

Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa

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Abstract Foraging behaviour and habitat selection occur as hierarchical processes. Understanding the factors that govern foraging and habitat selection thus requires investigation of those processes over the scales at which they occur. We investigated patterns of habitat use by African elephants (*Loxodonta africana*) in relation to vegetation greenness to investigate the scale at which that landscape attribute was most closely related to distribution of elephant locations. We analysed Global Positioning System radio-collar locations for 15 individuals, using the Normalized Difference Vegetation Index as a representation of vegetation greenness in a Geographic Information Systems framework. We compared the importance of vegetation greenness at three spatial scales: the total home range, the seasonal home range and the 16-day home range. During the wet season, seasonal home ranges for both sexes were associated with intermediate greenness within the total

home range; there was no evidence of selection based on greenness at finer scales. During the dry season, the strongest associations were within the 16-day home range: individual locations for males tended to be in areas of intermediate greenness, and those for females were in areas of intermediate and high greenness. Our findings suggest that the role of vegetation greenness varies with the scale of analysis, likely reflecting the hierarchical processes involved in habitat selection by elephants.

Keywords African elephant · Habitat selection · *Loxodonta africana* · Normalized Difference Vegetation Index (NDVI) · Scale

Introduction

Conclusions about the effects of environmental factors on the distribution of animal populations depend on the scales over which such relationships are investigated (Wiens et al. 1987; Boyce 2006). This is particularly true for large herbivores, whose forage resources occur in dispersed patches of varying but generally low quality (Westoby 1978; Belovsky 1984). As a consequence, herbivores are faced with a series of choices when searching for adequate nutrition, from selecting among plant or plant parts within a feeding station, to stations within a plant community, to communities within a landscape, to landscapes over a broader region (Senft et al. 1987). In this manner, selection of resources occurs as a nested hierarchy of choices; some factors have relevance at broader scales of decision-making and other factors have relevance at finer scales, determined by the requirements of a particular species and its perceptions of the patterns of resources and conditions in

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the environment (Wiens 1976; Senft et al. 1987). This hierarchy of selection has another consequence: with selection at any one level of the hierarchy, options at finer scales become constrained (Johnson 1980). Thus, for example, selection of a feeding station limits options for plants and plant parts that are subsequently available, also contributing to scale-dependent effects of environmental factors on animal distribution.

Distribution of large herbivores is determined in large part by plant phenology, which, in turn, influences the nutritional quality of forage (i.e., digestibility or protein content; Langvatn and Hanley 1993; Fryxell et al. 2004). Choice of patches by foraging herbivores depends on the amount of food available in that patch, but also the digestibility. Thus, an herbivore must balance forage availability, which affects intake rate, against forage nutritional quality, which influences digestive efficiency (Wilmshurst et al. 1995). Movements on the landscape, then, reflect animals as they select patches based on forage biomass and quality, feed in those patches and then depart when forage resources reach a critical level of depletion (Searle et al. 2005).

For African elephants (*Loxodonta africana*), a growing understanding of forage selection and patch use has developed through the use of global positioning system (GPS) technology and remote sensing imagery such as the Normalized Difference Vegetation Index (NDVI). The NDVI imagery gives a representation of the spatial and temporal variability in the biomass and nutritional quality of vegetation (i.e., greenness; Huete et al. 2002; Parker 2003; Pettorelli et al. 2005a), and a growing number of studies have demonstrated that movements, habitat use and distribution of elephants are associated with the greenness characteristics of the landscape (Murwira and Skidmore 2005; Chamaillé-Jammes et al. 2007; Young et al. 2009; Loarie et al. 2009a, b). It might appear obvious that greener vegetation is more beneficial to a foraging elephant, but the mechanisms underlying that association remain vague. For example, a single element of a Moderate Resolution Image Spectrometer (MODIS) NDVI image is a pixel that covers a 6.25-ha area containing, for savannas, a mixture of tree canopy and herbaceous ground cover (Scholes and Archer 1997), both of which contribute to the greenness of that pixel (Archibald and Scholes 2007) but represent qualitatively different resources to a herbivore (Owen-Smith and Cooper 1989).

Understanding the scales at which NDVI greenness is related to distribution of elephants will assist in uncovering the mechanisms that link greenness values on a remote sensing image to vegetation attributes on the landscape and to presence of elephants. Furthermore, misinterpretation of patterns is possible when an incorrect scale is chosen for investigation (Wiens 1989). Thus, the correct choice of

scale is essential to accurately relate distribution of animals to resources or conditions, and where information about the correct scale is lacking, investigation of patterns at several scales might reveal that at which a factor has its strongest influence (Morris 1987; Wiens 1989; Kotliar and Wiens 1990). Given these problems, our objective was to investigate the level of the foraging hierarchy at which elephants respond to biological attributes represented in an NDVI image.

