Research

Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant

C. L. Roever, R. J. van Aarde and K. Leggett

C. L. Roever (mail@carrieroever.com) and R. J. van Aarde, Conservation Ecology Research Unit, Dept of Zoology and Entomology, Univ. of Pretoria, Hatfield, South Africa 0083. – K. Leggett, Univ. of New South Wales Arid Zone Research Station, Univ. of New South Wales, NSW 2880, Australia.

Resource selection function (RSF) models are commonly used to quantify species/habitat associations and predict species occurrence on the landscape. However, these models are sensitive to changes in resource availability and can result in a functional response to resource abundance, where preferences change as a function of availability. For generalist species, which utilize a wide range of habitats and resources, quantifying habitat selection is particularly challenging. Spatial and temporal changes in resource abundance can result in changes in selection preference affecting the robustness of habitat selection models. We examined selection preference across a wide range of ecological conditions for a generalist mega-herbivore, the African savanna elephant *Loxodonta africana*, to quantify general patterns in selection and to illustrate the importance of functional responses in elephant habitat selection. We found a functional response in habitat selection across both space and time for tree cover, with tree cover being unimportant to habitat selection in the mesic, eastern populations during the wet season. A temporal functional response for water was also evident, with greater variability in selection during the wet season. Selection for low slopes, high tree cover, and far distance from people was consistent across populations; however, variability in selection coefficients changed as a function of the abundance of a given resource within the home range. This variability of selection coefficients could be used to improve confidence estimations for inferences drawn from habitat selection models. Quantifying functional responses in habitat selection is one way to better predict how wildlife will respond to an ever-changing environment, and they provide promising insights into the habitat selection of generalist species.

Understanding the complex, dynamic interaction between species occurrence and habitat is essential to predict and manage responses of species to natural or anthropogenic environmental changes. Some ecologists therefore rely on resource selection function (RSF) models to quantify these species/habitat interactions. RSF models compare samples of used and available resource units to estimate the relative probably of occurrence based on resource characteristics (Boyce et al. 2002, Manly et al. 2002). This multivariate approach is becoming progressively more flexible and can incorporate cumulative effects for human development (Houle et al. 2010), intraspecific competition (McLoughlin et al. 2010), and predation (Hebblewhite et al. 2005). RSF models can also be used to inform conservation management decisions because they offer spatially explicit and predictive models of species occurrence (Johnson et al. 2004, Aldridge and Boyce 2007). Knowledge of habitat selection is integral for habitat protection and augmentation (Johnson et al. 2004, Aldridge and Boyce 2007), the restoration of species to previously unoccupied habitat (Merrill et al. 1999), and the identification of dispersal corridors (Chetkiewicz and Boyce 2009) as well as attractive sinks (Nielsen et al. 2006). Such knowledge

may aid in conservation planning that aims to ensure the viability of the population, the connectivity among subpopulations in a metapopulation, or restore the spatial structuring of populations (van Aarde and Jackson 2007).

One of the main limitations of RSF models, however, is that the estimate of selection is contingent upon the sample of availability (Beyer et al. 2010). For example, if use of a resource remains constant but local availability decreases, then the parameter estimate will change from avoidance to selection. In a habitat selection framework, this is known as a functional response (Mysterud and Ims 1998). Functional responses in habitat selection can be an artifact of sampling intensity (Beyer et al. 2010), however they can also be driven by behavioral changes is selection. As a resource becomes more scares on the landscape, an animal needing to meet some daily requirement, be it nutritional, physiological, or social, must spend a disproportionate amount of time utilizing that resource. Consequently, selection for a resource changes as a function of its availability. The presence of a functional response severely limits the application of an RSF model created for one location to a different area where availability is not equivalent (Boyce et al. 2002, Manly et al.

2002, Beyer et al. 2010). Under natural conditions resources are seldom equally available across the distributional range of a species. RSF models therefore are typically not applied beyond the bounds of a study area unless independent validation data exists and, when they are, caveats are stipulated. Models that are accurate outside of the study area are hailed as robust (Boyce et al. 2002, Wiens et al. 2008). Spatially robust models most often occur for habitat specialists, where species/habitat associations are simple and resilient to changes in availability (Boyce et al. 2002).

Temporal variation in resource availability can also limit the predictive ability of habitat selection models (Wiens et al. 2008). Seasonality in resource abundance, even within the same region, can alter the selection patterns of a species as food preferences change (Boyce et al. 2002). Habitat specialists may be less sensitive to seasonal changes as they are often tied to a single food source or habitat type. For example, northern spotted owls in California are always closely associated with mature forest (Meyer et al. 1998), and wolverines are closely associated with high-elevation subalpine habitats (Copeland et al. 2007). Conversely, a generalist species like grizzly bears have vast shifts in diet (Munro et al. 2006), and consequently habitat selection preferences change as seasons change (Nielsen et al. 2002).

So what do ecologists do when confronted with a generalist species where habitat associations are more complex? Boyce et al. (2002) suggest that selection by generalist species be analyzed across a range of environmental conditions, to quantify how selection changes as a function of availability. Instead of being viewed as problems to be overcome, functional responses can instead be used to predict selection in different regions where resources abundance varies (Boyce et al. 2002, Matthiopoulos et al. 2011). To incorporate a functional response into an RSF model, a random coefficient in a mixed-effects model can be used (Gillies et al. 2006, McLoughlin et al. 2010); however, a random coefficient can only be applied to one habitat covariate within a model. For many generalist species, a functional response is present for more than one habitat covariate; therefore, separate models are required for each sub-population (Boyce et al. 2002, Nielsen et al. 2002). The use of separate models also allows one to use the information theoretic approach to determine whether different habitat covariates are important in different regions or seasons (Burnham and Anderson 2002).

Despite the call to study multiple populations of generalist species to better understand patterns in habitat selection, this advice is rarely followed, largely due to the data requirements for such an analysis. In this paper, we examine habitat selection of a generalist herbivore species, the African savanna elephant *Loxodonta africana*, among seven populations in eight countries across southern Africa. Elephants are ideally suited for a study on functional responses in habitat selection because they are widely distributed across southern Africa where they occupy landscapes ranging from the deserts of Namibia to the dense, wet forests of Mozambique. Their diets also vary seasonally; individuals shift from mainly grazing on tender grasses in the wet season to mainly browsing on the leaves, twigs, branches, and bark of trees in the dry season (Codron et al. 2011).

