RELATING RESOURCES TO A PROBABILISTIC MEASURE OF SPACE USE: FOREST FRAGMENTS AND STELLER'S JAYS

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Abstract. Many analytical techniques that assess resource selection focus on individual relocation points as the sample unit and classify resources as either used or available. Commonly, the relative use of each resource is quantified as the number of observations in each resource class or the proportional occurrence of a resource within a home range. We believe that a more accurate estimate can be summarized by a utilization distribution (UD). We present an analytical approach that explicitly incorporates a probabilistic measure of use, as defined by the UD. We used animal relocation points and fixed-kernel techniques to determine a UD within a home range. We related this probabilistic measure of use to categorical and continuous resource variables using multiple regression. Regression errors accounted for spatial autocorrelation so that the significance of regression coefficients could be appraised for each animal and averaged across animals. This allowed us to quantify the individualistic nature of resource selection and test for consistency in use of resources by a population. Sample sizes in population assessments correctly reflected the individual animal as the experimental unit. We used this technique in a geographic information system setting to examine the importance of local-scale (forest cover) and landscape-scale (degree of fragmentation, proximity to edges and human use areas) attributes to breeding season habitat selection by 25 radio-tagged Steller's Jays (*Cyanocitta stelleri*) in western Washington State, USA. Individual jays varied significantly in habitat use, but most (20) concentrated their use in areas with many vegetation patches or in areas with extensive edge between forest and nonforested land cover. This confirmed our prediction that jays prefer fragmented habitat and forest edges and helped to explain why jays are most abundant in fragmented landscapes. However, we refined our understanding of why they used such habitats by demonstrating that landscape attributes affected use of local habitat features: high-contrast edges were used most if they were associated with small human settlements and campgrounds. Use of patchy and edgy areas within home ranges may be reinforced by natural selection because jays that inhabited areas with complex-shaped patches and concentrated their activity in such areas were most likely to fledge young. Concentration of use along forest–human land use interfaces may explain the greater risk of nest predation to other birds in such settings.

Key words: Cyanocitta stelleri; edge effect; fragmentation; habitat selection; habitat use; kernel; nest predation; resource selection; resource utilization function; spatial autocorrelation; Steller's Jay; utilization distribution.

INTRODUCTION

Many analytical techniques are available to quantify resource selection by animals (Erickson et al. 2001, Manly et al. 2002). Commonly, resource attributes where animals are observed are compared to attributes at sites that are considered available (Thomas and Taylor 1990). A comparison of use vs. availability may take several forms, including simple univariate comparisons of categorical resources (Neu et al. 1974) to sophisticated multivariate techniques such as discrete-choice modeling (Cooper and Millspaugh 1999, 2001)

and logistic regression (Manly et al. 2002) that incorporate continuous and categorical resource variables. Each technique has advantages and disadvantages (Alldredge and Ratti 1986, 1992, Aebischer et al. 1993, Leban et al. 2001), so choosing among them ultimately depends on objectives of the research, the types of data available, and assumptions of the data and analytical procedures (Alldredge and Ratti 1986, 1992).

Problematic assumptions inherent in these procedures include inappropriate level of sampling and inadequate sample size, the unit-sum constraint (i.e., use of all levels of a categorical variable sums to 1), and arbitrary definition of habitat availability (Aebischer et al. 1993). Compositional analysis and logistic regression avoid the unit-sum constraint and allow specific consideration of differential habitat use by individuals
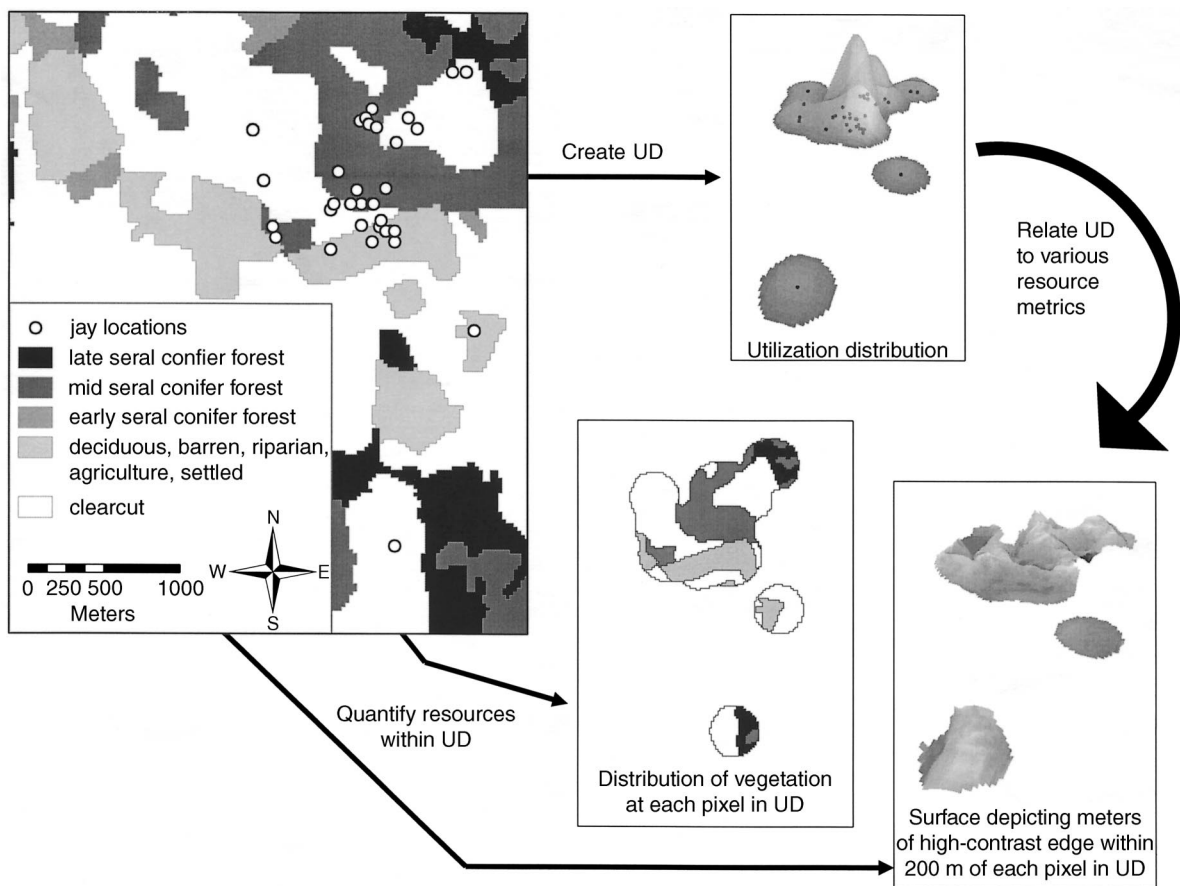
FIG. 1. Calculation of a resource utilization function for a single Steller's Jay. First, the jay's location estimates (upper left) are converted into a three-dimensional utilization distribution (UD; upper right) using a fixed-kernel home range estimator. The height of the UD indicates the relative 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, we 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 × 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.

(Aebischer et al. 1993, Erickson et al. 2001). Discrete choice helps to refine the scale at which availability is defined (Cooper and Millspaugh 1999, 2001). Mahalanobis distance techniques map resource use of populations without considering resource availability (Clark et al. 1993). Despite such advancements, even these analytical procedures are limited by the inability to account for resource use of variable intensity within an area of interest (e.g., an animal's range; Marzluff et al. 2001).

