

Analysis of Resource Selection Using Utilization Distributions

JOSHUA J. MILLSPAUGH,¹ *Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources, Columbia, MO 65211, USA*

RYAN M. NIELSON, *WEST Inc., 2003 Central Avenue, Cheyenne, WY 82001, USA*

LYMAN McDONALD, *WEST Inc., 2003 Central Avenue, Cheyenne, WY 82001, USA*

JOHN M. MARZLUFF, *College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195, USA*

ROBERT A. GITZEN, *College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195, USA*

CHADWICK D. RITTENHOUSE, *Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources, Columbia, MO 65211, USA*

MICHAEL W. HUBBARD, *Missouri Department of Conservation, 2901 W. Truman Boulevard, Jefferson City, MO 65109, USA*

STEVEN L. SHERIFF, *Missouri Department of Conservation, Conservation Research Center, 1110 S. College Avenue, Columbia, MO 65201, USA*

Abstract

Often resource selection functions (RSFs) are developed by comparing resource attributes of used sites to unused or available ones. We present alternative approaches to the analysis of resource selection based on the utilization distribution (UD). Our objectives are to describe the rationale for estimation of RSFs based on UD, offer advice about computing UD and RSFs, and illustrate their use in resource selection studies. We discuss the 3 main factors that should be considered when using kernel UD-based estimates of space use: selection of bandwidth values, sample size versus precision of estimates, and UD shape and complexity. We present 3 case studies that demonstrate use of UD in resource selection modeling. The first example demonstrates the general case of RSF estimation that uses multiple regression adjusted for spatial autocorrelation to relate UD estimates (i.e., the probability density function) to resource attributes. A second example, involving Poisson regression with an offset term, is presented as an alternative for modeling the relative frequency, or probability of use, within defined habitat units. This procedure uses the relative frequency of locations within a habitat unit as a surrogate of the UD and requires relatively fewer user-defined options in the modeling of resource selection. Last, we illustrate how the UD can also be used to enhance univariate resource selection analyses, such as compositional analysis, in cases where animals use their range nonrandomly. The UD helps overcome several common shortcomings of some other analytical techniques by treating the animal as the primary sampling unit, summarizing use in a continuous and probabilistic manner, and relying on the pattern of animal space use rather than using individual sampling points. However, several drawbacks are apparent when using the UD in resource selection analyses. Choice of UD estimator is important and sensitive to sample size and user-defined options, such as bandwidth and software selection. Extensions to these procedures could consider behavioral-based approaches and alternative techniques to estimate the UD directly. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):384-395; 2006)

Key words

bandwidth, compositional analysis, habitat use, kernel, Poisson regression, radio-tracking, resource selection, spatial autocorrelation, utilization distribution.

Radio-tracking of study animals using either Global Positioning System (GPS) or Very High Frequency (VHF) technology can provide accurate and cost-effective information on animal locations and movements (Millspaugh and Marzluff 2001). Resource selection studies often use radio-tracking data and Geographical Information System (GIS) technology to provide information on the types of resources or habitats selected by study animals (Manly et al. 2002). Such studies allow managers to identify geographic ranges, conserve important resources, understand the consequences of management actions (McDonald and McDonald 2002), and map the potential distribution of animals based on model predictions (Fielding and Bell 1997).

Technological advancements are allowing wildlife researchers to map resources and animal use at larger scales with increasingly finer resolutions. When GPS collars are used, animal movements may be monitored continuously. With GIS, multiple aspects of an area's land cover composition, spatial arrangement, and habitat quality can be mapped with high accuracy over large areas (e.g., Knick et al. 1997). To take advantage of such high-resolution data sets,

analytical tools have been developed that enable investigators to relate continuous measures of resource use by animals to multiple resources in a spatially explicit manner (e.g., Marzluff et al. 2004).

Despite recent advancements in resource selection analyses (Cooper and Millspaugh 1999, 2001, Manly et al. 2002), many analytical procedures treat the response variable as a dichotomous variable. One common procedure classifies sites as either used or unused based on observed locations and then compares used to unused resources with logistic regression on predictor variables. Another common procedure involves comparison of a sample of used units to a sample of available units (Manly et al. 2002, Buskirk and Millspaugh 2006). However, these procedures do not account for variability in the intensity of use among habitat units where locations were recorded.

Alternatively, resource use could be quantified along a continuum, by measuring the amount of use throughout an animal's range. Ecologists have summarized that continuum of use by estimating UD (Fig. 1; Van Winkle 1975). Utilization distributions estimate the intensity or probability of use by an animal throughout its home range (Van Winkle 1975, Kernohan et al. 2001). Using the UD in resource selection analyses offers an

¹ E-mail: MillspaughJ@missouri.edu

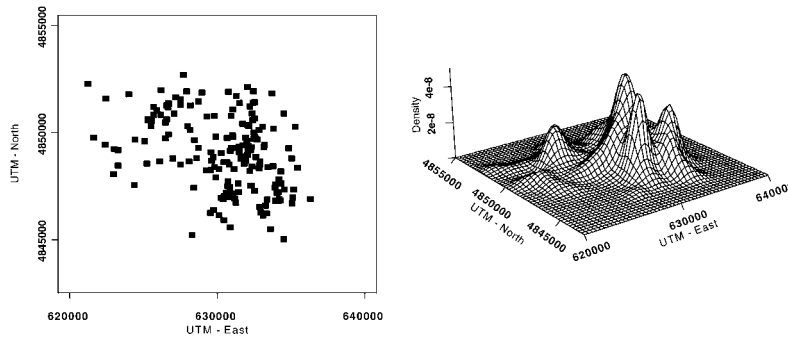


Figure 1. An example of a fixed-kernel utilization distribution with least-squares cross-validation smoothing (right) for elk locations (left) in Custer State Park, South Dakota (reprinted from Millspaugh et al. 2000).

alternative metric that summarizes resource use as a continuous and probabilistic process. Traditional resource selection analyses depend on correct classification of habitat at exact locations, which may be problematic when telemetry error exists (Withey et al. 2001). A UD approach avoids this problem because use at an estimated location is a smoothed function of all telemetry locations, which avoids the need to place locations in specific habitat patches. In addition, estimating and analyzing separate UDs for each study animal correctly treats the animal as the primary sampling unit (Aebischer et al. 1993, Otis and White 1999, Erickson et al. 2001). Despite these potential advantages, several important issues must be considered, such as selection of bandwidth values that determine the level of smoothing (Kernohan et al. 2001), sample size versus precision of estimates, and UD shape.

In this article, we summarize the analysis of resource selection with UDs using 3 examples. We begin by providing an overview of UD estimation techniques and factors affecting their performance. We also briefly discuss recent statistical developments in kernel estimation that may improve UD estimation. In the first example, we demonstrate methods that express the correlation between UDs and sets of spatially defined resources (Marzluff et al. 2004). The second example demonstrates a procedure that uses a generalized linear model (e.g., Poisson or negative binomial regression) with an offset term to model the relative frequency, or probability of use, within habitat units. Both procedures estimate coefficients of resource selection functions (RSFs) that quantify the probability of resource use as a function of predictor variables measured on habitat units. Last, we extend compositional analysis (Aebischer et al. 1993) by incorporating the UD in cases where space use within the home range is nonrandom. Our objectives are 1) to describe the rationale for estimation of RSFs based on UDs, 2) to offer advice about computing UDs and RSFs, and 3) to illustrate their use in resource selection studies.

Utilization Distribution Estimation

Estimation of a 3-dimensional UD surface or probability density function (Silverman 1986) facilitates 3 related goals. First, it allows for traditional home-range calculation by estimating the area corresponding to any desired probability of use (e.g., 95% home-range area by UD volume; Worton 1989). Second, the overall joint probability of use or overlap by 2 or more animals can be estimated (Seidel 1992, Millspaugh et al. 2000, 2004a,b). Third, the UD can be used to estimate the probability of use

within any specific area and to measure the intensity of use at specific coordinates (Marzluff et al. 2001, 2004). Thus, managers can conserve important resources and understand the consequences of management actions (Manly et al. 2002, McDonald and McDonald 2002). This article focuses on the last goal—analyzing resource selection as a function of predictor variables measured on habitat units.