Here, we develop habitat selection models at the scale of the home range that includes factors elephants are known to respond to: water (de Beer et al. 2006, Harris et al. 2008), slope (Wall et al. 2006), vegetation structure (Harris et al. 2008, Loarie et al. 2009, Young et al. 2009), and human presence (Hoare and Du Toit 1999, Harris et al. 2008, Jackson et al. 2008). We test for differences in male and female selection in the wet and dry seasons using the information theoretic approach to first quantify support for competing models. Then using the full model, we examine how the selection coefficients changed as a function of availability within an individual's home range (Hebblewhite and Merrill 2008, Houle et al. 2010). Our main objective was to quantify spatial functional responses, examining temporal functional responses only at a course, two-season scale. Specifically, in the more arid, western portion of the study area, we expect water and tree cover to be important covariates in habitat use in response to the limited availability of water (Leggett 2006) and the shortage of trees that provide shade (Kinahan et al. 2007) and offer some forage for elephants (Loarie et al. 2009). In the more mesic, eastern portion of the study area, we expect elephant's selection of tree cover to be unimportant for selection because trees are more plentiful and should, consequently, not limit elephant selection (Mysterud and Ims 1998, Illius 2006). We further expect a functional response to human presence, as elephants often come into conflict with people (Hoare 1999, Jackson et al. 2008). Thus, elephants in more remote areas would show greater indifference to human presence.

Methods

Study area

The study area comprised a large portion of the distributional range of elephants in southern Africa and included portions of Angola, Botswana, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe (Fig. 1). The region included a desert/grassland mosaic in the west, dry woodlands in the central region, and mesic forest in the east. Seasonal rainfall patterns drive vegetation structure (Sankaran et al. 2005). Mesic regions to the east had greater rainfall and hence greater tree cover compared to western portion of the study area (Table 1). Topographic conditions also varied, with more dramatic changes in elevation near the western and eastern coasts and relatively flat, unvarying terrain in the central region. Human density was low over much of the study area, with pockets of increased human densities near major waterways and roadways.

Elephant data

Elephants (n = 102) were captured and collared with Africa Wildlife Tracking GPS collars (model SM 2000E; Africa Wildlife Tracking, Pretoria, South Africa) between December 2002 and September 2010. Collars were programmed to relocate individuals at varying intervals, ranging from 1 to 24 h, with most elephants having multiple interval settings during the collaring period. Telemetry locations
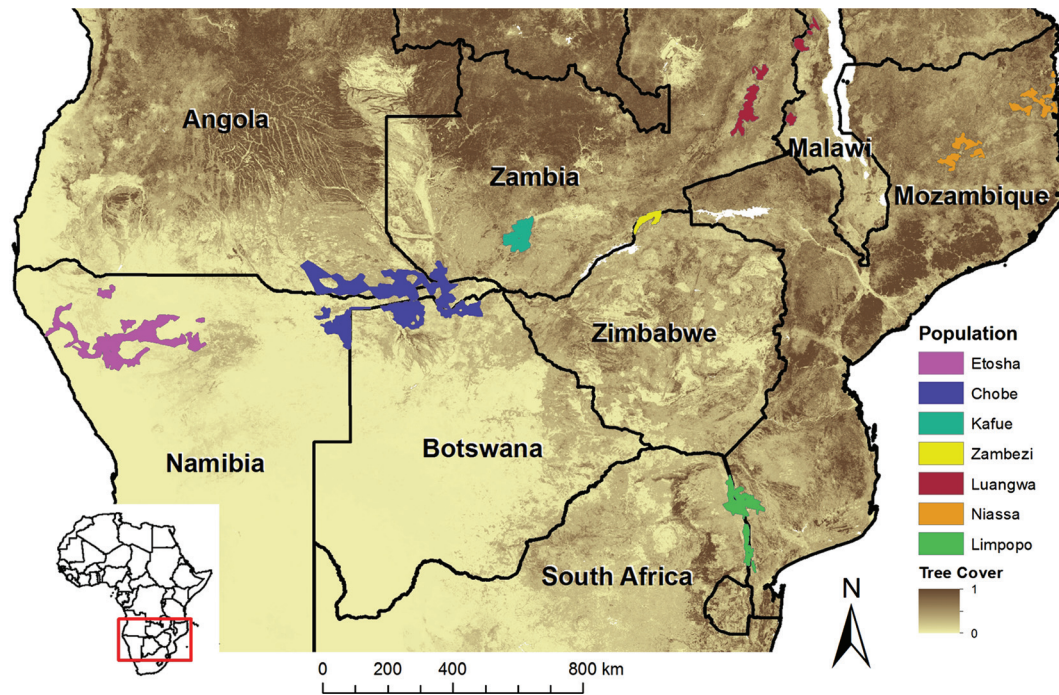
Figure 1. Map of the study area located in eight countries in southern Africa. Elephant local convex hull home ranges were grouped into seven populations (Etosha, Chobe, Kafue, Zambezi, Luangwa, Niassa, and Limpopo) based on study site. Proportion of tree cover is presented.

were divided into two seasons and combined across years. Core wet season was defined as December through March inclusive, and core dry season was defined as June through September (Young et al. 2009). Locations in the transition months of April, May, October, and November were omitted from the analysis. Only individuals with > 100 locations per season were retained for the analysis, resulting in 35 167 locations among 86 individuals for the dry season and 43 141 locations among 88 individuals for the wet season analysis.

Home ranges were generated separately for the core wet and dry season for each individual using the local convex hull (LoCoH) nonparametric kernel method (Getz et al. 2007). The adaptive sphere of influence (a-LoCoH) algorithm was used to construct kernels, with a equal to the furthest distance between any two locations (Getz et al. 2007). LoCoH home ranges, which ranged in area

from 50 to 9000 km², fit tightly around telemetry locations often leaving holes, which we believed were unrealistic. To reduce these holes, home ranges were further buffered by 3 km, the mean distance elephants within our study traveled during a 12 h period. Home ranges were created using R software (R Development Core Team 2010), along with the packages 'adehabitat' (Calenge 2006) and 'NNCH' (Getz and Wilmers 2004).

