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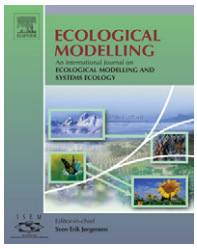

A synoptic model of animal space use: Simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships

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ABSTRACT

We propose a simple multivariate model for describing and understanding animal space use that estimates an animal's probability of occurrence as an explicit function of the animal's association with a fixed spatial area (i.e., home range), the spatial distribution of resources within that area, and the occurrence of other animals. We begin with a null model of space use to describe an animal's utilization distribution in the absence of effects from environmental covariates. We then use this null model as the foundation for a set of candidate models of space use that incorporate different combinations of environmental covariates where each model is chosen to reflect various hypotheses about important drivers of space use. Models are parameterized via maximum likelihood using location data collected from individuals at discrete times (e.g., telemetry) and spatially explicit environmental covariates. Information theoretic criteria are used to select the model(s) with most support from the data. The best model(s) is then used for both estimating the animal's home range and for inferring the relative importance of various environmental factors on space use. As an example, we applied our approach using male white rhino (*Ceratotherium simum*) location data collected in Matobo National Park, Zimbabwe. The best synoptic model was able to capture the complexities of the utilization distribution while the model structure and parameter estimates provided a basis to infer the importance of various ecological factors affecting male rhino space use.

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1. Introduction

Understanding animal space use is a critical component of many ecological investigations. Because animal space use is the result of physiological and behavioral adaptations to particular environmental characteristics, ecologists have long sought to describe where animals live and, more importantly, to understand the important factors affecting space use. Among the most prominent and widespread of these factors are: (1) the tendency for animals to remain in a particular area or home range due to site fidelity (Smith, 1976; Shields, 1983; White and Garrott, 1990; Wauters et al., 2001; Selonen and Hanski, 2003) or territorial behavior (Burt, 1943; Ostfeld, 1990; Newton, 1992; Adams, 2001); (2) the distribution of required or selected resources (Bergerud, 1974); and (3) the location of other animals (e.g., mates, competitors, predators and prey; Wauters et al., 2000).

One of the most common factors affecting animal space use is the tendency for most animals to confine their activities to a particular area or home range (Burt, 1943). This tendency

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might be the result of territorial behavior (Krebs and Davies, 1991; Adams, 2001), the need to continually provision a den or nest site, or behavior designed to increase knowledge of the location of important resources (Powell, 2000) or escape routes (Stamps, 1995). Within a home range, many animals selectively use certain habitats more than others. Because of an ultimate association with food and escape cover, habitat selection is typically assessed for environmental characteristics such as plant species composition, vegetation structure, and topography (Morrison et al., 1998). Beyond site fidelity and habitat selection, the presence or absence of other animals also may affect space use. Pressures of avoidance and attraction are usually related to mating opportunities (Emlen, 1973), predator–prey relationships (Mech, 1977; Murray et al., 1994) or competition (Pimm and Rosenzweig, 1981; Maurer, 1984; Morris, 1987).

Two general approaches have been taken for studying animal space use. One is a mechanistic approach that seeks to model animal space use using fundamental models of animal movement processes (Moorcroft and Lewis, 2006). Under this approach, general diffusion-advection models are built based on hypothesized behaviors (e.g., attraction to a home range center and aversion to foreign scent marks) governing an animal's movements. This is a powerful approach because hypothesized determinants of space use can be directly incorporated into the models and predictions from the models can be compared against observed location data to identify support for different hypotheses. Additionally, these models can be used to predict changes in space use resulting from changes in behavior or the spatial distribution of important factors. However, despite the power of this approach it is not widely used by ecologists likely due to computational expense and lack of generality (Kernohan et al., 2001).

The second approach is to estimate relevant parameters from a general, statistical model fit to observed location data. For example, animal home ranges are often estimated by fitting one or more statistical models (e.g., bivariate normal, kernel density) to location data obtained on a particular individual. While this approach often results in quite realistic representations of space use, it lacks an explicit connection to the behavioral and ecological process affecting animal space use, thus researchers must rely on post hoc analyses to infer anything about generating mechanisms of the observed space use. Similarly, analyses of resource selection within an animal's home range often begins by estimating the home range with one of the aforementioned statistical models and then comparing observed use of resources to their availability within the home range boundary (e.g., Borger et al., 2006; Thomas and Taylor, 2006).

Although the statistical modeling approach has traditionally analyzed each process (e.g., home range, resource selection, relationships among individuals) separately, recent work relating animal movements and resource selection has stressed the benefits of modeling these processes simultaneously. For example, Matthiopoulos (2003b) described an approach for modeling habitat preference as a function of accessibility and preference based on possible movement paths. Similarly, Rhodes et al. (2005) suggested that models used to infer habitat selection should take into account the probability of selecting a habitat dependent on its spatial context within the home range. Therefore, to study habitat selection, Rhodes et al. (2005) developed a model of the probability of moving from one location to the next as a function of the animal's current location, the distance to the home range center, and habitat selection. With a similar goal in mind, we describe a synoptic model for describing and understanding space use of individual animals that simultaneously models space use as a function of multiple, interacting behavioral and environmental factors. Our model differs from that of Matthiopoulos (2003b) and Rhodes et al. (2005) in that instead of modeling the movement process, we take a more general approach by modeling the resulting utilization distribution as a function of environmental covariates. The synoptic model is closest to what May (1978) characterized as a phenomenological model intermediate in complexity between general, statistical models and complex, mechanistic models based on detailed behavioral processes.

