ESTIMATION OF HABITAT SELECTION FOR CENTRAL-PLACE FORAGING ANIMALS

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Abstract: Analyses of habitat use for individuals occupying discrete home ranges are typically based on comparison with null models that implicitly assume no spatial context for habitat use within the home range. For species that regularly return to a central place, a more appropriate null model for estimation of habitat selection may be that of a declining expectation of resource use with distance from the central place, such as a nest site. When this null expectation is ignored and a uniform-use expectation is used for central-place foragers, we predicted (1) positive bias of selection for habitat types near the central place, and (2) bias will increase with the degree to which habitat types are spatially correlated to the central place. We explored these predictions with simulated data, using a range of selection intensities and spatial correlations. Results from the simulations confirmed our predictions: biases were large and positive for those habitat types proximal to the central place. To correct for these biases, we included distance from the central place as an explanatory variable in habitat selection models of simulated central-place foraging, and we found that including distance as a linear factor successfully reduced these biases. We then applied these models to field data from northern spotted owls (*Strix occidentalis caurina*) and red-cockaded woodpeckers (*Picoides borealis*). For both species, distance-based models performed better than the nonspatial (uniform) model: the models were both statistically superior and produced results more in concordance with our biological understandings. Estimates of selection for habitat types that were disproportionately located near the central place were lower in the distance-based models than in the uniform model, corroborating the results from the simulations. The simple distance-based models we used provide a reasonable means to estimate foraging habitat selection for animals for which a central place can be identified.

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The science of biological conservation often involves the assessment of the effects of habitat modification on individuals, which can then be scaled up to population level effects. An understanding of the patterns and intensity of resource selection by individuals in heterogeneous environments is central to animal ecology and wildlife management. Key to understanding such patterns is the estimation of both pattern and magnitude of habitat selection. Typically, methods for the analysis of habitat selection have been applied across taxa without regard to differences in species' behavioral or physiological ecology, or to the landscapes animals occupy.

The general definition of a "selected" resource has been a resource used in a proportion greater than that which is available, or conversely, "avoided" when use is proportionally less than available (Neu et al. 1974, Johnson 1980; White and Garrott 1990:186). Difficulties with this approach include defining what constitutes "available" habitat, and what the appropriate null model of no differences in the likelihood of use should be. The problems associated with the assessment of availability are not trivial, and an incorrect definition of habitat availability can lead to erroneous conclusions concerning habitat selection (Warnock and Takekawa 1995, McClean et al. 1998).

Estimation of habitat selection has been a persistent source of confusion and potential bias. Despite the recognition that habitats are not uniformly distributed, most of the recent advances in statistical methods for evaluating foraging habitat selection continue to be based on tests for selection given a set of resources that are implicitly assumed randomly distributed within a given area (Neu et al. 1974, Thomas and Taylor 1990, Aebischer et al. 1993, Manly et al. 1993, Cherry 1996). Recently, Otis (1997, 1998) developed statistical methods that allow for spatial patterns of habitat within a home range. None of the methods, however, account

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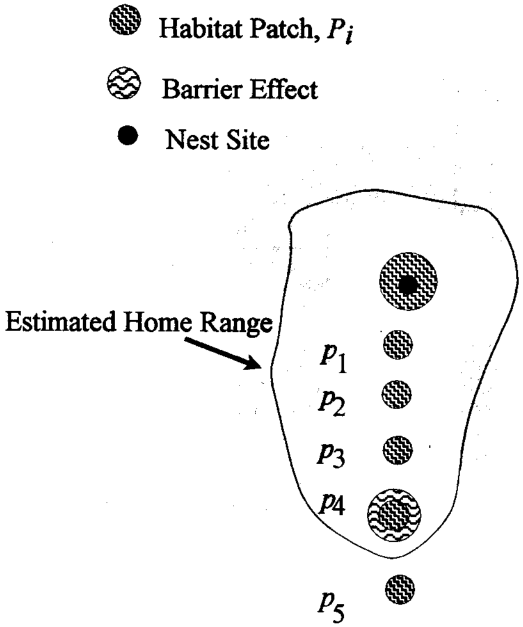

Fig. 1. Schematic representation of the uniform and central-place null model of habitat selection. In the uniform model, each patch (or grid cell) of habitat has the same expected use ($p_1 = p_2 = p_3 = p_4$), and patches outside of the estimated home range boundary have an expected use of zero ($p_5 = 0$). Under the central-place model, the probability of use is a function of distance from the central place. The probability of use is expected to decline with distance from the central place; the null expectation under the central-place model is $p1 > p2 > p3 > p4 > p5$. Barriers to use, such as landscape patterns, topographical constraints, and distance to conspecifics may also affect availability of habitat types. For example, if p_4 is surrounded by a habitat that limits use of p_4, then the null expectation for habitat use is lower for p_4 than for a patch of equal distance from the central place.

for differences in the availability or use of resources that are due to the behavioral ecology of a species. Availability of habitat types to an individual animal may vary because of the presence of predators or conspecifics, landscape patterns such as patch size (Otis 1997, 1998), and distance from a central place, such as a nest site (Fig. 1).

