MICROHABITAT ANALYSIS USING RADIOTELEMETRY LOCATIONS AND POLYTOMOUS LOGISTIC REGRESSION

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Abstract: Microhabitat analyses often use discriminant function analysis (DFA) to compare vegetation structures or environmental conditions between sites classified by a study animal's presence or absence. These presence/absence studies make questionable assumptions about the habitat value of the comparison sites and the microhabitat data often violate the DFA's assumptions of an equal covariance structure and multivariate normality. An alternative is to generate an ordinal measure of site-use intensity from radiotelemetry locations. This measure is derived from the percentage of total telemetry points of a study animal that are found at use-only sites, overcoming many of the problems associated with defining "absence" sites. The use-intensity response is then modeled as a function of microhabitat variables using ordered polytomous logistic regression (PLR). Unlike DFA, PLR does not require covariance equality or multivariate normality, and allows categorical microhabitat variables. The classification error of the microhabitat model developed with PLR is then assessed by jackknifing. This technique is demonstrated with an example analysis of the foraging microhabitat of the northern spotted owl (*Strix occidentalis caurina*). The resulting model correctly classified 78% of the sample stands in the jackknife evaluation. For animals with site fidelity and radiotelemetry data, the proposed technique may provide a robust alternative for microhabitat analysis.

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Effective species management and conservation require understanding of wildlife habitat requirements. Although habitat can be analyzed at many scales, it is often broadly classed in 2 levels: extensive or macrohabitat analysis identifying the general environmental factors, plant cover, or seral stage of an animal's habitat; and intensive or microhabitat analysis that focuses on uncovering specific vegetation structures or environmental conditions important to the study species (Morrison et al. 1992). Macrohabitat analysis provides essential information on potential habitat areas in a diverse landscape. An animal, however, may respond to specific vegetation structures or abiotic conditions rather than the whole suite of structures associated with a general macrohabitat condition (Hilden 1965; Green 1971; Dueser and Shugart 1978; Smith et al. 1981). Vegetation structure and environmental conditions are highly variable within a plant association or seral stage, hence habitat quality will vary greatly within a general vegetation type. To effectively model a species' microhabitat, the vegetation structures associated with selected habitat need to be identified.

Most microhabitat analyses have used the concept of a niche gestalt (James 1971) based on Hutchinson's multidimensional niche theory (Hutchinson 1957, 1978). An animal's niche is defined as the "hypervolume" in the n-dimensional space of environmental characteristics which describes the conditions in which the species is found. The animal's multidimensional niche is inferred from a multivariate analysis of a suite of environmental variables measured across a range of sites (Capen 1981, Shugart 1981). This approach has been used to develop single-species habitat models (Verner et al. 1986) by management agencies to evaluate the habitat quality of different areas (e.g., the Habitat Suitability Index [Fish and Wildl. Serv. 1981]).

However, the common analysis used in developing these habitat models relies on 2 questionable methods which weaken the results (Noon 1986): (1) niche characteristics are inferred from a comparison of presence sites (where the study animal was observed) and absence sites (where the study animal was not observed); and (2) the comparison is based on a questionable application of discriminant func-

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tion analysis (DFA). Detecting or not detecting an animal at a site provides little information on the site's habitat value, and does not establish that the absence site is actually avoided. Furthermore, using DFA for habitat models requires the assumption that the independent variables, in this case the suite of environmental measures, have a joint multivariate normal distribution with a common covariance structure across all sites (both presence and absence sites) (Johnson 1981). Ecological datasets rarely meet these conditions and DFA is not robust to major departures from the multivariate normality assumption, such as when categorical variables are included in the analysis (Hassler et al. 1986). The predictive power of single-species habitat models could be improved by using a better site-suitability measure than the dichotomous presence/absence and a statistical method which does not require covariance equality and multivariate normality for the habitat variables' joint distribution.

An alternative method for single-species microhabitat analysis is to generate a ranked, polytomous (many-valued) relative measure of animal use based on radiotelemetry data. Ordinal polytomous logistic regression is then used to model changes in use-intensity across sites as a function of changes in environmental conditions, providing a new method for niche inference. Multi-year radiotelemetry data on reproducing animals provides a relative measure of site use-intensity based on the percentage of telemetry points in an animal's home range which occur at a sample site. The relative measures are the basis of general categories of use-intensity (e.g., low, medium and high). In contrast to presence/absence microhabitat analysis, this technique provides an ordered, categorical measure of animal use while avoiding assumptions about no-use sites. Ordinal polytomous logistic regression is a class of general linear models (McCullagh and Nelder 1989) which relate an ordinal dependent variable (e.g., use-intensity categories) to a collection of independent variables (e.g., microhabitat measures), which may include both continuous and categorical variables (McCullagh and Nelder 1989, Anderson 1984). PLR makes no direct assumptions about the independent variables' distributions. A jackknife technique is used to assess the robustness of the final selection of microhabitat measures for predicting animal-use intensity. We will first discuss the techniques of these 2 steps, and then give an example of these methods applied to microhabitat analysis of the northern spotted owl.