Materials and methods

Study area This study occurred from November 2005 to November 2007 in Kruger National Park (KNP) and the adjacent private reserves (Balule, Klaserie, Letaba, Manyeleti, Sabisand, Timbavati, Umbabat) in northeastern South Africa. The private reserves were once separated by fences, but those fences were removed, allowing animals to move freely among the reserves and KNP. The climate in the region was semi-arid; at nearby Orphen, annual mean rainfall was approximately 550 mm (Gertenbach 1980). The study period included two wet seasons (November–March) and two dry seasons (April–October) defined from mean monthly rainfall. Soils in KNP are broadly divided into a less-fertile granitic zone in the west and a more fertile basaltic zone in the east (Venter et al. 2003). Vegetation communities were wooded savanna, with knobthorn (*Acacia nigrescens*), marula (*Sclerocarya birrea*) and mopane (*Colophospermum mopane*) dominant on the eastern basaltic soils, and *Combretum* spp. and mopane dominating the western granitic soils (Venter et al. 2003).

Study organism As non-specialist foragers, elephants have diets that consist of browse and grass in varying quantities (Codron et al. 2006). Elephant feeding can have a substantial effect on growth and mortality of woody vegetation; thus, elephants make an important contribution to processes that determine savanna vegetation structure (Scholes and Walker 1993; Riginos and Grace 2008). As of 2006, the KNP elephant population size was approximately 12,430 (0.63 km⁻²), and the private reserves had a combined abundance of approximately 2,829 (0.98 km⁻²; Blanc et al. 2007). Elephants for this study were captured by wildlife veterinarians using standard procedures. Captured animals were fitted with GPS collars (Africa Wildlife Tracking, Pretoria, South Africa) that download via a cellular telephone (GSM) network. The collars were accurate to within 10 m and recorded one location every 5 h.

Habitat model We developed a habitat model in a geographic information system (GIS) based on vegetation greenness. Vegetation was represented by MODIS NDVI

imagery, having a temporal resolution of 16 days and a spatial resolution of 250 m. This imagery provides a measure of spatial and temporal variability in the quantity and nutritional quality of vegetation (Huete et al. 2002; Pettorelli et al. 2005a; Van Bommel et al. 2006) and has demonstrated close correspondence with aboveground vegetation biomass for savannas (Huete et al. 2002). Furthermore, it has utility as an explanatory variable for habitat use by animals (Pettorelli et al. 2005a; Van Bommel et al. 2006) and by herbivores in particular (Musiega and Kazadi 2004; Mueller et al. 2008). The range of greenness values was 0–10,000, with larger values representing greener vegetation. In addition to greenness, we included elevation as a covariate because of its potential to influence conclusions about effects of greenness. For elevation, we used a digital elevation model (DEM) having a spatial resolution of 90 m. Although location of water sources is recognised to have an important effect on the distribution of elephants (Western and Lindsay 1984; Chamaillé-Jammes et al. 2007; Harris et al. 2008), there was incomplete information on water sources in the study area. However, water points were known to be abundant and widely available and thus likely to have a minimal effect on elephant location. For these reasons, water sources were omitted as a component of the habitat model. Habitat models were developed in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA).

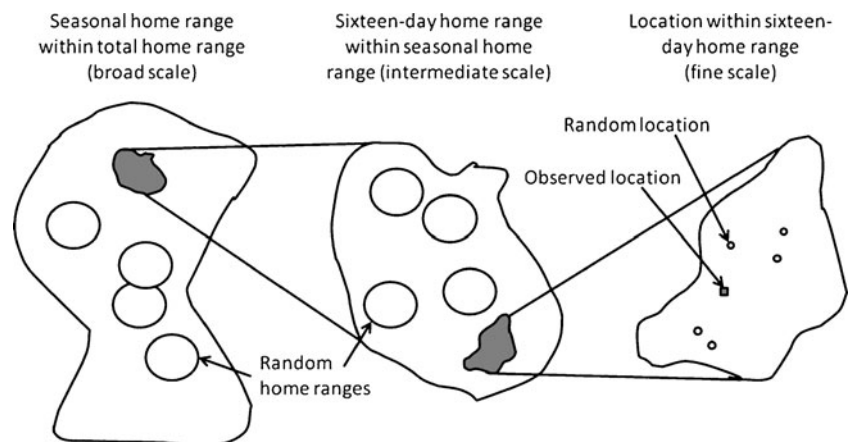
Data analysis To investigate the hierarchical nature of selection by elephants for greenness and elevation, we analysed relationships between elephant locations and these variables at three scales: within 16-day home range (fine scale), within seasonal home range (intermediate scale), and within total home range (broad scale; Fig. 1). The finest scale of analysis was limited by the temporal resolution of the NDVI imagery (16 days). To evaluate selection by elephants, we compared observed use (by GPS location) with random use within the 16-day home range. We

estimated a 95% adaptive kernel with least square cross-validation (Worton 1989, Blundell et al. 2001) using Home Range Tools for ArcGIS (<http://flash.lakeheadu.ca/~arodgers/hre/>). Within that home range, we placed random locations at a ratio of 10:1 random/used to be sure that available habitat was accurately represented (Manly et al. 2002). Values for NDVI and DEM associated with each used and random location became the data used in subsequent analyses. The same procedure was repeated to produce a sample of used and random values for each 16-day period covering the 2-year study.