Several methods for estimating home-range size have been developed over the past few decades. However, few techniques, other than kernel methods (Silverman 1986, Worton 1987, 1989), directly estimate a probability function corresponding to the UD. Previous probabilistic methods (reviewed by White and Garrot 1990) are inferior to kernel approaches in most contexts (Kernohan et al. 2001). For example, kernel methods make no assumption about UD shape and offer flexibility in estimating distributions. Moreover, extensions to the kernel method, particularly bandwidth selection, are under continued development by statistical researchers. However, we emphasize that no method is uniformly superior (Kenward et al. 2001, Kernohan et al. 2001, Getz and Wilmers 2004). In a single study addressing multiple goals, a different method may be most appropriate for each goal. For purposes of this article, we are most interested in accurately quantifying the UD within the home-range boundary for purposes of predicting the relative probability of occurrence through RSF estimation. We are assuming a typical VHF telemetry study with telemetry observations collected on a systematic schedule throughout the season of interest (Garton et al. 2001). Sample size recommendations are given assuming independence among observations (Garton et al. 2001). We focus on 3 issues relating to kernel UD-based estimates of space use: selection of bandwidth values, sample size versus precision of estimates, and UD shape and complexity.

Bandwidth Options

The bandwidth, or smoothing parameter, controls the neighborhood size within which observed locations contribute to the density estimate at a point (Silverman 1986). The most fundamental smoothing option is whether the bandwidth is held constant across the area for which density estimates are calculated (fixed kernel) or whether it is allowed to vary across this area such that the degree of smoothing varies with the density of nearby locations (variable or adaptive kernel). Allowing the bandwidth to vary so that smoothing is greater in the tails of the distribution, where uncertainty is higher, is intuitively appealing (Silverman

1986:100) because greater smoothing inherently considers uncertainty in the UD estimate. However, in UD simulations (Seaman et al. 1999), the simple form of adaptive kernel commonly used in home-range analyses (Silverman et al. 1986:101, Seaman and Powell 1996) had higher bias than a fixed-kernel approach based on the relative mean square error. Even with distributions containing sharp boundaries, this form of adaptive kernel was slightly worse than the fixed kernel (Getz and Wilmers 2004). Therefore, a fixed-kernel approach may be preferable to this form of an adaptive kernel (Kernohan et al. 2001) when estimating home range extent.

For both fixed-kernel and adaptive-kernel approaches, an automatic bandwidth selection method is desired. For the adaptive kernel, an automatic method can choose the pilot bandwidth that is locally adapted. Ecological studies have focused on 2 automatic bandwidth-selection methods, the reference or normal method (REF) and least squares cross-validation (LSCV). A third class of methods includes plug-in (PI) and solve-the-equation methods (STE; Wand and Jones 1995). Kernohan et al. (2001:144–145) reviewed general properties of these 3 classes of methods in the context of home-range estimation. The REF method is optimal if the true distribution is bivariate normal but often performs poorly for mixtures of bivariate normals (Seaman et al. 1999, Gitzen and Millspaugh 2003). The LSCV approach outperforms REF and is used commonly in home-range studies. However, it suffers from high sampling variability and a tendency to select overly small bandwidth values when there is fine-scale clustering in the data (Silverman 1986), even with large data sets (Amstrup et al. 2004). The PI/STE approaches are recommended as the best general-selection methods by some experts (Wand and Jones 1995) and have been applied in recent UD studies (Roloff et al. 2001, Amstrup et al. 2004). However, potential weaknesses of PI and STE approaches should be examined in the context of UD studies. These approaches tend to have a positive bias and may over-smooth real peaks in the underlying density (Loader 1999:191–192), which might result in a loss of resolution in the UD estimate. Thus, if an animal is selecting resources on a fine scale, over-smoothing the peaks might remove the chance of detecting important resource-selection patterns.

Based on simulations of bivariate, normal-mixture distributions, none of these bandwidth methods is uniformly best for estimating the UD with the fixed-kernel method. Variation in comparative bandwidth performance was high under most simulation conditions (Gitzen et al. 2006). High sampling variability “reflects the difficulty of bandwidth selection and the problem of resolving uncertainty in the data” (Loader 1999:192). Such uncertainty is inherent when estimating complex distributions from often-small sample sizes and probably will remain significant despite continued refinement of bandwidth methods. That is, despite refined smoothing options, UD methods will likely not be able to overcome problems of few telemetry locations. For UD estimation, little attention has been paid to handling this bandwidth-selection uncertainty. In detailed study of a single distribution, bandwidth uncertainty can be accounted for by examining how the estimated distribution varies as the bandwidth changes (Silverman 1986, Marron and Chung 2001). Space-use studies, in contrast, seek to draw population-level ecological inference based on

numerous UD-based estimates (e.g., of home-range size). Therefore, detailed examination of single distributions versus bandwidth variation is of minor interest.

Sample Size and Precision

There is no general variance expression for kernel estimators, so sample-size guidelines must be developed from simulations or detailed case studies of real data. For fixed-kernel estimation with LSCV, Seaman et al. (1999) recommended a minimum sample size of 30–50 locations when estimating home-range size at outer contours (e.g., area encompassing 95% of the volume in the UD). For any bandwidth method, performance will improve as sample size increases, up to some threshold (e.g., 90 or 100 locations for LSCV) where little improvement in an individual animal’s seasonal UD is observed with more locations (Seaman et al. 1999). This does not negate the need to consider carefully the bandwidth selection method in relation to what UD property is estimated. For example, with bivariate, normal-mixture distributions, at a sample size of 150, REF usually had higher absolute error in 95% home-range estimates than LSCV did with a sample size of 50 (Gitzen and Millspaugh 2003). However, in overall distribution overlap between estimated and true distributions, REF with $n = 150$ generally was slightly better than LSCV with $n = 50$.

In the most recent applications of the UD, density estimates are calculated at grid points spaced across the study area, and then, density estimates are used as the dependent variable for examining resource selection (e.g., Case I below; Marzluff et al. 2004). The effects of sample size and bandwidth on the precision of these estimates need further consideration. For example, the tendency of LSCV to choose a very low bandwidth for some data sets could result in relatively high-use points being classified as very low-use areas. Examination of the relative precision of point-specific density estimates has been addressed briefly in the statistical literature. This examination has focused on how much sample size must be increased with increasing dimensions in multivariate kernel analysis to maintain a specific relative precision in density estimates at the center of the distribution (Silverman 1986:93–94, Scott 1992:198–199).

UD Shape and Complexity

Kernel UD estimators implemented to date essentially assume that the underlying distribution lacks sharp boundaries between used and unused areas. Getz and Wilmers (2004) illustrate several distributions with sharp boundaries and discontinuities. For example, they generated “donut” distributions with a hole of unused area in the center of the region, or patterns with a sharp circular boundary around the outside of the home range, and relatively high space use at the inner and outer boundaries. Such distributions are realistic when roads, park boundaries, or natural features, such as lakes, create sharp boundaries between used and unused areas. Predictably, typical kernel methods handle such boundaries poorly even with high sample sizes (Getz and Wilmers 2004). With the use of a symmetric kernel (e.g., normal kernel), a peak in use just inside the boundary will result in high estimates of space used in unavailable areas outside of the boundary. Kernel methods clearly should be modified in the case of such sharp boundaries. In the univariate context, various solutions to this problem have been developed (e.g., Wand and Jones 1995:46–49, Cowling and Hall 1996) that deal well with boundary effects (Hall

and Tao 2002:544). Müller and Stadtmüller (1999) developed a multivariate boundary kernel approach that has not been implemented in available software. Local-likelihood density estimators (Hjort and Jones 1996, Loader 1999) offer an alternative to kernel approaches that may be particularly useful when such irregularities are present.

