feeder	4.244	1.179	12.969	1	<0.001	1.934	6.554	69.698	6.919	702.055
≤ 2 Vegetation types versus ≥ 4 Vegetation types	-1.346	0.676	3.962	1	0.047	-2.672	-0.021	0.26	0.069	0.98

3 Vegetation types versus ≤ 2 Vegetation types	0.911	0.496	3.379	1	0.066	-0.06	1.883	2.488	0.941	6.573
3 Vegetation types versus ≥ 4 Vegetation types	-0.435	0.712	0.374	1	0.541	-1.83	0.96	0.647	0.16	2.611
Medium sized home range versus Large sized home range	-0.561	1.082	0.268	1	0.604	-2.682	1.56	0.571	0.068	4.761
Medium sized home range versus Small sized home range	0.113	0.624	0.033	1	0.857	-1.111	1.336	1.119	0.329	3.805
Medium-to-large sized home range versus Large sized home range	-1.776	1.022	3.022	1	0.082	-3.778	0.226	0.169	0.023	1.254
Medium-to-large sized home range versus Medium sized home range	-1.215	0.599	4.109	1	0.043	-2.39	-0.04	0.297	0.092	0.961
Medium-to-large sized home range versus Small sized home range	-1.102	0.63	3.057	1	0.08	-2.338	0.133	0.332	0.097	1.143
Small sized home range versus Large sized home range	-0.674	1.104	0.372	1	0.542	-2.837	1.49	0.51	0.059	4.438
Low level of space use versus High level of space use	1.272	0.685	3.442	1	0.064	-0.072	2.615	3.566	0.931	13.663
Medium level of space use versus High level of space use	1.191	0.677	3.097	1	0.078	-0.135	2.517	3.29	0.873	12.397

Medium level of space use versus Low level of space use	-0.081	0.573	0.02	1	0.888	-1.203	1.042	0.923	0.3	2.836
Medium-to-high level of space use versus High level of space use	1.37	0.649	4.454	1	0.035	0.098	2.642	3.934	1.103	14.038
Medium-to-high level of space use versus Low level of space use	0.098	0.6	0.027	1	0.87	-1.078	1.274	1.103	0.34	3.577
Medium-to-high level of space use versus Medium level of space use	0.179	0.594	0.09	1	0.764	-0.986	1.344	1.196	0.373	3.833