2. A synoptic model of space use

To model the space use of a particular animal, we begin with the assumption that the individual under investigation has a true distribution of space use in an area over the analysis period. Often called the *utilization distribution*, this distribution is a quantitative measure of the relative time spent in an area over the period of study (Jennrich and Turner, 1969; Van Winkle, 1975; Katajisto and Moilanen, 2006). Specifically, we define $s(x)$ as a function describing the probability density of finding the animal under investigation at location x during the period of study (i.e., utilization distribution). We recognize that the form of $s(x)$ is the result of species-specific behaviors and life history strategies as well as individual responses to the spatial and temporal distribution of environmental factors. Our data consist of a vector of n spatial coordinates (i.e., locations) taken at discrete times that are assumed to be a sample of independent observations from $s(x)$. Associated with each location are the values of k environmental variables that will be used as covariates to model an individual's utilization distribution.

Instead of fitting a single model to the data, we suggest researchers formulate a set of models reflecting different assumptions and/or hypotheses about an individual's space use. If the models are constructed based on ecological hypotheses, then an information theoretic approach can be used to determine the relative support for each model and thus the relative degree of support for the corresponding ecological hypothesis (Burnham and Anderson, 2002; Johnson and Omland, 2004; Horne and Garton, 2006). Thus, the model(s) with the most support from the data can be used not only as an estimate of $s(x)$, but also to infer the importance of various ecological factors affecting space use (Richards, 2005).

To guard against problems of over- and under-fit models, we suggest that researchers include models of varying complexity in the candidate set starting with a simple or "null" model of space use that assumes no other influence except the tendency to remain in an area. While it may be quite unrealistic to expect any animal to utilize space independent of any environmental effects, this model is an important starting point in that additional environmental covariates will only

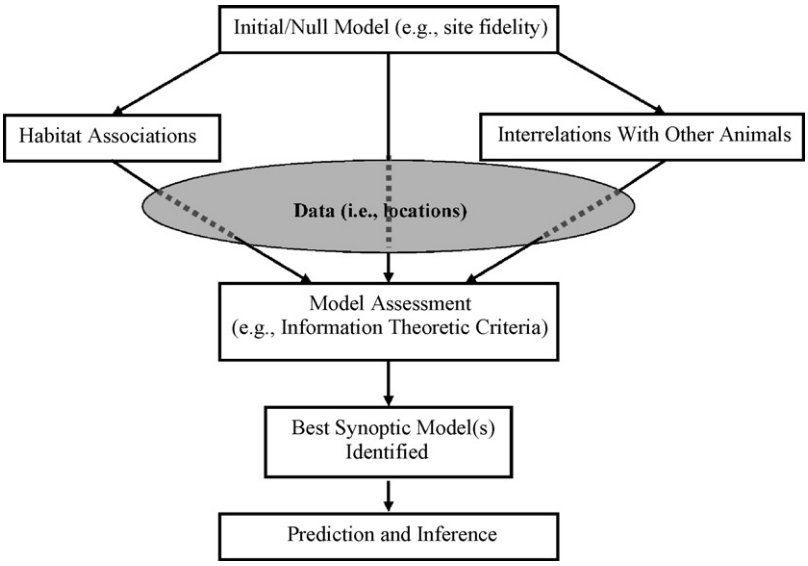

Fig. 1 – Schematic of a synoptic approach to modeling animal space use.

be included if there is sufficient support from the data. This initial model then serves as the basis for additional models of increasing complexity that are constructed by adding various combinations of environmental covariates. Actual variables will be species and hypothesis specific but should be selected based on a priori knowledge of a suspected influence on space use. After selecting the model with appropriate complexity, this model can then be used to estimate the utilization distribution, infer important drivers of space use, and to test ecological hypotheses (Fig. 1).

2.1. *Synoptic model description*

Similar to Manly et al. (1974, 2002:77) our model structure is based on the idea that there is a proportional change in use of an area attributable to each environmental covariate. First, we set $f_0(x)$ as the null model of space use in the absence of any effect from environmental covariates. The null model is chosen to describe the utilization distribution resulting from the behavioral and spatial processes in aggregate that give rise to an animal's home range. For example, $f_0(x)$ could be a bivariate normal distribution characterizing the space use of an animal that biases movements towards a central place (Dunn and Gipson, 1977; Okubo, 1980) or the exponential power model that allows for a more uniform distribution of space use (Horne and Garton, 2006).

Next, we assume a proportional increase or decrease in $f_0(x)$ caused by a spatially explicit environmental covariate where $H(x)$ is a function describing the environmental covariate. In the case of categorical variables, $H(x)$ can be an indicator function with $H(x) = 1$ if x is within the category type and 0 otherwise. For continuous covariates, $H(x)$ can equal the value of the environmental variable at position x, suggesting a linear relationship between the proportional change and the value of the variable or be some function of the environmental variable for non-linear relationships. Thus, a synoptic model describing the utilization distribution that incorporates a proportional increase or decrease in $f_0(x)$ caused by including one covariate is

$$s(x) = \frac{f_0(x) + \beta H(x) f_0(x)}{\int_x [f_0(x) + \beta H(x) f_0(x)]} \quad (1)$$

where β is an estimated selection parameter controlling the magnitude of the effect. To ensure $s(x) \geq 0$ (i.e., non-negative probability) and integrates to one, we set $\beta \geq -1$ and standardize $H(x)$ to range from 0 to 1.