Choosing the proportion of habitat types within a home range as a null model of availability (hereafter referred to as "uniform model") involves the implicit assumption that no factors other than habitat type affect its use. There are many cases, however, where this assumption is not reasonable (Otis 1997, 1998). The case we explore occurs when an individual exhibits central-place behavior such as foraging during the nesting season, when a bird regularly returns to a nest site. In this case, proportional use is a poor null model due both to the geometry of points radiating from a central place (principles of diffusion; e.g., Okubo 1977) and to biological mechanisms including energy efficiency (Pyke et al. 1977) and resource depletion. The use of a habitat patch by an individual exhibiting central-place behavior will be due both to the habitat's quality and proximity to the central place. To separate these 2 factors, we need a model which incorporates distance from the central place as well as the habitat characteristics that are of interest, which may include landscape characteristics (e.g., Otis 1997, 1998) as well as habitat type.

For central-place foraging animals, the use of resources decreases with increasing distance from a central place, such as a nest site. Interestingly, some home range estimators do take into account the expectation of a decrease in use with distance from a central place. For example, bivariate normal models assume random movement within a home range, but with decreasing probability away from the center (Jennrich and Turner 1969). The concept of multiple nodes and attraction points motivated Don and Rennolls (1983) to suggest a method for estimating home ranges that accounts for declining use of space with increasing distance from focal points. Surprisingly, this recognition has not motivated methods for estimating habitat selection, for which the proper null expectation of availability is so important. Despite numerous reassessments of statistical methods for analyzing use versus availability data, the central question of what is available to an individual has been largely ignored, which confounds selection with availability.

We do not contend that the choice of the habitat in which the central place is embedded is unimportant. Central places, such as nests, may be chosen based on proximity of high-quality foraging habitat. However, if the habitat requirements of the central place differ from the requirements associated with other activities, such as foraging, then the choice of an incorrect null model could lead to misleading inferences about habitat selection associated with these other activities.

We propose a general use versus availability model in which selection is defined as deviation from a null model where the expectation is a function of the distance from a central place, such as a nest. The distance function is estimated directly from data on locations of an in-

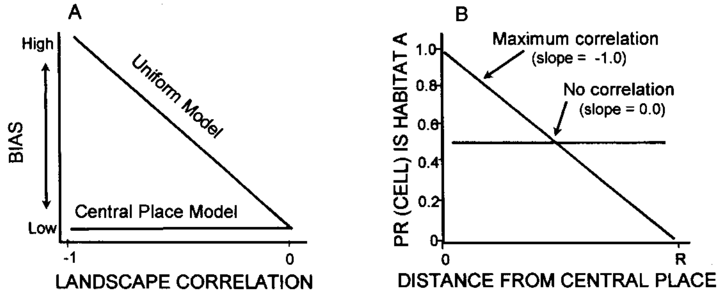

Fig. 2. Predictions of the bias in estimators of habitat selection under the uniform and central-place null models. (A) Bias increases under the uniform-use model as the spatial correlation of the landscape increases, whereas bias is low and independent of the level of spatial correlation under the central-place model. (B) Spatial correlation can be understood as the slope of the relation of the probability that a habitat cell was of the same type in which the central place was embedded with distance from the central place, with a maximum distance equal to the greatest distance, *R*, an individual was located from the central place.

dividual. We evaluated the technique by using Monte Carlo simulations of idealized central-place foragers in stylized landscapes. In these simulations, we predicted 2 patterns of bias within a central-place foraging framework (Fig. 2A). Our first prediction is that the estimated level of selection under the uniform model is biased whenever the spatial distribution of habitat patches is not random within a home range (Fig. 2A). Specifically, the estimate of selection ratios for habitat types near the central place will be positively (negatively) biased if the probability of encountering these types declines (increases) with distance from the central place (Fig. 2). We expected percent bias to be positively related to the level of spatial correlation of the landscape (Fig. 2A). Our second prediction is that bias is reduced when an appropriate distance function is included in the model structure, and therefore bias should be independent of the level of spatial correlation (Fig. 2A).

We illustrate the methodology with data from northern spotted owls and red-cockaded woodpeckers for which a central place is identified and foraging habitat use is evaluated from repeated locations of individuals.