The vast majority of resource selection techniques quantify use by relying on the individual observations as experimental units (Thomas and Taylor 1990, Manly et al. 2002). However, individual locations are not independent (Otis and White 1999). If P values are of interest (Johnson 1999, Burnham and Anderson 2002), the use of individual locations as experimental units constitutes pseudoreplication (Hurlbert 1984) and artificially inflates the statistical power of the analytical technique. Instead of focusing on individual locations, use may be better described by an animal's spatial and temporal use of space, and a familiar quantification of this is the home range (Aebischer et al. 1993). Within the home range, however, use is rarely uniform. Rather, some areas are commonly used and others rarely used (e.g., Marzluff et al. 1997). In contrast to assuming that use is uniform within the home range boundary (Aebischer et al. 1993), differential use could be quantified using the utilization distribution (UD; van Winkle 1975, Kernohan et al. 2001).

The utilization distribution (see Fig. 1) is a probability density function (Silverman 1986) that quantifies an individual's or group's relative use of space (Kernohan et al. 2001). It depicts the probability of an an-

imal occurring at each location within its home range as a function of relocation points (White and Garrott 1990:146). Although, the UD has been used to define areas of frequent or "core" use (Samuel et al. 1985), to incorporate geographically referenced time budgets into home range calculations (Samuel and Garton 1987), and to assess animal interactions (Seidel 1992, Millspaugh et al. 2000), it has not been used to relate relative space use to resource attributes.

In this paper, we describe a procedure that relates UDs to resources in a spatially explicit way. We assume that space use relates to resource use and that the UD quantifies this relationship by providing a continuous and probabilistic measure of use throughout the area of interest. Advantages of using the UD for this end include: (1) increasing the sensitivity of resource selection studies by quantifying use within a home range with a probabilistic and continuous metric; (2) reducing the impact of location error because a continuous plane, rather than single points, are used to estimate resource use; (3) eliminating concerns about independence of points (Swihart and Slade 1997) because a systematic sampling strategy with short time intervals and autocorrelated data may provide more accurate UD estimates; (4) correctly treating the animal (or group of animals) as the experimental unit rather than the point estimate; and (5) considering the entire distribution of animal movements instead of focusing solely on individual sampling points.

We develop Resource Utilization Functions (RUFs) to express the correlation between the UD and sets of spatially defined resources. This extends the Resource Selection Functions of Manly et al. (2002) to the case in which use is continuous rather than discrete (i.e., used or not used). The coefficients of the RUF indicate the degree to which an animal, a social unit, or population utilizes resources within some pre-defined area (e.g., a home range). Our objectives are to: (1) develop the theoretical underpinning of RUFs, (2) provide direction for calculating RUFs, and (3) illustrate the use of RUFs to understand how land cover and landscape pattern, especially fragmentation and edges, affect Steller's Jay (*Cyanocitta stelleri* [J. F. Gmelin 1788]) ranging behavior and reproduction.

THEORY OF RESOURCE UTILIZATION FUNCTIONS

Utilization distributions

Resource utilization functions rely on the continuous, probabilistic measure of animal space use provided by a utilization distribution. Height of a UD [$\hat{f}_{UD}(x, y)$ at location (x, y)] represents the amount of use at that location relative to other locations in the plane (Silverman 1986); see Fig. 1. Utilization distributions can be estimated from point processes, e.g., as observed locations of animals, using probability density functions such as kernel techniques (Worton 1989, Kernohan et al. 2001). Kernel density estimation tech-

niques have been applied in the statistical literature for many years (Silverman 1986, Scott 1992, Kernohan et al. 2001) and recently have been evaluated as estimators of space use by animals (Seaman and Powell 1996, Hansteen et al. 1997, Ostro et al. 1999, Seaman et al. 1999). Accurate kernel estimation assumes that 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 (>30–50 point estimates) 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 (Worton 1989, Kernohan et al. 2001).

Relating UDs to resources

Utilization distributions can be related to resources using multiple regression. We are simply interested in accounting for variation in the height of the UD (the dependent variable) attributable to variation in some set of measured resources (the independent variables). Issues relevant to any regression application must be addressed. It is important to first determine if a linear or non-linear model is appropriate because some animals may use moderate levels of a resource more than either minimum or maximum values (Marzluff 1986). Ordinary regression assumptions must be met (e.g., homoscedasticity and normality of the independent variable, lack of outliers, and sufficient sample size) or when they are not met alternative procedures or transformations should be used and potential biases appraised (Draper and Smith 1981). In addition to these usual considerations, regressing resources on animal use in a spatially-explicit setting requires us to consider the appropriate resolution for measuring animal use and resources and necessitates investigations of spatial autocorrelation.

Considering appropriate resolution, theoretically amounts to defining the scale (specifically, the extent and grain; Wiens 1989) at which the study organism responds to resources of interest. In practice this is done by deciding the outer boundary of the UD (extent), the bandwidth or "smoothing factor" used by kernel techniques to estimate the UD (grain of resource use), the resolution or cell size at which resources are mapped (grain of resource), and, in some cases, the extent over which landscape features are integrated.

The spatial extent of resources for the animal or population under study defines resource "availability." This might be defined objectively as the total extent of space used by an animal (e.g., the 100% kernel boundary), or subjectively defined as a high-use "core area," or a large study area (i.e., a pooled population distribution). We prefer an objective definition because this begins to standardize the determination of space use. Subjective definitions of space use are inconsistent and

arbitrary; they have plagued studies of resource selection for decades (Kernohan et al. 2001, Marzluff et al. 2001). We suggest that the 100% fixed-kernel home range boundary be used to define the extent of space use for several reasons. First, with adequate sample sizes ($>$30–50 location estimates), fixed kernels perform well at the outer boundary (Seaman et al. 1999). Second, kernels attach some uncertainty around each location coordinate; therefore, additional area just beyond each point is included. This is realistic because there is generally uncertainty about relocation coordinates (e.g., mapping error, telemetry error; Withey et al. 2001). Third, and perhaps most importantly, a 100% fixed kernel estimates a 100% probability function for that animal, i.e., there was a 100% chance of finding the animal in this area based on the sampling strategy used. For this reason, it is critical that the sampling strategy accurately reveals use patterns of the animal (Garton et al. 2001); an incomplete or biased sampling scheme will produce an incomplete or biased kernel estimate of the UD, even if the 100% boundary is used.

The grain at which organisms perceive resources is difficult to know, but is certainly related to their sensory and locomotory abilities (Vos et al. 2001). Where insights into perception are possible, the kernel bandwidth, which controls the degree of UD smoothing, and resource resolution, which is often dictated by mapping resolution, can be adjusted to match it. Note that UD and resource resolution are separate issues; each is calculated independently of the other prior to their joining. Although kernel approaches are cell-based, cell size has little influence on UD calculation; the smoothing parameter is far more important. Resource utilization by animals that perceive and react to small-scale variation should have small smoothing parameters so that UD surface estimates can closely match small changes in concentrations of observed animal locations. Resource utilization by animals that are likely to perceive and react to resources over larger areas should have larger smoothing parameters that produce smoother UD estimates, indicative of a coarse-grained resource consumer. User selection of smoothing parameters (bandwidth values), although advantageous to reflect perception capability of a study organism, should not be done without good justification. Rather, objective selection methods are preferred because they minimize error in UD estimation (Worton 1989, Kernohan et al. 2001), and standardize analyses. Although least squares cross-validation is commonly used to objectively define smoothing (Gitzen and Millspaugh 2003), other options including ''plug-in'' and ''solve-the-equation'' are promising for defining the UD of animals with fine- and coarse-grained movement patterns (Kernohan et al. 2001).

Perception of resources by animals may also affect decisions about how finely to map resources. Although this is relevant, it would be prudent to map resources at a scale fine enough to capture important resource variation, even if one thinks this is not perceptible to the study organism. This is reasonable because fine-scale maps can be converted to coarse-scale ones, but not vice versa. Resolving resources at multiple scales could even be used to help determine the perceptive abilities of a study organism. The resolution at which animal use is most closely aligned with resource variation may signal the perceptual grain of the organism. In practice, the minimum resolution available is often set by technology rather than biology. Readily available, remotely sensed resource maps usually have a resolution of only 20–50 m.