The majority of elephants within this study roamed freely and were not confined to parks, countries, or other intangible human boundaries (van Aarde and Ferreira 2009). However, fences were present along the borders of Etosha National Park and along international boundaries in Khaudum Game Reserve and Kruger National Park. For analytical purposes elephants were grouped by study site, hereby referred to as populations, resulting in seven populations: Etosha, Chobe, Kafue, Zambezi, Luangwa, Niassa,

Table 1. General description of some local conditions within each study site (population). The presence of water was calculated independently for the dry and wet seasons. High human use was defined as a human density of > 16 people km⁻² using LandScan (2008) human population data.

| Population | Mean slope (degrees) | Mean proximity to water (km) | | Mean percent tree cover | Percent area of high human use | Density of roads (km km⁻²) | Mean elephant home range (km²) |
		Dry season	Wet season				
Etosha	4.6	10.6	6.2	8.9	0.1	0.07	573
Chobe	0.6	18.5	18.9	10.8	0.8	0.04	1431
Kafue	1.0	5.6	9.1	18.7	0.5	0.06	482
Zambezi	3.8	2.0	2.3	17.9	21.9	0.20	143
Luangwa	2.3	6.0	5.4	21.0	12.8	0.12	378
Niassa	2.0	19.6	19.0	30.1	27.3	0.02	543
Limpopo	1.9	4.6	4.5	17.5	1.0	0.16	845

and Limpopo (ordered from west to northeast, with the most southern population, Limpopo, last; Fig. 1). Population names were often based on the nearest major protected area for convenience.

Habitat covariates

Habitat covariates were chosen based on their known or suspected influence on elephant space use. In order to ensure that direct comparisons could be made among models, habitat was described using covariates that could be applied to all populations, thereby avoiding site-specific variables such as categorical land cover descriptors. The structure and greenness of vegetation is known to be an important predictor of elephant space use because it provides both food and shade (Kinahan et al. 2007, Harris et al. 2008, Loarie et al. 2009, Young et al. 2009). Vegetation structure was characterized using the Moderate Resolution Imaging Spectrometer (MODIS) Vegetation Continuous Fields product (Hansen et al. 2006), from which we estimate the proportions of tree cover at a resolution of 0.25 km^2, defined as woody vegetation > 5 m in height (Hansen et al. 2002). An enhanced vegetation index (EVI) was used to quantify greenness (Pettorelli 2006). For the core wet and dry seasons, EVI layers for the 8 yr of this study were obtained and used to calculate mean EVI within a season at a resolution of 0.64 km^2.

Water was located using geospatial data from Tracks4 Africa (2010) and man-made watering point data supplied by conservation authorities. Water body locations were then validated against Landsat imagery, and missing water bodies were hand-digitized. Separate water layers were made for each season, with the core wet season including all water categories and the core dry season including only main rivers, river deltas, lakes, dams, and man-made watering holes. Distance to water was then calculated for telemetry locations within each season.

Elephants typically avoid humans and human disturbance (Hoare and Du Toit 1999, Harris et al. 2008), particularly during daylight hours when humans are more active (Jackson et al. 2008). We included several covariates that reflect the land-use patterns of people. Human density was estimated with LandScan (2008) human population data at a resolution of 1 km^2. Hoare and Du Toit (1999) found that elephants avoided areas with > 15.6 people km^{-2}; therefore, we identified areas with > 16 people km^{-2} (rounding up) and calculated the distance from each elephant location to

these pixels. Road data were obtained from Tracks4Africa (2010). Studies of other large mammals have shown an avoidance of high-traffic volume roads but neutral or positive selection for low-traffic volume roads which potentially facilitate movement (Chruszcz et al. 2003, Dickson et al. 2005); therefore, roads were categorized based on size. We determined distances of locations to main roads (freeway, national, or main roads) and secondary roads (all other road categories).

Finally, elephants avoid steep slopes due to their large body size (Wall et al. 2006), so we included slope derived from a 90×90 m resolution digital elevation model (Jarvis et al. 2006) in our analyses. All geospatial analysis was completed using the spatial analyst extension of ArcGIS 9.3.1 (ESRI 2009) and Geospatial Modeling Environment (Beyer 2011).

Habitat selection models

Habitat selection was modelled separately for the seven elephant populations and for males and females, with one collared female actually representing a breeding herd with several adult females and their offspring. Elephant locations (1) were compared to randomly generated locations (0) using a mixed effect logistic regression model for location i and individual j, taking the form:

$$w(x_{ij}) = \exp(\beta + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_j)$$

where $w(x_{ij})$ is the resource selection function, β_n is the coefficient for the n-th predictor variable x_n, and γ is the random intercept for animal j (Manly et al. 2002, Gillies et al. 2006). The random intercept was used to control for the lack of independence of points within individuals and differences in sample size among individuals (Gillies et al. 2006). We implemented a design III approach (Thomas and Taylor 1990, Manly et al. 2002), whereby random locations were generated within the home range of each elephant at a density of 3 points km^{-2}. At this density, contamination (i.e. use and available locations occurring within the same raster pixel) was $< 15\%$ for the habitat covariate mapped at the coarsest resolution (800×800 m), and was therefore negligible (Johnson et al. 2006).

We used model selection procedures (Burnham and Anderson 2002) to determine which habitat covariates had the greatest influence on resource selection for each of the seven populations. Seven a priori candidate models were ranked using Bayesian information criterion (BIC; Table 2).

Table 2. Candidate models considered when assessing habitat selection by elephants across southern Africa. The number of fixed and random parameters (K) is presented.

Model	Model structure	K
1. Null		2
2. Landscape	Slope + Distance to water + (Distance to water)^2	5
3. Water and food	Distance to water + (Distance to water)^2 + Proportion tree	5
4. Slope, water, and food	Slope + Distance to water + (Distance to water)^2 + Proportion tree	6
5. Human density	Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	6
6. Limiting factors	Slope + Distance to water + (Distance to water)^2 + Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	9
7. Full	Slope + Distance to water + (Distance to water)^2 + Proportion tree + Distance to humans + Distance to main road + Distance to secondary road + (Distance to secondary road)^2	10

BIC was used as it favours more parsimonious models compared to Akaike's information criterion (AIC), which favours complex models when sample sizes are large (Burnham and Anderson 2002, Grueber et al. 2011). Variables that were highly correlated (Pearson's r > 0.6) were not included in the same model. Correlations occurred between tree cover and mean EVI (Pearson's r = 0.68). Because tree cover is an indicator of both food resources and thermoregulatory needs (i.e. shade cover; Kinahan et al. 2007), tree cover was used in subsequent models. All continuous variables were tested for the potential presence of a nonlinear relationship with the inclusion of a quadratic term in a univariate analysis and by examining histograms. Model fit of the top-ranked model for each population was evaluated using k-fold cross validation (k = 5) and the Spearman rank correlation coefficient (Boyce et al. 2002). Analyses were conducted in R software (R Development Core Team 2010) using the lme4 package (Bates and Maechler 2010).