METHODS

Central Place Model: Theory

We assumed that each foraging trip starts and ends at the central place. In the single-prey model often used in foraging theory (Stephens and Krebs 1986), the trip continues until the animal acquires prey, at which time the animal returns to the central place (Orians and Pearson 1979). In this type of foraging, the probability of searching an area of a given size (referred to as a cell) at distance *d* from the central place is the probability that a trip is at least *d* in length (and hence could pass through the cell) times the reciprocal of the number of potential cells that exist *d* away from the central place. If the organism searches with equal probability in all directions around the central place, then the number of areas of unit size searched which exist *d* away from the central place will be proportional to the circumference of a circle of radius *d*:

$$n_d \propto 2\pi d \propto d,$$

where n_d is the number of areas *d* distance away from the central place. If we assume that an organism with each trip travels at least *d* from the central place, and if $P\ [c_d]$ is the conditional probability of searching a given cell at distance *d* given that the organism traveled at least that far, then

$$P[c_d] \propto \frac{1}{d}.$$

The unconditional probability of use at distance *d* for a central-place forager is therefore

$$U_d \propto \frac{1}{d} P[d],$$

where $P[d]$ is the probability that the trip extended to a distance of at least *d* from the center.

The $1/d$ density function is a consequence of geometrical principles, while $P[d]$ is a function of the biology of the organism, the sampling methods, or both. For example, $P[d]$ may incorporate aspects of resource depletion, predator avoidance, conspecific competition, or how locational data were collected (e.g., lower probability of detecting the animal when the animal is far from the nest site). An example of a simple null model (Model 1) for $P[d]$ assumes that foraging trips from the central place are of random length and direction extending to a maximum travel distance R. $P[d]$ is therefore a linear function of d, such that

$$P[d] = k - \frac{k}{R}d,$$

where k is a scaling constant forcing the function to integrate to 1.0.

When the biology of the organism is more fully specified, other null models may be appropriate. For example, a null model for an individual that captures a single prey item followed by a return to the central place (single prey loader; Stephens and Krebs 1986) with no physiological or survival costs would be based on the following logic. The animal starts at the central place, conducts a random walk searching for prey, and then returns when successful. If prey are equally likely to be found at all locations, then the probability of the search reaching a particular distance away from the center is simply the probability that prey was not found at some closer point, such that

$$P[d] = 1 - (1 - p_c)^{md},$$

where p_c is the probability of capturing a prey item per cell searched, and m is the average number of cells searched per unit distance traveled from the center.

Clearly, there are a large number of potential models associated with different behavior patterns, but, regardless of the model, the expected probability of using a cell will decrease with distance from the central place at a rate at least proportional to $1/d$. In our simulations to evaluate bias of estimators of habitat selection, we chose Model 1 as the most parsimonious model of central-place behavior.

Estimation Procedures

We used logistic regression to estimate selection as the odds ratio (Hosmer and Lemeshow 1989:40) of use between 2 habitat types. We assumed a data structure in which the sample unit was a particular cell within a real or simulated home range. The dataset originated from a sample of cells in which the individual was located through a sampling process (such as radiotelemetry) and a sample of randomly selected cells. The binary response variable was coded as 1 if an individual was located in a particular cell, and zero if the cell was a randomly selected cell. Habitat type and distance from the central place were explanatory variables measured from each sample cell. For analyses of the northern spotted owl and red-cockaded woodpecker data, we used a model that included distance variables, habitat types, and the interaction of the habitat type in which the central place was embedded and distance such that

$$\text{logit}(\hat{\pi}) = B_0 + B_1D + B_2D^2 + B_3D^3 + \sum_{j=1}^{(k-1)} (B_{(3+j)}X_j) + B_cDX_c.$$

This logistic regression model describes the probability of a cell being "used" as a function of a set of explanatory variables, where $\hat{\pi}$ is the maximum likelihood estimate of the probability that an individual was located in the specified cell during the sampling process, and the regression coefficients include B_o for the intercept, B_1 for the linear distance (D) variable, B_2 for the squared distance variable, and B_3 for the cubed distance variable; $\mathrm{B}_{(3+j)}$ for the jth type of habitat (X) variable, $j = 1 \ldots k$-1, where k is the number of habitat types; and B_c for the interaction of distance and the central-place habitat type (i.e., the type in which the central place was embedded). Distance was included as a polynomial to allow nonlinear distance effects. Habitat types, which were all categorical in our dataset, were treated as design or "dummy" explanatory variables (Hosmer and Lemeshow 1989:26), with k-1 design variables, each corresponding to a different type of habitat. Design variables were coded 1 if the cell was of the specified habitat type or zero if not. When habitat type is categorical, such as whether or not the habitat was older conifer forest, there are k-1 habitat variables in the model (Hosmer and Lemeshow 1989:48). The kth habitat type that is not denoted as a design variable in the model is labeled the "reference" group (Hosmer and Lemeshow 1989:26). Reduced models, such as the uniform model which did not include distance variables, were compared to the complex model for analyses of field data (Table 1). In the present study, B_o cannot be estimated, because the sampling probabilities are unknown for the "used" cells for the field data; however,

Table 1. Comparison of Aikaike's Information Criterion differences (ΔAIC) and odds ratio from uniform and distance-based habitat selection models for northern spotted owls and red-cockaded woodpeckers. Models distinguish between cells with animal locations and random cells, or between cells used by the female and male northern spotted owl.