Study Designs for Resource Selection and the Utilization Distribution

Three different sample designs for resource selection studies were identified by Thomas and Taylor (1990), and a fourth was added by Erickson et al. (2001), providing a unified approach for considering analysis options. These study designs differ in the way use and availability data are summarized. In sample design I, individual animals are not uniquely identified, and resource availability is defined at the population level. Typically, design I involves recording the number of observations within specific resource types. For example, Erickson et al. (1998) estimated moose (*Alces alces*) winter habitat selection from aerial surveys within Innoko National Wildlife Refuge in Alaska. In such cases, the researcher assumes detection probabilities do not differ among habitat types. In study design II, locations are recorded for each of n unique individuals, and resource availability is defined at the population level. Often there is a goal of collecting 30–50 locations per season per animal. An example of sample design II involved female black bear (*Ursus americanus*) habitat selection determined from locations of radiocollared bears within a defined study area (Clark et al. 1993). Design III defines resource availability separately for each animal, and locations are recorded for each individual. Nielsen et al. (2002) provided an example of design III in an examination of habitat selection by grizzly bears (*Ursus arctos*) within individual home ranges. In designs I–III, available resources are assumed to remain unchanged during the study period. For design IV, the set of available resources is sometimes assumed to be unique for each point of use. Examples include sea ice selection by polar bears (*Ursus maritimus*; Arthur et al. 1996) and elk (*Cervus elaphus*) bed site selection (Cooper and Millsbaugh 1999).

The UD is most appropriate under designs II and III, when locations from unique individuals are collected and there is interest in documenting resource selection within a defined study area or individual home ranges. Design I is inappropriate because we need telemetry observations from unique individuals. Also, design IV considers use for each point of use, whereas UD approaches are based on the combination of all points for an individual. Utilization distribution methods for resource-selection studies involving data obtained under designs II and III should treat the animal as the primary sampling unit (Otis and White 1999), and thus a UD-based RSF should be estimated for each study animal. Most studies will be undertaken to obtain inference to the sampled population rather than an individual animal. A method for estimating a population-level model with data from n study animals is to fit the same model to each of the n individuals and then estimate population-level model coefficients using

$$\hat{\beta}_i = \frac{1}{n} \sum_{j=1}^n \hat{\beta}_{ij}, \quad (1)$$

where $\hat{\beta}_{ij}$ is the estimate of coefficient i for individual j . The variance of the estimated population-level model coefficients can then be estimated using

$$Var(\hat{\beta}_i) = \frac{1}{n-1} \sum_{j=1}^n (\hat{\beta}_{ij} - \hat{\beta}_i)^2, \quad (2)$$

which includes both intra-animal and inter-animal variation (Marzluff et al. 2004, Sawyer et al. 2004). Standard or bootstrap test statistics or confidence intervals could be used to assess the statistical significance of the population-level model coefficients. Equations (1) and (2) equally weight each study animal but can be adjusted to incorporate sampling weights. When inference is intended for an individual animal, or locations are pooled across animals (design I), then, spatial autocorrelation in the locations needs to be addressed (e.g., Marzluff et al. 2004) because standard errors will usually be biased low (Neter et al. 1996). Spatial autocorrelation arises because the kernel analysis used to construct the UD induces a correlation between the deviations in neighboring pixels. However, if the animal is treated as the experimental unit and Eqs. (1) and (2) are used to estimate a population-level model, spatial autocorrelation in the individual locations can be ignored (Aebischer et al. 1993, Erickson et al. 2001) because individual model coefficients are unbiased even when autocorrelation is present (Liang and Zeger 1986, McCullagh and Nelder 1989, Neter et al. 1996). Random-effects models could also be used to estimate both population-level parameters and parameters for individual animals, but these models tend to be complex and can suffer from convergence problems. In such cases, Markov chain Monte Carlo (MCMC; Link et al. 2002) or Bayesian (D. Thomas, University of Alaska, Fairbanks, personal communication) procedures might prove useful.

Using the UD to Estimate an RSF

Utilization distributions can be related to resources in different ways (e.g., Marzluff et al. 2004, Neatherlin and Marzluff 2004). If there is only interest in relating a single, categorical variable to an animal's UD, a conceptually simple approach is to calculate a Relative Concentration of Use for each resource value (Neatherlin and Marzluff 2004). The Relative Concentration of Use is the ratio of the estimated probability of use of all patches of a particular resource to the occurrence of the resource type within the area of interest (e.g., the animal's home range). Concentration of use is analogous to other selection coefficients that relate a measure of resource use to a measure of resource occurrence (Manly et al. 2002). Concentration of use improves on traditional selection coefficients because it integrates relative selectivity throughout the area of interest, uses the animal instead of the relocation point as the primary sampling unit (Otis and White 1999), and measures use as a continuous random variable. In case III below, we extend this concept and illustrate how the UD can be used to enhance compositional analysis in cases in which animals use their range nonrandomly.

Individual animal density estimates from the UD (designs II or III) can be regressed on continuous or categorical resources, resulting in a Resource Selection “Probability” Function as defined by Manly et al. (2002) or a “Resource Utilization Function” (RUF; Marzluff et al. 2004). The phrase “Resource

