

Predator-specific landscapes of fear and resource distribution: effects on spatial range use

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Abstract. Although ecologists have long recognized that animal space use is primarily determined by the presence of predators and the distribution of resources, the effects of these two environmental conditions have never been quantified simultaneously in a single spatial model. Here, in a novel approach, predator-specific landscapes of fear are constructed on the basis of behavioral responses of a prey species (vervet monkey; *Cercopithecus aethiops*), and we show how these can be combined with data on resource distribution to account for the observed variation in intensity of space use. Results from a mixed regressionspatial regressions analysis demonstrate that ranging behavior can indeed be largely interpreted as an adaptive response to perceived risk of predation by some (but not all) predators and the spatial availability of resources. The theoretical framework behind the model is furthermore such that it can easily be extended to incorporate the effects of additional factors potentially shaping animal range use and thus may be of great value to the study of animal spatial ecology.

Key words: *Cercopithecus aethiops*; geographic information system (GIS); habitat selection; kernel density estimation; multi-predator environment; perceived predation risk; resource distribution; spatial autocorrelation; spatial regression; utilization distribution.

INTRODUCTION

Central to the study of animal ecology is an understanding of how animals utilize their environment over space and time. Such knowledge is not only fundamental to the study of the distribution and social organization of a species but also, and ever increasingly more so, in directing conservation and wildlife management efforts. In investigating nonmigratory patterns of space use, two closely associated concepts are generally thought to be of particular relevance: the home range and the utilization distribution (Johnson 1980, Anderson 1982, Worton 1989). For mammals, the home range has traditionally been described as “that area traversed by the animal [social unit, group] in its normal activities of food gathering, mating and caring for young” (Burt 1943:351). As an analytically more explicit concept though, the home range can be defined by a utilization distribution based on locational observations of the animals (Hayne 1949, Jennrich and Turner 1969). Probabilistic interpretations of this (van Winkle 1975) have allowed a quantitative expression of the intensity of space use within an area of interest and are increasingly being recognized as instrumental to a detailed interpre-

tation of patterns in animal ranging behavior (e.g., Marzluff et al. 2004, Horne et al. 2007).

The way in which animals exploit their spatial environment is thought to be driven primarily by the distribution of resources and the presence of predators (Schoener 1971, Mangel and Clark 1986). These factors exert their influence in fundamentally different ways though: whereas the influence of resource distribution is mainly a direct effect of local availability, the impact of predators is predominantly indirect (i.e., trait-mediated; e.g., Preisser et al. 2005). This implies that, while the distribution and density of resources are informative predictors of a species’ spatial ecology, predator distribution and density per se are not. Instead, behaviorally complex animals adjust their use of space to their perception of the distribution of predation risk (Lima and Dill 1990, Brown and Kotler 2004, Cresswell 2008).

Perceived predation risk has often been expressed in terms of vigilance or giving-up densities to create “landscapes of fear” (Brown et al. 1999, Laundré et al. 2001). However, although these landscapes elegantly express the trade-offs animals make between nutrient acquisition and, amongst others, the costs of predation (Brown 1988), they do not measure perceived predation risk *sensu stricto* (Searle et al. 2008). Moreover, in a multipredator environment (Lima 1992), they do not convey information of the impact of different predators on the phenotypic traits (such as ranging behavior) of prey animals. Nevertheless, the concept of a landscape of fear is both powerful and appealing to studies of

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animal space use, provided it can be modified to exclusively reflect perceived predation risk. Unfortunately, in most mammalian taxa behavioral traits revealing an animal's perception of the distribution of predator guild-specific predation risk are difficult to assess. Primates, however, may constitute a notable exception.

Most primates live in multipredator environments and have consequently evolved distinct behavioral responses to the various predators they encounter (Cheney and Wrangham 1987). What is more, the predator guild-specific alarm responses of some species are easily recognized by human observers, and in this respect vervet monkeys (*Cercopithecus aethiops*) have received considerable attention (e.g., Cheney and Seyfarth 1981). In addition, vervet monkeys are readily habituated to observer presence and hence allow collection of highly detailed information on range use and resource distribution in conjunction with data on perceived predation risk. By recording the location and type of alarm responses and subjecting these to the same techniques routinely used to estimate utilization distributions, probabilistic and predator guild-specific landscapes of fear can be constructed. Given the ease with which vervet monkeys alarm responses can be recognized, they are a particularly suitable species to assess the impact of fear on animal space use.

This study develops a spatial model of the ranging behavior of a group of free-ranging vervet monkeys. The model simultaneously incorporates trait-mediated effects of the presence of multiple predators as well as the direct effects of resource distribution. In doing so it is the first empirical model to combine the influence of both predation and resource distribution into a single quantitative model of animal range use in a spatially explicit way.