For models with multiple interacting covariates, we assume that any additional covariate results in a proportional change in the utilization distribution. Thus, for $i = 1$ to k covariates the synoptic model of space use is

$$s(x) = \frac{f_0(x) \prod_{i=1}^{k} (1 + \beta_i H_i(x))}{\int_x \left[f_0(x) \prod_{i=1}^{k} (1 + \beta_i H_i(x)) \right]}. \quad (2)$$

The denominator of Eq. (2) is the normalizing factor for a weighted distribution (Patil and Rao, 1978; Lele and Keim, 2006) and for most combinations of initial models and environmental covariates will be analytically intractable. As an approximation, we suggest dividing the landscape into m discrete grid cells and calculating

$$A \sum_{j=1}^{m} \left[f_0(x_j) \prod_{i=1}^{k} (1 + \beta_i H_i(x_j)) \right] \approx \int_x \left[f_0(x) \prod_{i=1}^{k} (1 + \beta_i H_i(x)) \right]$$

where A is the area of each grid cell. Instead of calculating the approximation across the entire landscape, the extent of the grid can be fixed to incorporate nearly all (e.g., >0.99) of the cumulative probability.

The synoptic model $s(x)$ is a probability density function with parameters describing the null model of space use $f_0(x)$, symbolized by θ, and the k-dimensional vector of selection parameters β describing the selection for or against environ-

mental covariates. These parameters can be estimated for a given a set of $q = 1$ to n observed locations x_q by maximizing the log-likelihood function

$$L(\theta, \beta) = \sum_{q=1}^{n} \ln \left[\frac{f_0(x_q|\theta) \prod_{i=1}^{k} (1 + \beta_i H_i(x_q))}{\int_x \left[f_0(x|\theta) \prod_{i=1}^{k} (1 + \beta_i H_i(x)) \right]} \right] \quad (3)$$

For our example application of the synoptic model, we maximized the log-likelihood function numerically using the Simplex algorithm (Press et al., 1986) programmed in Visual Basic. However, we suggest future applications of the synoptic model could make use of an improved technique called "data cloning" for calculating maximum likelihood parameter estimates and their standard errors (Lele et al., 2007).

2.2. *Interpretation of model structure and parameters*

While we do not wish to suggest there is a single model structure that must be used to apply our general approach, the model described by Eq. (2) has several desirable properties. First, the null model of space use $f_0(x)$ represents our hypothesis as to how the animal would use space in the absence of any effects from environmental covariates. Thus, if $f_0(x)$ is based on hypothesized movement processes (e.g., a bivariate normal from centrally biased random walk or a uniform distribution for a territorial animal), then the synoptic model allows researchers the opportunity to link mechanistic-based assumptions of animal movement to a statistical model of space use.

Second, there is a straightforward interpretation of the selection parameters for each environmental covariate in relation to their effect on space use. Because Eq. (2) represents the probability of occurrence for a given set of values of the environmental covariates, we can use odds ratios to determine the importance of a single or combination of environmental covariates on space use where the odds ratio represents the proportional change in the utilization distribution resulting from a change in the value(s) of the environmental covariate(s). This odds ratio for one set of covariate values $H(a)$ versus another $H(b)$ is calculated as

$$\delta(a, b) = \frac{\prod_{i=1}^{k} (1 + \beta_i H_i(a))}{\prod_{i=1}^{k} (1 + \beta_i H_i(b))}. \quad (4)$$

If interest is in a single covariate j, when the values for all other covariates are fixed (i.e., $H_{i,i\neq j}(a) = H_{i,i\neq j}(b)$), Eq. (4) simplifies to

$$\delta_j(a, b) = \frac{1 + \beta_j H_j(a)}{1 + \beta_j H_j(b)}. \quad (5)$$

The odds ratio for covariate j can be interpreted as how much more or less likely we are to find the animal in an area for a given value of $H_j(a)$ versus another value $H_j(b)$. For example, if H_j were a habitat type, $\hat{\delta}_j$ is an estimate of how much more or less likely the animal is to be in that habitat type (i.e., $H_j(a) = 1$) versus out of that habitat type (i.e., $H_j(b) = 0$). When $\delta = -1$ to 0, there is a proportional decrease in the utilization distribution, when $\delta = 0$ there is no change, and when $\delta > 0$ there is a proportional increase. Because negative associations are scaled differently than positive associations, it is important to recognize these differences when interpreting δ. For example, a negative change of $\delta = -0.5$, meaning the animal is half as likely to be found in an area, would be the same magnitude as a positive effect of $\delta = 2$ which means it is twice as likely to use the area. Thus, the estimated selection parameters ($\hat{\beta}$s) provide a way to estimate the proportional change in space use attributable to each covariate in isolation or in combination with other model covariates.

