

INCORPORATING RESOURCE UTILIZATION DISTRIBUTIONS INTO THE STUDY OF RESOURCE SELECTION: DEALING WITH SPATIAL AUTOCORRELATION

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Abstract: An accurate estimate of resource use by an animal can be summarized by regressing local- and landscape-level resources on an individual animal's or population's utilization distribution (UD) in a spatially explicit way. The resulting equation is termed a Resource Utilization Function and the regression coefficients indicate the intensity, direction, and consistency of resource use. However, using the UD as a response variable requires sampling individual pixels within the UD, which introduces spatial autocorrelation into the data, potentially affecting results and conclusions regarding resource use by the study animal. We discuss methods to remove the spatial autocorrelation so that the significance of regression coefficients for each resource can be evaluated for each animal. By using this methodology, we are able to quantify the individualistic nature of resource selection and test for consistency in use of resources by a population. We demonstrate the effects of removing spatial autocorrelation on individual parameter estimates of resource use by individual animals using radio telemetry data for 25 radio-tagged Steller's jays (*Cyanocitta stelleri*) in western Washington. The technique of removing spatial autocorrelation from our samples allows the use of pixel-level sampling of the UD in future resource selection studies.

Key words: habitat selection, habitat use, kernel, GIS, multiple regression, resource selection, resource utilization function, Steller's jay, spatial autocorrelation, utilization distribution, spatially-autocorrelated regression error

Many analytical techniques are available to quantify resource selection by animals (Manly et al. 1993, Erickson et al. 2001, Boyce et al. 2002). Recently, regressions of local- and landscape-level resource attributes have been related to continuously varying measures of space use by animals (Marzluff et al. In Press). This approach produces a Resource Utilization Function (RUF) that relates resources to the height of a utilization distribution (UD). As a probability distribution that quantifies an individual's or group's relative use of space, the utilization distribution is an excellent representation of variation in space use (Kernohan et al. 2001). Moreover, even with limited sampling of animal locations, estimation of Uds with fixed kernel procedures accurately reflect the true UD (Seaman et al. 1999). The coefficients associated with each variable in the RUF quantify the intensity, direction, and consistency of resource use much like they do in Manly et al.'s (1993) resource selection functions (RSFs). However, RUFs improve on more commonly used approaches like RSFs because they are not limited to discrete designations of resource use (used versus not used or used versus "available"). RUFs relate the degree of resource use to any measurable aspect of a resource that can be mapped.

Many resource selection techniques quantify use by relying on individual observations or radio locations as experimental units (Thomas and Taylor 1990, Manly et al. 1993). However, individual locations are not independent (Otis and White 1999) which artificially increases the statistical power of a test statistic. Quantification of resource use may be better described using a single composite measure from each animal (Johnson 1980, Millsap and Marzluff 2001). This has recently taken the form of a selection coefficient (Manly et al. 1993) or a log-ratio-transformed component of a composition (Aebischer et al. 1993) derived by comparing used to available resources. We extend this approach by examining variation in use within a "home range." This correctly relies on individuals or groups of individuals (ranges of populations, herds, etc.) as the experimental unit (Otis and White 1999) and objectively designates all areas used by the animals of interest as "available." Environmental autocorrelation is normal (Scheigg 2003) and results in spatial clumping of resources. This complicates analysis of Uds because it will lead to spatial autocorrelation of resource use. In addition, home range estimates using fixed kernel estimates use bandwidth as a smoothing factor (Kernohan et al. 2001) to extrapolate single point locations across a surface, explicitly introducing spatial autocorrelation into the UD. Spatial autocorrelation within samples will invalidate the assumption of independence among observations required by statistical hypothesis testing, and inflate the probability of a type I error (Legendre 1993, Legendre et al. 2002) because of underestimates of variance associated with parameter coefficients (Lennon 1999, 2000). While de Solla et al. (1999) used Monte Carlo

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simulation to demonstrate that spatial autocorrelation in radio locations did not affect home range size estimates using kernelling methods, we are concerned with the potential effects of spatial autocorrelation on coefficient estimates for resource use by individuals. Estimating parameters with a statistical framework that assumes no spatial autocorrelation in the samples when it is present will lead to variance estimates that are smaller than the actual variability of the data, increasing the likelihood of finding significance in explanatory variables in hypothesis testing. If, however, the effects of spatial autocorrelation are either removed before fitting a model or are explicitly incorporated in the statistical model used, variance estimates should be smaller than those of the incorrectly specified model mentioned above and conclusions of significance will be unbiased.