Choice of resource resolution is especially important to estimation of RUFs because grid cells within the kernel home range eventually become the sampling units where the UD and the resource are measured. Therefore, the UD and the resources are eventually measured at the same resolution, usually that of the resource with the finest resolution. Resolving the UD more finely than the resources (the UD is continuous) is inconsequential because any finer scale variation in use will only be associated with the coarser (i.e., constant) value of the resource.

Selection of resource variables involves more than consideration of resolution. Resource variables should not be linear combinations of one another (multicollinear), but they also do not need to be completely independent. Multiple regression procedures will produce best linear unbiased estimates of parameter coefficients even when collinearity exists among independent variables (McCullagh and Nelder 1990, Neter et al. 1990). Biological reasoning should be used to determine the need to include correlated variables in the RUF. Decisions about correlated variables will be common because spatially explicit landscape variables are often correlated, even if they measure relatively distinct landscape properties (e.g., area, shape, connectivity, or diversity).

Spatial autocorrelation is a common property of ecological distributions (Schiegg 2003) that must be addressed in the development of a RUF. Ordinary Least Squares (OLS) regression is based on the assumption that deviations in the UD, given the resource attributes, are independent. However, the kernel analysis induces a correlation between the deviations in neighboring pixels that must be adjusted to obtain efficient estimates of the regression coefficients. Failure to adjust for spatial autocorrelation will invalidate the assumption of independence among observations required by statistical hypothesis testing and will 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).

Spatial autocorrelation can be addressed by fitting a regression model to the UD with spatial correlation as a function of the distance between the pixels. We suggest using a stationary model from the Matern class, i.e., the correlation is a function of the Euclidean dis-

tance between two locations (Handcock and Stein 1993), with range determined by the bandwidth used in each individual animal's kernel density estimate (Hepinstall et al., *in press*). The two model parameters are (1) ρ, the range of spatial dependence, measured in meters; and (2) θ, the smoothness of the UD surface, measured in the number of derivatives of the UD surface. Operationally, this means that the UD surfaces realized from this model will have continuous $\lceil \theta - 1$ derivatives (almost certainly) where $\lceil$ is the integer ceiling function. For example, values of $\theta > 1$ mean that the UD is smooth enough to have one derivative existing. Larger values of θ are associated with smoother UD estimates. Specifically, the $\lceil \theta - 1$ derivatives of the surfaces satisfy a Lipschitz condition of any order less than $\lceil \theta - \theta$. That is, there exists $C, \delta > 0$ such that $|\hat{f}_{\text{UD}}(x, y) - \hat{f}_{\text{UD}}(x', y')| < C|(x, y) - (x', y')|^a$ for $x, y, x', y' \in R$ almost certainly, if $|(x, y) - (x', y')|$ $< \delta$ and $a + \theta < \lceil \theta$. 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 increasingly is being used to model continuous spatial processes because of its flexibility of form and its ability to capture a wide range of spatial dependencies. Because the model is an approximation to the complex correlation induced by the kernel analysis, we suggest using a maximum likelihood procedure to jointly estimate the spatial variance of $\hat{f}_{\text{UD}}(x, y)$, the RUF coefficients, and the smoothness of the surfaces individually for each animal. The range (of smoothness) should be 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 (Hepinstall et al., *in press*).

Resource utilization coefficients

The coefficients in the RUF indicate the importance of each resource to variation in the UD. Their sign indicates whether use increases (+ sign) or decreases (− sign) with increase in the quantity of the resource. Their magnitude indicates the change in UD for a unit change in the quantity of the resource if the quantities of all the other resources are held fixed. Unstandardized regression coefficients are necessary if the RUF is to be used to predict expected use of resources (e.g., to map expected use throughout a species' range based on observed use within a sample of individual home ranges). However, use of standardized coefficients allows comparisons of the relative influence of resources on animal use, regardless of the measurement scale quantifying the resource (Zar 1986). Consider two resources that are equally correlated with use, but one

has values of 1–4 and the other of 10 000–40 000. Their standardized coefficients will be equal despite the fact that their unstandardized coefficients differ by four orders of magnitude. The standardized partial regression coefficients for each resource variable β_j can be estimated as

$$\hat{\beta}_j = \hat{\beta}_j^* \frac{S_{xj}}{S_{\text{RUF}}} \tag{1}$$

where $\hat{\beta}_j^*$ is the maximum likelihood estimate of $\hat{\beta}_j^*$, the partial regression coefficient from the multiple regression equation; S_{xj} is the standard deviation of the values of resource j; and S_{RUF} is the estimate of the standard deviation of the UD values.

The estimates of the standardized coefficients could also be used to rank the relative importance of each resource. The significance of the coefficients ($\hat{\beta}_j^*$ or $\hat{\beta}_j$) can be determined as usual in regression because spatial correlation is assumed to be a function of the distance between pixels. This is a limited application of the technique, but it is analogous to typical studies that relate abundance of animals or locations of a collection of unmarked animals to resources (Thomas and Taylor [1990] I and II designs).

If the study design allows UDs to be derived for many individual animals (the Type III design of Manly et al., and the preferred design; Otis and White 1999), then more analytical options exist. An average RUF, $\hat{\bar{\beta}}_j^*$, could be developed for mapping the expected use of *n* animals by averaging the unstandardized $\hat{\beta}_{ij}^*$ across the $i = 1, \ldots, n$ animals. If we assume that each animal is independent of other sampled animals, then the average RUF can be estimated from the estimates of the individual animal coefficients by a simple average (so that each animal is weighted equally) and the estimate will have variance

$$\text{Var}(\hat{\bar{\beta}}_j^*) = \frac{1}{n^2} \sum_{i=1}^{n} \text{SE}^2 \hat{\beta}_{ij}^*. \tag{2}$$

This variance quantifies our uncertainty in knowing $\bar{\beta}_j^*$ for the animals that we have observed. It does not include inter-animal variation.

The standardized coefficients can become independent variables in subsequent analyses (much as other selection coefficients can be used in secondary analyses; Aebischer et al. 1993). This allows us to test for population-wide consistency in selection and to rank the relative importance of each resource to the population. Here, coefficients for each resource for each animal become the independent, replicated measures of resource use. The H_0 that $\bar{\beta}_j = 0$ can be tested at the α probability level by determining whether the 1 − α confidence interval includes 0. Sample size is now the number of animals, not pixels or location estimates. Positive $\hat{\bar{\beta}}_j$ values that are significantly greater than 0 indicate use of a resource that is greater

than expected based on availability. Negative $\hat{\bar{\beta}}_j$ values that are significantly less than 0 indicate use of a resource less than expected based on availability. $\hat{\bar{\beta}}_j$ values can be compared to each other with standard t tests to determine whether some resources are used significantly more or less than other resources (Zar 1996). When determining confidence intervals and conducting hypothesis tests, it is conservative (variance is larger and confidence intervals wider) to view the coefficients as a random sample from a larger population of animals and include inter-animal variation in the calculation of variance. This can be done using standard sampling statistics, for example,

$$\mathrm{Var}(\hat{\bar{\beta}}_j) = \frac{1}{n-1} \sum_{i=1}^{n} (\hat{\beta}_{ij} - \hat{\bar{\beta}}_j)^2. \qquad (3)$$

Conservative estimation of variance captures all biologically relevant sources of variation in resource use by a population, but makes rejection of null hypotheses less likely. A less conservative, more precise estimate of sampling variation could be obtained by subtracting the variance due to estimating the individual coefficients (Eq. 2) from the total variance (Eq. 3).

The importance of each resource is also simply indicated by the proportion of animals whose use is significantly correlated with the resource. Inconsistent resource use within the population may prompt investigations of the scale of resource selection or of factors that mediate use, such as properties of animals or landscapes.