We can also evaluate the effect of each covariate in relation to changes in the null model of space use. Also from Eq. (2), the proportional change in the null model of use at any position x is given by

$$\frac{\prod_{i=1}^{k} (1 + \beta_i H_i(x))}{\int_x \left[f_0(x) \prod_{i=1}^{k} (1 + \beta_i H_i(x)) \right]} \quad (6)$$

When covariates are categorical and non-overlapping the proportional change in the null model caused by covariate j is

$$\frac{(1 + \beta_j)}{\int_x \left[f_0(x) \left(1 + \sum_{i=1}^{k} \beta_i H_i(x) \right) \right]}. \quad (7)$$

We note that under the special case when $f_0(x)$ is uniform, Manly's selection ratio (Manly et al., 2002:77) is a consistent estimator of Eq. (7) (see Appendix A).

In addition to estimates of odds ratios and selection ratios for each individual, researchers may also be interested in the population-level effect of each covariate. As our synoptic model is an estimate of an individual's space use, we refer readers to several recent developments in the application of mixed effects models to gain population-level understanding from individual-based models of space use (e.g., Borger et al., 2006; Gillies et al., 2006; Thomas et al., 2006). Our synoptic model is particularly amenable to the approach developed by Thomas et al. (2006) in which an individual-level model describing the probability of use is incorporated as a "data model" (i.e., Eq. (1), Thomas et al., 2006:406). Thus, to gain population-level estimates of selection, one would substitute our synoptic model for the data model in Thomas et al. (2006).

3. Example: space use of male white rhinos

As an example of how our synoptic model can be tailored to investigate a particular species' space use, we used location data collected on three adult male white rhinos from March 1994 to January 1995 in Matobo National Park, Zimbabwe (Rachlow et al., 1999). Matobo Park in southwestern Zimbabwe is characterized by steep, granite outcrops and

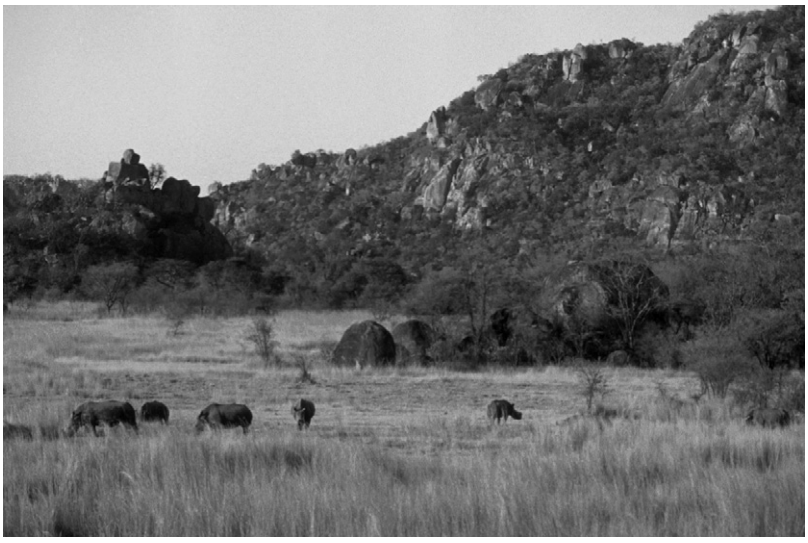

Fig. 2 – White rhinos in Matobo National Park, Zimbabwe.

boulders interspersed among mixed savanna vegetation that varies from open grasslands to dense shrub and woodlands (Fig. 2). Social behavior of adult white rhinos and patterns of space use differ dramatically between sexes. While adult females use non-defended areas that overlap widely among individuals (Rachlow et al., 1999), adult males mark territories with ritualistic defecation and urination behaviors, defending those territories against other adult males (Owen-Smith, 1971). Space use within home ranges appears to be influenced by a preference for short grass swards for foraging and the inability to readily negotiate steep rocky areas.

3.1. *Candidate models, model selection and interpretation*

Following the approach outlined in the previous section, we hypothesized that male space use might be influenced by: (1) territorial behavior; (2) habitat characteristics such as the distribution of steep inaccessible terrain and preferred forage; and (3) locations of female rhinos with the potential to be sexually receptive. We used the exponential power home range model as an initial or null model of space use. This is a convenient null model because a bivariate normal distribution is a particular case (i.e., shape parameter equals one). However, the additional shape parameter allows for platykurtic shapes up to and including a circular uniform distribution (i.e., shape parameter <1; Horne and Garton, 2006). To incorporate the influence of habitat associations related to topography and the distribution of preferred forage, spatially explicit covariates were derived based on percent slope and normalized difference vegetation index (NDVI; Kidwell, 1997). Percent slope (PS) was included as a continuous variable while areas where NDVI ranged from −0.38 to −0.16 were included as a categorical variable describing grassland and open woodland vegetation types (OPEN). Areas with high densities of potentially receptive females (i.e., non-pregnant females without calves or with calves ≥10 months of age) were characterized by calculating a fixed kernel density estimate using female telemetry locations (FD). To keep our analysis simple, we used the combined locations ($n = 203$) of seven females to calculate the density estimate recognizing a more exhaustive analysis might seek to estimate space use for each individual separately. In addition to these ecological influences, rhino space use was confined to areas within the Park boundary by a high-tension game-proof fence. Therefore, we had an additional categorical variable (PB) that defined areas outside the Park boundary.