Species and sex Model[b]	ΔAIC[c]	Odds ratio for habitat selection[a]				
		Older	Hardwood	Young	Longleaf	Marsh
Northern spotted owl (male)						
Habitat, distance, older × distance	0.0	11.0	0.9	1.1		
Habitat, distance	4.9	2.7	0.9	1.1		
Habitat, distance (polynomial)	5.7	2.6	0.8	1.1		
Habitat	34.2	2.9	0.9	1.2		
Distance	17.2	1.0	1.0	1.0		
Northern spotted owl (female)						
Habitat, distance, older × distance	29.3	7.3	1.2	2.0		
Habitat, distance	28.0	4.8	1.2	2.0		
Habitat, distance (polynomial)	0.0	3.6	0.9	1.7		
Habitat	128.3	6.1	1.3	2.5		
Distance	44.1	1.0	1.0	1.0		
Northern spotted owl (female vs male)						
Habitat, distance, older × distance	19.1	1.5	1.6	1.5		
Habitat, distance	17.1	1.5	1.6	1.8		
Habitat, distance (polynomial)	5.6	1.4	1.5	1.5		
Habitat	29.0	2.1	1.5	2.0		
Distance	11.7	1.0	1.0	1.0		
Distance (polynomial)	0.0	1.0	1.0	1.0		
Red-cockaded woodpecker						
Habitat, distance, longleaf × distance	0.0				0.5	0.3
Habitat, distance	1.7				1.7	0.2
Habitat, distance (polynomial)	0.4				1.7	0.2
Habitat	96.6				0.7	<0.1
Distance	19.4				1.0	1.0

[a] The odds ratio shown here is the ratio of the odds for selection of habitat types compared to a reference type, which included clearcuts (spotted owls) and pine plantation (red-cockaded woodpeckers). In the spotted owl example, odds ratios of the probability of use compared to the reference type are shown for older forests (nest-site type), hardwoods, and young forests. In the case of red-cockaded woodpeckers, odds ratios are reported for longleaf pine (nest-site type) and marsh habitat. For models that included only distance, the odds ratio is assumed to be 1.0 for habitat factors. Note that for models that included the interaction of habitat and distance, the odds ratio for the effect of habitat is a function of distance; for simplicity, the odds ratio reported is for a distance of zero meters from the nest site.

[b] Models investigated included habitat, which included variables for each type (northern spotted owls: clearcut, young, older conifer, hardwood; red-cockaded woodpeckers: pine plantation, longleaf pine, marsh), distance from the nest location, as a linear or as a third-degree polynomial function, and the interaction of both distance to the nest, and whether or not the habitat type was the type in which the nest site was embedded, and distance to the nest.

[c] Aikaike's Information Criterion differences (ΔAIC) represents a ranking of the best model (lowest AIC) with the other candidate models, such that $\Delta AICi = AICi -$ minimum AIC, where i denotes the ith model of the set of candidate models (Burnham and Anderson 1998).

the estimated odds ratio (described below) can be used to make inferences on selection patterns (Manly et al. 1993:127).

For analyses of the simulated data, the most general model included only the linear distance variable and a single habitat variable:

$$\text{logit}(\hat{\pi}) = B_0 + B_1 D + B_2 X,$$

where X is 1 if the cell was in Habitat A or zero if it was in Habitat B. We discuss 2 types of reduced models: (1) the uniform model, which includes only habitat variables; and (2) a distance-based model, in which distance is included as a covariate without the habitat variable. We used Akaike's Information Criterion (AIC) values to identify the most parsimonious models (Burnham and Anderson 1998).

In the context of this paper, the odds ratio is a measure of selection of a given habitat type relative to the reference type, with adjustments made for all other variables in the model. We estimated the odds ratio for the nth variable (r_n) as

$$\hat{r}_n = e^{\hat{B}_n}$$

(Hosmer and Lemeshow 1989:41). We used PROC LOGISTIC (SAS Institute 1994) to obtain parameter estimates.