APPLICATION TO STELLER'S JAY MANAGEMENT

Questions about resource use in Steller's Jays

Steller's Jays, common in western North America, are nest predators that search for and locate nests incidentally to foraging on insects, berries, and human handouts; see Plate 1). As such, their relative use of certain portions of a landscape indicates the risk of predation to open-nesting birds (Vigallon 2003), including the threatened Marbled Murrelet (*Brachyramphus marmoratus* [J. F. Gmelin 1789]; Nelson and Hamer 1995, Luginbuhl et al. 2001, Raphael et al. 2002). A new technique was needed to analyze resource use by jays because no existing technique removed our concerns about using individual location estimates to define resource use, or incorporated non-uniform use within the home range. Resource Utilization Functions remove these concerns and allow us to relate variation in use within the home range (a measure of nest predation risk) to measures of landscape fragmentation and edge resulting from logging, human settlement, and recreation.

Jay abundance is greatest in fragmented forest landscapes (Marzluff et al. 2000, Luginbuhl et al. 2001; see Plate 1). Therefore, we hypothesized that jays preferentially use: (1) forest–clearcut edges, (2) forest areas fragmented by small human settlements and camp-

grounds, and (3) landscapes characterized as complex, fragmented mixes of young and old forests. Here we test these hypotheses and demonstrate a typical resource utilization analysis. We calculate RUFs for jays and investigate resource selection coefficients to: (1) produce general equations of resource use for prediction throughout the study area, (2) quantify differences in selection among groups of jays, and (3) determine how resource selection correlates with demography.

Field data collection

Study site.—We studied jays on the western side of the Olympic Peninsula, north and south of Forks, Washington State (47°56′ N, 124°23′ W). The study area (details in Marzluff et al. 2000, Luginbuhl et al. 2001, Neatherlin 2002, Vigallon 2003) is characterized by steep topography and coniferous forest dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), sitka spruce (*Picea sitchensis* (Bong.) Carr.), and western redcedar (*Thuja plicata* Donn ex D. Don). Most land is reserved (Olympic National Park, Olympic National Forest) or managed for timber production (Washington State and private forest lands). Human settlement is light, but recreation is common (Neatherlin and Marzluff, *in press*).

Radio-tracking Steller's Jays.—We monitored the locations of 47 breeding adult Steller's Jays (determined by plumage and confirmed by behavior; Greene et al. 1998) during the nesting and chick-rearing season (April–September) from 1995 to 1998. Each individual was only monitored during one year and only one member of a breeding pair was observed each year. We fitted jays with 6-g, backpack-mounted (around the wings; Buehler et al. 1995) transmitters to facilitate our observations. We homed in (Mech 1983) on jays 1–3 times per week until we saw them or determined them to be within 200 m (based on lack of directionality in the radio signal). We recorded their locations on maps/photos of the study site, using a global positioning system in remote areas. During each 1–2 h focal observation period, we plotted the entire area used by a bird and then recorded 2–3 locations (extreme and mid points of area used) for subsequent definition of the home range. Known locations of birds at nests were not included. We occasionally recorded single locations of animals at their roosts. We purposely recorded few locations per day on each animal to maximize the number of birds that we could track and spread locations on each bird over the range of times and conditions encountered during the breeding season (Otis and White 1999).

We defined an animal as being "adequately sampled" if 30 locations were obtained; 25 jays were adequately sampled. Previous simulation studies indicate that, at minimum, 30–50 points drawn randomly from a variety of known distributions are sufficient for kernel methods to accurately define the home range (Seaman

TABLE 1. Definitions of (A) land cover attributes and (B) derived landscape pattern metrics that were related to utilization of home ranges by Steller's Jays.

Term	Definition
A) Land cover	
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
Nonforested lands	Urban areas, barren lands, agriculture, some very young regenerating lands
Water	Rivers, lakes, saltwater
B) Pattern of land cover in landscape	
Number of land cover patches	Measure of fragmentation equal to no. distinct land cover patches in landscape. Adjacent pixels of same land cover are joined to form a patch. In our case, no. patches equals patch density because total landscape area is held constant (12.6 ha). No. patches = 1, if all pixels are of same land cover, increasing to a maximum equal to total pixels in landscape.
Contrast-weighted edge density†	Measure of total edge (interface between patches of different land cover) in a landscape that equals the sum of all edge segments multiplied by a contrast weight divided by landscape area. This produces a quantity of edge (m/ha) within the landscape that we designed to be especially sensitive to mature forest - clearcut interfaces because these areas provide rich combinations of feeding opportunities for jays.
Index of juxtaposition and interspersion	Measure of intermixing of patch types that measures the probability of each patch being adjacent to all other patch types. Approaches 0 when some patch types are commonly found adjacent to each other, but other types are rarely found next to each other. Ranges to 100 when all patch types are equally adjacent to all other patch types.
Landscape mean patch shape index	Measure of patch complexity that is the average of all patch shapes in the landscape. Shape is calculated separately for all patches by dividing a patch's perimeter by the minimum perimeter possible for a square patch (maximally compact shape) of equal size. Equals 1 when patch is square or almost square, and increases without limit as shapes become more irregular.

Notes: Landcover was determined by classification of satellite imagery (see *Methods*) and landscape metrics were determined using FRAGSTATS (McGarigal and Marks 1995). For our analysis, ''landscape'' is a circular area with a radius of 200 m (12.6 ha) because Steller's Jays appear responsive to edges of this width (Marzluff et al. 2000). See Table 4 for actual ranges of landscape metrics in this study.

† Contrast weights: 1.0 for interface of late-seral forest with clearcut; 0.75 for interface of late-seral with nonforest or mid-seral with clearcut; 0.50 for interface of mid-seral with nonforest; 0.25 for interface of late-seral with early-seral, mid-seral with early-seral, early-seral with nonforest, or early-seral with clearcut; 0.10 for interface of late- with mid-seral or nonforest with clearcut; 0.0 otherwise. Edge density = 0 when no edge exists in the landscape, and increases without limit.

et al. 1999). In our case, the increase in range size with sampling effort (i.e., incremental analysis) suggested that an average of >75% of the entire range was defined by 30 locations; 95% confidence intervals around these means include 100% definition of the area used. Our definition of adequate sampling is supported by the lack of a positive correlation between the number of location estimates and the size of the home range of adequately sampled animals ($r = -0.14$, $n = 25$, $P = 0.50$; correlation between sample size and size of the minimum convex polygon home range, which is known to be most sensitive to sample size, Kernohan et al. 2001).

Determining fecundity.—We observed radio-tagged adult jays throughout the breeding season to determine their success at fledging nestlings. Nests were rarely found, but jays only fledged a single brood each year, and fledged young conspicuously followed parents, begged noisily, and were therefore easily detected and counted. We observed each jay for 2–3 hours for a minimum of 20 days during the breeding season (March–September). Nine of the jays that we followed were never seen in the company of fledglings; we termed them ''unsuccessful.'' Sixteen jays successfully fledged young. The number of young fledged only varied from 1 to 5 per nest (2.88 ± 0.26 fledglings; mean ± 1 SE); these birds were classified as ''successful.''

Defining a RUF for Steller's Jays

Our approach consists of four basic steps (Fig. 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 grid cell within the UD, (3) determine the associated resources at the same cells, and (4) relate height of the UD to resource values cell-by-cell to obtain coefficients of relative use of resources.

Estimating the UD.—We used fixed-kernel estimation with least squares cross-validation (Kernohan et al. 2001) in the ANIMAL MOVEMENTS extension of ArcView 3.1 (Hooge and Eichenlaub 1997) to estimate the UD. Least squares cross-validation is an iterative process that estimates the least biased smoothing factor

TABLE 2. Resource utilization functions (RUFs) for Steller's Jays during the breeding season in the forests of Washington State's Olympic Peninsula. Positive coefficients indicate that use increases with increasing values of the resource.