METHODS

Study species and field site

The vervet monkey species complex (*Cercopithecus aethiops* subspecies) is both common and abundant throughout most of sub-Saharan Africa (Willems 2007). Vervet monkeys live in multi-male multi-female groups that typically average just below 20 individuals and maintain an opportunistic, yet principally frugivorous diet. Their relatively small body size (males, 4–8 kg; females, 3–5 kg) in combination with a diurnal and semi-terrestrial, semi-arboreal lifestyle make vervet monkeys susceptible to predation by a wide range of mammalian, avian, and reptilian predators (Enstam and Isbell 2007). Predator classification by semantic vocalizations occurs (Seyfarth et al. 1980), and these alarm calls elicit adaptive behavioral responses that are easily recognized by a human observer.

Fieldwork was conducted at the Lajuma Research Centre in the western part of the Soutpansberg mountain range, South Africa (23°02' S, 29°26' E). The study site (described in Willems 2007) is set in a mountainous

environment with on-site elevation ranging from 1150 to 1750 m. The local vegetation is characterized by a complex mosaic of habitat types belonging to the unique Soutpansberg mist-belt forest group and comprises structural and floral elements of the forest, thicket, savannah, and grassland biomes (von Maltitz 2003). Though most large animals have historically been purged from the area, a healthy predator community prevails. Most notable with regard to vervet monkeys are: Crowned Eagle (*Stephanoaetus coronatus*), Verreaux's Eagle (*Aquila verreauxii*), chacma baboon (*Papio cynocephalus ursinus*), and leopard (*Panthera pardus*). Potentially dangerous and locally common species of snake include black mamba (*Dendroaspis polylepis*), boomslang (*Dispholidus typus*), Mozambican spitting cobra (*Naja mossambica*), puff adder (*Bitis arietans*), and African rock python (*Python sebae*). Although these snakes, with the exception of adult rock python, do not actively prey on vervet monkeys, they do pose a potential cause of mortality and could thus reasonably be expected to affect range use by the study group.

Collection of field data

A single group of free-ranging vervet monkeys was selected for extensive behavioral monitoring. All animals in the group (mean, $n = 17.8$; range, $n = 13$ – 24) were individually recognized and allowed the observer (E. P. Willems) to approach within 5 m without showing any notable behavioral response. Data were collected on a handheld computer (Palmtop Zire 21; Palm Europe, Berkshire, UK) with behavioral data collection software (Pendragon Forms 4.0; Pendragon Software, Libertyville, Illinois, USA) and a global positioning system (GPS) device (Garmin GPS 72; Garmin, Olathe, Kansas, USA), with supplementary data recorded in paper notebooks. The data presented here were obtained over the 12-month period from May 2005 to April 2006.

Range use.—The group was followed on foot for seven successful days each month, yielding a total of 84 follow days over the observation period. Successful follow days were defined as days on which the animals could be followed traveling from sleeping tree to sleeping tree without losing audiovisual contact over a continuous period exceeding 60 min. Geographic coordinates were collected on the center of mass of the group (Altmann and Altmann 1970) at 30-min intervals throughout the day. Accuracy of these measurements averaged 6.9 ± 2.3 m ($n = 2040$).

Perceived predation risk.—The time, nature, and cause of alarm responses were scored on an all-occurrence basis (Martin and Bateson 1993). In order not to lose contact with the animals during these events and to allow audiovisual confirmation of predator type, geographic coordinates were not measured directly by GPS. Instead, the locations were estimated a posteriori from detailed field notes and by calculation. This involved the assumption of a straight trajectory at a constant speed of progression between the two 30-min interval GPS

fixes immediately preceding and following an event. A total of 385 alarm responses was recorded and could be categorized into the following predator guild classes: eagle, $n = 215$; baboon, $n = 57$; leopard, $n = 15$; snake, $n = 12$; and unknown, $n = 86$. It is important to note that alarm responses assigned to a certain predator guild will not always have equated to the actual presence of a predator. These "false" alarms nevertheless express the monkeys' perception of predator-specific risk and are therefore equally informative as "correct" alarm responses. Although sample sizes were quite small for some predator guilds, as little as 10 locational observations have been found to permit reliable inference using the statistical procedures employed in this study (Börger et al. 2006). Alarm responses classified as unknown were discarded from further analysis.