At the intermediate scale, we compared observed 16-day home ranges with random home ranges, within a seasonal home range estimated from all of an individual's locations for each dry and wet season using 95% adaptive kernel methods. At that scale, use was defined as the average NDVI and DEM values within the 16-day home range polygons estimated for the fine-scale analysis, and those values were compared with the average NDVI and DEM values within random home ranges (Katnik and Wielgus 2005). For each observed home range, we randomly selected ten locations. We then buffered each random location by an amount that would produce a circular home range of area equal to the area of the observed home range. Analysis at the broadest scale occurred in a similar manner, except that observed seasonal home ranges for each individual were compared with random home ranges within that individual's total home range, estimated from locations covering the 2-year study period.

We used logistic regression to estimate how degree of use varied with changes in greenness and elevation (Manly et al. 2002). The response variable was whether a location or home range represented observed or random use. The explanatory variables were NDVI and DEM. Individual elephant was also included in the model as a random effect to account for multiple observations for the same animals (Gillies et al. 2006). We conducted a separate analysis for each sex, season and scale. Because of difficulties with

Fig. 1 Spatial scales used in this analysis



convergence failures when fitting the models, we converted continuous NDVI and DEM variables into categorical variables having five levels (i.e., one to five, associated with low to high greenness or elevation; Table 1), with each level having the same number of observations. Convergence failures occur when the algorithms for fitting a model do not converge on maximum likelihood estimates for that model (Allison 2004). A common cause for convergence failure is when there are prominent divisions in the frequency distribution of one of the explanatory variables (Allison 2004). If boundaries between category levels are such that a one level spans both some of the observations and some of the prominent divisions, then those divisions cease to be a problem, and the model converges on a maximum likelihood estimate. To avoid using an arrangement of categories that produced a desired or biased outcome, both the number of levels and the divisions between levels were chosen arbitrarily. As a consequence of the categorization of the NDVI variable, interpretation of the degree to which elephants showed selection for each level of greenness and NDVI were based on use relative to the lowest category.

Small sample size and strongly non-normal data distribution caused difficulties with model fitting and parameter estimation for the broad and intermediate scales. To solve this problem, we used a Monte Carlo bootstrapping approach to estimate model parameters and 95% confidence intervals for all scales (Manly 2007). To do this, we selected randomly and with replacement a sample data set of size equal to the original data set. Next, we fitted the logistic model with NDVI, DEM and individual random effect as variables and saved the parameter estimates. We repeated the process 1,000 times to produce a bootstrapped distribution of estimates for each regression parameter. The

parameter estimate was the average estimate of those 1,000 iterations, and the 95% confidence intervals (CI) were the 2.5% and 97.5% quantiles of the bootstrapped distribution. Because we used categorical data for this analysis, we estimated a separate parameter and CI for each category of greenness and elevation above the lowest category. Each parameter was the estimated difference between that category and the lowest category, and the CI indicated the degree to which that difference was greater than zero. When a confidence interval contained zero, we interpreted that category and the lowest category to be used equally. An interval that did not contain zero was evidence that a category was used more or less than the lowest category. When one of the CI end-points was roughly equal to zero, we judged that to be suggestive but inconclusive evidence of a difference in use between that category and the lowest category. We conducted the statistical analysis in R (R Development Core Team 2008) with the function “lmer” in library “lme4” (Bates et al. 2008).

Results

We analysed location data for 15 elephants (four female, 11 male). There was a total of 27,519 locations across all animals, with locations per animal ranging from 1,353 to 2,695. Six elephants had data for both years of the study.

Wet season Female elephants demonstrated evidence of selection among greenness categories for the broad scale only (Table 2, Fig. 2). Wet-season home ranges were associated with category 4 greenness more than with the lowest category of greenness; placement of wet-season home ranges with respect to the other categories appeared to be no different than to the lowest category. Because analysis at the broad scale involved averages over relatively large areas, there was reduced variability in NDVI values, and thus, category 2 greenness was not represented for females during the wet season. Also, a strongly non-normal distribution of parameter estimates was apparent from the asymmetrical confidence intervals, which supports the use of bootstrapping methods to estimate parameters and confidence intervals. There was no evidence for selection among greenness categories at the intermediate or fine scales (Table 2, Fig. 2).