Jay group	n	Mean estimates of unstandardized RUF coefficients (1 SE)†		
		$\hat{\bar{\beta}}_0^*$	$\hat{\bar{\beta}}_{\text{no. patches}}^*$	$\hat{\bar{\beta}}_{\text{edge}}^*$
All jays	25	1.32 (0.1)	0.09 (0.01)	0.005 (0.001)
Jays <1 km from human activity	10	1.74 (0.1)	0.11 (0.014)	0.03 (0.001)
Jays >5 km from human activity	15	1.04 (0.1)	0.08 (0.014)	0.01 (0.001)
Jays >5 km from human activity in fragmented landscape	9	1.1 (0.13)	0.09 (0.014)	−0.009 (0.001)
Jays >5 km from human activity in contiguous landscape	6	0.95 (0.20)	0.07 (0.02)	−0.01 (0.002)
No clearcuts in home range	5	2.38 (0.18)	0.02 (0.02)	0.04 (0.002)
Clearcuts in home range	20	1.06 (0.09)	0.11 (0.01)	−0.004 (0.008)

Notes: The RUF at location x is modeled as: $\text{RUF}(x) = C(x)\beta + Z(x)$ where β is the vector of unstandardized RUF coefficients corresponding to $C(x)$, the vector of resource utilization characteristics: (patch number, contrast-weighted edge density, juxtaposition and interspersion of patches, patch shape, mature forest, and clearcut; see Table 1 for definitions). The final term $Z(x)$ measures the spatial variation in RUF induced by the kernelling. It is modeled as a mean-zero Gaussian random field with empirically estimated Matern correlation function.

† Standard errors were calculated using Eq. 2, which quantifies the uncertainty in our estimation of resource use by each individual jay rather than uncertainty in how this sample of jays represents the larger population of jays on the Olympic Peninsula.

(that with the lowest mean integrated square error; Worton 1989). We defined the spatial extent of space use as the 99% fixed-kernel home range boundary. This reduced subjectivity (as previously discussed) to the maximum extent possible using program Animal Movement (100% boundaries are not calculated), and limited our inference about resource use to the area inhabited by the animal, based on relocation points. This certainly contains areas used most by jays, but radio-tracking effort determines how much of the true home range is likely to be estimated by kernel techniques (our largest samples suggest that our efforts captured >75% of total space use). Because we defined the spatial extent of our analysis as the home range, we investigated resource use relative to resource occurrence within the home range. We could have included areas beyond the home range (where use would be ~0) if we were interested in larger scale assessments of resource use.

Measuring the density estimate.—We estimated resource use at each grid cell throughout the home range by measuring the average height of the kernel density estimate over each cell. We developed an ArcView 3.1 extension for this purpose (FOCAL PATCH; available online).[5]

Measuring resources.—We used 1988 and 1990 Landsat thematic mapper satellite images of the Olympic Peninsula to classify land cover throughout the landscape including our study areas. Our base vegetation map was obtained from the Washington Department of Natural Resources. Land cover was originally classified from 1988 and 1990 Landsat thematic mapper satellite images to six forest cover types at 25-m resolution (Green et al. 1993). This database was updated twice to reflect timber harvest through 1991 and

1993 (estimated accuracy of harvest mapping was 90–98%). The harvest change detection used a comparison of satellite imagery to detect areas that were converted from forested cover to the clearcut class (Collins 1993). Recent (1993 to present) harvest immediately around each study stand was delineated during fieldwork and was used to update the base map for analyses immediately adjacent to the stand. The six types of land cover that were delineated are defined in Table 1.

We used this land cover classification to measure five resource attributes at each 25×25 m cell within jay home ranges: (1) the land cover type, (2) contrast-weighted edge density, (3) interspersion–juxtaposition index, (4) number of patches, and (5) mean shape index (see Table 1 for definitions; see McGarigal and Marks [1995] for calculation formulas). To determine the last four attributes, we used an analysis window with radius 200 m centered on each cell. We retained the minimum grain available to characterize resource variability (25 m) and used 200 m as the landscape extent because nest predation rates are highest within 200 m of edges in our study area (Marzluff et al. 2000, Raphael et al. 2002), suggesting that predators like jays respond to landscape attributes at this scale.

We measured land cover and landscape pattern at each grid cell using FOCAL PATCH. FOCAL PATCH interfaces with PATCH ANALYST (Rempel et al. 1999) to calculate landscape metrics for a circular area with user-defined radius centered on each grid cell. Any mapped resource can be associated with a cell with this "moving window" approach. The final result of running FOCAL PATCH is the production of a table with a row for each cell in the analysis area (home range, in our case) and columns corresponding to cell location, resource use, and the measured resource attributes (e.g., land cover type and landscape metrics) for the specified circular area. This can be exported

Table 2. Extended.

$\hat{\bar{\beta}}^*_{\text{juxtaposition}}$	$\hat{\bar{\beta}}^*_{\text{patch shape}}$	$\hat{\bar{\beta}}^*_{\text{mature forest}}$	$\hat{\bar{\beta}}^*_{\text{clear}}$
−0.0002 (0.0003)	0.14 (0.05)	−0.14 (0.01)	−0.29 (0.03)
−0.005 (0.0003)	−0.50 (0.07)	0.01 (0.05)	−0.56 (0.07)
0.001 (0.0005)	0.56 (0.08)	−0.29 (0.04)	−0.10 (0.04)
0.002 (0.0005)	0.50 (0.09)	−0.53 (0.05)	−0.15 (0.05)
−0.001 (4E-7)	0.64 (0.14)	0.07 (0.06)	−0.03 (0.07)
−0.008 (3E-7)	−0.93 (0.09)	0.30 (0.1)	0 (0)
−0.001 (1E-7)	0.40 (0.06)	−0.24 (0.03)	−0.27 (0.03)

(Table header: Mean estimates of unstandardized RUF coefficients (1 SE)†)

from ArcView to additional statistical analysis software packages.

Relating UD measurements to resource measurements.—We used multiple linear regression techniques to relate resource attributes (i.e., the independent resource variables) to the continuous measure of use (i.e., height of the UD estimate). We regressed resource values at each cell within an animal's home range to the corresponding value of the UD at that cell. We regressed six resource variables simultaneously on use to account for the four landscape pattern metrics and important land cover variation (two dummy variables that distinguished mature forest {% mid-/late-seral forest cover} from clearcut land {% clearcut land cover}, and settled land {% barren/urban/early-seral forest cover}) described in Table 1. This produced $n = 25$ unstandardized $\hat{\beta}^*_j$'s (one per jay). We derived the population-level RUF by assuming that each jay's use of land was independent (jays were scattered over a 26 000 km² study area), averaging $\hat{\beta}^*_j$ and computing variance with Eq. 2.

Because adjacent grid cells taken from the kernel analysis induced spatial autocorrelation into our data, we developed a maximum likelihood estimator of regression coefficients that assumed spatially dependent errors. Formally, the model is

$$\hat{f}_{\text{UD}}(x, y) = \mathbf{V}(x, y)^T \beta + Z(x, y) \qquad x, y \in R \quad (4)$$

where $\mathbf{V}(x)$ is the vector of resource attributes at the location (x, y) within the region R of positive density for the bird, and β values 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 $\hat{f}_{\text{UD}}(x, y)$ at different location within the range induced by the kernelling. We modeled $Z(x, y)$ as a mean-zero Gaussian process with the following correlation function:

$$\text{Cor}[Z(x, y), Z(x', y')]$$
$$= K_{\rho,\theta}[\sqrt{(x - x')^2 + (y - y')^2}] \quad (5)$$

where

$$K_{\rho,\theta}(d) = \frac{1}{2^{\theta-1}\Gamma(\theta)}\left(\frac{d}{\rho}\right)^{\theta} B_{\theta}\left(\frac{d}{\rho}\right) \quad (6)$$

where Γ is the gamma function and B_{θ} is the modified

Bessel function of the third kind and order θ discussed by Abramowitz and Stegun (1970). We provide access to the **R** statistical and graphing environment and a RUF analysis package that applies this Matern correlation function (Handcock and Stein 1993) to the data table from FOCAL PATCH.[6]

USE OF LOCAL- AND LANDSCAPE-SCALE RESOURCES BY JAYS

Describing resource use with RUFs

We present a variety of RUFs for Steller's Jays in Table 2. The RUF for all 25 jays indicates highest use of areas within their home range that have high densities of land cover patches, high densities of contrast edge, low juxtaposition of land covers, complex-shaped landcover patches, and an abundance of young forest/barren/agricultural/settled land cover relative to mature forests or clearcuts. This equation describes the average resource utilization using only the variance associated with estimating the individual resource utilization coefficients; we did not account for inter-bird variation. This is a valid representation of our certainty in estimating the average coefficients, given our sample of 25 jays, which is useful for projecting resource use by these jays over a larger region. However, individual jays varied considerably in their use of specific resources. Most jays (20/25) significantly concentrated their activities in regions of their home range that either had abundant high-contrast edges (10 jays), many patches (14 jays), or both edges and patches (4 jays; Fig. 2, Table 3).