To test the presence of functional responses, we used a two-step approach (Hebblewhite and Merrill 2008, Houle et al. 2010). First we modelled habitat selection for each individual, so that all covariates could vary in slope and intercept, using the full model (model 7, Table 2). We then assessed how the selection coefficient of a given covariate changed as a function of the mean value of that covariate within the individual's home range (log transformed). Significance was evaluated using a linear regression. Where models displayed heterogeneity of variance, generalized least squares were used instead of a simple linear regression (Zuur et al. 2010). This procedure could only be applied to covariates with linear selection coefficients (i.e. slope, proportion tree, distance to people, and distance to main roads).

Results

Dry season RSF models

The top-ranked model was the full model (model 7) for all female and most male (4 of 6) populations during the dry season (Table 3). The top models provided good fit to the data using k-fold cross validation expect for Niassa females (Spearman rank $r_s = 0.48$, and p > 0.05) and Chobe males ($r_s = 0.62$, and p > 0.05; Table 3). The inclusion of all variables in most top-ranked models was counter to our expectations that selection for some covariates would be less important as availability changed. This indicated that all variables examined in this study were important to elephant habitat selection irrespective of availability during the dry season. The strength and direction of covariates was consistent across most populations in the top-ranked models. Elephants from most populations selected areas of low slope (9 of 13), high tree cover (10 of 13), far distances from people (8 of 13), and close proximity to main road (8 of 13; Table 4). Populations varied in the maximum distance elephants traveled from water, ranging from 6 km in the Zambezi to 79 km in the Chobe population. Despite this, elephants in most populations (9 of 13) selected areas near and far from water at greater frequencies than random (Table 4, Fig. 2). Only Niassa females selected areas of intermediate distances from water during the dry season (i.e. the selection coefficient had a hump-shaped curve). Selection for secondary roads was less consistent across populations. Males and females in Niassa and Limpopo along with Etosha females and Chobe males selected areas of intermediate distance from secondary roads; whereas, the elephants from the remaining populations selected areas near to secondary roads or areas both near and far from these roads.

Wet season RSF models

In the wet season, Etosha, Chobe, Kafue, and Zambezi populations continued to have the full model (model 7) as the top-ranked model for both sexes (Table 3). However, among the more easterly populations, Luangwa, Niassa, and Limpopo, the top-ranked model was the limiting factors model (model 6) for those females and for Limpopo males. Of these eastern populations, only Luangwa males had a top-ranked model that included tree cover, indicating

Table 3. The top ranking model using Bayesian information criterion (BIC) for female and male elephant habitat selection in the dry and wet season. Top model weight (w) is presented along with Spearman rank correlation coefficient ($\bar{r}_s$) and significance for model fit.

	Females			Males		
	Top model	w	$\bar{r}_s$	Top model	w	$\bar{r}_s$
Dry season						
Etosha	7. Full	1.00	0.96*	7. Full	1.00	0.96*
Chobe	7. Full	1.00	0.96*	7. Full	1.00	0.62
Kafue	7. Full	1.00	0.98*	7. Full	1.00	0.96*
Zambezi	7. Full	1.00	0.96*			
Luangwa	7. Full	0.73	0.95*	5. Human density	0.95	0.79*
Niassa	7. Full	0.97	0.48	7. Full	1.00	1.00*
Limpopo	7. Full	0.82	0.95*	6. Limiting factors	0.88	1.00*
Wet season						
Etosha	7. Full	0.62	0.98*	7. Full	1.00	0.84*
Chobe	7. Full	1.00	0.89*	7. Full	1.00	0.99*
Kafue	7. Full	1.00	1.00*	7. Full	0.95	0.87*
Zambezi	7. Full	1.00	0.83*			
Luangwa	6. Limiting factors	0.99	0.73*	7. Full	1.00	0.95*
Niassa	6. Limiting factors	0.88	0.61	5. Human density	1.00	0.03
Limpopo	6. Limiting factors	0.98	0.89*	6. Limiting factors	0.73	0.99*

Table 4. Parameter estimates of the top-ranked BIC model for each population in the dry (a) and wet (b) season. Estimates for which confidence intervals do not cross zero are indicated by (∗). Missing values (−) occur when a given parameter was not included in the top model.

(a)

	Females						
	Etosha	Chobe	Kafue	Zambezi	Luangwa	Niassa	Limpopo
Slope	−0.12*	0.39*	0.24*	−0.15*	−0.05*	−0.03*	−0.06*
Distance to water†	−4.10*	−0.54*	−0.24	−0.73	−1.41*	3.18*	−4.64*
(Distance to water†)2	1.10*	0.12*	−1.64*	−4.71*	0.37*	−0.70*	3.58*
Proportion tree	27.67*	4.31*	3.72*	1.81*	0.77*	1.55*	1.07*
Distance to humans	0.24*	0.04	−1.08*	1.37*	0.41*	−0.18	−0.45*
Distance to main road†	−0.16*	0.06*	0.76*	0.29*	−0.05	1.27*	−0.54*
Distance to secondary road†	1.83*	−0.20*	−0.81*	−7.67*	−1.58*	3.88*	0.86*
(Distance to secondary road†)2	−1.28*	−0.04	0.33*	8.62*	0.80*	−0.73*	−0.55

	Males					
	Etosha	Chobe	Kafue	Luangwa	Niassa	Limpopo
Slope	−0.12*	0.15*	−0.03	−	−0.21*	−0.20*
Distance to water†	−0.56*	−1.08*	−1.09*	−	−1.59*	−2.73*
(Distance to water†)2	0.09*	0.13*	0.20	−	0.36*	1.03*
Proportion tree	−22.74*	3.72*	3.42*	−	2.44*	−
Distance to humans	0.06*	0.05	−0.34*	1.26*	1.23*	−0.61*
Distance to main road†	−0.12*	−0.12*	0.04	−0.10	−0.41*	−0.66*
Distance to secondary road†	−2.50*	0.71*	−2.25*	−0.16	1.71*	0.47*
(Distance to secondary road†)2	0.58*	−0.05*	0.62*	−0.53	−0.96*	−0.41*

†Distance measures were in km and multiplied by 0.1 to facilitate model convergence.