Because we use pixel-level samples within the UD (our response variable), our methodology requires the removal of the effects of spatial autocorrelation when relating variables from pixel-level data within an animal's home range to the UD values. Many different techniques to account for or remove the effects of spatial autocorrelation have been used for different types of analysis (e.g., inflating variance estimates for modeling bird abundance: Vernier et al. 2002; detecting species associations using a random patterns test: Roxburgh and Chesson 1998; autologistic models for predicting species presence: Augustin et al. 1998).

In this paper we describe a procedure that relates UD to resources in a Geographic Information System (GIS) environment and illustrate how to remove the effects of spatial autocorrelation when looking at individual pixels within a UD of an individual animal. As an example, we test the effect of spatial autocorrelation on the significance and sign of parameter estimates for selection of resources by individual Steller's Jays (*Cyanocitta stelleri*).

METHODS

Radio-tracking Steller's Jays

We used radio locations from 25 adequately sampled (>30 locations; Seaman et al. 1999) breeding Steller's Jays during the nesting and chick-rearing season (April – September) from 1995-1998. Each individual was only monitored during one year. We fitted jays with 6g, back-pack mounted transmitters to facilitate our observations. We homed in on jays 1-3 times per week and recorded their locations on maps/photos of the study site. A global positioning system was used to record locations in remote areas. During each 1-2 hr focal observation period we plotted the entire area used by a bird, then recorded 2 - 3 locations (extreme and mid points of area used) for subsequent definition of the home range.

Quantifying Resources

We used a vegetation map derived from 1998 and 1990 Landsat Thematic Mapper imagery (Green et al. 1993) to delineate six land cover types at 25 m resolution: *late seral coniferous forest* (> 70% crown closure of conifer, with > 10% crown closure in trees > 21" DBH and < 75% hardwood/shrub); *mid seral coniferous forest* (> 70% crown closure of conifer, with < 10% crown closure in trees > 21" DBH and < 75% hardwood/shrub); *early seral coniferous forest* (> 10% and < 70% crown closure of conifer and < 75% hardwood/shrub); *clearcut/meadow/hardwood* (< 10% crown closure of conifer or > 75% hardwood); *water*; *non-forest lands* (urban areas, barren lands, agriculture, some very young regenerating lands). We used this land cover classification to measure six resource attributes at each 25m x 25m pixel within jay home ranges: (1-3) the land cover type (condensed as Mature forest = late seral and mid seral coniferous forest; Clearcut/meadow/hardwood; and Young forest and anthropogenic lands = young seral coniferous forest and non-forested lands), (4) contrast-weighted edge density, (5) interspersed-juxtaposition index, and (6) mean shape index (see McGarigal and Marks 1995 for calculation formulas; edges between mature forest and regenerating forest or settled areas received greatest weight). To determine the last three metrics, we used an analysis window with radius 200m centered on each pixel.

We defined the spatial extent of space use as the outer boundary of the 99% fixed kernel home range (Worton 1989; de Solla et al. 1999). This reduced subjectivity and limited our inference about resource use to the area inhabited by the animal based on relocation points. Jays may have selected their home ranges based on resources available at a larger scale than we are investigating.