Habitat type and resource distribution.—Information on the spatial distribution of habitat types and key resources such as sleeping trees and surface water was obtained using a variety of techniques. Firstly, a detailed land cover map of the study area was constructed on the basis of extensive field surveys, analyses of a time series of historic aerial photographs (stemming from surveys conducted by the South African government in 1957, 1965, 1972, 1983, 1993, 1997, and 2003), and semi-random vegetational quadrat sampling (Brower et al. 1997). The 10 habitat types thus identified within the home range were demarcated on an ortho-rectified Quickbird satellite image that served as a base map (local effective ground resolution, 0.56 m; *available online*).² Secondly, the course of year-round water sources and the locations of known sleeping trees were captured by GPS. Lastly, habitat-specific estimates of food availability were developed from a detailed dietary analysis using focal animal sampling (Martin and Bateson 1993), monthly phenological transects recording availability and abundance of food items from the main food species (accounting for >40% of total feeding time), and habitat-specific density estimates of these food species as obtained from semi-random quadrat sampling (for a more detailed description of the methodology, see Willems 2007).

All information was imported into a geographic information system (GIS; ArcGIS Desktop 9.0 [ESRI 2004]) using DNR Garmin 4.4 software (Whately et al. 2004). Data were projected into the Universal Transverse Mercator coordinate system (datum, WGS 1984; zone, 35 S) and cell size of output rasters (calculated below) was set to 5 m to approximate GPS accuracy as achieved in the field.

Parameter calculation

Range use.—The intensity of space use was quantified by a utilization distribution calculated through kernel density estimation. This statistical procedure is one of the

more robust and most widely applied techniques for range use analyses in current animal ecology and relies on nonparametric algorithms to calculate a probability density surface from a set of Cartesian points (for an extensive mathematical treatise, see Silverman 1986). In terms of range use by the study group this translates into the estimation of the probability of occurrence within the study area, based on GPS measurements taken on the center of mass of the group. To assure that the utilization distribution was proportional to the amount of time the animals spent at each location, only GPS coordinates collected at a constant time interval ($n = 2040$) were included in the analysis (Seaman and Powell 1996). A fixed Gaussian kernel relying on least-squares cross-validation (LSCV) to parameterize its bandwidth (Gitzen et al. 2006) was chosen in the Home Range Tools extension for ArcGIS (Rodgers et al. 2007). Within this probabilistic framework, home range size was subsequently calculated at 114 ha by a 99% volume isopleth (Anderson 1982). The resulting home range area and underlying utilization distribution are depicted in Fig. 1.

Perceived predation risk.—Fixed kernel density estimation using LSCV bandwidth parameterization was also employed to create predator guild-specific density distributions of alarm responses. The outcomes of this were divided by the utilization distribution to generate a measure of the probability of an alarm response occurring at each location within the home range per amount of time the monkeys spent there. These probabilistic and predator guild-specific landscapes of fear are presented in Fig. 2.

Habitat type and resource distribution.—The 10 habitat types within the animals' home range were ranked in order of increasing food availability per surface area (number of food items per hectare). Although structural aspects of a habitat (e.g., visibility) are also of importance, these are already indirectly incorporated in the landscapes of fear and, here then, habitat type is exclusively equated with food availability. Since food availability in four habitats was estimated to be zero (or close to zero), these were lumped together, resulting in the following habitat ranking scheme: 0, cliffs, marsh-, shrub-, and woodland; 1, tall forest; 2, grassland; 3, bushland; 4, short to low forest; 5, riverine forest; 6, thicket. Access to sleeping sites and surface water was expressed as the distribution of shortest Euclidean distances to the nearest known sleeping tree and year-round water source. Graphical representations of habitat type and resource distribution are given in Fig. 2.

Statistical analysis

Any investigation of animal space use must analytically address the inherently spatial character of ranging data. A lot of debate currently exists on how best to deal with spatial autocorrelation within ecological data because, apart from containing valuable biological information, spatial autocorrelation also greatly com-

² (<http://www.digitalglobe.com>)