(b)

	Females						
	Etosha	Chobe	Kafue	Zambezi	Luangwa	Niassa	Limpopo
Slope	−0.15*	0.24*	0.03	−0.17*	−0.10*	−0.07*	−0.10*
Distance to water†	0.64*	0.11	−0.51	0.93	−0.39*	−0.22*	−0.55
(Distance to water†)2	0.15*	−0.04*	−1.48*	−1.17	0.16*	0.01	0.71*
Proportion tree	7.52*	2.44*	2.83*	1.66*	−	−	−
Distance to humans	−0.09*	0.10*	−0.85*	1.18*	0.37*	−0.52*	0.15
Distance to main road†	0.03	−0.04*	0.25*	−0.11*	0.07*	0.69*	−0.40*
Distance to secondary road†	−1.00*	0.34*	−2.26*	−5.12*	−0.67*	1.08*	2.98*
(Distance to secondary road†)2	0.23*	−0.04*	0.67*	6.04*	0.21*	−0.05	−2.11*

	Males					
	Etosha	Chobe	Kafue	Luangwa	Niassa	Limpopo
Slope	−0.07*	0.08	0.05	−0.13*	−	−0.35*
Distance to water†	−0.29*	−0.21*	−0.63*	−2.77*	−	0.56
(Distance to water†)2	0.15*	0.09*	0.01	1.51*	−	−0.34
Proportion tree	−14.80*	3.39*	3.11*	2.25*	−	−
Distance to humans	0.31*	−0.13*	0.15	2.06*	−0.57*	−0.03
Distance to main road†	−0.02	0.13*	−0.32*	0.22*	0.01	−0.21*
Distance to secondary road†	−1.37*	−0.33*	−0.20	−2.11*	1.05*	0.17
(Distance to secondary road†)2	0.30*	0.00	0.05	0.97*	−0.60*	−0.41*

†Distance measures were in km and multiplied by 0.1 to facilitate model convergence.

that during the wet season tree cover was not an important predictor of elephant habitat selection in these populations. This was concurrent with our expectations that tree cover would be less influential for elephants in more mesic environments. The top models provided good fit for most populations during the wet season; however, model fit was poor for Niassa females and males ($r_s = 0.61$ and 0.03, respectively, and $p > 0.05$; Table 3). Selection for water during the wet season was more variable across populations than it was in the dry season. Luangwa and Limpopo females selected areas both near and far from water, Zambezi and Chobe females selected intermediate distance from water, Kafue and Niassa females selected areas close to water, and Etosha females selected areas far from water. Half of the males (3 of 6) selected areas both near and far from water, while the remaining three were variable in selection (Fig. 2). This variability in selection indicated a functional response to water seasonally. Selection for low slopes (8 of 13), high tree cover (7 of 13), and far distances from people (8 of 14) was similar to the dry season. However, selection for main roads was
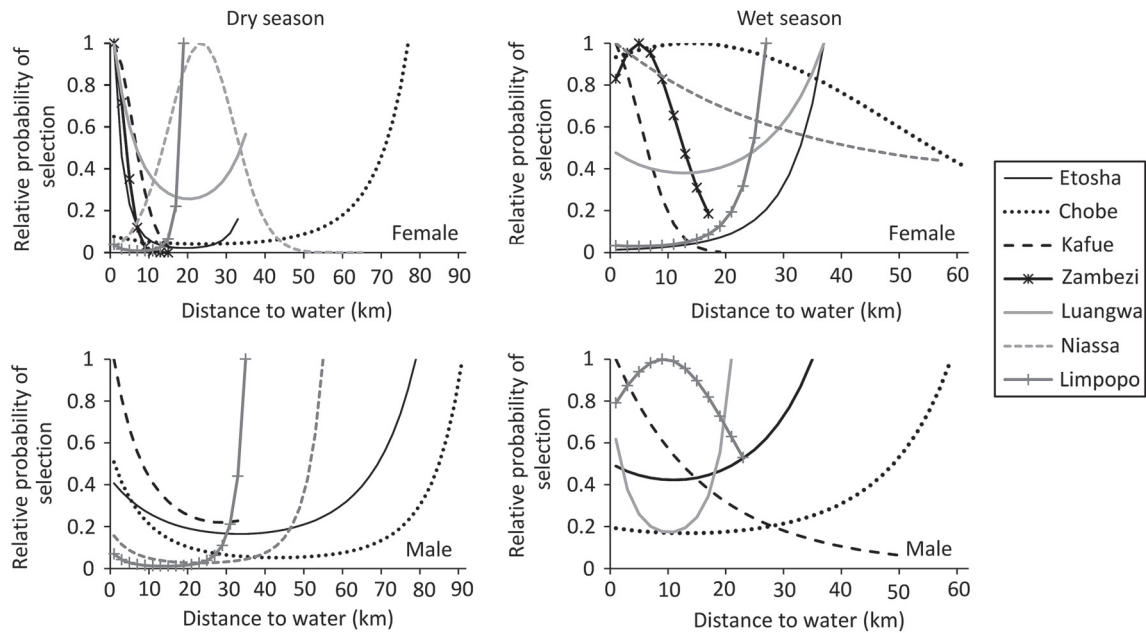
Figure 2. Relative probability of selection of water for females and males in the dry and wet seasons as a function of the distance to water. Values for each population are displayed only across the range of distances observed within that population.

counter to dry season selection, with nearly equal numbers avoiding (6 of 13) and selecting (7 of 13) main roads. In the wet season, selection for secondary roads continued to be as variable as it was in the dry season.

Functional responses

When comparing the selection coefficient for a given covariate to the mean value of that covariate within an individual's home range, we found a significant functional response for proximity to humans during the dry season (R^2 adjusted = 0.04, p = 0.03; Fig. 3). As the mean distance from humans increased (i.e. as there were fewer people within the home range) selection for people decreased. We expected selection for proximity to human to be less significant when elephants were far from human development; however, we did not find this pattern. Instead, we found a general pattern of avoidance when they were far from people and high heterogeneity in the selection coefficient when elephants were close to people.

While the functional responses tested were not significant within a linear regression model for all other covariates examined, the variability of selection coefficients at varying levels of resource abundance indicated similar patterns as observed with the proximity to humans covariate. Because of heterogeneity of variance in the slope and tree cover models, generalized least squares techniques were used. While most elephants selected areas of low slope, when the home range of an individual was located in a relatively flat area, the selection coefficient was more variable (Fig. 3). A similar pattern occurred with tree cover. When the proportion of tree cover within an individual's home range was low, the variability in the selection coefficient increased with some individuals having relatively strong selection for trees. Functional responses for distance to main road were not

significant during either season and displayed no heterogeneity of variance.