For the rhino synoptic model, we used Eq. (2) with $k = 4$ environmental covariates. The initial exponential power model was defined as

$$f_0(x) = \frac{2}{c2\pi a^2 \Gamma(c)} \exp\left[-\left(\frac{\|x-\mu\|}{a}\right)^{2/c}\right] \quad (8)$$

where Γ is the gamma function, μ is the center of the distribution, $a > 0$ is the scale parameter, $c > 0$ is the shape parameter, and $||x-\mu||$ denotes the distance between x and μ (Horne and Garton, 2006). Additional potential covariates for the synoptic models were $H_1(x) = \text{PB}$ which took a value of 1 if outside the Park boundary and 0 otherwise; $H_2(x) = \text{PS}$ with values of PS standardized to range from 0 to 1; $H_3(x) = \text{OPEN}$ which took a value of 1 if inside the open cover type and 0 otherwise; and $H_4(x) = \text{FD}$, a continuous variable standardized to range from 0 to 1 (Fig. 3).

Five a priori competing models were constructed to describe space use by male rhinos. Four of these models included various combinations of the environmental covariates chosen to reflect hypotheses of space use including: (1) space use is constrained by the park boundary but is unaffected by percent slope, presence of the open covertype, or the density of available mates (ExpPower + PB); (2) space use is affected only by the park boundary and habitat selection (ExpPower + PB + PS + OPEN); (3) space use is affected only by the park boundary and the location of sexually receptive female rhinos (ExpPower + PB + FD); (4) space use is affected by the park boundary and the combined influence of habitat and female density (ExpPower + PB + PS + OPEN + FD). The last

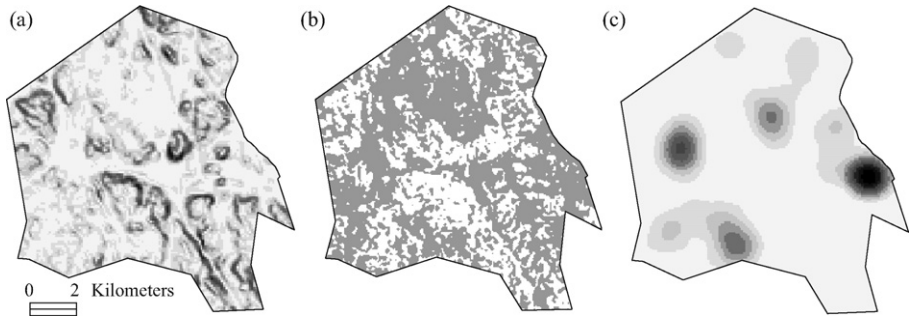

Fig. 3 – Environmental covariates used to model space use by male white rhinos. Covariates included (a) percent slope, (b) grassland/open woodland cover type, and (c) female white rhino density. Standardized values for each covariate ranged from 0 (light areas) to 1 (dark areas).

model (ExpPower) we included was simply the exponential power model without any covariates.

Because all rhinos were restricted to areas within the park boundary, the selection parameter for models containing covariate PB was not estimated but set to −1 indicating no probability of use outside the Park. All other model parameters including the location, scale, and shape parameters for the exponential power as well as the selection parameters were estimated by numerical maximization of the likelihood function, Eq. (3), using the Simplex algorithm (Press et al., 1986).

To select the best model from the candidate set, we used a variant of AIC corrected for small sample size (AIC_c; Johnson and Omland, 2004; Horne and Garton, 2006). While we identified the information theoretic (IT) best model by the lowest AIC_c, we considered models with AIC_c scores within 3 of the lowest AIC_c to be competing best models (Burnham and Anderson, 2002; Horne and Garton, 2006).

We estimated the utilization distribution for each rhino using parameter estimates from the IT best model. We determined the magnitude of the effect of the environmental covariates on each rhino's space use from estimates of the selection parameters $\hat{\beta}$ from the IT best model. We used the odds ratio δ, Eq. (4), as a measure of the proportional change in space use caused by the environmental covariates.

4. Results

The best model for estimating the utilization distribution of all three male rhinos included combinations of habitat and female density covariates (Table 1). The full model containing all covariates had the lowest AIC_c for all three males. For M09, models without all three environmental covariates performed substantially poorer suggesting that space use by M09 was affected by the location of females, the open covertype, and percent slope. However, for males M05 and M25, there was more model selection uncertainty. Models without female density but including habitat covariates performed almost as well for males M05 and M25 and a model without the habitat covariates (open covertype and percent slope) but including female density performed well for male M05.

Using estimates of the selection parameters from the IT best model for each individual, we were able to infer the magnitude of the effect each environmental covariate had on individual space use. Odds ratios suggested that space use of all males was positively associated with female density and the open covertype while negatively associated with increasingly steep slopes (Table 2). For example, M05 was 0.01 times less likely to be in an area with the highest slope (32% slope) compared to an area with the lowest slope (0% slope); ~3 times more likely to be in the open covertype as opposed to out of this covertype; and ~7 times more likely to be in an area char-

Table 1 – Summary of *a priori* candidate models used to estimate the utilization distribution of three male white rhinos

Rhino ID	Model[a]	K	ΔAIC_c	w_i
M05 ($n=36$)	ExpPower + PB + FD + OPEN + PS	7	0	0.536
	ExpPower + PB + FD	5	1.12	0.306
	ExpPower + PB + OPEN + PS	6	2.60	0.147
	ExpPower + PB	4	8.88	0.006
	ExpPower	4	9.21	0.005
M09 ($n=44$)	ExpPower + PB + FD + OPEN + PS	7	0	0.929
	ExpPower + PB + FD	5	5.14	0.071
	ExpPower + PB + OPEN + PS	6	37.66	0.000
	ExpPower + PB	4	56.28	0.000
	ExpPower	4	74.58	0.000
M25 ($n=57$)	ExpPower + PB + FD + OPEN + PS	7	0	0.507
	ExpPower + PB + OPEN + PS	6	0.06	0.492
	ExpPower + PB + FD	5	14.83	0.000
	ExpPower + PB	4	19.22	0.000
	ExpPower	4	52.46	0.000

Table includes number of telemetry locations (n), number of estimated model parameters (K), the difference between each model and the model with the lowest AIC_c (ΔAIC_c), and the Akaike weight (w_i).