Monte Carlo Simulation Procedures

We generated circular landscapes with 2 habitat types: (1) a type which was selected (Habitat A), and (2) a type which was neutral (Habitat B). We determined habitat use of a given cell by simulating a constant speed path which moved outward from the central place at a random azimuth and distance and then returned along the same path (Model 1). At systematic intervals with a time frequency no greater than 1 sample/"round trip," the location of the simulated animal was sampled, and the habitat type and distance associated with that location was recorded. The 2 time intervals, movement of the individuals and the sampling process, were arbitrary; however, the sampling interval was much less frequent than the movement interval. The habitat type, either Habitat A or B, was determined stochastically based on the distance from the central place and the spatial correlation of the landscape we investigated (Fig. 2B). For example, if there was no spatial correlation (Habitat A and B distributed randomly), the probability that a given cell was Habitat A was 0.5 for all distances from the central place. If the spatial correlation was −1.0, then the probability that a cell was Habitat A declined from approximately 1.0 adjacent to the central place to zero at the perimeter of the landscape ("*R*" distance; Fig. 2B). Random numbers between zero and 1 were generated for each cell. The random number was compared to the assigned probability of a cell being Habitat A based on the distance from the central place and the spatial correlation of the landscape. If the random number was less than the cell probability, then the cell was classified as Habitat A; otherwise, the cell was classified as Habitat B. Availability of habitat types was estimated from randomly selected points, which were generated via a uniform distribution within the "landscape" extending to the greatest distance an individual could have been located (*R*). This procedure is similar to that used in field studies to obtain "used" and "available" locations within a home range boundary (e.g., sampling Design III of Manly et al. [1993:7]). Relative selection was modeled in terms of the probability of leaving a currently occupied habitat cell. The probability of moving to an adjacent cell at each time interval was 1.0 if the cell was of Habitat B (neutral habitat), and $1/S_a$ if the cell was Habitat A. Thus, the odds ratio for the habitat type in which the central place was embedded (Habitat A) was $r = S_a$.

In each landscape, we varied the distribution of Habitat A in relation to the central place, but we retained approximately equal proportions of Habitat A and B. We evaluated the effect of the spatial correlation with a slope of 0.0 (no correlation) to −1.0 (no Habitat A at *R*; Fig 2B) at 0.2 intervals and odds ratios of 1 (no selection), 2, 4, and 6 (6 times as likely to select Habitat A relative to Habitat B). We generated a single set of approximately 20,000 "used" cells and 20,000 randomly selected cells for each level of selection and spatial correlation. The large sample size is assumed to produce unbiased and precise estimates of the expected value of the statistics used in the estimation method, and the resulting parameter estimates can be used to calculate the expectation bias (sensu Burnham et al. 1987:214).

We estimated the odds ratios for use of Habitat A relative to Habitat B. We compared the known odds ratios with those estimated under habitat models with and without distance as a covariate modeled as a linear function. Estimated odds ratios greater than the true odds ratio (positive bias) indicate that the distance-related effects were confounded with habitat use. For example, if the habitat rules specified that an organism encountering Habitat A would be 4 times as likely to stay in Habitat A when compared to Habitat B, the unbiased odds ratio for Habitat A would be 4. Percent relative bias (PRB) was computed as

$$\mathrm{PRB} = \left(\frac{(\hat{r} - r)}{r}\right) \times 100,$$

where $\hat{r}$ is the estimated odds ratio.

Field Procedures

We applied the models to northern spotted owls and red-cockaded woodpeckers, species that exhibit central-place foraging behavior. We recorded habitat type and distance to the nest site for each used (radio or visual location) and randomly selected cell (Geographic Information System pixel) within an area defined by either the area within the home range (spotted owls) or within a circle with the radius equal to the maximum distance an individual was located from its nest (woodpecker). Distance was included in the models as either a linear function or as a cubed polynomial. We reported the estimated odds ratio of each habitat type compared to a reference type, and we reported the linear distance effect as the percent change in the probability of use of a grid cell/100-m from the nest. Subsets of models included 1 or more of the following effects: (1) habitat, (2) distance, and (3) the interaction of distance and whether or not the habitat was the type in which the nest was located. The latter effect, the interaction of habitat and distance, estimated the change in selection intensity of the nest habitat type in relation to distance from the nest site. We chose the habitat type in which the nest was embedded for illustrative purposes; any or all of the habitat types could have been incorporated into the model as interaction effects. We compared models with AIC.

Northern Spotted Owl.—Locations of a pair of northern spotted owls were collected in the central Coast Ranges of Oregon during the breeding season (1 Mar–31 Aug) of 1988 (J. A. Thraillkill, Oregon State University, personal communication). Locations were estimated from radiotelemetry bearings taken approximately once per day for nocturnal locations and once per week for diurnal locations. We pooled habitat types to include only clearcut (<10 yr), young conifer (10–79 yr), older conifer (≥80 yr), and hardwood forests. The nest was located in older conifer.

We included 91 locations in the male dataset and 86 in the female datasets, and 500 locations selected randomly from within the pairs' home range, which we estimated using the 100% minimum convex polygon method (White and Garrott 1990:148). In addition to sex-specific models, we constructed a model to evaluate the hypothesis that selection for habitat types did not differ between the male and female. For this analysis, only owl locations were used; we assumed all habitats were equally available to the pair of owls. The response variable was coded 1 if a particular cell was used by the female or coded zero if used by the male.