Discussion

Although savannah elephants are generalist mega-herbivores with wide ecological tolerances, we found consistency in their habitat selection patterns, lending insight into the biology of the species. Elephants in most populations and both seasons had the full model (model 7) as the top-ranked BIC model. This is not unexpected given that for inclusion in BIC models, we considered covariates which relate to some biological process or limiting factor for elephants (e.g. food, water, terrain, and human presence). We did, however, find that in the wetter, eastern populations (Luangwa, Niassa, and Limpopo) tree cover was not an important predictor of elephant use in the wet season, as expected. The decline in the importance of the vegetation covariate suggested a functional response for vegetation, where its importance declines both temporally (within these populations as increased rainfall makes food more readily available) and spatially (across populations as vegetative cover increases). This functional response was not supported when we examined the abundance of tree cover within each individual's home range. However, when we further excluded non-significant selection coefficients from the analysis to reflect their lack of importance in those models, the function response was significant in the dry season (p = 0.02).

Our results also revealed evidence of a temporal functional response for water. Water is a limiting factor for elephants, as demonstrated by their close association with watering holes in the dry season (de Beer et al. 2006, Harris et al. 2008, Shannon et al. 2009, Young et al. 2009) and their population increases when supplemental water is provided (Owen-Smith et al. 2006). In the dry season, most
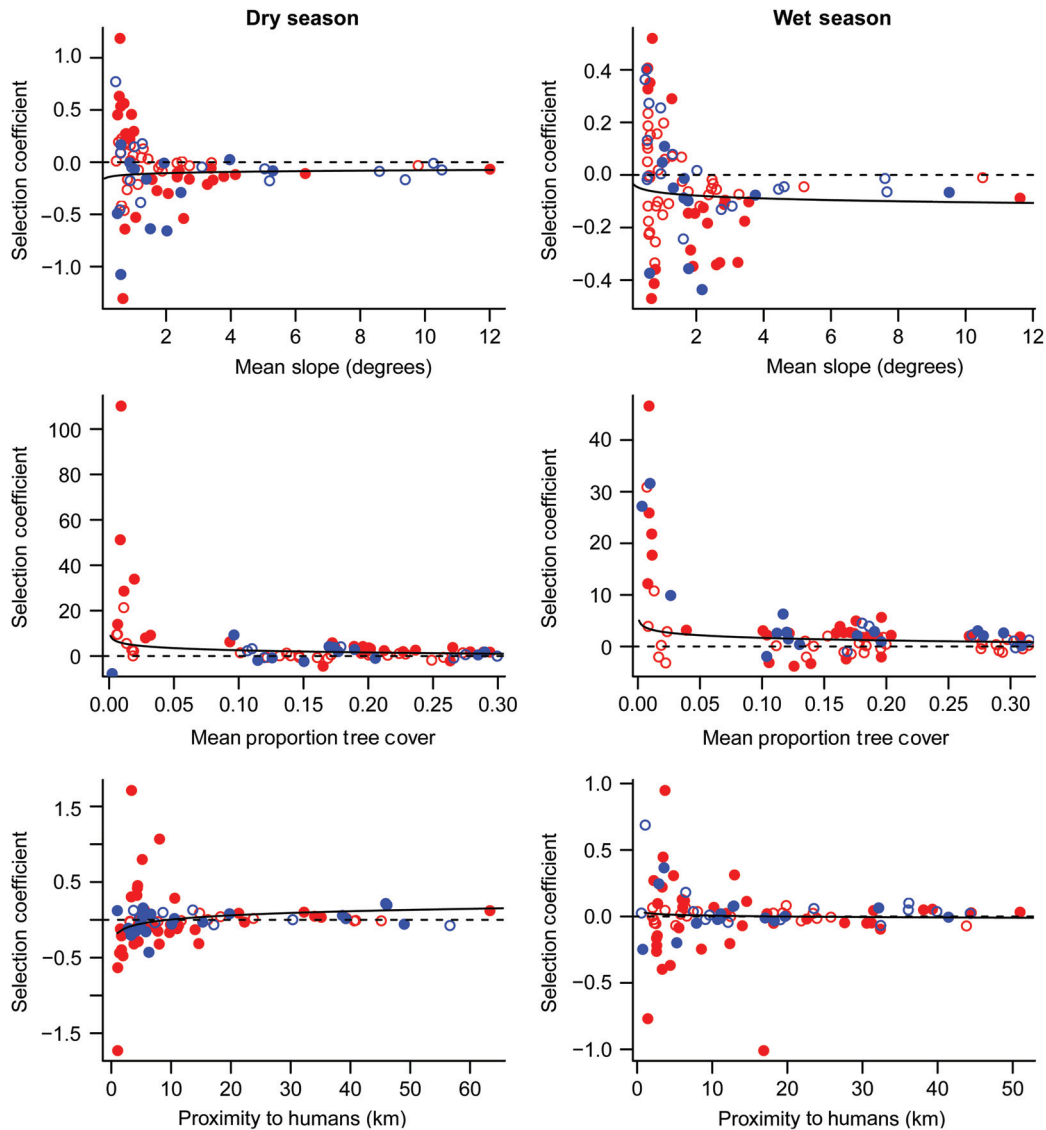
Figure 3. Functional responses in habitat selection for female (red) and male (blue) elephants. Selection coefficients were estimated for each individual using a resource selection function model and were modeled as a function of the mean slope, tree cover, or proximity to humans within each home range. Both significant (filled circle) and non-significant (open circle) selection coefficients were modeled.

populations (9 of 13) selected areas near and far from water; whereas, in the wet season, selection for water was highly variable, with individuals selecting areas near, far, and of intermediate distance from water (Fig. 2). The change in selection for water as a function of season suggests a functional response, as higher rainfall during the wet season results in greater abundance and wider distribution of water throughout the study area. However, we did not find a spatial functional response for water as expected. The more mesic, eastern populations had similar selection patterns for water in the dry season, indicating that water was a limiting factor, even in these wetter regions.

Selection for low slopes, high tree cover, and far distance from people was consistent across populations and seasons and was similar to previous studies of elephant selection patterns (Hoare and Du Toit 1999, Wall et al. 2006, Kinahan et al. 2007, Harris et al. 2008, Loarie et al. 2009). The real ecological insight gained from studying elephant selection across a large spatial scale, however, comes from the heterogeneity of variance displayed in the functional responses. Previous research into function responses of habitat selection has not reported such heterogeneity in variance. This could be an artifact of low sample size, as most studies have few individuals along the continuum of available abundance (Hebblewhite and Merrill 2008, Houle et al. 2010). However, heterogeneity of variance in habitat selection should be expected for some habitat covariates. Slope, for example, does not limit elephant movement when the home range is situated in a relatively flat area. As a result, we found high variability in the selection coefficients in these locations. When elephant home ranges occur in areas with variable topography, slope became a limiting factor. Consistent negative selection coefficients show that elephants living in such areas selected flat topography.