[a] ExpPower refers to the exponential power distribution used as the null model; PB is a categorical covariate defining areas within the Park boundary; FD is a continuous covariate related to the density of females in an area; OPEN is a categorical variable defining areas with a grassland or open woodland covertype; and PS is a continuous variable for percent slope.

Table 2 – Parameter estimates[a] for the synoptic model used to describe space use by three male white rhinos

Rhino ID	μ_x	μ_y	a	c	PS[b]	OPEN[b]	FD[b]
M05	646309	7729348	2831	0.53	0.010	3.02	6.78
M09	638919	7722865	6184	0.63	0.468	2.36	41.38
M25	649985	7724209	4292	0.10	0.023	1.58	2.48

[a] Four parameters were estimated for exponential power function used as the null model including the center of the distribution in the x and y dimensions (μ_x, μ_y), the shape parameter (a), and the scale parameter (c). Selection parameters were estimated for the three environmental covariates including percent slope (PS), grassland or open woodland covertype (OPEN), and female density (FD).

[b] Instead of reporting the selection parameter estimates from the synoptic model (i.e., the β in Eq. (2) in the text), we report the odds ratios representing the proportional change in the utilization distribution attributable to each variable. In Eq. (5) in the text, $H_j(a) = 1$ and $H_j(b) = 0$.

acterized as having the highest female density compared to the lowest density.

The previous results were for each covariate when the rest were held constant. Using Eq. (4) we can also compare two scenarios containing the full suite of environmental covariates. For example, how much more likely is M05 to be in an area with 2% slope, 0.5 relative female density, and in the open covertype versus 10% slope, 0.7 relative female density, and not in the open covertype? Entering −0.99, 2.02, and 5.78 for the estimated betas of PS, OPEN, and FD as well as 0.06 and 0.31 for the standardized slope values of 2% and 10%, respectively, gives

$$\delta = \frac{[1 + (-0.99)(0.06)][1 + 2.02(1)][1 + 5.78(0.5)]}{[1 + (-0.99)(0.31)][1 + 2.02(0)][1 + 5.78(0.7)]} = 3.16$$

where the first term in brackets is for percent slope, the second is for the open covertype and the third is for female density. Thus, M05 is approximately three times more likely to be in the first area as opposed to the second.

Resulting estimates of the utilization distributions based on the IT best model for each animal revealed space use patterns that were highly irregular and multimodal (Fig. 4) reflecting the patchy distribution of influential environmental covariates. Generally, areas characterized by the open covertype with high female density and low slope had high probability of use whereas areas without these characteristics were used less. Traditionally, such complex distributions could only be described using non-parametric models (e.g., kernel smoothing). However, our synoptic model demonstrates that by incorporating additional spatial covariates, parametric models are able to capture the complexity of patterns of space use that have escaped them in the past.

5. Discussion

Animal space use is inherently a multivariate process and we believe an understanding of this process is best achieved by explicitly modeling the utilization distribution as a function of several interacting ecological processes and environmental pressures. The synoptic model allows researchers to estimate an individual animal's utilization distribution as a function of multiple, spatially explicit, environmental covariates. When coupled with an analysis of the odds ratios using the estimated parameters, the model can also be used to infer the strength of the effect various environmental factors have on space use. As a secondary benefit, our synoptic model offers an avenue by which estimates of animal home ranges are likely to be improved by including additional spatially explicit information other than location coordinates.

By using the synoptic model, researchers can evaluate the strength of evidence for different hypotheses about the ecological processes affecting animal space use. Thus, the best

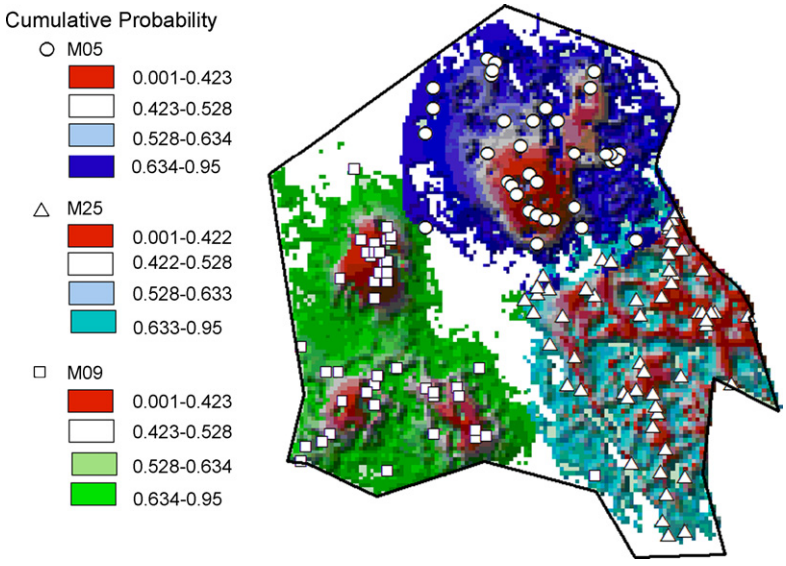

Fig. 4 – Estimated utilization distribution for three male white rhinos (M05, M09, M25) in Matobo National Park, Zimbabwe, based on a synoptic model of space use. Contour lines follow areas of equal probability with the outer extent defining the 95% home range for each individual.