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METHODS

Previous Microhabitat Analysis

Most single-species microhabitat studies use a binary classification of sample sites such as presence/absence or use and random. In these studies, vegetation and site characteristics are compared between an area where the animal was located and one in which it was not, with microhabitat niche characteristics inferred from the differences (e.g. Martinka 1972, Conner and Adkisson 1976, Whitmore 1981, Mills et al. 1993). Modeling an animal's microhabitat from this type of comparison involves 2 questionable assumptions: (1) presence sites are suitable habitat, and (2) absence sites are unsuitable habitat.

Presence sites may be identified from single or multiple observations of the study species at a location. However, locating an animal at a site does not indicate that the site is suitable habitat. The site may have little or no habitat value if the animal is merely moving through the area. A further problem is that different sites may serve different habitat functions. For example, the collection of presence sites may contain both foraging and resting areas, each with potentially distinct microhabitat qualities. Some studies have identified presence sites only when a particular behavior is displayed, such as singing by the study bird (James 1971, Holmes 1981). This approach increases the odds that a particular site is valued habitat and that microhabitat is being compared between areas used in the same manner.

The selection of absence sites is especially problematic. Johnson (1981) pointed out that 3 possible conditions may exist at a site where the species is not detected: (1) habitat is unsuitable;

(2) habitat is suitable but the species is absent for other reasons, such as a low population or inter-specific competition; and (3) habitat is suitable and the species is present but not detected. Presence/absence studies assume the first condition always holds when any of the 3 explanations are possible. The resulting microhabitat analysis will not be useful, and perhaps even misleading, if absence sites are actually suitable habitat.

These uncertainties blur the distinction between presence/absence sites (Johnson 1981). The presence/absence analysis has a fundamental flaw: comparison sites do not come from distinct sample populations, and the actual habitat value of the use and nonuse sites is unknown. Developing a more robust model of animal microhabitat requires a measure of use that avoids absence or random comparison sites.

Statistical Analysis of Microhabitat Models

Discriminant function analysis is the general statistical method most often used to infer microhabitat characteristics from a comparison of use and nonuse sites. Unfortunately, microhabitat data seldom, if ever, meet the 2 main assumptions that underlie DFA: (1) the covariance matrix of the independent variables (microhabitat measures) is identical for both the use and nonuse sites, and (2) the independent variables have a multivariate normal joint distribution. The covariance structure of habitat measures would be expected to differ among use and nonuse sites for most study species (e.g. variance in snag volume among presence and absence sites for cavity-nesting birds). Unequal covariance structure will distort the classification equations (Lachenbruch 1975, Williams 1981) and the distortion will be more acute if sample sizes are disproportionate such as when more absence or random sites are sampled than presence sites (Holloway and Dunn 1967, Pimentel 1979, Morrison 1984). DFA's assumption that independent variables have a multivariate normal joint distribution is difficult to test and is a condition unlikely to be met by microhabitat data. Furthermore, because categorical measures cannot be multivariate normal by definition, discriminant function analysis should not be used when microhabitat measures include categorical data (Press and Wilson 1978, Noon 1986).

Two other basic methods for modeling microhabitat selection have also been proposed, both of which use maximum likelihood techniques and therefore have less restrictive data requirements than DFA. The first, binary logistic regression (Capen et al. 1986, Brennan et al. 1986, Manly et al. 1993), assumes that comparison sites come from distinct populations, and relies on the identification of use sites and nonuse, or absence, sites. The second relies on comparison of a sample of available sites with a sample of use sites based on log-linear or proportional hazards models (Manly et al. 1993). Manly et al.'s approach avoids the necessity to identify nonuse sites and attempts to estimate relative probability of use (or absolute probability of use if sampling fractions are known).

Proposed Technique

Identifying the individual features important to an animal's microhabitat using only presence/absence comparisons is difficult when the environmental conditions of the use sites are highly correlated with each other while strongly differing from available but avoided sites. For example, a comparison of old-growth use sites and avoided clearcut or young-forest sites can do little to identify the particular features important to an old-growth associated species because the vegetation structure is too distinct between the contrast sites. In these conditions, a microhabitat analysis is needed which can tease apart a complex suite of environmental conditions within the species' preferred habitat type. One approach to a more robust analysis is to compare an ordinal gradient of use preferences against subtle microhabitat changes within the preferred use sites.