Quantifying Animal Space Use

The UD is a bivariate function where height ($\hat{f}_{UD}(x,y)$) at location (x,y) represents the amount of use at that point relative to other locations (Silverman 1986; Figure 1). Kernel density estimation techniques have been applied in the statistical literature for more than a decade (Silverman 1986, Scott 1992, Kernohan et al. 2001) and have recently been evaluated as estimators of space use by animals (Worton 1989, Seaman and Powell 1996, Hansteen et al. 1997, Ostro et al. 1999, Seaman et al. 1999). Accurate kernel estimation assumes sampling is sufficient to

quantify relative differences in use (Garton et al. 2001). Simulation evaluations demonstrate that kernel-based estimators better represent differential space use than other UD techniques with adequate sample sizes and perform well under complex spatial point patterns (Seaman et al. 1999). Consequently, kernel-based estimators have become the standard for non-mechanistic models of animal movements (Kernohan et al. 2001). It is by computing the UD and using the associated probability density function ($\hat{f}_{UD}(x,y)$) throughout the UD that we can quantify a probabilistic measure of animal space use. We estimated the optimal bandwidth for each home range using least squares cross validation (Seaman and Powell 1996, Kernohan et al. 2001).

Relating Animal Use to Resources in a GIS Environment

Our approach consists of four basic steps (Figure 1): 1) estimate the UD using fixed kernel techniques (Seaman and Powell 1996), 2) measure the density estimate (i.e., the height of the UD) at each pixel within the UD, 3) determine the associated resources at the same pixels, and 4) relate height of the UD to resource values pixel by pixel using multiple regression to obtain coefficients of relative use of resources.

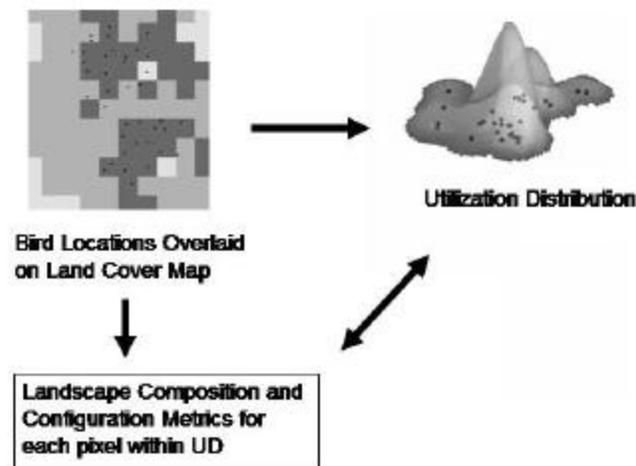


Figure 1. Schematic showing how we calculated a resource utilization function for a single Steller's jay. First, the jay's location estimates (upper left) are converted into a 3-dimensional utilization distribution (UD; upper right) using a fixed-kernel home range estimator. Second, resource attributes (e.g., landscape composition and configuration) are derived from resource maps within the area covered by the UD. The height of the UD is then related to these attributes on a pixel by pixel basis with multiple regression techniques that adjust the assumed error term for spatial autocorrelation.

We term the resulting regression equation the Resource Utilization Function (RUF) because it extends Manly et al.'s (1993) Resource Selection Function to the case where measured use is continuous rather than discrete (i.e., used or not-used). We regressed resource values at each pixel within an animal's home range to the corresponding value of the UD at that pixel. We measured multiple resources (land cover, edge, and fragmentation) at each pixel and related all resources to use simultaneously with multiple linear regression. Because the kernelling procedure induced spatial autocorrelation into our data, we developed a maximum likelihood estimator of regression coefficients that assumed spatially-dependent errors. Ordinary Least Squares (OLS) regression is based on the assumption that the deviations in the UD given the resource attributes are independent from pixel to pixel. However, the kernelling procedure induces a correlation between the deviations in neighboring pixels that must be adjusted for to produce efficient estimates of the regression coefficients. To do this we fit a spatial regression model to the UD with spatial correlation as a function of the distance between the pixels. Formally the model for the UD is:

$$\hat{f}_{UD}(x, y) = V(x, y)^T \mathbf{b} + Z(x, y) \quad x, y \in R$$

where $V(x)$ is the vector of resource attributes at the location (x, y) within the region R of positive density for the bird, and \mathbf{b} are the corresponding RUF coefficients. The spatially varying term $Z(x, y)$, $x, y \in R$ is a random field over R that approximates the correlation among values of $\hat{f}_{UD}(x, y)$ at different locations within the range induced by the kernelling. Because our landscape is continuous, simultaneous autoregressive (SAR) or conditional autoregressive (CAR) techniques, which operate on discrete, irregular lattices were not used. Instead we model $Z(x, y)$ as a mean-zero Gaussian process with correlation function:

$$Cor[Z(x, y), Z(x', y')] = K_{r, q} \left(\sqrt{(x - x')^2 + (y - y')^2} \right).$$

where

$$K_{r, q}(d) = \frac{1}{2^{q-1} \Gamma(q)} \cdot (d/r)^q B_q(d/r)$$

where Γ is the gamma function and B_q is the modified Bessel function of the third kind and order q discussed by Abramowitz and Stegun (1964, sec. 9). This is the Matern correlation function (Handcock and Stein 1993). It is a stationary model (i.e., the correlation is a function of the Euclidean distance between the two locations). The two parameters are the spatial range of dependence (r) and the smoothness of the UD surfaces themselves (q). The units of the range are meters, while the smoothness is the number of derivatives of the UD surfaces. Operationally, this means the UD surfaces realized from this model will have continuous $\lceil q \rceil - 1$ derivatives (almost certainly) where $\lceil \cdot \rceil$ is the integer ceiling function. For example, for values of q greater than 1 indicates that the UD is smooth enough to have one derivative existing. Larger values of q are associated with smoother UD estimates. Specifically, the $\lceil q \rceil - 1$ derivatives of the surfaces satisfy a Lipschitz condition of any order less than $\lceil q \rceil - q$. That is, there exists $C, d > 0$ such that $|\hat{f}_{UD}(x, y) - \hat{f}_{UD}(x', y')| < C |(x, y) - (x', y')|^a$ for $x, y, x', y' \in R$ almost certainly, if $|(x, y) - (x', y')| < d$ and $a + q < \lceil q \rceil$. The range is determined by the rate of decrease of the correlation between estimates of the UD with distance. Thus the covariance function captures the key characteristic of the estimates in a relatively parsimonious manner. The Matern model is being increasingly used to model continuous spatial processes because of its flexibility of form and its ability to capture a wide range of spatial dependencies. As the model is an approximation to the complex correlation induced by the kernelling, we used a maximum likelihood procedure to jointly estimate the spatial variance of $\hat{f}_{UD}(x, y)$, the RUF coefficients and the smoothness of the surfaces individually for each animal. The range (of smoothness) was set by the bandwidth used in each individual animal's kernelling procedure. Although the spatial correlation model is only approximately correct, the estimates of the regression coefficients based on it will be much closer to optimal than the OLS estimates as the fitted correlation function will be closer to the true correlation than the uncorrelated values implicit in OLS.

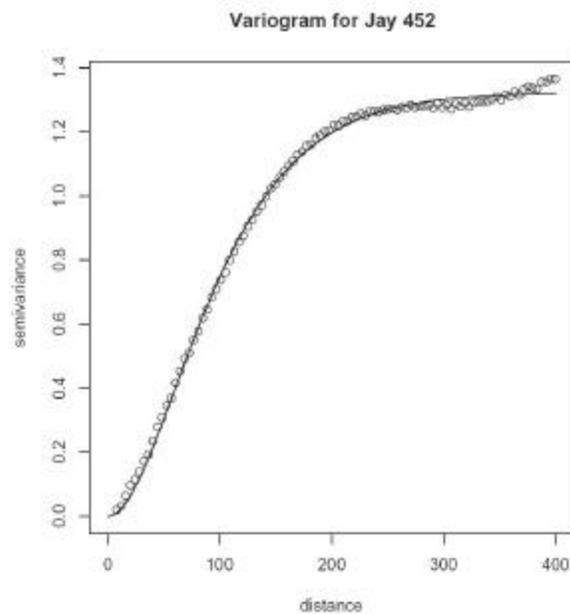
Subsequent analysis can use the individual coefficients for each resource for each animal as independent, replicated measures of resource use to test for population-level consistency in selection. Because the individual coefficients are easy to estimate directly using OLS regression, but require additional steps to estimate using a spatial correlation model, it is important to understand the effects that spatial autocorrelation have on the estimates of coefficients. We compared the coefficients (β_j 's) and their significance at the $\alpha = 0.05$ probability level for each resource variable (i) for each jay before and after correcting for spatial autocorrelation. Because positive β_j 's that are significantly greater than 0 indicate a positive correlation with use of a resource and significantly negative β_j 's indicate a negative correlation with use of a resource, any changes in sign before versus after correction for spatial autocorrelation are especially important.