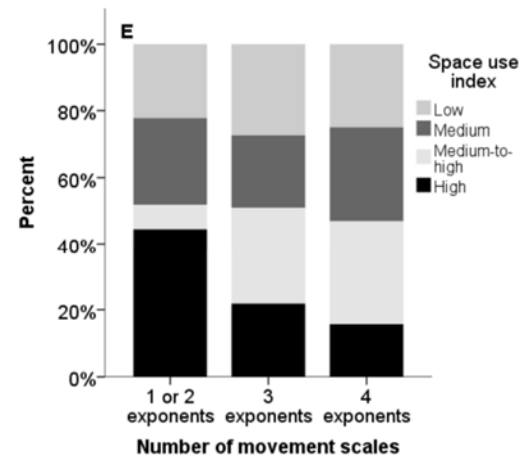
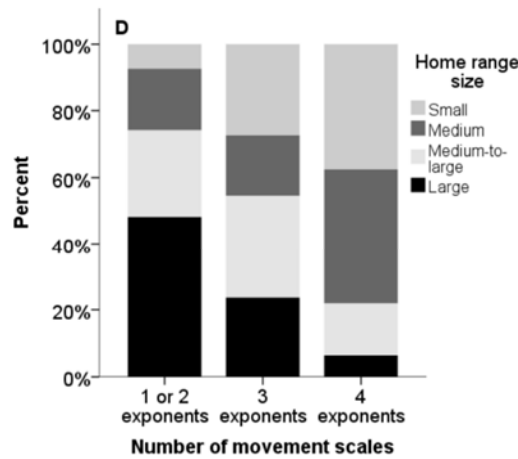
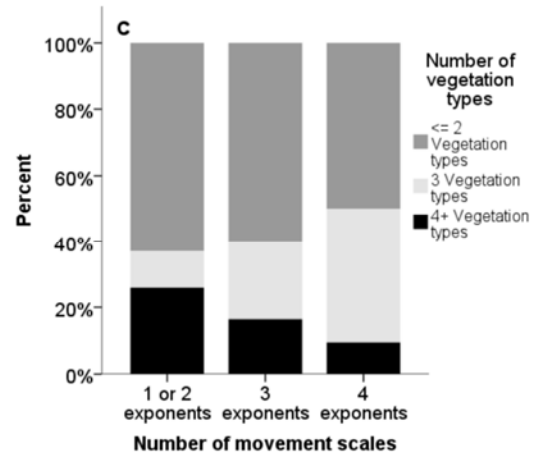
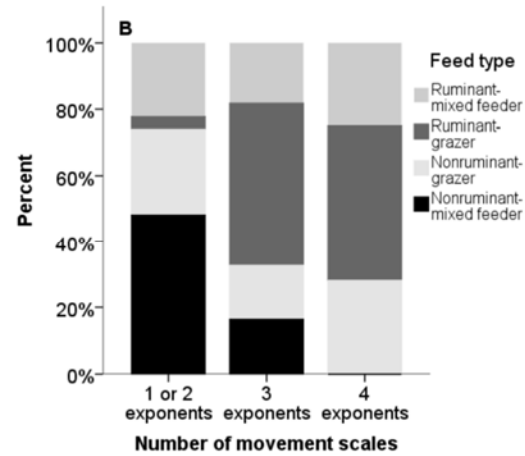
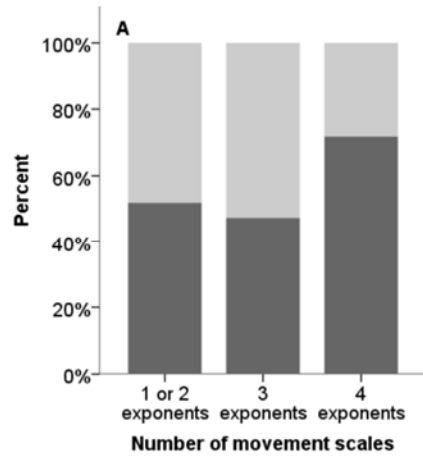


Figure.3: The effect of (A) season; (B) feeding type; (C) number of vegetation types; (D) home range size; and E) level of space use on the number of movement scales indicated by the percentage of data subsets which produced 1 and 2, 3 or 4 movement scales.

As non-ruminant mixed feeders were driving the odds ratios in the above analysis, we ran an additional ordinal regression analysis where they were excluded from the model. In this case there was also a lower number of movement scales detected for wet versus dry season ($X^2(1) = 4.682, p = 0.030$), But neither the feeding type (Wald $X^2(2) = 1.674, p = 0.433$), the number of vegetation types (Wald $X^2(2) = 3.228, p = 0.199$), home range size (Wald $X^2(3) = 6.292, p = 0.098$), or space use index (Wald $X^2(3) = 7.002, p = 0.072$) had any significant effect on the prediction of the scale of movement.

6. Discussion

Spatial variation in the African landscape results in a heterogeneous distribution of resources that are influenced by rainfall and temperature along seasonal cycles (Birkett et al., 2012; Cornélis et al., 2011). Large herbivores select different habitats and show different movement patterns during times of low versus high resource availability (Birkett et al., 2012; Venter and Watson, 2008). Surface water sources can dry up, which influences the trade-off foragers face between nutritional requirements and surface-water constraints when forage quantity is reduced (Redfern et al., 2003). Forage quality and quantity are most affected near water sources because animals tend to congregate in these areas due to water dependency (Redfern et al., 2003). The reduced forage quantities during dry years forces large herbivores to travel further from water sources to meet their nutritional requirements (Redfern et al., 2003; Venter and Watson, 2008). The fact that, in general there were fewer movement scales detected in the wet season versus the dry season suggest that when animals were forced to trade-off forage quality and quantity during the dry season (Redfern et al., 2006), they moved further between forage areas and water sources in order to satisfy their forage requirements (Venter and Watson, 2008).