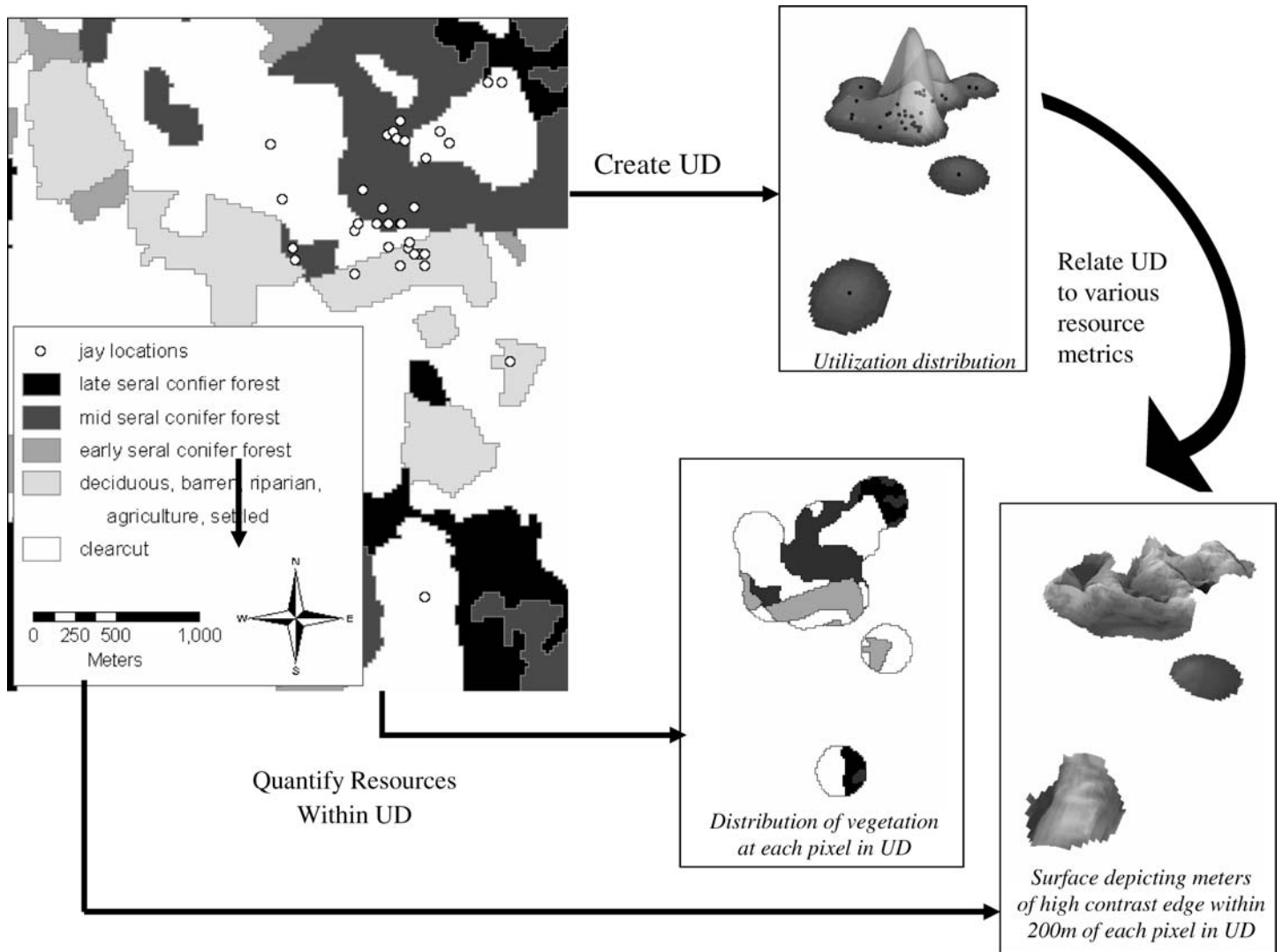


Figure 2. Calculation of a resource utilization function for a single Steller's jay. First, the jay's location estimates (upper left) are converted into a 3-dimensional utilization distribution (UD; upper right) using a fixed-kernel home-range estimator. The height of the UD indicates the relative probability of use within the home range. Greater heights indicate areas of greater use as inferred from regions of concentrated location estimates. Second, resource attributes are derived from resource maps within the area covered by the UD. For example, Marzluff et al. (2004) calculated a continuous resource measure (contrast-weighted edge density; lower right; highest at interfaces between late-seral forest and clearcuts or urban areas) and a categorical resource measure (vegetative land cover; lower left) at each grid cell center within the area of the UD. The height of the UD (relative use \times 100) is then related to these local (e.g., vegetation cover; lower left) and landscape (e.g., contrast-weighted edge density; lower right) attributes on a cell-by-cell basis with multiple regression techniques that adjust the assumed error term for spatial autocorrelation (reprinted from Marzluff et al. 2004).

Selection Function” is also used with the implicit assumption that a probability density function is being estimated (i.e., in this case, a map providing the probability of occurrence throughout the region of interest). The estimated regression coefficients indicate how resources relate to variation in the underlying probability density function and their magnitude indicates the change in probability for a unit change in the quantity of the resource if the quantities of all the other resources are held fixed.

Case I: Relating UD to Resources—Using Multiple Regression Adjusted for Spatial Autocorrelation

Forest fragmentation is hypothesized to increase the risk of nest predation on several bird species (Marzluff and Restani 1999). However, mechanisms increasing risk are poorly understood (Andr n 1992). We suspected that nest predators may be more abundant and more likely to concentrate their foraging activities in patchy or edgy

environments created by forest loss. We tested this idea by relating use by the Steller's Jay (*Cyanocitta stelleri*) to continuous and categorical measures of land cover composition and arrangement (Marzluff et al. 2004). Here, we summarize analytical methods and findings to illustrate how UD's can be related to resources.

The Marzluff et al. (2004) approach consists of 4 basic steps (Fig. 2): 1) estimate the UD using nonparametric procedures, such as fixed kernel techniques (Seaman and Powell 1996, Kernohan et al. 2001); 2) measure the height of the UD (i.e., probability density estimate) at each habitat unit (e.g., pixel in the GIS) throughout the entire UD surface (i.e., home range); 3) determine the resources at the same pixels; and 4) use multiple regression to relate UD height to the predictor variables. In addition to these steps, Marzluff et al. (2004) accounted for spatial autocorrelation using the Matern correlation function (Handcock and Stein 1993).

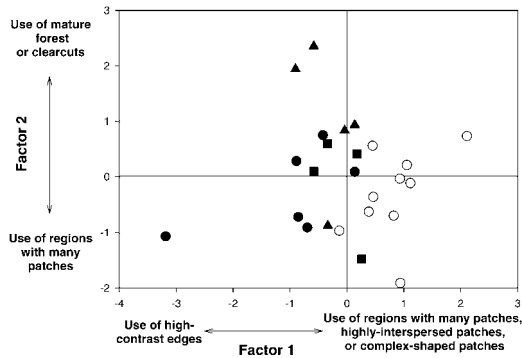


Figure 3. Ordination of resource selection tendencies by 25 individual Steller's jays on Washington's Olympic Peninsula. Factor 1 from the principal components analysis accounted for 33.6% of the explained variation and was correlated most closely with the use of high-contrast edge ($r = -0.83$) and use with respect to patch shape ($r = 0.78$). Factor 2 accounted for 29.8% of the explained variation and was most closely associated with the use of mature forests ($r = 0.77$) and clear cuts ($r = 0.77$). The significance of resource utilization coefficients in individual jay RUFs is indicated by symbol type. ○ = Significant use of patches, ● = Significant use of edges, ■ = Significant use of patches and edges, ▲ = No significant use of patches or edges (reprinted from Marzluff et al. 2004).

For the 25 jays used in this example, the average RUF for the population was:

$$f(x) = 1.3 + 0.9(\text{no. patches}) + 0.005(\text{m of high-contrast edge}) - 0.0002(\text{juxtaposition of land cover}) + 0.014(\text{patch-shape index}) - 0.4(\text{mature forest}) - 0.29(\text{clear cut}). \quad (3)$$

The average variance of the resource utilization coefficients was estimated by

$$Var(\hat{\beta}_j^*) = \frac{1}{n^2} \sum_{i=1}^n se^2(\hat{\beta}_{ij}^*) \quad (4)$$

where the inter-bird variation was not incorporated. Equation (4) represents the average uncertainty in coefficients, based on regression of the height of the UD on the number of units in the home ranges, given the 25 jays and the specific user-defined options selected for UD estimation. Individual jays varied considerably in their use of specific resources. Most jays (20/25) significantly concentrated their activities in regions of their home

ranges that either had abundant high-contrast edges (10 jays), many patches (14 jays), or both edges and patches (4 jays; Fig. 3).

To rank resource use by the study population, Marzluff et al. (2004) compared standardized RUF coefficients (Zar 1996). For example, the number of patches was the most important predictor of a jay's location; jays tended to use patchy areas more than uniform ones (Table 1). The variation around standardized $\hat{\beta}_j$ is considerable, which results from the inclusion of inter-bird variation (Eq. 2), thereby allowing inference from the sample of jays to the population, assuming that the 25 birds were selected randomly or in some representative fashion. Marzluff et al. (2004) used the more conservative approach of including all sources of variance (Eq. 2) rather than basing the estimation of sampling variance only on inter-bird variation (Eq. 4) because, in their example, inter-bird variation was an order of magnitude larger than the variance associated with estimating the resource utilization coefficients of individual jays. The large inter-bird variation in resource use emphasizes the individuality in resource use exhibited by the study population.

Case II: Estimating an RSF Using Poisson Regression with an Offset Term

As an alternative to case I, the analysis of case II defines habitat units as circular or rectangular areas centered on points across the study area or home range of each animal and can be applied to location data obtained under sample designs I–III. Given a large number of unbiased locations for each animal (Withey et al. 2001, Frair et al. 2004), the relative frequency of locations within a habitat unit provides a surrogate UD as the relative frequency of animal locations occurring in each sampled habitat unit. Using GIS, one can identify a large number of possible habitat units within a study area, selected by random or systematic sampling procedures. The habitat units should include an area small enough to detect changes in animal concentrations but large enough to ensure multiple locations will occur in some units. If possible, habitat units of different sizes should be investigated to help determine the effects on estimated coefficients. Selection of habitat unit size is analogous to the amount of smoothing introduced by selection of different bandwidths in estimation of a UD by kernel methods.