As with the females, male elephants also demonstrated evidence of selection among greenness categories for the broad scale only (Table 2, Fig. 2). Wet-season home ranges were associated more with intermediate and high levels of greenness (categories 3–5) than with the lowest category of greenness. Also, as with the female analysis, category 2 greenness was not represented at the broad scale. There was

Table 1 Categorization of Normalized Difference Vegetation Index (NDVI) and elevation (DEM) in metres, in the Kruger-private reserve transboundary region, South Africa, 2005–2007

Variable	Category	Lower limit	Upper limit
DEM	1	209	344
	2	345	368
	3	369	394
	4	395	430
	5	431	555
NDVI	1	144	3,018
	2	3,019	3,745
	3	3,746	4,648
	4	4,649	5,600
	5	5,601	9,952

DEM digital elevation model, NDVI Normalized Difference Vegetation Index

Table 2 Regression estimates for African elephant (*Loxodonta africana*) in the Kruger-private reserve transboundary region, South Africa, 2005–2007

Season	Sex	Scale	No. animals	No. used locations or home ranges	Variable	Category	Bootstrap results					
							Estimate	95% LCL	95% UCL			
Wet	Female	Broad	4	7	DEM	2	15.80	-1.39	21.76			
						3	10.04	-10.11	19.40			
						4	15.44	-1.24	21.20			
					NDVI	5	15.97	-1.01	21.77			
						3	-3.01	-19.47	1.84			
						4	17.43	0.56	21.35			
		Intermediate	4	50	DEM	5	-4.46	-20.33	2.08			
						2	1.21	-0.04	2.60			
						3	-0.24	-1.66	1.17			
					NDVI	4	-0.15	-1.45	1.14			
						5	0.38	-0.82	1.79			
						2	0.10	-15.27	15.89			
		Male	Male	Broad	11	15	DEM	3	0.95	-1.39	15.90	
								4	1.75	-0.28	16.64	
								5	1.15	-0.92	15.96	
							NDVI	2	-0.02	-0.15	0.10	
								3	-0.24	-0.39	-0.11	
								4	-0.27	-0.44	-0.13	
	Intermediate			11	112	DEM	5	-0.15	-0.32	-0.01		
							2	-0.12	-0.30	0.06		
							3	-0.20	-0.36	-0.03		
						NDVI	4	-0.07	-0.22	0.09		
							5	0.02	-0.13	0.17		
							2	17.62	0.51	20.37		
	Fine			Male	Broad	11	15	DEM	3	18.28	16.91	19.71
									4	18.10	16.82	19.41
									5	-0.24	-0.99	0.80
								NDVI	3	15.21	0.22	18.74
									4	19.09	17.76	20.64
									5	15.99	0.90	19.92
		Intermediate	11		112	DEM	2	0.07	-0.72	0.95		
							3	0.25	-0.45	1.10		
							4	0.14	-0.53	0.95		
						NDVI	5	-0.14	-0.89	0.80		
							2	-0.78	-2.39	0.87		
							3	0.30	-0.57	1.57		
Fine		11	7975		DEM	4	0.59	-0.21	1.67			
						5	0.56	-0.25	1.68			
						2	-0.16	-0.25	-0.08			
					NDVI	3	-0.10	-0.17	-0.02			
						4	-0.16	-0.24	-0.09			
						5	-0.17	-0.24	-0.09			
Fine	11	7975	DEM	2	0.03	-0.09	0.16					
				3	0.01	-0.09	0.10					
				4	-0.04	-0.13	0.06					
			NDVI	5	-0.05	-0.14	0.04					
				2	0.03	-0.09	0.16					
				3	0.01	-0.09	0.10					

Table 2 (continued)

Season	Sex	Scale	No. animals	No. used locations or home ranges	Variable	Category	Bootstrap results						
							Estimate	95% LCL	95% UCL				
Dry	Female	Broad	4	6	DEM	2	-5.05	-20.87	19.06				
						3	-16.51	-19.98	0.84				
						4	-5.14	-20.81	19.47				
						5	2.11	-19.69	22.30				
		NDVI	3	14.86	-0.61	36.72							
			4	-4.84	-20.27	18.37							
			Intermediate	4	58	DEM	2	-0.65	-1.65	0.32			
							3	-4.50	-18.02	-1.30			
		4					0.27	-0.71	1.17				
		5					-0.87	-1.63	-0.11				
		NDVI	2	0.07	-0.77	0.94							
			3	0.26	-0.62	1.08							
	4		-0.31	-1.71	0.85								
	5		0.14	-0.98	1.05								
	Fine	4	4054	DEM	2	-0.13	-0.23	-0.03					
					3	-0.27	-0.39	-0.15					
					4	-0.28	-0.42	-0.16					
					5	-0.11	-0.23	-0.02					
					NDVI	2	0.07	-0.02	0.16				
						3	0.14	0.05	0.23				
						4	0.11	0.00	0.22				
						5	0.11	-0.01	0.21				
					Male	Broad	11	15	DEM	2	17.93	16.77	19.24
										3	18.16	16.93	19.45
4										16.50	-0.09	18.50	
5										-0.08	-0.40	0.17	
NDVI	3	0.53	-0.86	2.00									
	Intermediate	11	157	DEM						2	0.39	-0.12	0.91
3						0.47	-0.04	0.99					
4						-0.18	-0.86	0.42					
5						-0.19	-1.18	0.59					
NDVI						2	0.24	-0.18	0.70				
						3	0.05	-0.46	0.52				
Fine	11	11615	DEM	2		-0.16	-0.21	-0.11					
				3	-0.24	-0.29	-0.18						
				4	-0.24	-0.31	-0.18						
				5	-0.18	-0.26	-0.10						
				NDVI	2	0.02	-0.03	0.06					
					3	0.10	0.05	0.15					
4	0.06	0.00	0.12										
5	-0.13	-0.23	-0.04										