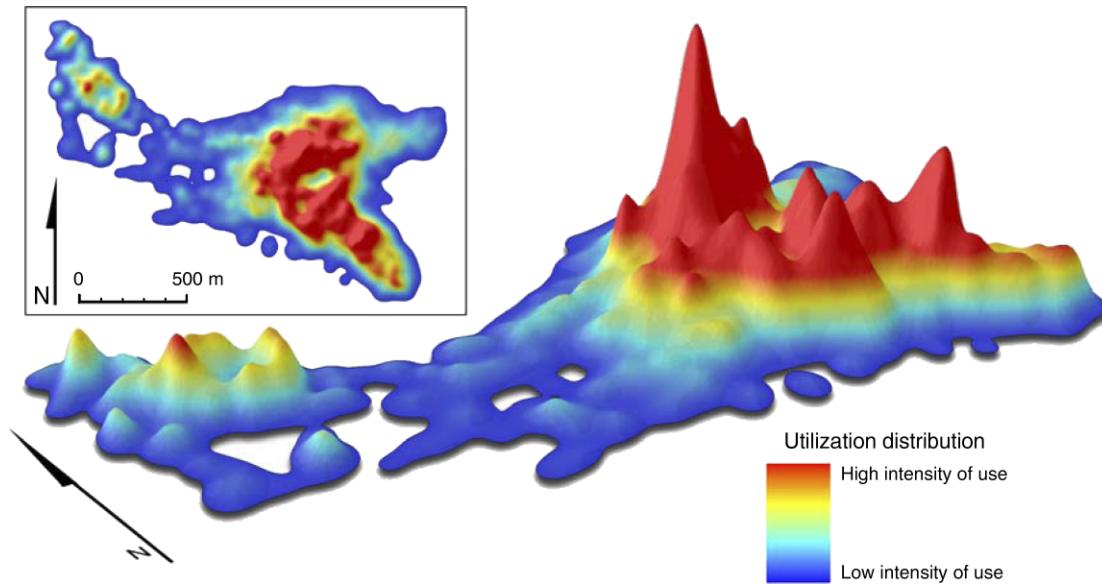


FIG. 1. Home range area of the study group (114 ha) as obtained through kernel density estimation. Peaks and color coding of the utilization distribution are proportional to the intensity of space use. Fieldwork was conducted on vervet monkeys (*Cercopithecus aethiops*) at the Lajuma Research Centre in the western part of the Soutpansberg mountain range, South Africa.

plicates analysis (Legendre 1993). If uncontrolled for, it may lead to pseudoreplication (Hurlbert 1984), overestimation of effective sample size, inflated significance values (Clifford et al. 1989), and even a systematic bias toward certain explanatory variables (Lennon 2000, but see Diniz-Filho et al. 2003, Hawkins et al. 2007). Because of this, spatial autocorrelation has often been removed from data prior to analysis. Unfortunately, this not only incurs a great loss of information but also compromises the accuracy and biological validity of ensuing findings since statistically independent data cannot adequately capture the biological essence of animal range use (De Solla et al. 1999). Moreover, autocorrelation within ranging behavior can be highly informative (e.g., Cushman et al. 2005).

A random set of 1000 points within the animals' home range was selected for analysis, and parameter values at these locations were extracted. The spatial pattern within this set of sample points was assessed by visual inspection of correlograms and global Moran's I values (Fig. 3). To account for the level of autocorrelation thus exposed in all variables, statistical significance of exploratory Spearman's correlation analyses was calculated from adjusted (i.e., geographically effective) degrees of freedom following Dutilleul (1993). A spatial regression analysis was subsequently employed to determine the extent to which the observed variation in intensity of space use could be ascribed to each of the predictor variables acting simultaneously. To meet parametric assumptions, the utilization distribution was log-transformed prior to this analysis and habitat type was recoded into six dummy variables in order of increasing food abundance. Lastly, the most appropriate

framework for the regression analysis was determined, and, given the presence of significant spatial autocorrelation in both the response and predictor variables, a mixed regressive-spatial regressive (or lagged predictor) model was deemed most suitable (Florax and Folmer 1992). In matrix notation the general specification of this model is given by

$$\mathbf{y} = \rho\mathbf{W}\mathbf{y} + \boldsymbol{\beta}\mathbf{X} + \boldsymbol{\gamma}\mathbf{W}\mathbf{X} + \boldsymbol{\varepsilon}$$

where \mathbf{y} is the $n \times 1$ vector of observations on the response variable, ρ is the spatial autoregressive parameter, \mathbf{W} is an $n \times n$ weights matrix that formalizes the spatial relationships between sample points, $\boldsymbol{\beta}$ is the $k \times 1$ vector of regression parameters associated to \mathbf{X} , \mathbf{X} is the $n \times k$ matrix of observations on the predictor variables, $\boldsymbol{\gamma}$ is the $k \times 1$ vector of spatial cross-regressive parameters associated to \mathbf{X} , and $\boldsymbol{\varepsilon}$ is the $n \times 1$ vector of independent and normally distributed error terms.

Conceptually, this model can be understood as a standard regression model (the regressive term; $\boldsymbol{\beta}\mathbf{X}$) complemented by two spatial sets of predictor variables. The first set (the autoregressive term, $\rho\mathbf{W}\mathbf{y}$) is calculated from the average value of the response variable at neighboring sample points, whereas the second (the cross-regressive term, $\boldsymbol{\gamma}\mathbf{W}\mathbf{X}$) incorporates average values of all predictor variables at these points. The degree to which neighboring sample points exert their influence is determined by the row-standardized weights matrix \mathbf{W} (Anselin 2002). In the model developed here, this matrix was set to contain nonzero neighbor weight elements (w_{ij}) to specify the relationships among all sample points as a distance decay function. On the basis of corrected Akaike Information Criteria (AIC_c) selection criteria