A better model of single-species microhabitat could be developed if site comparisons did not rely on absence locations and a statistical analysis was used where assumptions are not violated by the measurement data. In contrast to the binary habitat-use measure provided by presence/absence data, radiotelemetry data can provide a relative measure of animal preference for use-only sites. A measure of the animal's use is derived from the percentage of total telemetry points which occur in any 1 area. The method requires no assumptions about unused areas as only areas with known, repeated use are assigned measures and included in the model building. Differences in the level of use-intensity among sites are analyzed against changes in microhabitat conditions using ordered polytomous logistic regression. The robustness of the final

PLR model is assessed using the existing data set and a jackknife technique.

Radiotelemetry Data

Telemetry data have been used to establish migration patterns (Mech and Frenzel 1971, Fritts et al. 1984) home range size (Trent and Rongstad 1974, Solis and Gutierrez 1990), activity (Marshall and Kupa 1963), predation (Mech 1967), macrohabitat preferences (Nelson 1979, Forsman et al. 1984) and mortality (Cook et al. 1967, Dumke and Pils 1973, Franzmann et al. 1980) of a study animal. For animals with site and home range fidelity, telemetry can also capture the animal's relative use patterns over a longer time period and larger area than can field observations of an animal's presence (Turkowski and Mech 1968, White and Garrott 1990). Telemetry locations identify particular use-sites and the frequency with which the study animal returns to each area.

Caution, however, should be used when inferring habitat quality from site use-intensity. The amount of time an animal spends in 1 area does not necessarily correspond to the site's habitat value. For example, an animal may spend only 5 minutes a day drinking, yet if water is scarce, the site is essential to the animal's survival (Morrison et al. 1992). While telemetry information cannot remedy this problem of interpretation, it can provide a larger sample of site use than field observations of species presence or absence. Telemetry increases the area and time period over which the animal can be followed, allows for night tracking, and reduces human observer effects on the animal's behavior (Mech 1983). While no sampling procedure can reveal an animal's perception of a site's habitat value, we believe telemetry provides the best approximation of animal-use preferences.

In microhabitat analysis, site characteristics are the study focus rather than individuals or groups of animals. The scale and definition of a site depends on an animal's autecology and how sites can be spatially delineated from surrounding areas. A site identified by telemetry should be the area around a location that is relatively homogenous for the environmental conditions that may be important to the study animal, such as a similar plant association, seral stage, disturbance history, or microclimate conditions.

For telemetry to provide unbiased information on use-intensity patterns, locations should be classified and screened in an effort to standardize sample sites. Three general guidelines are proposed: (1) only telemetry data for successfully reproducing animals should be selected; (2) telemetry locations should be classified by factors possibly affecting microhabitat selection or quality (e.g., season, species behavior, and the animal's sex); (3) locations should be screened for independence and a maximum error size.

Reproductive success of the study animal should be a minimum qualification for selecting habitat for measurement. Habitat quality cannot be measured by sighting-intensity or animal density alone. Demographic factors such as reproductive success, fledgling survival and mortality should also be considered (Van Horne 1983). This qualification is particularly important for species that occupy marginal habitat without reproducing when their preferred habitat type is not available (Krebs 1971, Lidicker 1975, Atwood 1980, Thomas et al. 1990).

Telemetry datasets include many more location samples than presence/absence observations and therefore many different types of microhabitats (i.e., foraging, roosting, nesting). Whenever possible, sample locations should be categorized by factors such as the animal's sex, the season and the type of behavior, to avoid collecting samples from different populations (Pimentel 1979). While all microhabitat studies face this problem, an advantage of telemetry data is that sample locations can be standardized by season, sex, and possibly behavior activity (inferred from the time of day).

Telemetry should be screened so that locations have a standardized error and are temporally independent. Location errors can be estimated with the size of the polygon formed by the intersection of 3 or more telemetry vectors (Lenth 1981, Mech 1983, White and Garrott 1990). Although the size of an acceptable polygon will depend on the scale of an animal's movements and the heterogeneity of the use area, any telemetry error polygon which overlaps areas with distinctly different vegetation (e.g., a forest and an adjacent clearcut) should be discarded. Autocorrelation between telemetry locations must also be examined as statistical methods generally require independent observations. The location of an animal at any one time influences its location in the immediate future. To insure that telemetry locations are not autocorrelated (Swihart and Slade 1985), enough time must elapse between observations for the locations to be independent. Telemetry locations taken in less than the required elapsed time should be deleted from the dataset before analysis.

Having selected a sub-sample of telemetry locations screened by these criteria, a relative measure of use-intensity can be developed. This measure is relative as no analysis can claim, for example, that a site with 5 telemetry points is preferred habitat over a site with 4 telemetry points. Still, the approach provides general categories of use-intensity derived from a longer-term, larger-area sample than standard field observations of species presence. The screened telemetry points are mapped and use-sites identified by point clusters. The number of telemetry points at each site, as a percentage of the total selected telemetry points for each animal, is calculated. The sites are then classified into relative use-intensity categories based on their telemetry percentages (e.g., low, medium, and high). The number of categories should be the most parsimonious grouping of cluster patterns found in a frequency distribution of the sites by telemetry percentages.