Elephant generally had a lower number of movement scales, compared to all the other feeding types. Elephants concentrate their foraging within areas of high forage availability that are sufficiently close to water and large enough to optimize the efficiency of foraging (De Knecht et al., 2011). Surface-water is a strong determinant of elephant spatial use, and may take precedence over the role that landscape heterogeneity plays in their movement (de Beer and van Aarde, 2008; De Knecht et al., 2011). Elephants are also able to change their diet from graze to browse in times with low resource availability (Codron et al., 2006; de Boer et

al., 2000; Shannon et al., 2013), which enabled them to stay closer to water resources compared to grazers.

Large herbivores exhibit distinct scales in movement that are in many cases related to habitat heterogeneity (Frair et al., 2005; Redfern et al., 2003). More movement scales would thus be expected as herbivores move through a mosaic of vegetation patches of variable suitability (more heterogeneous) compared to more homogeneous vegetation. In this study while vegetation heterogeneity would appear to have had an effect on number of movement scales, the relationship was not strong. We used broad landscape scale vegetation types (Mucina and Rutherford, 2006) as there was a lack of a finer scale standardized habitat maps for all the reserves.

Because the larger herbivores feed at a coarser grain scale (Prins and Van Langevelde, 2008), we expected them to have fewer movement scales because they interact with their habitat in a less complex manner. However, the results did not convincingly support our hypothesis, because animals with large home ranges were equal in movement scale to those animals with smaller home range sizes. The number of movement scales difference between animals with medium-to-large home ranges versus animals with medium sized home ranges seemed to be driven by the larger species, such as eland and African buffalo, generally having two or three movement scales, which occurred mainly in the medium-to-large home range size grouping. Other species, such as blue wildebeest, red hartebeest, plains zebra and Cape mountain zebra which are considered medium sized grazers, grouped in both the medium-to-large and the medium sized home ranges, and generally moved with a wider (2, 3 and 4) number of movement scales.

The hypothesis that species which are more restricted by fences would have fewer movement scales was confirmed by this study. Because large migratory movements are limited by fences (Boone and Hobbs, 2004; Loarie et al., 2009; Naidoo et al., 2012) we expected animals to have fewer movement scales when exposed to this restriction. This result has significant implications for protected area management, as it shows that an important part of these species natural ecological processes, i.e. the migratory process and extensive ranging behaviour, is prevented from functioning as it should (Shannon et al., 2006). The implication

is that large herbivores that were able to migrate and/or range further, as seasonal forage changes took place, in order to make use of the suitable forage resources in the broader landscape, are now not able to do this. This in turn increases pressure on local forage resources that could result in unnatural overgrazing (de Beer and van Aarde, 2008; Shannon et al., 2006).

Identifying movement scale determinants of large herbivores can benefit their management and conservation, as it allows an understanding of herbivore species spatial dynamics, impacts, and associated ecological processes. Scales are defined by rates of foraging and ecosystem processes, while boundaries between units, at each scale, are defined by animal behaviour (Senft et al., 1987). The results indicate that large herbivore movement behaviour is complex in scale which has important implications for conservation management in protected areas (Coe et al., 1976; Cumming et al., 2010; Delsink et al., 2013). In order for managers to effectively manage protected areas and associated biodiversity they need take cognisance of the different scales animals operate under. This should be followed by implementation of management action at appropriate scales to prevent scale mismatch (Cumming et al., 2010; Delsink et al., 2013).

Our study was limited to only a few species and ecosystems which may have limited the ability to make general robust conclusions. Further, ecosystem-focused research, which includes a wider range of species, are recommended.

7. Conclusion

Our results suggest that intrinsic factors such as large herbivore traits, and extrinsic factors such as, surface water, vegetation heterogeneity, interspecific competition and fences influences the scales at which animals move. Anthropogenic influences caused by management actions, for example construction of artificial water holes and fences, have an effect on animal movement that could have significant impacts on ecosystems in protected areas (de Beer and van Aarde, 2008; Redfern et al., 2003). Protected area managers should thus be aware of scale complexity in animal movement in order to initiate appropriate conservation management action.

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