Given this approach, and considering that counts of animal locations are often modeled using Poisson distributions, Poisson

Table 1. Estimates of standardized parameter coefficients (β) for 25 Steller's jays nesting on the Olympic Peninsula of Washington State. P values test the null hypothesis that the average $\beta = 0$, given $n = 25$ jays. Relative importance of resources is indicated by the magnitude of β . Consistency in selection at the population level is indicated by the significance of β and the number of jays whose use was either positively or negatively associated with each attribute (from Marzluff et al. 2004).

Resource attribute	Mean standardized β	95% Confidence interval	P ($\beta = 0$)	No. of jays with use significantly associated with attribute	
				+	-
No. of patches	+0.11 ^a	-0.57-0.28	0.19	14 ^a	9
Contrast-weighted edge	+0.06 ^a	-0.13-0.26	0.50	10 ^a	9
Mature forest	-0.05	-0.18-0.08	0.45	12	8
Clear cut	-0.04	-0.17-0.09	0.51	6	9
Interspersion-juxtaposition	-0.01 ^a	-0.14-0.16	0.87	11	8 ^a
Patch-shape index	+0.01 ^a	-0.11-0.14	0.84	9 ^a	12

^a Use in direction predicted if jays select for edgy, fragmented areas within their home range.

regression with an offset term can be used to model the relative frequency, or probability of use, within a habitat unit. However, other generalized linear models, such as negative binomial regression, may also be appropriate. The approach presented here extends the Heisey (1985) method by modeling the probability of use based on continuous and categorical resource attributes and does not require partitioning of resources into “used” or “available” classes.

If locations are pooled across animals (e.g., design I) or inferences are made regarding an individual’s selection pattern, dependencies in relocations and over-dispersion should be investigated. If a population-level model is estimated under sample designs II or III using Eqs. (1) and (2), small-to-moderate over-dispersion (McCullagh and Nelder 1989) and spatial autocorrelation in the Poisson model is irrelevant because estimates of model coefficients are still unbiased (Liang and Zeger 1986, McCullagh and Nelder 1989), although the estimators may not be very efficient.

The Poisson model for the expected relative frequency of locations in habitat unit i is

$$\ln[E(r_i)] = \ln(\text{total}) + \beta_0 + \beta_1 x_1 + \dots + \beta_p x_p, \quad (5)$$

which is equivalent to

$$\begin{aligned} \ln[E(r_i/\text{total})] &= \ln[E(\text{Relative Frequency}_i)] \\ &= \beta_0 + \beta_1 x_1 + \dots + \beta_p x_p, \end{aligned} \quad (6)$$

where r_i is the number of recorded locations for the animal within habitat unit i , total is the total number of locations for the marked animal across all habitat units, and the predictor variables are denoted by x_1, \dots, x_p . The offset term $\ln(\text{total})$ in Eqs. (5) and (6) is a quantitative variable whose regression coefficient is set to 1.0. Because the offset in this model is the same for all sampled habitat units within the study area or home range for a particular animal, it is absorbed into the estimate of β_0 , and ensures the response variable being modeled is the relative frequency or probability of use, instead of the counts of use. For most habitat units, predictions of relative frequency or probability of use based on this model should be very small. As is common in statistical modeling, there is a danger of making predictions beyond the region of observations used to fit the model (Neter et al. 1996). A large prediction based on the case II model, particularly >1 , likely indicates the model is not appropriate for the particular levels of predictor variables.

Individual models can be evaluated and adjusted for over-dispersion by fitting the full model (i.e., all variables considered) and estimating the amount of over-dispersion (McCullagh and

Nelder 1989). Use of the negative binomial distribution in place of the Poisson in the above context would also allow for over-dispersion. However, for small-to-modest amounts of over-dispersion, the differences in parameter estimates between Poisson and negative binomial models can be neglected (McCullagh and Nelder 1989).

The Poisson regression approach outlined above differs from case I in 3 ways. First, it uses empirical data as the response variable when estimating the RSF, avoiding difficulties with differences in user-defined and software options in kernel estimation. However, this procedure requires the habitat unit area be specified, with user-defined options similar to the grid-cell size in the RUF analysis and the bandwidth (the neighborhood size) in kernel estimation. Second, it allows for nonconstant error variance, which can occur when modeling count data. Third, use of the offset term in the Poisson model should restrict predictions of probability of use to the $[0, 1]$ interval for sampled habitat units in the analysis and ensures predictions are nonnegative for all other habitat units. This simple approach to modeling relative frequency of use is a surrogate for estimating and modeling a UD surface. However, more investigation is needed before it is known how a certain density of recorded locations is necessary before reliable, precise estimates of probability of use can be obtained.

To facilitate a direct comparison between methods of cases I and II, we used the same data from the 25 jays. Habitat units for this analysis were defined as 200-m-radius buffers centered on each grid cell within the home ranges, which corresponds to the grain at which researchers thought jays responded to habitat changes (Marzluff et al. 2004). Using a random starting point, a systematic sample of 2,000 habitat units was drawn from each home range, with the exception of 1 jay with a smaller home range. A systematic sample of 1,500 habitat units was taken from jay 5343. The population-level model was estimated as

$$E(\text{Relative Frequency}) =$$

$$\exp \left[\begin{array}{l} -2.7040 + 0.1081(\text{no. patches}) \\ -0.0005(\text{m of high-contrast edge}) \\ +0.0005(\text{juxtaposition of land cover}) \\ +0.0105(\text{patch-shape index}) \\ -0.1239(\text{mature forest}) - 0.8315(\text{clear cut}) \end{array} \right]. \quad (8)$$

Standard errors and 95% confidence intervals based on $n = 25$ jays for the population-level model are presented in Table 2. None of the parameters for the habitat variables were found to be statistically significant for this model, as also noted by Marzluff

Table 2. Estimates of parameter coefficients (β) for 25 Steller’s jays nesting on the Olympic Peninsula of Washington State, based on the Poisson-regression model of the utilization distribution (UD) surface (case II). The 95% confidence intervals for the average jay were calculated using the standard error of the sample of $n = 25$ coefficients.

Resource attribute	Mean β	SE (β)	95% Confidence interval
No. of patches	0.1081	0.0596	-0.015-0.231
Contrast-weighted edge	-0.0005	0.0061	-0.013-0.012
Mature forest	-0.1239	0.1029	-0.336-0.088
Clear cut	-0.8315	0.8020	-2.487-0.824
Interspersion-juxtaposition	0.0005	0.0018	-0.003-0.004
Patch-shape index	0.0105	0.3116	-0.633-0.654

et al. (2004). Thus, high individual variation in resource use by jays was confirmed.

Regardless of the need for further evaluation of the individual models, the results from this analysis are similar to the population-level results from the analysis presented as case I. Clear-cut and mature forest areas had negative relationships with the expected probability of use for the average jay, whereas locations with a high number of patches and a large patch-shape index experienced more use. However, all the estimated coefficients had 95% confidence intervals encompassing zero (Table 2), because of high individuality in resource use by jays, indicating the need for a larger sample size or further variable selection, or perhaps, individual variation should be the focus rather than population-level inferences. Understanding individual variation in resource use is important for managers and researchers and can be understood by relating individual jay resource coefficients to other aspects of their home ranges as done by Marzluff et al. (2004).

Case III: Using the UD to Extend Compositional Analysis

Aebischer et al. (1993) were the first to propose use of compositional analysis, a multivariate analysis of variance, for studies of wildlife habitat selection. The technique is based on procedures outlined by Aitchison (1986) and is appropriate for designs II and III. Habitat use is defined by the proportion of each habitat type throughout an individual animal's use area (e.g., total home range, core area). Availability is similarly defined as the proportional occurrence of habitat types, but at a larger scale (e.g., study area; Johnson 1980).