model can be used not only for describing the size, shape, and location of the home range, but also probing why the home range takes that form. In our example, the best synoptic model indicated that multiple environmental factors influenced space use by male rhinos. There was a strong negative relationship between probability of use and the steep, rocky slopes. This relationship is likely due to morphological constraints of rhinos that render them incapable of moving readily through steep, loose terrain or because of the energetic demands of climbing. Additionally, the synoptic model implies that male rhinos were typically found in areas with foraging resources (i.e., open cover type) and high densities of potentially receptive females.

Despite these general trends in rhino space use, it should be noted that there was significant model selection uncertainty for two of the males. For M05, the limited number of locations ($n = 36$) and likely correlations among covariates resulted in ambiguities as to whether habitat selection or the location of females in isolation were the main drivers of space use or whether all of these factors collectively contributed to determining the space use. Similarly, there was not clear evidence that including female density provided a better model of space use for M25 than a model containing only habitat covariates. In regards to these ambiguities, we remind readers first and foremost that these results were only used as an example application of the synoptic model. However, we expect our results are not atypical of those that will be encountered when the synoptic model is used for future studies. Therefore, we emphasize that results from the synoptic model should be incorporated into a population-level analysis as previously discussed in the section on interpreting the model structure and parameter estimates. We also note that many of these ambiguities can only be alleviated by increasing sample size and thus, providing more power to specify the relationships and then by following up on inferences obtained from observational studies with manipulative experiments.

Our rhino example demonstrated another practical benefit of using environmental covariates to model space use. Frequently, animal home ranges include areas that, because of certain characteristics, are inaccessible or completely avoided (e.g., a lake within the home range of a terrestrial animal, or the terrestrial environment for an aquatic species). In our example, the rhinos at Matobo Park were confined to areas within the Park by an impassible fence. Similar to Matthiopoulos (2003a), this prior knowledge can be incorporated into the model by defining inaccessible areas and setting the selection parameter equal to −1. However, if these relationships are not known the synoptic model offers a way to estimate them contemporarily through the likelihood function.

5.1. *Home range estimation and resource selection using a synoptic model*

With few exceptions (e.g., Matthiopoulos, 2003a,b), most empirical models for estimating animal home ranges are based solely on location coordinates and do not allow researchers to incorporate additional ecological factors that affect occurrence into the model. Likewise, habitat selection analyses generally fail to incorporate spatial processes such as home range behavior (Thomas and Taylor, 2006). However, researchers have begun to develop models that combine home range behavior and habitat selection into one analysis. For example, Matthiopoulos (2003a) recognized that home range estimation could be improved by incorporating the spatial distribution of environmental factors (e.g., location of a nest or the distribution of food) into kernel density estimates, provided researchers have a priori knowledge of their effects. Our model differs from the approach of Matthiopoulos (2003a,b) in that no a priori estimates of habitat selection are required. Instead, these relationships are estimated simultaneously with the utilization distribution by combining location data with readily available data on spatially explicit environmental covariates.

Simultaneously coupling home range models with resource selection into a single model has additional benefits beyond improving estimates of the utilization distribution. The purpose of the initial/null model is to represent space use in the absence of any effect from environmental covariates. In essence, the null model is defining the "availability" of resources upon which subsequent selection behavior operates. This is a critical step that enables researchers to remove the effect of primary behavioral processes (e.g., central tendency around the home range center) from analyses of resource selection. Recognizing this deficiency in resource selection analyses, important contributions were made by Matthiopoulos (2003b) who described an approach to examine habitat preference that accounted for accessibility of habitats and Rhodes et al. (2005) who described a model for incorporating home range behavior into habitat selection analyses. Our approach differs from that of Matthiopoulos (2003b) and Rhodes et al. (2005) in that instead of modeling the movement process with the goal of inferring habitat selection, we construct a phenomenological model of the resulting probability distribution of space use. The model is constructed in such a way that the effects of home range behavior, habitat selection and interrelations with other animals can be taken into account while estimated parameters within the model can be used to infer the strength of the effect these factors have on an animal's space use.

5.2. *Assumptions of the synoptic model*

Finally, we discuss several structural and statistical assumptions of the synoptic model and subsequent parameter estimation as they relate to the biological realities of animal movements and data collection. First, we have assumed that the utilization distribution of the animal under investigation is fixed over the analysis period. This assumption has traditionally been accommodated by setting a temporal boundary for home range estimation or resource selection (e.g., seasonal estimates) and we believe this approach is appropriate for the synoptic model as well. However, a better approach would be to apply the synoptic model in the context of a mixed effects model to determine temporal processes associated with changes in animal space use and insure that home range size and patterns of habitat selection were not changing over the analysis period (Borger et al., 2006).