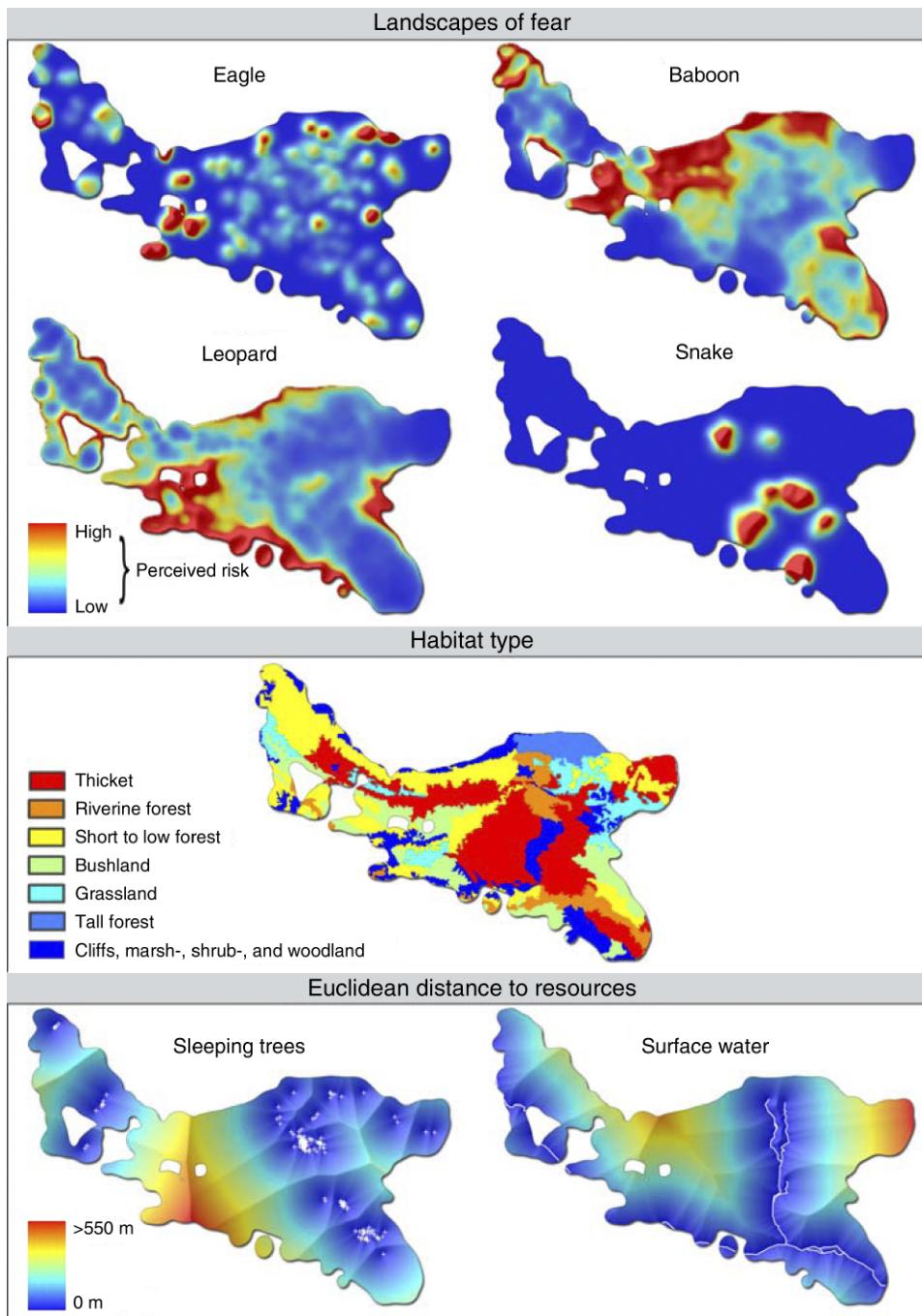


FIG. 2. Graphical representations of the environmental variables considered in all spatial analyses to account for the observed variation in the intensity of space use by the study group.

(Burham and Anderson 2002), the effect of neighbor j on location i was modeled to equal the inverse quadratic geographic distance d between locations i and j ($w_{ij} = 1/d_{ij}^2$).

Analyses were conducted using the Spatial Analysis in Macroecology package (SAM 2.0: Rangel et al. 2006), while global Moran's I values were calculated by the Rook's Case add-in for Excel (Sawada 1999).