A refined measure of use might be considered when the investigator wants to compare animal use within the home-range boundary to what is available in the study area. In the Aebischer et al. (1993) approach, once the outer boundary is delineated, either habitat use is assumed to be proportional to the raw proportion of the home-range polygon comprised of that patch, or nonrandom use within that boundary is simply ignored. Yet, nonrandom use should be our baseline expectation; there is little reason to assume that use will be completely random once the home-range boundary is established. The UD offers an ideal technique to overcome this issue because it allows us to incorporate more information about use within the home-range boundary. By incorporating the UD, we can directly estimate the amount each habitat is used. Each habitat can then be weighted by its estimated amount of use, so that both the proportion of that habitat within the home range and the amount of use of that habitat are integrated. This should provide a more accurate measure of selection because the UD allows us to quantify the disproportionate use of some habitats. We call our modification that incorporates the UD, the "weighted compositional analysis," and the traditional Aebischer et al. (1993) approach, the "unweighted compositional analysis." In our example, we first examine whether data show the expected pattern of nonrandom distribution within the home-range boundary. If this expected result is obtained, weighted compositional analysis is expected to give better insight into selection.

Our example used radiotelemetry data from 14 cow elk equipped with VHF transmitters in Custer, South Dakota, USA. For this example, all individuals had >50 locations during the spring season. First, we used Monte Carlo simulations to evaluate

whether radiotelemetry locations from these 14 elk showed deviations from complete spatial randomness (CSR; Diggle 1983). Under the assumption of CSR, intensity of use would be constant throughout each animal's home range, and locations would not be clustered in portions of the range. We calculated the empirical distribution function (EDF) of "origin-to-point nearest neighbor distances" ("point-to-nearest-event distances," F -hat; Diggle 1983, Kaluzny et al. 1997) for the observed locations and for points generated from completely random distributions. This metric estimates the proportion of points on a specified grid within distance d of the nearest point in the set of n locations (Kaluzny et al. 1997). We calculated F -hat for the observed locations. To examine whether the observed EDF was consistent with CSR, we generated 200 sets of random (randomly distributed x and y coordinates) locations within the 100% minimum convex polygon and calculated F -hat for each random set at the same set of distances used to calculate F -hat for the observed locations. We used the S+ Spatial Stats module (Kaluzny et al. 1997) in S-PLUS 2000 (MathSoft, Inc., Cambridge, Massachusetts) to evaluate the CSR assumption for each of 14 elk location sets.

Our results, summarized in Fig. 4, demonstrate that nearly all individuals exhibited some degree of spatial nonrandomness in space use within their home range. Based on these results, we concluded that use within the home range is not random, and thus, a weighted measure of resource use may give more accurate estimates of resource selection. We note that it is possible for randomness to be rejected, but for the unweighted analysis to give accurate results under some conditions if use of a habitat varies widely among patches of that habitat. For example, highly clumped location patterns could indicate high use of one patch of a habitat, low use of another patch of that habitat, and overall similarity of use versus availability of that habitat. However, in such a situation, a weighted and unweighted analysis should produce identical results.

Next, we developed UDs for each individual elk using fixed kernel techniques and PI smoothing. We used a normal kernel for all density estimates (Silverman 1986). To remain consistent with other resource selection studies and to reduce potential bias from the tails of the UD, we included only 95% of the UD (by volume). We overlaid the UD grid on the habitat patch GIS map using ArcView 3.2 (Environmental Systems Research Institute, Redlands, California) and summed the raw UD values by patch type. For each habitat type, we divided the summed UD value by the total UD value of all patches (i.e., 0.95) to obtain a UD-weighted estimate of use for each habitat type for each individual animal.

We compared the results of compositional analysis using the unweighted approach (Aebischer et al. 1993) and our weighted UD method. We used 7 habitat types based on habitat structural stage; these included early successional (ponderosa pine <20.3 cm diameter, breast height [dbh]), low canopy-closure forest (ponderosa pine stands >20.3 cm dbh and <40% canopy closure), mid canopy-closure forest (ponderosa pine stands >20.3 cm dbh and 41–70% canopy closure), high canopy-closure forest (ponderosa pine stands >20.3 cm dbh and 71–100% canopy closure), fire-killed forest, meadows, and other (habitats that occurred in low proportion). We subtracted differences in the log-transformed availability data from the log-transformed use data for each animal

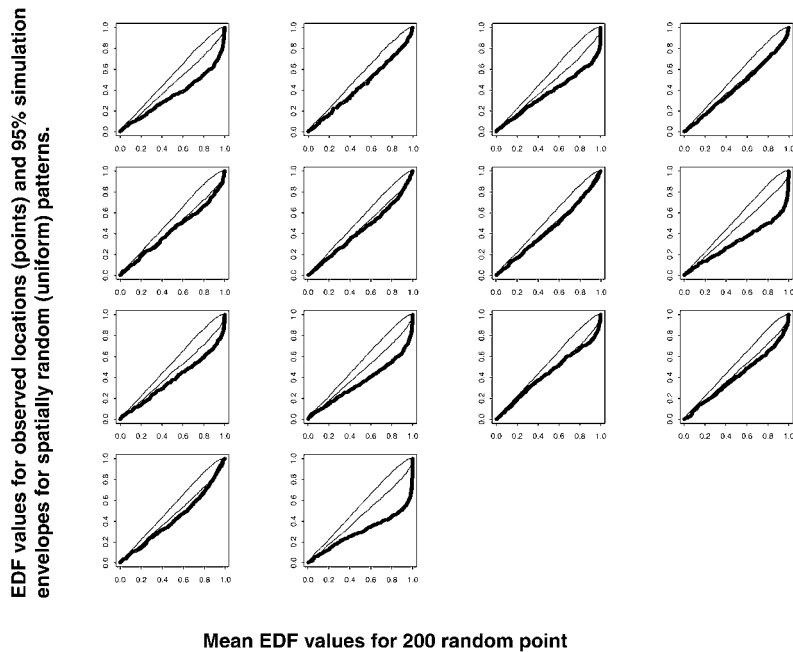


Figure 4. Plots represent the empirical distribution function (EDF) values of origin-to-point-nearest-neighbor distances for observed locations from 14 radio-collared elk used in case III (points) or 95% confidence envelopes from 200 spatially random patterns (lines) vs. the mean EDF values from these 200 uniform patterns.

and then tested for overall selection using Wilks' lambda statistic. When use differed from availability, we calculated the mean and standard deviation for the log-ratio differences, which were used to rank each habitat type. We used *t*-tests to assess difference between ranks and to determine where selection differed by habitat pairs (Aebsicher et al. 1993, Erickson et al. 2001).

When comparing the unweighted and weighted UD methods, we observed changes in overall habitat rankings and differences in significant habitat pair comparisons, despite relatively little change in use patterns (Fig. 5). Although the highest-ranked habitat (mid canopy-closure forests) and the lowest-ranked habitat (early successional) remained the same, important ranking differences were noted among other habitat types for the 2 analysis techniques. For example, the meadow habitat type was the second-most selected habitat when incorporating the UD, whereas the unweighted UD method ranked it below low, mid, and high canopy-closure habitat types.

The weighted compositional analysis approach retains the ease of interpretation of traditional compositional analysis but incorporates additional information on use as estimated by the UD. The additional biological insight obtained by using the UD, compared with unweighted compositional analysis, will be greatest when use within the home-range boundary is highly nonrandom. Our simplistic example demonstrates that nonrandomness in space use within the home range can affect conclusions of resource selection studies when not considered, even in cases where clustering is modest (Fig. 5). In our example, elk apparently used the meadow habitat to a greater degree than was represented by computing the proportion of that habitat within the home-range boundary. Thus, those areas where intensive use is likely to occur might be underrepresented in the traditional analysis, particularly if certain resource types do not occur in great proportion within the home-range boundary. This finding has important management impli-

cations because important resources occurring in limited amounts might be ranked low in the unweighted model. Conversely, it is likely that underused habitats could be weighted more heavily in cases where that resource is prevalent, yet used little. Both of these problems can be addressed by incorporating the UD to quantify use.