DEM digital elevation model, *NDVI* Normalized Difference Vegetation Index, *LCL* lower confidence limit, *UCL* upper confidence limit

Presented are bootstrapped coefficient estimates and 95% confidence intervals for variables elevation (DEM) and vegetation greenness (NDVI)

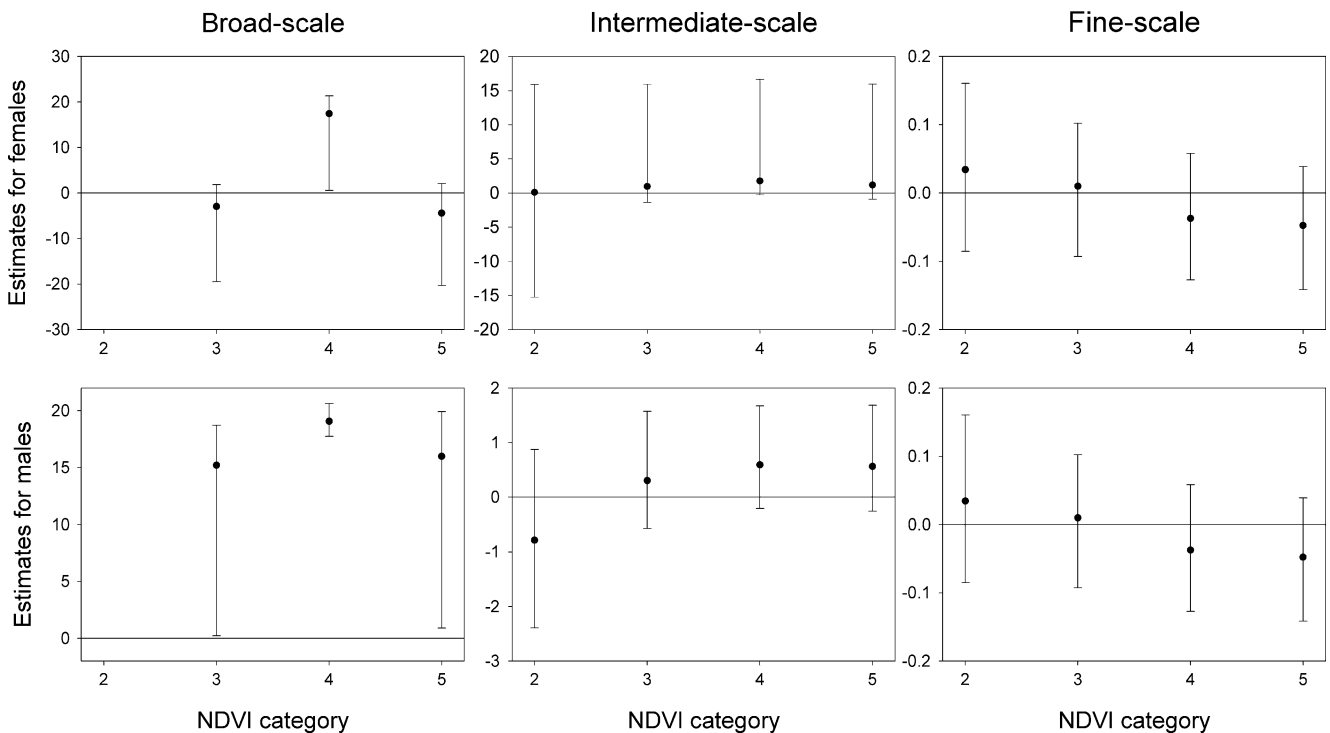


Fig. 2 Wet-season selection of greenness (NDVI) at the within-total-, within-seasonal- and within-16-day-home-range scales for African elephants in the Kruger-private reserve transboundary region, South Africa, 2005–2007. Presented are bootstrapped point estimates and

95% confidence intervals showing selection of variable categories relative to the lowest category. The horizontal lines represent no difference from the lowest (first) category

no evidence for selection among greenness categories at the intermediate or fine scales (Table 2, Fig. 2).

Dry season There was weak evidence that seasonal home ranges for females were associated more with category 3 greenness than with greenness for the lowest category (Table 2, Fig. 3). Categories 2 and 5 were not represented at the broad scale, in part, because of the reduced variability in values associated with averages over seasonal home ranges, but also because of reduced variation in greenness as vegetation dies back through the dry season. While there was no evidence of selection at the intermediate scale, at the fine scale, elephant locations were associated more with intermediate levels of greenness (categories 3 and 4) than with that of the lowest level (Table 2, Fig. 3).

For male elephants at the broad scale, there was no evidence that seasonal home ranges were placed within the total home range according to greenness; as with females, fewer than five categories were represented for greenness at the broad scale of analysis (Table 2, Fig. 3). At the intermediate scale, there was no evidence of placement of 16-day home ranges according to greenness in seasonal home ranges. At the fine scale, locations were more positively associated with intermediate greenness, but more negatively associated with high greenness, than they were with the lowest category of greenness (Table 2, Fig. 3).