One of the main criticisms of RSF models is that they are limited in their ability to make predictions in

different areas or at different times (Garshelis 2000, Manly et al. 2002). Some authors contend that using information gained about functional responses in selection could help remedy this problem (Boyce et al. 2002, McLoughlin et al. 2010, Matthiopoulos et al. 2011). For elephants, selection at the scale measured in this study was relatively consistent and the measured functional responses were not significant; consequently, we do not believe that the function responses discovered here could be used towards those ends. However, researchers could use information about heterogeneity of variance to better estimate the confidence around habitat selection models applied to new regions, especially when no data on habitat selection is available. For example, in relative flat areas close to people, one would expect much more variable selection patterns and less accurate estimates of habitat selection for elephants based on the functional responses observed in this study.

Among the covariates examined, the human presence covariates were least consistence across populations. While elephants generally avoided humans, variability in selection increased as individual home ranges were in closer proximity to people (Fig. 3). Selection for road covariates was also variable between populations (Table 4a, b). This variability in elephant selection was counter to our expectations that humans would have little influence on selection when elephants were far from people. However, the variability in selection for human-use features is not an uncommon pattern in selection by generalist species where humans are both a source of food because of crops and a potential threat, and likely indicates that individual elephants were using different strategies when near human development. In grizzly bears, for instance, some individuals become habituated to human food sources or use human settlements as a refuge from more dominant individuals (McLellan and Shackleton 1988, Mattson et al. 1992), while others avoid humans due to the increased mortality risk (Gibeau et al. 2002, Wielgus and Vernier 2003). Human-use features may also co-occur with areas preferred by wildlife, such as near rivers and the more fertile floodplains (Roever et al. 2008). Roads within protected areas, for example, are often established along the best game viewing routes, such as near rivers and watering holes. The threats posed to elephants by roads within protected areas should be minimal (Blake et al. 2008) and could confound inferences drawn about selection of roads located outside of protected areas. Spatial scale is also likely influencing the patterns observed for human use features. Avoidance of humans is likely occurring at a broader spatial scale; whereby the elephant home range was already situated in a low human-density area (Hoare and Du Toit 1999), thus within-home range selection patterns were more variable.

This study represents an amalgamation of habitat selection theory for elephants across southern Africa; however, a study area of this size, particularly in the developing world, creates unique challenges. To make comparisons across regions, the habitat covariates chosen had to be consistent across the study area. Unfortunately, GIS data quality often varies from one country to the next, so while detailed geospatial data were available for South Africa, Namibia, and Mozambique, information was often lacking for Malawi, Zambia, and Zimbabwe. Consequently, we used global datasets which, while excellent in quality, use larger spatial resolution (the smallest being 90 × 90 m for slope but increasing to 500 × 500 m for tree cover). This larger resolution could help explain the poor model fit for Niassa females and Chobe males in the dry season and Niassa females and males in the wet season. Prediction of elephant habitat selection could be improved if fine scale information on vegetation characteristics and the presence of standing water across the seasons were available. As some of the world's most diverse and valuable wildlife resources are in the developing world, efforts should be made to increase the quality of geospatial data in these regions for the betterment of wildlife management.

Studying a generalist species over a wide spatial scale can lend insight into the biology of that species (Boyce et al. 2002), which could be particularly important in predicting changes in animal space-use in this ever-changing world. Our analysis confirms expectations that a generalist mega-herbivore showed a functional response, particularly when the relevant resource was uncommon or limiting (Mysterud and Ims 1998, Illius 2006). We also found that selection by this generalist species is more variable when at different levels of resource abundance, which can be used to better estimate confidence around model predictions. In southern Africa, elephant management strategies are moving towards reinstating a more natural, self-sustaining spatial dynamic through the development of transfrontier conservation areas (Hanks 2001, Western 2003, van Aarde and Jackson 2007). Current initiatives strive to remove fences around parks, reduce artificial water sources, and promote cooperation between countries, allowing wildlife access to greater and more natural roaming areas. However, information on how elephants will respond to these changes is lacking because experimentation on many large mammal species, particularly those of management concern, is not feasible. Consequently, researchers must work within the context of present-day landscapes. Conservation initiatives can benefit from relying on our illustrated functional responses to better predict elephant selection within changing landscapes.

References

Aldridge, C. L. and Boyce, M. S. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. – Ecol. Appl. 17: 508–526.

Bates, D. and Maechler, M. 2010. Linear mixed-effects models using S4 classes. – R package ver. 0.999375-37.

Beyer, H. L. 2011. Geospatial modeling environment. – Spatial Ecology, LLC.

Beyer, H. L. et al. 2010. The interpretation of habitat preference metrics under use-availability designs. – Phil. Trans. R. Soc. B 365: 2245–2254.

Blake, S. et al. 2008. Roadless wilderness area determines forest elephant movements in the Congo Basin. – PLoS One 3: e3546.

Boyce, M. S. et al. 2002. Evaluating resource selection functions. – Ecol. Model. 157: 281–300.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516–519.

Chetkiewicz, C. L. B. and Boyce, M. S. 2009. Use of resource selection functions to identify conservation corridors. – J. Appl. Ecol. 46: 1036–1047.

Chruszcz, B. et al. 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. – Can. J. Zool. 81: 1378–1391.

Codron, J. et al. 2011. Landscape-scale feeding patterns of African elephant inferred from carbon isotope analysis of feces. – Oecologia 165: 89–99.

Copeland, J. P. et al. 2007. Seasonal habitat associations of the wolverine in central Idaho. – J. Wildl. Manage. 71: 2201–2212.

de Beer, Y. et al. 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. – J. Arid Environ. 64: 412–421.

Dickson, B. G. et al. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. – J. Wildl. Manage. 69: 264–276.

ESRI 2009. ArcGIS ver. 9.3.1. – Environmental Systems Research Inst. (ESRI), Redlands.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measureing use, selection, and importance. – In: Boitani, L. and Fuller, T. K. (eds), Research techniques in animal ecology: controversies and consequences. Columbia Univ. Press, pp. 111–164.