Discussion

The main advantage of using the UD (or a surrogate) in resource selection analyses is the ability to consider resource use in a probabilistic manner throughout an animal's range and incorporate a continuous measure of use. Whereas most resource selection techniques have relied on a fixed definition of use of a point or unit during the study period (e.g., presence of an animal during an aerial survey), UD procedures account for differential use intensities throughout an animal's range. Therefore, emphasis shifts away from overall indices of use toward better understanding of the underlying pattern of space use during the study period. We believe this emphasis is appropriate given that animal use within the home range should be viewed in a probabilistic sense. With the recognition that all areas within the home range have some probability of use, the focus on RSF estimation addresses how resources change the probability density function. For some study designs (e.g., design III) the estimated spatial extent of what is used helps define the spatial bounds of what is available (i.e., home range). We view this situation favorably because under this scenario the comparison of use and availability is a continuous process (i.e., comparing intensity of use across the region considered available) versus a dichotomous one (i.e., used vs. available). Furthermore, by summarizing animal movements in a continuous and probabilistic framework, it becomes possible to quantify the degree of nonrandomness in resource use for analyses such as compositional analysis, and individual differences in resource use are highlighted and amenable to future analysis.

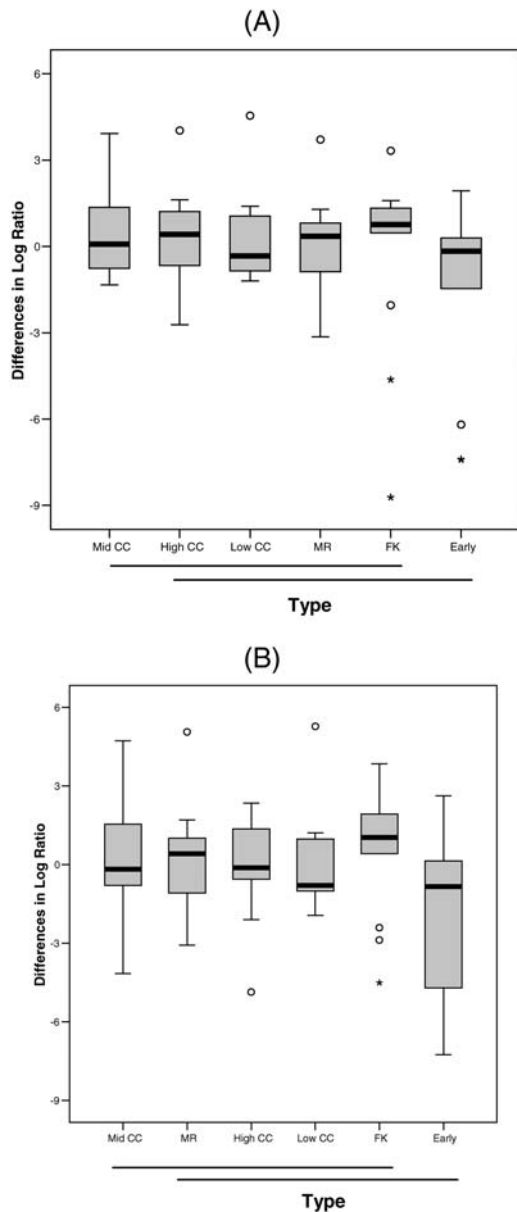


Figure 5. Box plots of differences in the log ratio based on the (A) unweighted and (B) weighted utilization distribution from the compositional analysis of 14 elk for 7 habitat types. Habitats appear in order of ranking on the x axis (i.e., the mid canopy-closure forest received the highest rank using both approaches). Habitats sharing underscore were not significantly different based on *t*-tests ($P < 0.05$). Mid CC = mid canopy-closure forest; MR = meadow; High CC = high canopy-closure forest; FK = fire-killed forest; Early = early successional.

Both cases I and II require selection of the covariates, including interactions and polynomial terms, to be included in the basic models fitted to the individual animals. This important step has been ignored in this article for the sake of brevity. Estimates of variation in estimates or coefficients of RSFs are relatively empirical in case II, but they are, as usual, conditional on the model used (e.g., Poisson regression) and covariates fitted. It is relatively more difficult to quantify variation of estimates and coefficients in case I because of bandwidth selection and other user-options in UD estimation. In earlier modeling of resource selection (e.g., Manly et al. 2002), the analyses and models depended on a fixed definition of “use” as measured by the study

protocol during the study period. Units were either “used” or “not used.” Use of the UD in estimation of an RSF allows the pattern of space use to be more appropriately modeled, but we grant that inferences continue to be limited to probability of use during the study period as measured by the study protocol.

Under sample designs I–III, a more traditional RSF estimation procedure has been to fit the coefficients of an exponential RSF using logistic regression (Manly et al. 2002) for a fixed definition of use of a point or unit during the study period. This procedure is an efficient method of RSF estimation because of its simplicity in comparing used locations to points or habitats considered available and the wide availability of standard logistic-regression software. Logistic regression in use-availability studies requires low probabilities of use for most habitat units and correct model specifications, otherwise assumptions are not guaranteed (Manly et al. 2002, Keating and Cherry 2004, Nielson et al. 2004). Generally, most resource selection studies involve relatively rare species or events (e.g., spotted owls, brown bear den sites), and when dealing with GIS data, there can be an extremely large number of possible habitat units within a study area, and thus, the probability of use for any one unit should be small. For any situation, the logistic-regression approach to use-availability data can be relied on to correctly rank the habitat units in order of importance (Keating and Cherry 2004).

Before application of UD methods, it is also necessary to consider the assumptions. First, given that the UD surface is estimated from sample points, we assume the UD accurately estimates the probability of use even in areas where the animal was not located. Increasing the number of observations will usually help UD estimation (Seaman et al. 1999), thus, integrating GPS data with UD procedures might be appropriate. Second, we assume that enough sample points have been obtained to estimate the UD. Sample size is a critical issue in kernel-based UD estimation (Seaman et al. 1999, Kernohan et al. 2001), and often, greater than 30–50 independent locations are required per animal to obtain an adequate surface and size fit. Thus, we recommend that studies with fewer than 30 locations during the period of interest per individual not use UD approaches. The UD method requires enough locations that the smoothed surface is adequate, whereas the more-empirical Poisson modeling requires that a substantial number of sample units contain one or more locations. The specific form of the kernel and bandwidth selection options is important, and consequently, computer software to estimate the UD should be considered. A careful review of the literature is necessary to ensure user-defined options are appropriately selected so that UD estimation is robust. Last, we acknowledge that problems with defining availability are still present, although less obvious, which ultimately influences management recommendations resulting from resource selection analyses. For example, if UD density values are related to resource attributes at grid points in some area (Marzluff et al. 2004), all grid points within that area (e.g., 95% home range) are treated as “available.” In a sense, the approach examines the intensity of use of available resources.

Management Implications

The choice of analysis in resource selection studies depends on study objectives, a given species’ ecology and habitat, the available

data, and assumptions of both the data and analysis. We provide an alternative framework for data analysis that should be considered 1) when locations from unique individuals are collected, and there is interest in documenting resource selection within a defined study area or individual home ranges (study designs II and III); 2) when differential use patterns exist within an animal's home range resulting in nonrandom use; 3) when there is interest in assessing the variability of individual animal resource selection patterns while allowing for population-level inferences; 4) when behavior-specific resource selection is important; 5) when resource data can be readily mapped and joined with animal UD's; and 6) when designation of "used and available resources" is problematic. Advantages over other procedures are likely greatest when designation of "used and available points" is problematic, placement of animal locations in specific habitats is difficult (e.g., telemetry error), and nonrandom use patterns within the home range exist. Thus, UD-based approaches help overcome some problems with several commonly used procedures. In addition to properly treating the animal as the sampling unit (Otis and White 1999), UD procedures rely on the pattern of animal space-use rather than using individual sampling points. By considering resource use in a probabilistic manner, RSF estimation identifies how resources directly change the probability density function. Despite issues with UD estimation, these benefits outweigh the potential drawbacks in many circumstances.