RESULTS

Utilization distributions for Steller's Jays on Washington's Olympic Peninsula showed a high level of spatial autocorrelation. The range value for each jay was derived from the fixed kernel home range estimate using least-squares cross validation (LSCV) and input into the spatial regression model (mean = 140, median 160, range 54 to 268). The smoothing parameter estimated by the spatial regression model gives an indication of the spatial

autocorrelation. Spatial autocorrelation between contiguous pixels was high: the smoothing parameter ranged from 0.11 to 2.22 derivatives of the UD with a mean of 0.86 and a median of 0.25 for our 25 jays. Hence the estimates of UD ranged from continuous but very rough (0.11) to over twice differentiable (2.22). Thus the estimates exhibit substantial local variability. Figure 2 shows the plotted semivariogram for a jay with a smoothness MLE of 1.97 with a fit line superimposed. The spatial autocorrelation for this bird extended 250m from a focal pixel. The close fit between the observed data (the circles) and the form of the semivariogram curve indicates that the Matern form grossly fits our data. While the Matern function has infinite range, the effect range in this example is 250m.

Figure 2. Semivariogram (semivariance plotted versus lag distance) for Steller's jay number 452 with fitted line of trend superimposed. The point at which the line levels off is termed the range



and corresponds to the distance at which two samples (pixels in our case) are no longer spatially autocorrelated.

Despite the high degree of spatial autocorrelation in our data, removing it did not greatly alter our conclusions about resource use by Steller's Jays (Table 1). For all six resource variables, the β_j 's were as often or more often significant when the effects of spatial autocorrelation were removed and only five coefficients (of approximately 150 estimated) changed sign (Table 1). After adjusting for autocorrelation, 20 of the 25 jays concentrated their use in areas within their home ranges that were characterized by abundant patches and/or more edge. However, the difference between the mean β_j for each resource variable was minimal except for clearcut/meadow/hardwood and the mean variance estimate was approximately halved for our corrected β_j 's (Table 2). The relative magnitude and sign of corrected coefficients indicate that jays concentrated their use in areas within their home range that had high densities of landcover patches, high densities of contrast edge, low juxtaposition of landcover classes, complex-shaped landcover patches, and an abundance of young forest relative to mature forests or clearcuts (See Marzluff et al. In Press for more details)

Table 1. Number of RUF coefficients (β s) for 25 Steller's Jays nesting on the Olympic Peninsula of Washington State that were significantly different from zero ($\alpha = 0.05$) before and after correction for the effects of spatial autocorrelation.

Resource Attribute	Number of Jays with significant β estimates		
	Before Correction	After Correction	Number of Jays where β changed signs
Number of Patches	18	23	1
Contrast-weighted Edge	18	19	0
Mature Forest	15	23	2
Clear cut	14	15	0
Interspersion - Juxtaposition	19	19	2
Patch Shape Index	20	21	0

Table 2. Mean ($n = 25$) value for RUF coefficient estimates (β) before (Un) and after (Corr) correcting for spatial autocorrelation and the difference between the two estimates for the six resource variables tested.

Resource Attribute	Mean ($n = 25$) β estimate			Standard Error β estimate		
	Uncorrected	Corrected	Difference (Corr-Un)	Uncorrected	Corrected	Difference (Corr-Un)
Number of Patches	0.098	0.095	0.003	0.071	0.038	0.033
Contrast-weighted Edge	0.005	0.005	-0.001	0.006	0.003	0.003
Mature Forest	-0.160	-0.139	-0.021	0.203	0.120	0.084
Clear cut	-0.263	-0.310	0.046	0.279	0.148	0.131
Interspersion - Juxtaposition	-0.001	-0.001	0.001	0.002	0.001	0.001
Patch Shape Index	0.111	0.136	-0.025	0.432	0.225	0.207

DISCUSSION and CONCLUSIONS

Animals move in response to resources in their environment which tend to be clumped adding spatial autocorrelation to sample data. This source of spatial autocorrelation is generally controlled for by adding a minimum time between subsequent observations. However, since the phenomenon we are interested in (resource use) is inherently a non-independent phenomenon, it would be more appropriate to use a statistical framework that explicitly models the spatial autocorrelation in the data.