To summarise, in the wet season, both sexes appeared to select seasonal home ranges that favoured intermediate or high levels of greenness, but there was no pattern of selection for finer scales. In the dry season, there was weak evidence that females selected intermediate levels of greenness, but it was clear for both sexes that locations favoured intermediate greenness and even avoided high greenness (i.e., males) in 16-day home ranges.

Discussion

The results presented demonstrate that relationships between landscape use and NDVI greenness change with the scale used for analysis. This result is consistent with those reported for a number of studies in other environments (e.g., sage sparrow [*Amphispiza bell*] and sage thrasher [*Oreoscoptes montanu*], Wiens et al. 1987; muskox [*Ovibos moschatus*], Schaefer and Messier 1995; mule deer [*Odocoileus hemionus*], Kie et al. 2002; and caribou [*Rangifer tarandus*], Gustine et al. 2006). For each of those systems, there was evidence that various environmental factors affected the distribution or movements of individuals, but those factors showed the clearest relationships at particular scales and particular levels of the resource selection hierarchy.

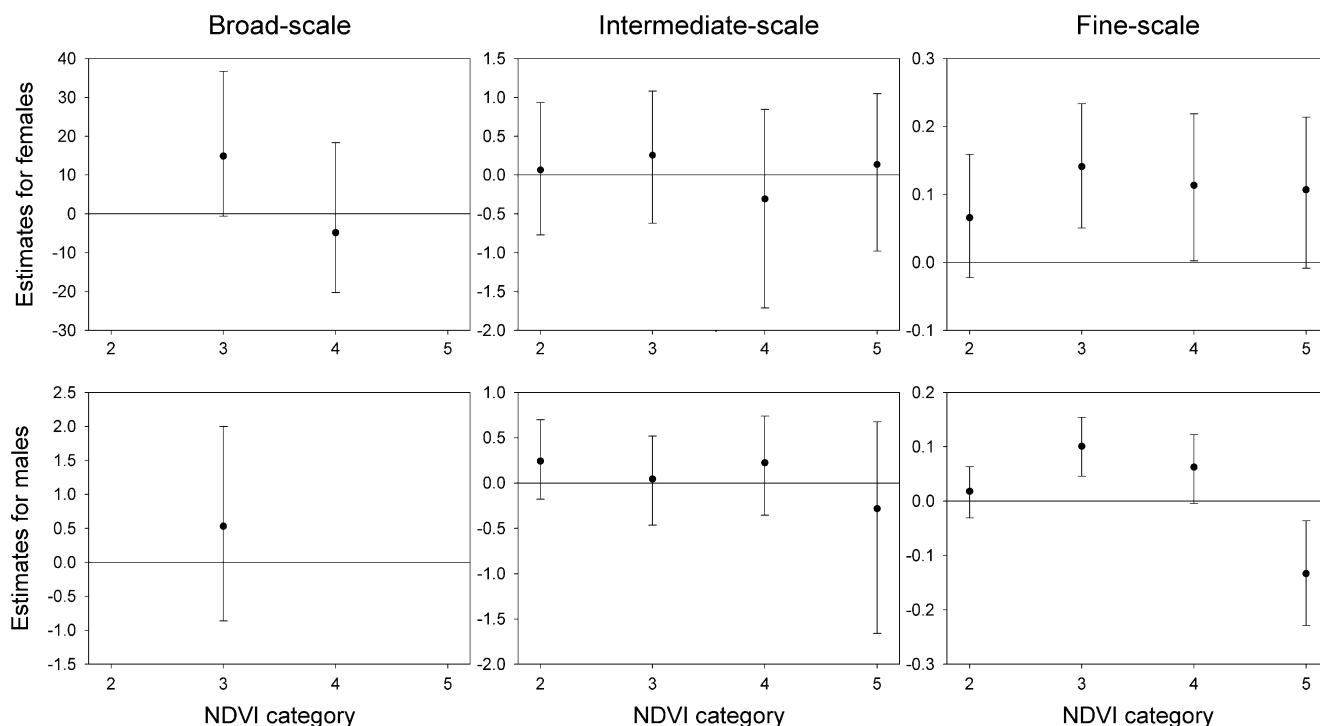


Fig. 3 Dry-season selection of greenness (NDVI) at the within-total-, within-seasonal- and within-16-day-home-range scales for African elephants in the Kruger-private reserve transboundary region, South Africa, 2005–2007. Presented are bootstrapped point estimates and

95% confidence intervals showing selection of variable categories relative to the lowest category. The horizontal lines represent no difference from the lowest (first) category

Broad-scale selection For seasonal home ranges within total home range, both males and females demonstrated evidence of selection for particular categories of greenness, but only in the wet season. For both sexes, wet-season home ranges appeared to be established in areas favouring higher greenness (categories 4 or 5). This is consistent with elephants establishing home ranges based on forage productivity during the growing season and with elephants in more productive environments having smaller home ranges (Young et al. 2009). It is also consistent with elephants being less constrained by locations of water sources when establishing home ranges at that time of year (Smit et al. 2007; de Beer and van Aarde 2008; Harris et al. 2008; Young et al. 2009). The constraint of water sources might have been operating during the dry season, such that greenness played less of a role in home range establishment. Ideally, our analysis would have included locations of water sources as a covariate, and an effect of greenness in the dry season might have been more apparent if we had accounted for variation explained by a variable such as “distance to water”.