Also, the ability to directly evaluate behavior-specific resource selection should be viewed favorably because we can begin to understand why animals use resources disproportionately (Marzluff et al. 2001).

Acknowledgments

J. Millspaugh is grateful to the Missouri Department of Conservation; University of Missouri; University of Washington; South Dakota Department of Game, Fish, and Parks; U.S. Forest Service; U.S. Fish and Wildlife Service; Boise Cascade Corporation; the Prairie Fork Conservation Fund; and the Rocky Mountain Elk Foundation for support of his resource selection research. He also thanks A. Cooper, G. Brundige, B. Kernohan, A. Rodgers, J. Skalski, and his coauthors for discussions on UD estimation and application. Discussions with E. D. Ford and T. P. Cardoso initiated the use of Monte Carlo tests of randomness under case III. J. Marzluff's work was stimulated by interaction with M. Handcock, P. Hurvitz, J. Millspaugh, and E. Neatherlin. It was supported by The University of Washington, Washington Department of Natural Resources, U.S. Forest Service, Pacific Northwest Research Center, Rayonier Timber, Weyerhaeuser, U.S. Fish and Wildlife Service, Port Blakely Timber, and Sustainable Ecosystems Institute. We appreciate helpful comments from J. Nichols and D. Strickland on an earlier draft of this manuscript.

Literature Cited

- Aebischer, N. J., P. A. Roberston, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Aitchison, J. 1986. *The statistical analysis of compositional data*. Chapman and Hall, London, United Kingdom.
- Amstrup, S. C., T. L. McDonald, and G. M. Durner. 2004. Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin* 32:661–679.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794–804.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77:215–227.
- Beringer, J., J. J. Millspaugh, J. Sartwell, and R. Woeck. 2004. Real-time video recording of food selection by captive white-tailed deer. *Wildlife Society Bulletin* 32:648–654.
- Buskirk, S. W., and J. J. Millspaugh. 2006. Metrics for studies of resource selection. *Journal of Wildlife Management* 70:in press.
- Clark, J., J. E. Dunn, and K. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57:519–526.
- Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566–575.
- Cooper, A. B., and J. J. Millspaugh. 2001. Accounting for variation in resource availability and animal behavior in resource selection studies. Pages 243–274 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Cowling, A., and P. Hall. 1996. On pseudodata methods for removing boundary effects in kernel density estimation. *Journal of the Royal Statistical Society B* 58:551–563.
- Diggle, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic, London, United Kingdom.
- Erickson, W. P., T. L. McDonald, and R. Skinner. 1998. Habitat selection using GIS data: a case study. *Journal of Agricultural, Biological, and Environmental Statistics* 3:296–311.
- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studied with radio-marked animals. Pages 211–242 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Fielding, A. L., and J. F. Bell. 1997. A review of methods for assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and L. B. Hawthorne. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 16–42 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27:489–505.
- Gitzen, R. A., and J. J. Millspaugh. 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildlife Society Bulletin* 31:823–831.
- Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed kernel analysis of animal range use. *Journal of Wildlife Management*: in press.
- Hall, P., and T. Tao. 2002. Relative efficiencies of kernel and local likelihood density estimators. *Journal of the Royal Statistical Society B* 64:537–547.
- Handcock, M. S., and M. L. Stein. 1993. A Bayesian analysis of kriging. *Technometrics* 35:403–410.
- Heisey, D. M. 1985. Analyzing selection experiments with log-linear models. *Ecology* 66:1744–1748.
- Hjort, N. L., and M. C. Jones. 1996. Locally parametric nonparametric density estimation. *Annals of Statistics* 24:1619–1647.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kaluzny, S., S. C. Vega, T. P. Cardoso, and A. A. Shelly. 1997. *S+ spatial statistics*. Springer-Verlag, New York, New York, USA.
- Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68:774–789.
- Kenward, R. E., R. T. Clarke, K. H. Hodder, and S. S. Walls. 2001. Density and

- linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. *Ecology* 82:1905–1920.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Knick, S.T., D. Dyer, and D. L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61:75–85.
- Liang, K. Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* 73:13–22.
- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277–291.
- Loader, C. R. 1999. *Local regression and likelihood*. Springer-Verlag, New York, New York, USA.
- Manly, B. F. J., L. L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second edition. Kluwer Academic, Boston, Massachusetts, USA.
- Marron, J. S., and S. S. Chung. 2001. Presentation of smoothers: the family approach. *Computational Statistics* 16:195–207.
- Marzluff, J. M., and M. Restani. 1999. The effects of forest fragmentation on avian nest predation. Pages 155–169 in J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. *Forest fragmentation: wildlife and management implications*. Brill Academic, Leiden, The Netherlands.
- Marzluff, S., T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. Pages 310–326 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Marzluff, J., J. Millspaugh, P. Hurvitz, and M. A. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Second edition. Monographs on statistics and applied probability number 37. Chapman and Hall, London, United Kingdom.
- McDonald, T. L., and L. L. McDonald. 2002. A new ecological risk assessment procedure using resource selection models and geographic information systems. *Wildlife Society Bulletin* 30:1015–1021.
- Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. *Journal of Wildlife Management* 64:994–1003.
- Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2004a. Herd organization of cow elk in Custer State Park, South Dakota. *Wildlife Society Bulletin* 32:506–614.
- Millspaugh, J. J., R. A. Gitzen, B. J. Kernohan, M. Larson, and C. Clay. 2004b. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32:148–157.
- Millspaugh, J. J., and J. M. Marzluff, editors. 2001. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Müller, H. G., and U. Stadtmüller. 1999. Multivariate boundary kernels and a continuous least squares principle. *Journal of the Royal Statistical Society B* 61:439–458.
- Neatherlin, E. A., and J. M. Marzluff. 2004. Campgrounds enable American crows to colonize remote native forests. *Journal of Wildlife Management* 68:708–718.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*. McGraw-Hill, Boston, Massachusetts, USA.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13:45–56.
- Nielson, R. M., B. F. J. Manly, and L. L. McDonald. 2004. A preliminary study of the bias and variance when estimating a resource selection function with separate samples of used and available resource units. Pages 28–34 in S. Huzurbazar, editor. *Resource selection methods and applications*. Omnipress, Madison, Wisconsin, USA.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63:1039–1044.
- Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Verification of a spatially explicit habitat model for Rocky Mountain elk. *Journal of Wildlife Management* 65:899–914.
- Sawyer, H., R. M. Nielson, L. L. McDonald, and D. Strickland. 2004. Sublette mule deer study: long-term monitoring plan to assess potential impacts of energy development on mule deer in the Pinedale Anticline Project Area. Western EcoSystems Technology, Inc., Cheyenne, Wyoming, USA. <http://www.west-inc.com/big_game_reports.php>. Accessed 2005 July 10.
- Scott, D. W. 1992. *Multivariate density estimation: theory, practice, and visualization*. Wiley, New York, New York, USA.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Seidel, K. D. 1992. *Statistical properties and applications of a new measure of joint space use for wildlife*. Thesis, University of Washington, Seattle, USA.
- Silverman, B. W. 1986. *Density estimation for statistics and data analysis*. Chapman and Hall, London, United Kingdom.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322–330.
- Van Winkle, W. 1975. Comparison of several probabilistic home-range models. *Journal of Wildlife Management* 39:118–123.
- Wand, M. P., and M. C. Jones. 1995. *Kernel smoothing*. Chapman and Hall, London, United Kingdom.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic, San Diego, California, USA.
- Withey, J. C., T. D. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pages 43–69 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, San Diego, California, USA.
- Worton, B. J. 1987. A review of models of home range for animal movement. *Ecological Modeling* 38:277–298.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Zar, J. H. 1996. *Biostatistical analysis*. Fourth edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Associate Editors: Strickland and McDonald.