Red-Cockaded Woodpecker.—Red-cockaded woodpecker data were collected from southcentral Florida at the Avon Park Air Force Range (L. Backus, Archbold Biological Station, personal communication). Either the male or the female of a single colony was followed visually from April 1995 through March 1996; only a single bird was followed during any given time period. We pooled data from the pair because the male and female of a colony foraged together (L. Backus, personal communication). Locations (n = 411) were typically taken every 10 min for 1 day/month between the time the bird left the roost tree in the morning until at least 1300, or until it entered and remained in a roost tree for the evening. Random locations (n = 100) were selected within a 1.5-km radius of the nest, which was the greatest distance a bird was located from the nest. Three habitat types occurred in the study area with a frequency of >1 observation for the random or bird data: pine flatwoods (primarily longleaf pine [*Pinus palustris*]), pine plantation (primarily slash pine [*P. elliottii*]), and marsh, in which trees were located along its margin. The nest tree was located in pine flatwoods.

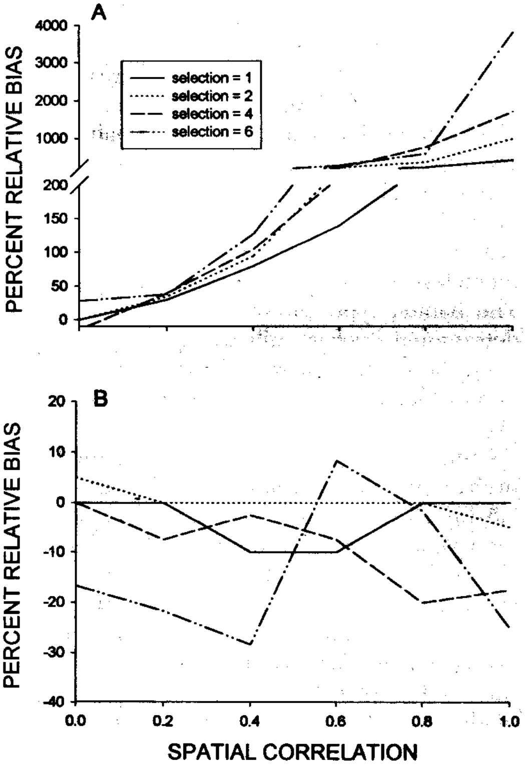

Fig. 3. Percent relative bias of estimates of selection intensity in relation to the spatial correlation of the landscape and the true selection intensity of simulated data. To facilitate presentation, the *X*-axis represents the absolute value of the spatial correlation.

RESULTS

Simulation Results

Bias was positively associated with the degree of the spatial correlation of the landscape, and the intensity of selection when distance was not incorporated into the model (Fig. 3A). Bias was greatest when both selection intensity and spatial correlation were high (Fig. 3A). For example, PRB was >3,000% when the selection intensity was 6 and the spatial correlation was −1.0 (Habitat A clustered near the central place). Bias was lowest when the spatial correlation was zero (no relation between habitat patch type and distance from the central place).

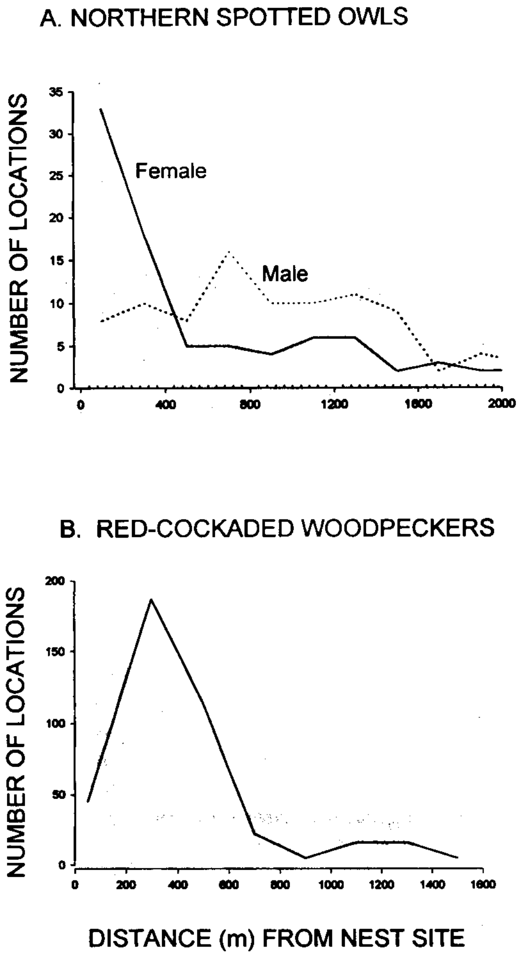

Fig. 4. Frequency distribution of distance from the nest site for (A) a pair of northern spotted owls radiotracked in western Oregon during the nesting season (Mar–Aug 1988), and (B) a pair of red-cockaded woodpeckers visually followed from April 1995 to March 1996. The female spotted owl (A) was located more frequently near the nest site than the male. Similar to the northern spotted owls, locations of the red-cockaded woodpeckers declined rapidly with distance from the nest (B).