Several previous studies of elephant home range dynamics relate the size, location and changes of home ranges to vegetation productivity or heterogeneity (Grainger et al. 2008, de Beer and van Aarde 2008). Simple productivity should be related to abundance and quality of forage, but

heterogeneity is relevant because elephants are more likely to find required resources within a home range if there is wide variation in structure and composition of the plant community to provide those resources (Murwira and Skidmore 2005). Overall, smaller home ranges are associated with higher vegetation productivity and more heterogeneous vegetation because elephants range over shorter distances to meet their requirements (Grainger et al. 2008, Young et al. 2009).

To contrast with those studies, our analysis took a somewhat different approach. Rather than investigate the dynamics of existing home ranges in response to landscape attributes, we compared regions where an individual had established a home range to where it had not. Such an analysis lends a different perspective on habitat selection by elephants because it addresses the degree to which one factor (greenness) promotes occupancy of an environment by individuals [i.e., Johnson's (1980) second-order selection]. Once an individual has selected a home range, the size and shape of that home range should reflect the animal's movement and selection of resources within the home range [i.e., Johnson's (1980) third-order selection]. Both approaches are valuable, but they provide slightly different information on the role of greenness on elephant distribution.

A further difference is that we focussed on average productivity of vegetation within seasonal home ranges

rather than heterogeneity of vegetation. Because our goal was to compare among scales of selection, averages facilitated that comparison most easily: at the finest scale was a greenness value for a single pixel, which itself is an average of the greenness among the vegetation found within that pixel. An understanding of the role of vegetation heterogeneity at multiple scales (Kie et al. 2002) would provide still further information on the factors affecting elephant distribution across the savanna biome.

Intermediate-scale selection There was no evidence that 16-day home ranges were established selectively with respect to greenness for either sex or season. A home range based on 16 days is likely to be arbitrary with respect to elephant biology, but that limit was imposed by the temporal resolution of the MODIS NDVI imagery we used. Initially, we treated this scale as representing selection at the scale of the “large patch” in a foraging hierarchy (i.e., one level above feeding station; Senft et al. 1987). Thus, this might represent large patches of resources that are occupied by an elephant herd until the resources are depleted to the point where those foraging animals depart and seek another large patch (Charnov 1976, Bailey et al. 1996, Searle et al. 2005). To represent that patch-level selection, depletion and departure, a resolution more appropriate to the foraging behaviour of an elephant should be considered. For example, the 16-day home range for one of our study animals was 3.3 km², which would contain approximately 50 250×250-m pixels. Based on behavioural observations for elephants in Sengwa, Zimbabwe, patch selection occurs on the order of 0.25 km², or over a linear distance of 500 m (2 pixels) and a time period of approximately 1 day (Guy 1976). Murwira and Skidmore (2005) further demonstrated that presence of elephants was optimally related to vegetation heterogeneity over a linear distance of 457–734 m (2–3 pixels). Time in a patch and movements between patches likely vary considerably across African elephant range and are influenced by local conditions, climate and soils (Young et al. 2009, Loarie et al. 2009b), but the results of Guy (1976) and Murwira and Skidmore (2005) suggest that the use of 16 days as a representation of large-patch selection likely resulted in a mismatch between the scale of elephant biology and that of the MODIS NDVI imagery.

Fine-scale selection During the wet season, there was no evidence of selection of particular greenness categories at the finest scale of analysis. This was likely a consequence of selection having occurred already at broader scales. As generalist herbivores with a mixed feeding strategy (Codron et al. 2006), the most active resource selection might have already occurred at the scale of the large patch, based on a broader perception of the quality of forage items available

once a large patch is occupied. Thus, any feeding station within that large patch is likely to be favourable for an animal with a broad tolerance for food types. Contributing to the absence of a pattern at the fine scale in the wet season might be a mismatch of scales between the resolution of our spatial data (250 m) and that at which elephants choose feeding stations.

During the dry season, however, there was stronger evidence for differential selection among greenness categories, with both sexes appearing to favour sites of intermediate greenness. For males, there was evidence that the greenest category was used less than the lowest category of greenness. During the dry season, areas with the highest greenness values contain vegetation that is dying back most slowly. That vegetation also is likely dominated by unpalatable, evergreen shrubs that are heavily defended by anti-herbivory compounds (Owen-Smith and Cooper 1989). Selection of locations of intermediate greenness in the dry season might reflect selection for patches having forage of moderate nutritional quality (e.g., grass that is dying back but still palatable) and avoidance of patches with abundant woody species that have a large influence on NDVI values but are also high in plant defence compounds.