Some variation in use of patch or edgy areas of the home range was correlated with other properties of the landscape. Concentrated use of areas with many patches was stronger if clearcuts were present in the home range ($\hat{\bar{\beta}}^*_{\text{patch}} = 0.11$) than if they were absent ($\hat{\bar{\beta}}^*_{\text{patch}} = 0.02$). Jays with clearcuts concentrated their use in patchy areas, but not in the highest contrast edges (there were many high-contrast interfaces between clearcuts and forest). Jays without clearcuts made extensive use of mature forest and concentrated their use in high-contrast edge areas because in their home ranges such

[6] URL: ⟨http://csde.washington.edu/~handcock/ruf⟩
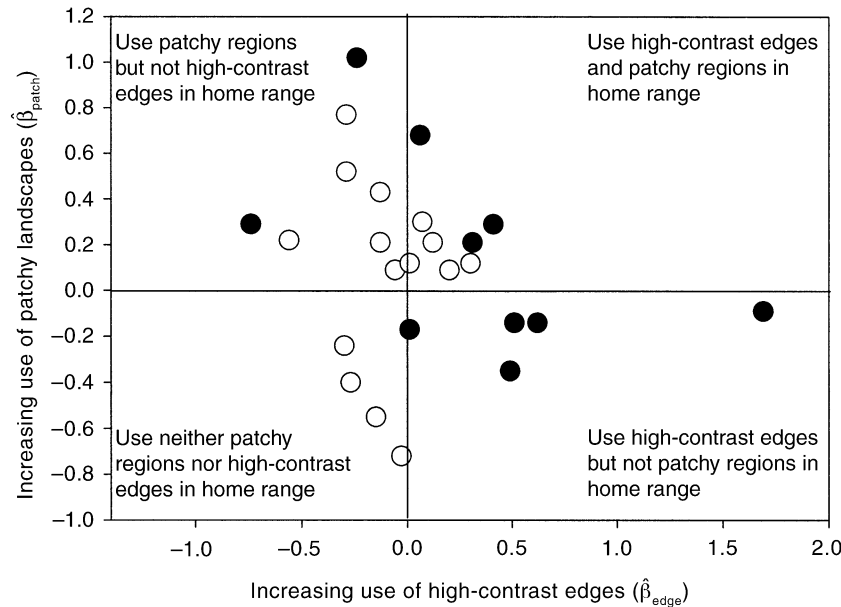
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FIG. 2. The influence of human activity on use of edges and patches by Steller's Jays. Jays tended to use either patchy or edgy areas in their home ranges rather than areas with both or neither attributes. Jays ($n = 10$, solid circles <1 km of a human activity center (campground, small town, or picnic area on the Olympic Peninsula) used high-contrast edges (interfaces between anthropogenic or clear-cut areas and mature forests) more than did jays ($n = 15$, open circles) >5 km from human activity (high-contrast edges for those jays were interfaces between clear-cuts and mature forests).

areas were limited and represented interfaces between forests and settled areas or campgrounds (probably offering supplemental food). Likewise, proximity to small human settlements and campgrounds appears to affect use of edges (Fig. 2). High-contrast edges were used more if they were near settlements or campgrounds (often the edge was the forest–human area interface; $\hat{\overline{\beta}}^*_{edge} = 0.31 \pm 0.20$, mean ± 1 SE) than far from such activity (where high-contrast edges are only forest–clearcut interfaces; $\hat{\overline{\beta}}^*_{edge} = -0.01 \pm 0.06$; $F_{1,24} = 5.4$, $P = 0.03$). We did not include proximity to human settlement and recreation as a variable in the calculation of a RUF because it is a property of an

entire home range; it does not vary among grid cells within a home range. Variation in other aspects of the home range, which was substantial (Table 4), did not strongly correlate with resource use. Only one correlation out of 58 was significant (correlation between $\hat{\overline{\beta}}^*_{clear}$ and the proportion of range covered with clearcuts, $r = -0.41$, $P = 0.05$), indicating that home range size and the amount of most land cover types and configurations (edges, patch number, degree of land cover interspersion) characterizing each home range did not strongly influence resource use within the home range.

Documenting factors that are associated with variation in the RUF coefficients may improve the repre-

TABLE 3. Estimates of standardized RUF coefficients ($\hat{\overline{\beta}}$) for 25 Steller's Jays nesting on the Olympic Peninsula.

Resource attribute	Mean standardized $\hat{\beta}$	95% confidence interval	P ($\overline{\beta} = 0$)†	No. jays with use significantly associated with attribute	
				+	−
Number of patches	+0.11‡	−0.57–0.28	0.19	14‡	9
Contrast-weighted edge	+0.06‡	−0.13–0.26	0.50	10‡	9
Mature forest	−0.05	−0.18–0.08	0.45	12	8
Clearcut	−0.04	−0.17–0.09	0.51	6	9
Interspersion–juxtaposition	−0.01‡	−0.14–0.16	0.87	11	8‡
Patch shape index	+0.01‡	−0.11–0.14	0.84	9‡	12

Notes: Relative importance of resources is indicated by the magnitude of $\hat{\overline{\beta}}$. Consistency in selection at the population level is indicated by significance of $\hat{\overline{\beta}}$ and the number of jays whose use was either positively or negatively associated with each attribute.

† P values test the null hypothesis that the average $\overline{\beta}$ is zero, given $n = 25$ jays.

‡ Use is in the direction predicted if jays select for high-edge, fragmented areas within their home range.

TABLE 4. Size, composition, and landscape patterns within Steller's Jay home ranges.

Attribute	Minimum	Maximum	Mean	1 SE
Range size (ha)	5.0	429.0	80.0	16.0
Barren/urban land cover (%)	0	17.5	2.7	0.87
Mid-/late-seral forest cover (%)	11	88.4	55.8	4.8
Early-seral forest cover (%)	0	43.7	10.0	2.9
Clearcut land cover (%)	0	84.0	27.3	5.2
Number of landcover patches	3	69	19.4	3.5
Total contrast-weighted edge density (m/ha)	24.7	71.9	43.3	2.4
Index of juxtaposition and interspersion (%)	50.7	97.7	77.3	2.3
Landscape mean patch shape index	1.3	1.8	1.6	0.02

Notes: All statistics are based on a sample of 25 jays living on Washington's Olympic Peninsula. Range size was determined using the 99% contour of the fixed kernel estimator.

sentation of how a population uses resources and may increase successful projection of this use. Consider, for example, our findings that resource use varies with the occurrence of clearcuts and with proximity to human activity. We used this information to provide a series of predictive, landscape-sensitive, "conditional" RUFs (Table 2). Characterization and eventual projection of use for our population of jays (because we already determined resource use to be individualistic) would thus be a multi-step process in which the landscape conditions of an area were first determined, and then the correct model of use for that landscape was applied.