RESULTS

Exploratory analyses of spatial association.—Results from the spatial correlation analyses on the relationship between the utilization distribution and perceived predation risk, habitat type, and resource distribution are presented in Table 1. The intensity of space use was negatively associated with the landscapes of fear for

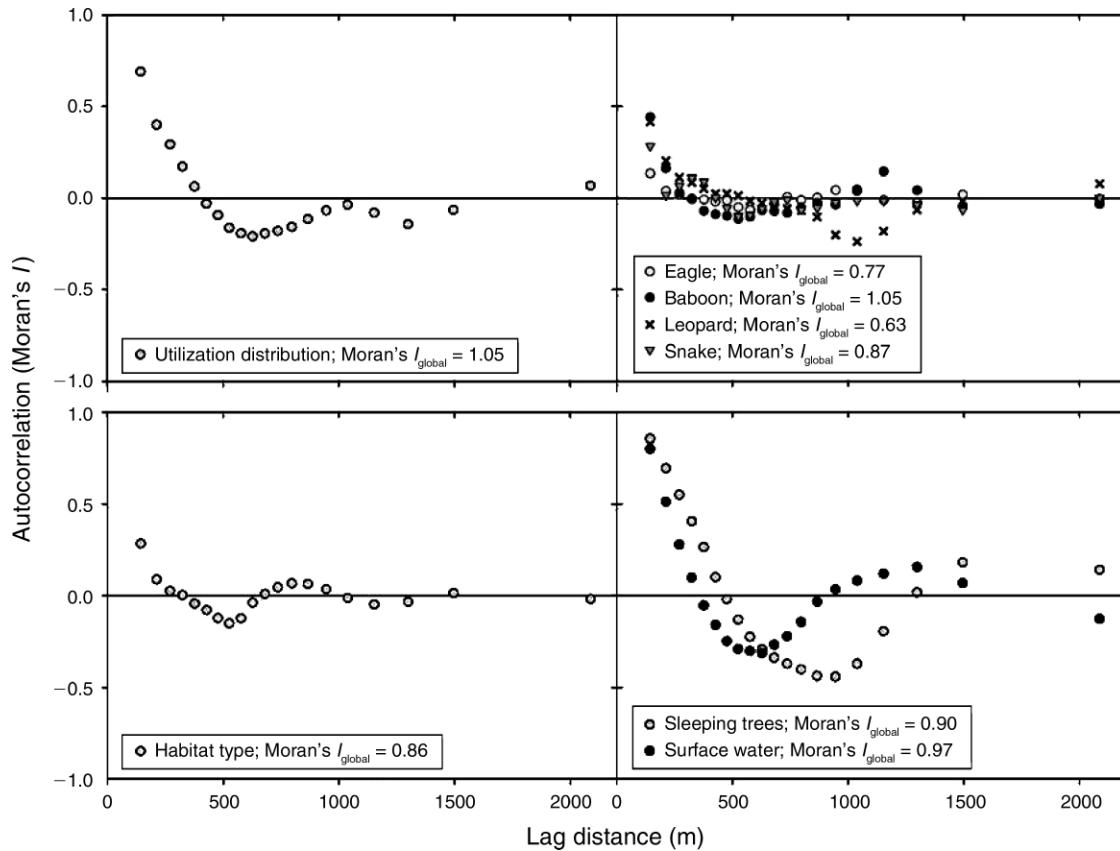


FIG. 3. Correlograms and global Moran's *I* values indicating the level of spatial autocorrelation within all variables. Moran's *I* has an expected value of close to zero in the absence of autocorrelation, whereas values around ± 1 signify very strong positive/negative spatial autocorrelation. Global values were calculated by taking the mean nearest-neighbor distance between sample points (17.08 m) as lag distance. Monte Carlo permutation tests revealed global autocorrelation levels in all variables to be significantly positive ($P < 0.005$; permutations, $n = 200$).

baboon and leopard as well as with the distance to sleeping trees and surface water. A positive association with habitat type, ranked according to increasing food abundance, was also established. No significant correlation was apparent between range use and the landscapes of fear for eagle and snake.

Spatial regression model.—A mixed regressive-spatial regressive model was developed to assess the extent to which the observed variation in intensity of space use could be ascribed to the simultaneous effects of all investigated variables. The full model revealed that the landscapes of fear for eagle and snake were nonsignificant predictors, and their exclusion yielded a better model as assessed by the AIC_c ($\Delta AIC_c = 7.87$; Appendix A). Parameter estimates and results from this AIC_c -selected model are presented in Table 2, and the spatial structure and distribution of error terms are given in Fig. 4. The intensity of space use was negatively related to the landscapes of fear for baboon and leopard and the distance to sleeping trees and surface water. Habitat selection also appeared to be of relevance as the two dummy-coded habitat types with the highest food availability per surface area (riverine forest and thicket)

were used significantly more often than those with the lowest food abundance (cliffs, marsh-, shrub-, and woodland). Overall, the model accounted for $>60\%$ of the variation in the utilization distribution of the study

TABLE 1. Spearman's correlation analyses ($n = 1000$) based on geographically effective degrees of freedom (Dutilleul 1993) between the intensity of space use (utilization distribution) and predator guild-specific perceived predation risk, habitat type (ranked in ascending order of food abundance), and resource distribution.