Getz, W. and Wilmers, C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. – Ecography 27: 489–505.

Getz, W. M. et al. 2007. LoCoH: nonparameteric Kernel methods for constructing home ranges and utilization distributions. – PLoS One 2: e207.

Gibeau, M. L. et al. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. – Biol. Conserv. 103: 227–236.

Gillies, C. S. et al. 2006. Application of random effects to the study of resource selection by animals. – J. Anim. Ecol. 75: 887–898.

Grueber, C. E. et al. 2011. Multimodel inference in ecology and evolution: challenges and solutions. – J. Evol. Biol. 24: 699–711.

Hanks, J. 2001. Conservation strategies for Africa's large mammals. – Reprod. Fert. Develop. 13: 459–468.

Hansen, M. et al. 2006. Vegetation continuous fields MOD44B, 2001 percent tree cover, collection 4. – Univ. of Maryland.

Hansen, M. C. et al. 2002. Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. – Remote Sens. Environ. 83: 303–319.

Harris, G. M. et al. 2008. Rules of habitat use by elephants Loxodonta africana in southern Africa: insights for regional management. – Oryx 42: 66–75.

Hebblewhite, M. and Merrill, E. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. – J. Appl. Ecol. 45: 834–844.

Hebblewhite, M. et al. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. – Oikos 111: 101–111.

Hoare, R. E. 1999. Determinants of human–elephant conflict in a land-use mosaic. – J. Appl. Ecol. 36: 689–700.

Hoare, R. E. and Du Toit, J. T. 1999. Coexistence between people and elephants in African savannas. – Conserv. Biol. 13: 633–639.

Houle, M. et al. 2010. Cumulative effects of forestry on habitat use by gray wolf (Canis lupus) in the boreal forest. – Landscape Ecol. 25: 419–433.

Illius, A. W. 2006. Linking functional responses and foraging behavior to population dynamics. – In: Danell, K. et al. (eds), Large herbivore ecology, ecosystem dynamics, and conservation. Cambridge Univ. Press, pp. 71–96.

Jackson, T. R. et al. 2008. Solutions for elephant Loxodonta africana crop raiding in northern Botswana: moving away from symptomatic approaches. – Oryx 42: 83–91.

Jarvis, A. et al. 2006. Hole-filled seamless SRTM data V3. – International Centre for Tropical Agriculture (CIAT).

Johnson, C. J. et al. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. – J. Appl. Ecol. 41: 238–251.

Johnson, C. J. et al. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. – J. Wildl. Manage. 70: 347–357.

Kinahan, A. A. et al. 2007. Ambient temperature as a determinant of landscape use in the savanna elephant, Loxodonta africana. – J. Therm. Biol. 32: 47–58.

LandScan 2008. High resolution global population data set. – Copyrighted by UT-Battelle, LLC, operator of Oak Ridge National Laboratory under Contract no. DE-AC05-00OR 22725 with the United States Dept of Energy.

Leggett, K. 2006. Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. – Pachyderm 40: 40–51.

Loarie, S. R. et al. 2009. Elephant seasonal vegetation preferences across dry and wet savannas. – Biol. Conserv. 142: 3099–3107.

Manly, B. F. J. et al. 2002. Resource selection by animals: statistical design and analysis for field studies. – Kluwer.

Matthiopoulos, J. et al. 2011. Generalized functional responses for species distributions. – Ecology 92: 583–589.

Mattson, D. J. et al. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark-pine seed crops. – J. Wildl. Manage. 56: 432–442.

McLellan, B. N. and Shackleton, D. M. 1988. Grizzly bears and resource-extraction industries – effects of roads on behavior, habitat use and demography. – J. Appl. Ecol. 25: 451–460.

McLoughlin, P. D. et al. 2010. Considering ecological dynamics in resource selection functions. – J. Anim. Ecol. 79: 4–12.

Merrill, T. et al. 1999. Defining landscapes suitable for restoration of grizzly bears Ursus arctos in Idaho. – Biol. Conserv. 87: 231–248.

Meyer, J. S. et al. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. – Wildl. Monogr. 139: 5–51.

Munro, R. H. M. et al. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. – J. Mammal. 87: 1112–1121.

Mysterud, A. and Ims, R. A. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. – Ecology 79: 1435–1441.

Nielsen, S. E. et al. 2002. Modeling grizzly bear habitats in the yellowhead ecosystem of Alberta: taking autocorrelation seriously. – Ursus 13: 45–56.

Nielsen, S. E. et al. 2006. A habitat-based framework for grizzly bear conservation in Alberta. – Biol. Conserv. 130: 217–229.

Owen-Smith, N. et al. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. – S. Afr. J. Sci. 102: 389–394.

Pettorelli, N. 2006. Using the satellite-derived NDVI to assess ecological responses to environmental change (Vol. 20, p. 503, 2005). – Trends Ecol. Evol. 21: 11.

Roever, C. L. et al. 2008. Grizzly bears and forestry II: grizzly bear habitat selection and conflicts with road placement. – For. Ecol. Manage. 256: 1262–1269.

Sankaran, M. et al. 2005. Determinants of woody cover in African savannas. – Nature 438: 846–849.

Shannon, G. et al. 2009. The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. – Divers. Distrib. 15: 776–783.

Thomas, D. L. and Taylor, E. 1990. Study designs and tests for comparing resource use and availability. – J. Wildl. Manage. 54: 322–330.

Tracks4Africa 2010. Tracks4Africa Enterprises. – Unit 8 Innovation Center, Western Cape, South Africa.

van Aarde, R. J. and Jackson, T. P. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. – Biol. Conserv. 134: 289–297.

van Aarde, R. J. and Ferreira, S. M. 2009. Elephant populations and CITES trade resolutions. – Environ. Conserv. 36: 8–10.

Wall, J. et al. 2006. Elephants avoid costly mountaineering. – Curr. Biol. 16: 527–529.

Western, D. 2003. Conservation science in Africa and the role of international collaboration. – Conserv. Biol. 17: 11–19.

Wielgus, R. B. and Vernier, P. R. 2003. Grizzly bear selection of managed and unmanaged forests in the Selkirk Mountains. – Can. J. For. Res. 33: 822–829.

Wiens, T. S. et al. 2008. Three way k-fold cross-validation of resource selection functions. – Ecol. Model. 212: 244–255.

Young, K. D. et al. 2009. Elephant spatial use in wet and dry savannas of southern Africa. – J. Zool. 278: 189–205.

Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol. 1: 3–14.