In all cases, bias was substantially reduced when we included distance in the model (Fig. 3B). Further, with the distance-based model, we failed to find a relation between PRB and the spatial correlation; PRB remained between −28 and 8% (Fig. 3B).

Northern Spotted Owl

For both the male and female northern spotted owl, the number of locations decreased with increasing distance from the nest (Fig. 4A). Similarly, older conifer forest had a decreasing probability of occurrence with increasing distance from the nest (−2.8%/100 m). Most telemetry locations were in older conifer (mean of 69.6%), whereas the home range contained only 40% of this habitat type. The model that included only habitat types as explanatory variables (uniform model) had the largest AIC, a value much greater than the model with the lowest AIC, suggesting it was a poor model (Table 1). Under the uniform model, older conifer was almost 3 times as likely to be selected as clearcuts (odds ratio = 2.9) for the male and over 6 times as likely for the female (odds ratio = 6.1). Under a model that included only distance (linear function) as an explanatory variable, the probability of use declined at a rate of 13.2%/100 m for the male and 23.7%/100 m for the female, reflecting the female's greater use of space near the nest. The most parsimonious model that described both the male and female data included distance and habitat types as explanatory variables (Table 1). The estimated odds ratios for older conifer tended to be lower under distance-based models than under the uniform model for both the male and the female (Table 1). The single best model for the male included not only distance and habitat type, but the interaction of distance and whether or not the habitat type was old conifer (Table 1).

We compared the habitat selection patterns between the male and the female directly by using the model in which the response variable was coded 1 for the female and zero for the male. Under the uniform model, we estimated over a two-fold higher selection of older conifer for the female relative to the male (Table 1). This result was not surprising, because the female was more likely to be near the nest than the male (Fig. 4A), and older conifer forest was most common near the nest site. Models that included distance as an explanatory variable performed best (Table 1). When distance was included in the model structure as a third-degree polynomial, the odds ratio for selecting older conifer decreased to 1.4 times as likely for the female than the male. This model was the most parsimonious among the set of candidate models that described the differences between the male and female space-use patterns (Table 1). Inclusion of habitat types in the model did not appreciably increase the ability to predict grid cells used by the female relative to the male, whereas distance from the nest site did.

Red-Cockaded Woodpecker

The pair of woodpeckers often foraged near the nest site and was selective of habitat type. Although observers located the pair of red-cockaded woodpeckers foraging as far as 1.5 km from the nest site, most (57%) locations were <400 m from the nest (Fig. 4B). With a distance-only model, the probability of use declined at a rate of 32.2%/100 m from the nest tree. The woodpeckers were primarily located in pine flatwoods (57%) and pine plantations (42%), whereas the home range was composed of 42% pine flatwood, 22% pine plantation, and 33% marsh. Under the uniform model, which included only habitat types as explanatory variables, pine flatwoods was estimated as "avoided" (odds ratio = 0.7) compared to pine plantation. The most parsimonious models of those evaluated included distance and habitat effects (Table 1). Including distance in the model affected the odds ratio of habitat selection. The likelihood to have been located in pine flatwoods compared to pine plantation increased from apparent avoidance (odds ratio = 0.7) to selection (odds ratio = 1.7). The change from avoidance to selection of pine flatwoods when distance was included in the model structure was due to the spatial correlation of the landscape. The relation of distance from the nest tree to the probability that a grid cell was plantation was negative (-26.4%/100 m); the relation to pine flatwoods was weak and positive (3.1%/100 m).

DISCUSSION

Estimates of selection for foraging habitat with both the simulated and field data were consistent with our predictions for animals that exhibit central-place behavior. With distance-based models, estimates of selection for the habitat type that was distributed near the central place were lower than estimates computed under the uniform model. The pair of northern spotted owls selected older conifer forests over younger forests as estimated under both the uniform model and the distance-based models. However, under the distance-based models, estimates of selection for older conifer were lower than under the uniform model due to the spatial correlation of the landscape—forests closer to the nest site were more likely to be older conifer, and closer forest stands were used more often than those further from the nest. The results from the simulations suggest that when the spatial correlation is accounted for in the modeling process, more accurate estimates of selection result. We found the distance effect was greater for the female than the male northern spotted owl, which was likely due to the greater time the female spent at the nest during incubation and brooding (Fig. 4A). Without distance in the model, the female northern spotted owl had a much higher estimated selection for older forests than the male. The best model had only distance as an explanatory variable, which suggested that the difference in use of habitat types was due to distance from the nest site and not to differences in patterns of habitat selection. As far as we are aware, there is no evidence of sexual differences in habitat selection.