Variable	Spearman <i>r</i>	Effective df	<i>P</i>
Perceived predation risk			
Eagle	0.291	292.27	0.282
Baboon	-0.122	85.04	0.022
Leopard	-0.612	115.71	<0.001
Snake	0.430	153.44	0.297
Habitat type and resource distribution			
Habitat type	0.374	351.52	<0.001
Sleeping tree	-0.443	49.08	0.003
Surface water	-0.296	60.61	0.005

Note: Fieldwork was conducted on vervet monkeys (*Cercopithecus aethiops*) at the Lajuma Research Centre in the western part of the Soutpansberg mountain range, South Africa.

TABLE 2. Parameter estimates and key statistics of the mixed regressive-spatial regressive model expressing the log-transformed utilization distribution as a function of predator guild-specific perceived predation risk, habitat type, and resource distribution as selected by corrected Akaike Information Criteria (AIC_c).

Environmental predictor	B	β	SE β	γ	SE γ	t ($\beta = 0$)	P
Landscapes of fear							
Baboon	-0.257	-0.277	0.019	0.773	0.035	-13.333	<0.001
Leopard	-0.448	-0.555	0.017	0.771	0.062	-26.141	<0.001
Habitat type (dummy coded)							
Tall forest	-0.016	-0.019	0.018	0.772	0.052	-0.883	0.377
Grassland	0.001	0.018	0.013	0.653	0.288	0.718	0.473
Bushland	-0.004	-0.006	0.015	0.718	0.193	-0.249	0.803
Short to low forest	0.029	0.049	0.015	0.697	0.222	1.863	0.063
Riverine forest	0.035	0.056	0.014	0.733	0.171	2.481	0.013
Thicket	0.088	0.129	0.018	0.760	0.123	4.838	<0.001
Euclidean distance to resources							
Sleeping trees	-0.339	-0.230	0.030	0.773	0.006	-11.271	<0.001
Surface water	-0.157	-0.107	0.029	0.773	0.006	-5.323	<0.001

Notes: Model particulars: $n = 1000$; $\rho \pm SE = 0.773 \pm 0.026$; $R^2 = 0.615$; $P < 0.001$; $AIC_c = -4123.62$. Terms are: B , unstandardized regression parameter; β , standardized regression parameter; γ , spatial cross-regressive parameter; ρ , spatial autoregressive parameter.

group. Note that results from the spatial regression model are in line with those from the independent correlation analyses based on geographically effective degrees of freedom. This is taken to underscore the robustness of current findings.

DISCUSSION

While it is widely recognized that animal space use is strongly driven by the presence of predators and the distribution of resources, no previous empirical study has quantified the combined effects of these two key environmental conditions. Here we developed a spatially

explicit model of the ranging behavior of a prey species foraging in a multipredator environment. The model is the first of its kind to simultaneously incorporate trait-mediated effects of predation and the direct effects of resource distribution. It is also unique in that it concurrently considers the independent influence of different predator guilds through the implementation of predator-specific landscapes of fear. The results indicate that fear of some (but not all) predators and local resource availability account for >60% of the total variation in the intensity of space use. Findings are briefly reiterated and interpreted below.

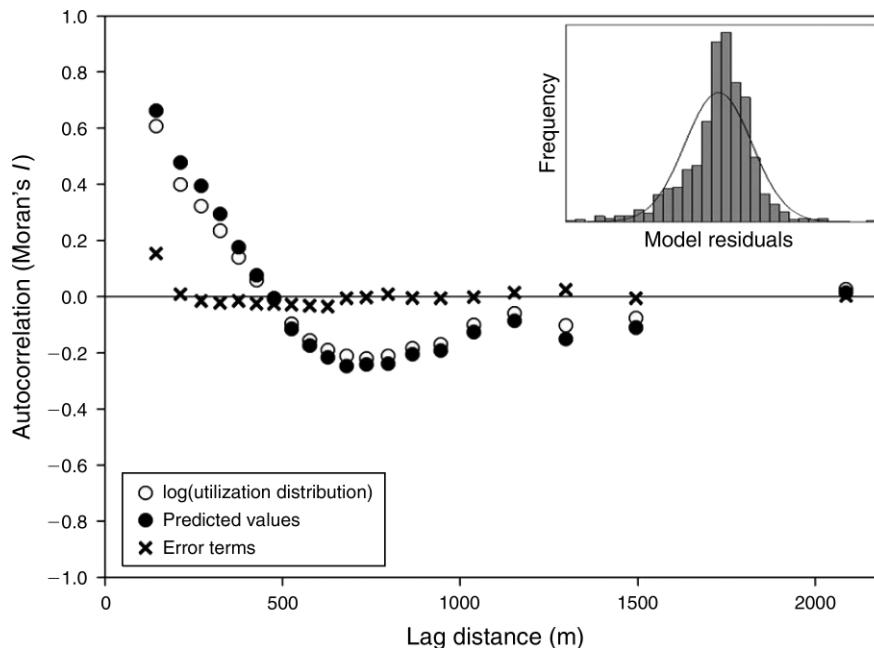


FIG. 4. Moran's I correlogram and histogram of the residuals from the mixed regressive-spatial regressive model selected by corrected Akaike Information Criteria (AIC_c). The figure illustrates that error terms were independent and normally distributed, thereby validating the model.