Ranking use of specific resources

The relative use of each resource by the study population of jays is indicated by the average absolute value of the standardized $\hat{\beta}_j$. In our example, the number of patches was the most important correlate of a jay's location; jays tended to use patchy areas more than uniform ones ($\hat{\beta}_{patch}$ is positive; Table 3). Other resource attributes were not as strongly related to use (all P's > 0.40); however, they varied in their relative ability to account for a jay's use within its home range (contrast edge was of secondary importance and use of

FIG. 3. Use of land covers (mean ± 1 SE) found within Steller's Jay home ranges. Means are calculated by summing the heights of the UD at each grid cell comprising a specific land cover within a jay's range.

clearcuts was of least importance; Table 3). Note that the variation around the standardized $\hat{\beta}_j$ is considerably greater than the variation that we calculated for the unstandardized $\hat{\beta}_j^*$ (Table 2). This is because we included inter-bird variation (Eq. 3), thereby allowing inference from our sample of jays to all jays in the population. We used the more conservative approach of including all sources of variance rather than basing our estimation of sampling variance only on inter-bird variation (Eq. 3 − Eq. 2) because, in our example, inter-bird variation was an order of magnitude larger than the variance associated with estimating the resource utilization coefficients of individual jays.

Analysis of RUF coefficients for forest land cover indicated that mature (combination of late- and mid-seral forest) and clear-cut forests were used less than young-seral forests, barren areas, agriculture, and settled areas, but this varied considerably among individuals (vegetation dummy variables indicate the use of mature and clear-cut land cover relative to young-seral forests, natural clearings, and anthropogenic areas). An alternative way to visualize this is to calculate the average height of the UD (actual use) for each type of land cover for each jay (Fig. 3). In this example, we only included jays that had a given land cover type available in the home range (e.g., only 10 jays had small settlements and campgrounds in their range). As hypothesized, jays with access to small settlements and campgrounds used them more frequently than any other land cover types, but overall differences in use among cover types were not significant (ANOVA of use by cover type $F_{4,87} = 0.74$, $P = 0.54$). Use of settled lands and campgrounds was marginally greater than use of clearcuts (LSD mean difference = −8.29, $P = 0.10$), presumably because of anthropogenic foods available in settlements and camps (Neatherlin and Marzluff, *in press*).

It might also be desirable to quantify all of the jays' responses to each land cover type. Those individuals that do not have a specific type available in their home range have $\beta = 0$ for that cover type (e.g., 15 jays did not have anthropogenic land in their range). In our study, such an analysis suggests that no land cover was significantly correlated with use of the home range
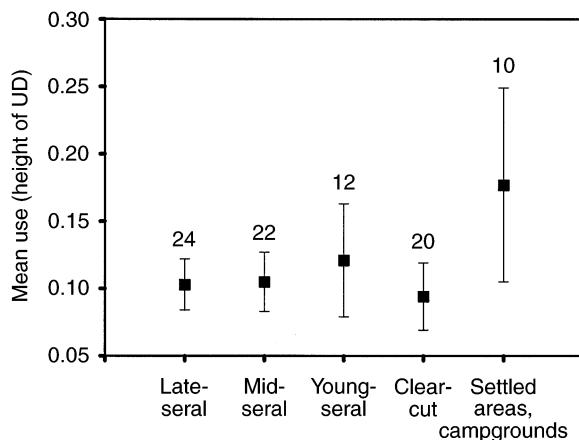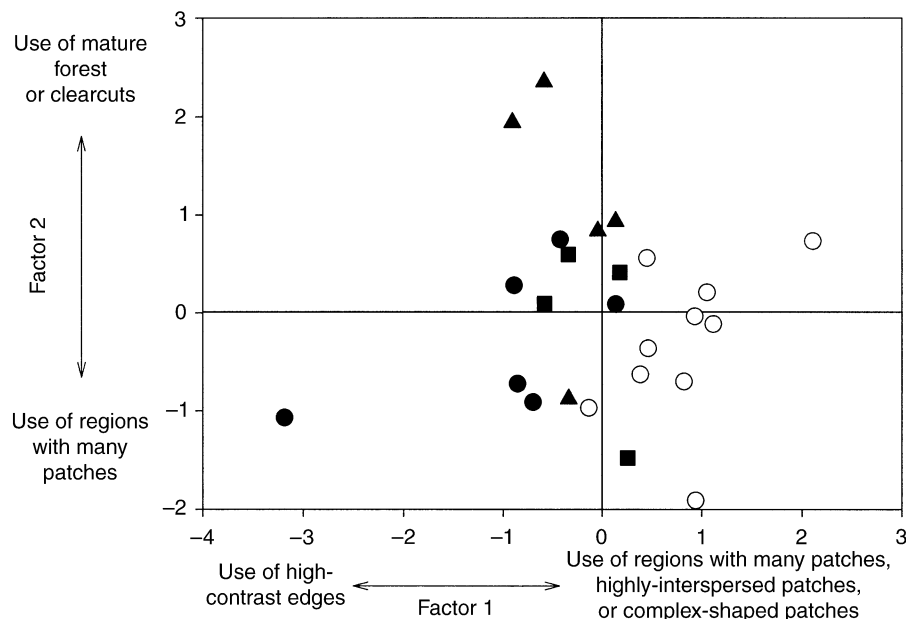
FIG. 4. Ordination of resource selection tendencies by 25 individual Steller's Jays on Washington's Olympic Peninsula. Factor 1 from the principal components analysis accounted for 33.6% of the explained variation and was correlated most closely with the use of high-contrast edge ($r = -0.83$) and use 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 clearcuts ($r = 0.77$). The significance of resource utilization coefficients in individual jay RUFs is indicated by symbol type: open circles, significant use of patches; solid circles, significant use of edges; solid squares, significant use of patches and edges; solid triangles, no significant use of patches or edges.

($F_{4,19} = 0.47$, $P = 0.76$). This was probably because placement of the home range, a form of resource selection itself, in some cases obviated the need to be selective within in the range, but in other cases exaggerated it.

Testing for preferential use of edges and fragmented regions in the home range

Our primary hypothesis about resource use by jays was that use would be greatest along edges and in fragmented portions of the home range. We quantified fragmentation with four distinct metrics (Table 1), but only contrast-weighted edge density and number of land cover patches were associated with use as we had predicted (Table 3). As we have already discussed, use was not consistent among jays in this population because, depending on proximity to human activity and occurrence of clearcuts in the home range, jays tended to use areas of abundant edge or abundant patches, but not areas with both aspects of fragmentation (Fig. 2). Factor analysis provided an alternative way to visualize individuality in resource use by jays and highlighted how significant, but distinct, resource use by individuals can lead to inconsistent resource use by a population (Fig. 4). We used the standardized resource selection coefficients as dependent variables in a principal component analysis. Two factors explained 63.5% of the variation in resource use among jays. These factors segregated jays into those associating significantly

with high-contrast edges and those associating significantly with areas rich in patches. Jays associating with both fragmentation dimensions were intermediate in the plot, whereas the few jays not associating with edges or patches tended to be most closely associated with mature forests or clearcuts.

We support the research hypothesis that Steller's Jays use fragmented landscapes more than contiguous landscapes because only five of 25 individuals did not significantly concentrate their use in portions of their home range with abundant edge or abundant patches (Table 3, Fig. 2). However, in-depth exploration of resource utilization coefficients provided a richer view of this relationship by highlighting individually distinct responses to fragmentation metrics and reasons for this individuality.

Relating use to demography

Relative use of particular resources may explain variation in breeding success of jays. We tested this using logistic regression to relate RUF coefficients, and other attributes of the home range, to success or failure of jays at fledging young. Natural selection may reinforce the use of patchy landscapes by jays because fledging success tended to increase with the abundance and use of complex-shaped patches and the abundance of midseral forests (P[success] $= -9.5 + 6.2$ {landscape patch shape index} $+ 4.3$ {RUF coefficient for use of

PLATE 1. (Left) Drawing of an Olympian Peninsula Steller's Jay holding a songbird's egg. These jays have blue-black crests on their mostly black heads. Their wings, body feathers, and tail are vibrant blue with black barring. They average 32 cm in length and 110 g in mass. (Right) Fragmentation of coniferous forests on Washington's Olympic Peninsula, resulting from timber harvest, provides stark edges between mature forests and regenerating clearcuts and an abundance of isolated forest patches. Steller's Jays use areas within their home ranges with abundant edges and forest patches more than contiguous, less fragmented forest areas. Drawing credit: Stacey M. Vigallon. Photo credit: John M. Marzluff.

complex-shaped patches} + 0.08 {average use of mid-seral forest}; $\chi^2_3 = 6.96$, $P = 0.07$).