Habitat selection inferences were model dependent in the case of the red-cockaded woodpeckers. Under the uniform model, pine plantations were estimated as "selected." With the distance-based models, plantations were "avoided" and pine flatwoods (longleaf pine habitat) were "selected," which is consistent with current understanding of red-cockaded woodpecker biology (Jackson 1994). The difference in the selection patterns detected in the models was due to the greater clustering of pine plantations near the nest site; the uniform model did not account for this spatial variation, whereas the distance-based models did.

In both the northern spotted owl and red-cockaded woodpecker examples, modeling based on the expectation of uniform use led to potentially erroneous conclusions. For the northern spotted owl, in which the nest site was embedded in preferred foraging habitat, the uniform use model led to the inference that females had stronger foraging preferences for old-growth forests than did males. For the red-cockaded woodpecker, proximity of plantations to the nest site led to the inference that plantations were preferred over longleaf pine stands for foraging. In both species, imprecise parameter estimates made the detection of selection difficult; however, the patterns under the uniform and the distance-based models were consistent with our predictions.

Conclusions on selection of habitat types are usually drawn from a sample of the population and not usually 1 or 2 individuals. We illustrated our methods by using few individuals. However, data from a population sample can be analyzed similarly. One approach is to estimate the selection parameters for each individual and then analyze the patterns of selection for the population via the set of individually estimated parameters (e.g., Manly et al. 1993:83), consistent with analysis of repeated measurements on experimental units (e.g., Ramsey and Schafer 1997:450). For example, the estimated odds ratio for selection of older forests by individuals can be the response variable in an analysis of variance (ANOVA). Explanatory variables in the ANOVA model could include composition of the landscape (e.g., percent of older forest within a home range), sex of the individual, season, or any number of environmental and biological variables of interest.

For individuals that exhibit central-place behavior, we demonstrated that bias of estimators of selection for foraging habitat under the uniform model will depend on the level of selection and the spatial correlation of the landscape. The bias of estimators of habitat selection can be extreme when habitat type is correlated with the distance from the central place, which often occurs with species that are selective of nesting habitat at large spatial scales, such as northern spotted owls (Ripple et al. 1997, Swindle 1998). Without explicitly accounting for factors affecting the availability of habitat, such as distance or other barriers to use, selection is confounded with availability, and incorrect management recommendations may be chosen. The likely result would be to favor the habitat that is most common near the central place and to discount the habitat located distant from the central place. We emphasize that an animal may select a nest site based on proximity to high-quality foraging habitat. In such cases, selection of foraging habitat may be explained by distance alone. It is thus important to evaluate nest-site selection independent of foraging selection to understand the biological basis of the selection patterns detected during the modeling process.

Patterns of space use for many organisms are likely to be clustered within a home range. For animals exhibiting central-place behavior, the probability of patch use rapidly declines with increasing distance from a central place strictly due to the relation of density to distance, $U_d \propto 1/d$. Therefore, if there are no other factors responsible for space-use patterns, patches nearer to the central place will have a greater probability of use than will distant sites. Ecological mechanisms that may affect the attractive force of the center may include energy expenditure (Pyke et al. 1977), resource depletion (Hamilton et al. 1967), predator avoidance (Werner et al. 1983), and factors related to care of young. Nonrandom space-use patterns occur in a large suite of species under broad ecological conditions for reasons unrelated to habitat selection.

In the central-place models that we presented, it is essential that there is a biological criterion for the decision to characterize a location as a central place independent of the observation of use. For example, if we simply choose the arithmetic mean of the location points as the central place, it will be centered on a place of use, and use of habitats near this central location will be discounted. Hence, without a biological understanding that there exists a formal central place, such as a nest site, and that use around such sites may differ from foraging selection, distance-based models should not be used. Although it is imperative that a central place exist, there are no assumptions on the habitat type in which the central place is embedded. When multiple sites exist that function as central places, such as roost or den sites, our method can be generalized to include distances from several locations.

For species, places, or seasons for which a central place is not identifiable, our method does not lead to improvements over the traditional assumption of uniform availability. Even for organisms that are not clearly linked to a central place, there may be nuclei of attractiveness, which has led to diffusion models that account for "centrally biased" random walks (Okubo 1977:133). Okubo describes 2 classes of such models. The first describes attractiveness to the center that diminishes with distance, and the other describes the opposite: attraction increases with increasing distance from the center. Further research on methods to separate selection from availability for studies in which a central place is not identified or does not exist would lead to much improved assessment of habitat selection.

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