To explore the effects of spatial autocorrelation when using Utilization Distribution (UD) to generate a resource utilization function (RUF) we used data from 25 Steller's Jays to generate 25 separate RUFs before and after the effects of spatial autocorrelation were removed. Our methods can be extended through the use of standardized estimates of coefficients to make generalizations about resource selection by animals (e.g., Marzluff et al. In Press). Although the amount of spatial autocorrelation in our pixel-level samples within the UD was high, the effect of removing spatial autocorrelation from the coefficients did not greatly alter our results. Of the six variables for 25 birds, only 5 (of 150 possible) changed the direction of their correlation. Our results show that, while estimates of variance derived from an incorrectly specified statistical form (e.g., OLS) to model spatially autocorrelated data may be smaller than the true variability in the data (e.g., Legendre 1993, Legendre et al. 2002, Lennon 1999, 2000), the true variance estimates when spatial autocorrelation is explicitly accounted for are actually smaller than the estimates from the incorrectly specified model.

The ability to account for spatial autocorrelation in the UD and explanatory variables improves on existing techniques by explaining a larger proportion of the variance in the response variable. The ability of the RUF to use all the information a researcher gathers on resources and their relative use by animals, its ease of application in a GIS environment, and its reliance on standard statistical procedures (i.e., calculation of probability density functions, multiple regression with error adjustments for spatial autocorrelation) make it an intuitive, flexible, and powerful advancement. The use of the Matern covariance model is standard in the field of spatial statistics. The models here were fit using the **geor** package within the **R** environment for statistical computing and graphics. Both are available free of charge from www.r-project.org and run on most computer platforms.

We anticipate analytical and biological advancements in our technique. Analyses will advance with continued research on point process models so that resource use can be directly related to resource properties in a spatially-explicit manner without the need to first derive a UD. The observed information can be more appropriately modeled as a realization of a spatial point process. We are exploring Poisson processes with non-parametric intensity functions and alternatives with second-order dependence. These methods estimate the UD directly and automatically adjust for the correlation without the need for an ancillary spatial correlation model. Biological advancements may occur with behaviorally-specific analyses of resource use (Cooper and Millspaugh 2001, Marzluff et al. 2001). This could be done by gathering a sufficient sample of locations where specific behaviors occurred and creating conditional (behavior-specific) utilization distributions (Marzluff et al. 2001). This quantification of use for a specific behavior could then be related to resources using the RUF technique. In this way, we would become increasingly knowledgeable of why animals use the landscape in nonuniform ways. Our study was of foraging jays; over 90% of our jay locations were made as jays searched for and procured food. Therefore, our RUF relates jays to food resources. Alternatively, one could have used only roost locations or nesting locations, for example, to construct RUFs for other important behaviors.

The choice of what analytical technique to use ultimately depends on characteristics of the data, study objectives, and assumptions of the data and analytical techniques. Each analytical procedure has several important assumptions and researchers should carefully consider which assumptions are most violated in their study (e.g., “can I adequately document resource availability?”). Important assumptions to consider include experimental unit designation (Aebischer et al. 1993), definitions of resource availability (Cooper and Millspaugh 1999), and use of points to quantify resource use (Aebischer et al. 1993). Towards this end, we suggest researchers use expert systems (Starfield and Bleloch 1986) to help determine which analytical techniques to use. Expert systems would allow an objective way of determining what technique to use based on study objectives and sampling limitations. It is our contention that the animal should be the experimental unit, quantifying resource availability is problematic, and that a continuous measure of space use through an animal’s range most adequately describes resource use. Our approach satisfies these needs without assuming that points directly represent use, or that comparisons of used and unused points (which could have been used at another time) are needed to quantify resource selection. For these reasons, we believe the RUF will be a useful technique for others studying resource selection.

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