DISCUSSION

Ecological insights

We developed a RUF for Steller's Jays to investigate how this species responded to land cover amount, type, and pattern (see Plate 1). It is important to understand this response because jays prey on the nest contents of a federally threatened species, the Marbled Murrelet, and human activity (timber harvest, settlement, recreation) affects the amounts, types, and patterns of land cover used by nesting murrelets in our study area (Nelson and Hamer 1995, Raphael et al. 2002). Our approach allowed us to demonstrate greater use of patchy and edgy forests by most jays, and concentrated use of edge habitat by jays that lived in landscapes including small human settlements and campgrounds. This pattern of resource use probably explains why predation on artificial murrelet nests is edge dependent only in settled and recreational areas (Raphael et al. 2002) and why fragmentation often leads to heightened nest predation in agricultural and urban landscapes (Marzluff and Restani 1999). We gained some insight into why jays appear to favor areas with abundant and complex-shaped patches; those that do had an increased likelihood of fledging young in one year. We may gain a better understanding of how natural selection affects resource use in the future, as survival and lifetime reproduction of jays exhibiting various sorts of resource use become known. The ability to document resource

use, understand why an observed pattern of use occurred, and finally project the implications of resource use to other species (such as the birds whose nests jays prey on) is an inherent strength of our RUF approach.

Because of its reliance on the UD, the RUF that we estimated predicts the probability of use based on any combination of resources that can be mapped. Unlike other techniques, the response variable is a continuous and probabilistic measure of space use. Resources can be discrete (e.g., cover types) or continuous (e.g., distance to water) and measured at the local (e.g., elevation) or landscape (e.g., edge density) scale. Many recent advancements in resource selection are either univariate (compositional analysis; Aebischer et al. 1993) or consider relocation points as simply used or available (logistic regression; Manly et al. 2002). The ability of the RUF to use all of the information that a researcher gathers on resources and their relative use by animals, its ease of application in a GIS environment, its ability to overcome some assumptions (e.g., independence of animal locations), 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.

Assumptions and limitations

Our approach has two primary assumptions. First, we assume that the UD can be accurately approximated from a sample of observations. The fixed-kernel technique that we used to estimate UDs is robust to rela-

tively small samples (>30; Seaman et al. 1999) and non-uniform distributions (Seaman et al. 1999). However, much remains to be investigated about how well all UDs actually represent animal space use and whether general space use is a good surrogate of resource use. Researchers should locate their animals so that observations accurately reflect use during the period of interest (e.g., different times of the day; Garton et al. 2001). The kernel function should be parameterized so that use of areas known to be unavailable (e.g., water for terrestrial animals) is not included. This requires special attention to sample size (Seaman et al. 1999) and the choice of bandwidth (smoothing parameter; Worton 1995, Kernohan et al. 2001). The choice of bandwidth is often seen as the most important aspect of kernel density estimation and should be selected carefully using objective criteria (Seaman et al. 1999, Kernohan et al. 2001, Gitzen and Millspaugh 2003). New methods of bandwidth selection (Kernohan et al. 2001) should be investigated as to their robustness to depiction of fine- and coarse-grained animal movements.

Second, inferences about resource use are dependent on the estimated spatial extent of the area used by animals, just as they are in all current techniques. This problem is unlikely to be solved until we understand more about why animals use resources. However, we can begin to understand the spatial extent of the used area by investigating resource use at multiple scales (Johnson 1980, Marzluff et al. 1997). For example, RUFs could be calculated by relating UDs to resources beyond the home range, within the home range, and within a core area of the home range where resource occurrence differs. Then, standardized RUF coefficients could be directly compared across scales to determine how relative use varies. We can also begin to understand how animals perceive resources at any given scale by quantifying resources within various distances of points in the area of interest. We did this at two distances (the immediate point and within 200 m of the point) and discovered that Steller's Jays responded more to the configuration of cover types (200-m scale) than to the actual cover type (Table 3).

Analysis of resource use at the individual animal level, rather than at the location level, is appropriate (Aebischer et al. 1993, Otis and White 1999) and biologically relevant. It is biologically relevant because it forces the researcher to investigate individual variability in resource use. Individuality is often extreme (Marzluff et al. 1997; our jay example). Recognition and quantification of individual resource use suggests a host of interesting investigations with practical significance. For example, we discovered that proximity to human activity and presence of clearcuts affected the use of edges and patches by jays (Fig. 2, Table 2). This can aid in projecting jay use in areas that we did not study, because we can tailor our predictive equations of use to local and landscape conditions. Taken

to an extreme, we could map jay use on a cell-by-cell basis by first determining the proximity of the cell to human activity and the presence of clearcuts within 200 m. Then, using the RUF appropriate to those conditions, we could calculate expected use (Table 2). Such a context-specific application of animal–resource relationships has the potential to significantly improve our ability to predict animal occurrence and response to resource manipulation. Using current techniques, we rarely accurately predict animal occurrence in one area using relationships derived from a different area (Knick and Rotenberry 1998), perhaps because we do not focus enough on variation in resource use and its explanation.

Focusing on individual variation in resource use also provides an intuitive way to relate resource use to demography. RUF coefficients can be related to survivorship, reproduction, or dispersal just like other individual attributes (e.g., sex, condition, age). This could have important applied, as well as theoretical, implications. In particular, we could rate resources by the relative contributions that their RUF coefficients make to demography. Those resources selected by especially fit individuals could then be favored in land management actions designed to increase population size.

Alternative procedures and future improvements

We anticipate analytical and biological advancements in our technique. Analyses will advance with continued research on point processes so that resource use can be directly related to resource properties in a spatially explicit manner without the need to first derive a UD. For example, better estimates of RUF coefficients may be obtained using Poisson processes with nonparametric 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.

Other alternatives for analysis currently exist. Using standard regression approaches, Akaike's Information Criteria (AIC) could be used to test specific a priori models about resource selection (Burnham and Anderson 2002). The approach recommended by Burnham and Anderson (1998) would (1) allow investigation of specific hypotheses, (2) facilitate parsimonious model selection, (3) help rank and compare candidate models, and (4) help avoid spurious correlations found in "data dredging" procedures. Also, model averaging techniques could be used with Akaike weights. In this case, inference would be based on the complete set of a priori models. This approach may help to reduce bias and improve precision in resource use (regression) coefficients (Burnham and Anderson 2002). Even if traditional "data dredging" techniques are used, model-averaging procedures may provide better inference than reporting one best model (Burnham and Anderson 2002).

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 behaviourally 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 as to why animals use the landscape in non-uniform ways. We studied foraging jays; >90% of our jay locations were made as jays searched for and procured food. Therefore, our RUF analysis 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 (Alldredge and Ratti 1986, 1992, Leban et al. 2001). 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). Toward this end, we suggest that researchers use expert systems (Starfield and Bleloch 1986) to help determine which analytical techniques to use. Expert systems are decision support tools that use a knowledge base consisting of pertinent questions, alternative solutions, and rules based on existing information. Use of expert systems would allow an objective way of determining what procedures to use based on study objectives, biology of the species, advantages and disadvantages of particular techniques, and sampling limitations. For example, an expert system could assist a researcher in selecting an appropriate bandwidth depending upon attributes such as the degree of clustering observed in points and the number of relocations. It is our contention that the animal should be the experimental unit, that 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 that the RUF will be a useful technique for others studying resource selection.

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