We assumed that our sample of animal locations were independent samples from the utilization distribution. How-

ever, it is well known that taking locations over relatively short time intervals introduces serial autocorrelation into the data (Swihart and Slade, 1985). Because our synoptic model is ultimately an estimate of the utilization distribution, we suggest that general recommendations for collecting telemetry data for home range estimation apply. In particular, we suggest researchers use a systematic sampling scheme to collect locations during the time period from which inferences will be drawn (Garton et al., 2001; Kernohan et al., 2001; Fieberg, 2007).

Last, we suggested that by using the synoptic model, researchers can shorten the distance between general statistical models and mechanistic models of animal space use. To do this using the model we presented, we have assumed two connections between the synoptic model and animal movements. First, we assumed that the null model is a good approximation of the space use of an animal moving without any influence from environmental covariates and secondly, we assumed that there was proportional change in the utilization distribution caused by each environmental covariate.

We used the exponential power model as a null model because a circular normal distribution characteristic of an animal that biases random movements towards a central place is a particular case (i.e., shape parameter equals 1) but also allows for a more uniform distribution of space use (i.e., shape parameter <1) that may be characteristic of territorial animals in homogeneous environments (Grant, 1968; Covich, 1976). While a direct connection can be made between a centrally biased random walk and a circular normal distribution (Dunn and Gipson, 1977; Okubo, 1980), currently there are no similar connections between movement processes and the exponential power model when the shape parameter does not equal 1. Future research should investigate these connections and seek to determine appropriate parametric distributions that can be used as the null model based on known movement behaviors or ecological hypotheses.

We chose to model the effect of environmental covariates as a proportional change in the utilization distribution because of agreement with other studies of resource selection. However, we are unaware of any studies that have provided a link between this assumption and actual hypothesized animal movements. We note that from a limited set of simulations of a centrally biased random walk within an area composed of categorical "habitat" types, there was support for a proportional change in the utilization distribution if the animal is more likely to stay inside the preferred habitat type than if there was no preference (Horne, 2005). Again, to provide a better link with the biological processes governing animal space use we suggest that future research should investigate the appropriateness of assuming a proportional change in the utilization distribution from real and simulated animal movement processes.

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Appendix A

Association between synoptic model weighting parameters and Manly's selection ratios.

We start with the synoptic model of animal space use,

$$s(x) = \frac{f_0(x)\prod_{i=1}^{k}(1+\beta_i H_i(x))}{\int_x \left[f_0(x)\prod_{i=1}^{k}(1+\beta_i H_i(x))\right]} \quad (A.1)$$

where, $s(x)$ = probability density of use at spatial location x; $H_i(x) = i = 1, \ldots, k$ spatially explicit environmental covariates; if covariates are categorical (e.g., habitat types), $H_i(x)$ is an indicator function that equals 1 if x is in category i and 0 otherwise. $f_0(x)$ = null probability density of space use (i.e., no effect of covariate(s) $H_i(x)$ on probability of use) β_i = weighting parameter.

If H_is are non-overlapping and categorical (i.e., habitat types), Eq. (A.1) becomes,

$$s(x) = \frac{f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)}{\int_x \left[f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)\right]} \quad (A.2)$$

Next, consider selection of habitat type j in H. In the following, we will show that when the null model of space use is uniform, Manly's selection ratio (Manly et al., 2002:77) is a consistent estimator of

$$\frac{(1+\beta_j)}{\int_x \left[f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)\right]} \quad (A.3)$$

Without changing the result of Eq. (A.3), we multiply Eq. (A.3) by $f_0(x)/f_0(x)$

$$\frac{f_0(x)(1+\beta_j)/\int_x \left[f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)\right]}{f_0(x)} \quad (A.4)$$

The numerator in Eq. (A.4) is the probability density of use at a position x in habitat j under the model that incorporates the effect of selection. The denominator in Eq. (4) is the probability density of use at position x in habitat j without selection (i.e., null model of space use).

If $f_0(x)$ is a uniform distribution (i.e., equal probability of use within a boundary), then without changing the result of Eq. (A.4) we can calculate the probability of using habitat j under the model with selection divided by the probability of using habitat j without selection by multiplying Eq. (A.4) by A_j/A_j where, A_j is the area of habitat j within the boundary of $f_0(x)$.

$$\frac{f_0(x)(1+\beta_j)/\int_x \left[f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)\right] A_j}{f_0(x)A_j} \quad (A.5)$$

Because the numerator of Eq. (A.5) is the probability of using habitat j under the selection model, it is equivalent to the

expected proportion of locations in this habitat type $E(O_j)$. Similarly, because the denominator in Eq. (A.5) equals probability of using habitat j without selection, it equals the proportion of habitat type j within the boundary of $f_0(x)$, symbolized as π_j. Thus, Eq. (A.5) equals $E(O_j)/\pi_j$ and because Eq. (A.3) is equivalent to Eq. (A.5),

$$\frac{(1+\beta_j)}{\int_x \left[f_0(x)\left(1+\sum_{i=1}^{k}\beta_i H_i(x)\right)\right]} = \frac{E(O_j)}{\pi_j}.$$

A consistent estimate of $E(O_j)/\pi_j$ is Manley's selection ratio o_j/π_j, where o_j is the observed proportion of locations in each habitat type (Manly et al., 2002:77).

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