The role of elevation Although not specifically a goal of this investigation, we recognise that elevation might nonetheless play a role in resource selection by elephants and have a scale-dependent influence on that selection. Moreover, it could influence conclusions about relationships between greenness and patterns of landscape use by elephants. There was evidence of selective use of elevation, depending on the season, at all three scales (Table 2).

Elephants have been reported to use lower-elevation areas during the dry season (Shannon et al. 2006), and this pattern was also apparent in our data at some scales of selection. There was evidence from our analysis that, if elephants showed any selectivity for particular elevations at the broad scale of analysis, they established home ranges at intermediate or higher elevations. Within those seasonal home ranges, however, selection appeared to be for the lower parts of those home ranges; this pattern was most apparent at the fine scale, but it also occurred in some cases at the intermediate scale. Elevation itself might be a landscape attribute that influences habitat selection, or it might be correlated with other resources or conditions that have those influences. The former situation might be a consequence of the high energetic cost for very large animals to traverse hilly landscapes (Wall et al., 2006). The latter situation could arise if environmental heterogeneity were associated with elevation and if elephants were selecting habitat based on vegetation heterogeneity (Grainger et al. 2008; Murwira and Skidmore 2005; Young et al. 2009) or aspect diversity at higher altitudes (Hebblewhite et al. 2008).

Furthermore, particular vegetation communities are associated with higher or lower elevations, for example, along a catena sequence (Venter et al. 2003) or with respect to a riparian zone (Rogers and O'Keefe 2003). Independent of vegetation productivity or leaf area, plants along such gradients might vary with respect to presence of key forage resources (e.g., marula, *S. birrea*; Morris et al. 2006) or overall palatability as a consequence of plant defences (Scholes and Walker 1993). Elephants favour *Acacia*-marula woodlands in the wet season (Shannon et al., 2006), and some elephants change their seasonal movements in response to the availability of fruits (White 1994). Thus, at least seasonally, such factors could influence the importance of elevation as an explanatory factor for the distribution of elephants in a manner that is independent of vegetation productivity as represented by an NDVI image.

NDVI as a predictor of animal distribution The utility of NDVI as a tool to understand the ecology of animals has been demonstrated for a number of species (Pettorelli et al. 2005b; Mueller et al. 2008; Bro-Jorgensen et al. 2008) and for elephants in particular (Wittemyer et al. 2007; Chamaillé-Jammes et al. 2007; Loarie et al. 2009a). A critical component of that understanding is in relating greenness to a mechanistic explanation of what determines animal distribution. Where NDVI is involved, that includes knowing the factors on the ground that contribute to the greenness value, and thus, the measurement of productivity represented in a pixel of an NDVI image.

For savannas, the proportion of the greenness signal caused by woody or herbaceous vegetation can vary from pixel to pixel, and thus, might give a different representation of how productive a site is (Archibald and Scholes 2007). In terms of understanding the mechanisms of resource selection by herbivores, that ratio can also influence the interpretation of greenness as an index of food, when part of that signal depends on grass characteristics and part depends on canopy cover, with each representing very different forage types for animals (Owen-Smith and Cooper 1989). In their analysis, Young et al. (2009) attempted to control for vegetation structure by analysing relationships between greenness and elephant distribution within vegetation structural classes, with each class having varying proportions of woody and herbaceous vegetation. Those classes were viewed to play a large role in the relationships between home range size and vegetation productivity and in how those relationships changed from dry to wet savannas. The implicit assumption is that, at such a broad scale, tree–grass ratios within pixels are constant, or if they vary, that variation is relatively unimportant.

At a finer scale of selection, tree–grass ratios within pixels lend a perspective on the mechanism causing selection that is missed when those ratios are ignored. High

greenness that is a consequence of canopy attributes invokes a very different foraging environment for an herbivore than does high greenness that occurs as a consequence of herbaceous ground cover. Knowledge of which vegetation component is dominant within a pixel further would produce different interpretation to the cause of selection of that pixel (e.g., selection for browsing opportunities or cover versus selection for grazing opportunities). For example, elephants in northern Kruger consume substantially more grass in the dry season, where the dominant browse species is phenol-rich mopane (*C. mopane*) than do southern elephants where mopane is less common (Codron et al. 2006). Based on NDVI greenness alone, such differences could easily be missed. Efforts to separate the contributions of woody and herbaceous components to the greenness signal would contribute greatly to revealing the mechanisms that drive resource and habitat selection by large herbivores at multiple scales in savanna biomes.

Conclusion

The role of scale requires careful consideration when attempting to determine the biological processes that influence the ecology of a particular species. Moreover, researchers investigating those processes risk misinterpretation of patterns if measurement occurs at an inappropriate scale. Our results suggest that selection of vegetation greenness, as represented by NDVI, was most apparent at the broadest and finest scales we considered. However, conclusions about the mechanisms leading to that selection were limited by lack of information about the relative contributions of trees and grass to the greenness values of NDVI imagery. Future efforts to understand habitat selection from remotely sensed data will have to separate those two components and thus contribute to a mechanistically based understanding of the role of vegetation greenness in the ecology of large herbivores.

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