Perceived predation risk

Probabilistic landscapes of fear for baboon and leopard were negatively associated with the utilization distribution of the study group. This suggests that these two (locally confirmed) predators each posed a threat that caused the monkeys to avoid areas where the respective risk of predation was perceived to be high. In contrast, the spatial distribution and local density of alarm responses to eagles and snakes did not affect range use significantly. The latter finding may reflect the notion that most on-site species of snake were not true predators of vervet monkeys, but the absence of a negative association between space use and the landscape of fear for eagle (a locally confirmed predator) was unexpected. A brief explanation seems in order.

Aerial predators typically monitor areas much larger than the ranges of their primate prey (Shultz and Noë 2002), and their ease of travel, acute eyesight, and unpredictable use of space over time (Roth and Lima 2007) result in an even distribution of risk within the horizontal plane over a prey's home range. Circumstantial statistical evidence for this comes from the relatively high number of geographically effective degrees of freedom (Table 1) and the approximately even spatial structure of the landscape of fear for eagle (Fig. 3). Together, this indicates a comparatively low and constant level of spatial autocorrelation within the distribution of perceived risk, which translates into a relatively flat landscape of fear for eagle (with some scattered and isolated peaks; Fig. 2). This implies that adjustment of vertical substrate use, rather than horizontal range use, is a more effective antipredation strategy against this predator guild. Further eroding the landscape of fear for eagle may have been the monkeys' vigilance, which is highly effective in detecting eagles at distances where no imminent risk of attack yet exists. Vigilance thereby makes timely adjustment of height in the vertical substrate possible and thus reduces the need to alter horizontal range use in response to the high risk of predation by eagles.

Habitat selection and resource distribution

Concurrent to adjustments caused by fear of baboon and leopard, range use was also affected by habitat selection and resource distribution. The study group spent more time in the two habitat types in which food was most abundant and in addition stayed close to sleeping trees and surface water. Although previous studies also related habitat characteristics and resource distribution to probabilistic measures of range use (e.g., Marzluff et al. 2004), these did not simultaneously consider risk effects of predators, thereby potentially neglecting a key factor in the ecology of the study animals (Creel et al. 2005, Fortin et al. 2005, Creel and Christianson 2008). What is more, regression parameters and *t* values of the current model (Table 2) even suggest that the effects of fear may exceed those of resource distribution. The integrated approach adopted here may

thus be critical to a more in-depth understanding of the relative strengths of the different factors shaping animal space use.

Synopsis and future directions

While the significance of predators and resources in determining range use have been widely acknowledged, analytical complications inherent to spatial data have impeded the assessment of the relative importance of these two factors. Consequently, and possibly exacerbated by the difficulties associated with measuring trait-mediated effects of predation, most spatially explicit range use studies to date have focused almost exclusively on the importance of resource distribution. Here we demonstrated how perceived risk of predation by certain predator guilds, habitat selection (based on food abundance), and resource distribution were all significant determinants of vervet monkey range use. Of particular importance was the finding that the effects of fear can exceed those of local resource availability. In this respect, the adoption of the concept of landscapes of fear proved highly informative and an important next step will be to compare these landscapes to the actual utilization distributions of predators and structural characteristics of a habitat, such as visibility and distance to refuges.

From an analytical perspective it is interesting to note that the mixed regressive-spatial regressive approach taken here outperformed other, more commonly applied spatial regression techniques (e.g., simultaneous [SAR], conditional [CAR], and moving average [MA] autoregressive models; Appendix B). The mixed regressive-spatial regressive model may thus offer substantial potential for future studies, and one obvious suggestion would be to incorporate additional variables into the regression framework. The effect of intraspecific competition, for example, could easily be investigated by including utilization distributions of neighboring groups as predictor variables into the model. This study will hopefully spur research into some of the spatial variables and techniques introduced here as they provide exciting new frameworks for future studies of animal ecology.

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APPENDIX A

Output of the full mixed regressive-spatial regressive model of space use by the study group (*Ecological Archives* E090-037-A1).

APPENDIX B

Residual correlograms of four methods of spatial regression (*Ecological Archives* E090-037-A2).