The transformation of telemetry locations is a categorization of an underlying continuous response variable, percentage of total animal locations, into ordinal groups of relative animal use such as low, medium and high. Discriminant function analysis, which assumes that groups being compared are samples from distinct populations, should not be used with this measure of use-intensity. Polytomous logistic regression is specifically designed for a multi-valued categorical dependent variable, even one derived from making an underlying continuous variable discrete. Polytomous logistic regression analyzes the gradient of animal use against changes in microhabitat, investigating the dependencies of animal use on the various microhabitat measures.

Polytomous Logistic Regression

Ordered PLR models an ordinally ranked dependent variable (e.g. animal-use intensity) as a function of multiple continuous or discrete independent variables (e.g. habitat measurements). While traditional binary logistic regression has seen increasing ecological application (Hassler et al. 1986, Shanubhogue and Gore 1987, Lenihan 1993, Trexler and Travis 1993), PLR has been used mainly in medical studies (Ashby et al. 1986, Hosmer and Lemeshow 1989). So far, wildlife studies have used only the binary form of logistic regression to model dependent variables (Capen et al. 1986, Brennan et al. 1986).

Binary and PLR make no direct assumptions about the multivariate distributions of the independent variables (McCullagh and Nelder 1989, Anderson 1984). Rather, logistic regression assumes that a particular functional relation holds between the dependent and independent variables: the posterior log odds ratio, or logit, of the dependent variable is a linear function of the independent variables. The logit form can arise from a wide range of assumptions regarding the multivariate distribution of the independent variables (Anderson 1972). The independent variables need not follow a multivariate normal distribution, nor is there any restriction on categorical independent variables as in DFA (Press and Wilson 1978). Model parameter estimates and significance tests are based on maximum likelihood estimation. The likelihood formulas are derived from distributional assumptions for the dependent variable (the logit assumption) and the sampling model underlying the data collection (Anderson 1984, Hosmer and Lemeshow 1989).

Polytomous logistic regression models the probability that a site belongs to use-intensity group i as a function of the site's observed microhabitat measures using the logit model of proportional odds (Anderson 1984, McCullagh and Nelder 1989). The model retains the information inherent in the ordinal rank of the dependent variables (e.g. low, medium, and high).

let $X = (x_1, x_2, x_3, \ldots x_n)$
= the vector of observed microhabitat measures for site A, and
$\Pi_i(X)$ = the probability that a site with microhabitat measures X belongs to use category i ($i = 1, \ldots, k$), (e.g., use-intensity groups with an ordinal rank),

then:

$$F_i(X) = \Pi_1(X) + \Pi_2(X) + \Pi_3(X) + \ldots + \Pi_i(X)$$
$$i = 1, \ldots, k - 1$$

$F_k(X) = \Pi_k(X) = 1 - F_{k\text{-}1}(X)$ is the 'cumulative probability' that a site with microhabitat measures X belongs to use categories 1,2, . . . or i. For example: $F_{low}(X) = \Pi_{low}(X)$, $F_{medium}(X) = \Pi_{low}(X) + \Pi_{medium}(X)$, $F_{high}(X) = 1 - F_{medium}(X)$.

The logit is defined as the natural logarithm of the cumulative odds:

$$L_i(X) = Logit(F_i(X)) = ln[(F_i(X)/(1 - F_i(X))]$$

PLR models the logit as a linear function of the independent variables:

$$L_i(X) = \alpha_i + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n$$

$$i = 1, \ldots, k - 1$$

$$L_k(X) = -(\alpha_{k-1} + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

$$i = k$$

$$\alpha_1 < \alpha_2 < \alpha_3 < \ldots < \alpha_{k-1}$$

For example: $L_{low}(X) = ln\,[(F_{low}(X))/(1 - F_{low}(X))] = \alpha_{low} + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n$.

Note that this relation implies that the logit functions, $L_i(X)$, for the various use-intensity categories are parallel planes which may differ only by their intercepts, not by the slopes of the microhabitat measures. This assumption of proportional odds can be tested in the process of fitting the model. Furthermore, if the intercepts for 2 use-intensity categories are statistically indistinguishable, the 2 categories cannot be differentiated by the independent variables (microhabitat measures) in the dataset.

The parameters, (α's, β's), are estimated using maximum likelihood techniques (Anderson 1984, Hosmer and Lemeshow 1989). This basis in maximum likelihood gives PLR 2 principle advantages over DFA. First, microhabitat measures need not have a multivariate normal distribution. Second, the ordinal rank of the dependent variable, (e.g. low, medium, and high-use-intensity categories), is retained in model development. Discriminant function analysis models the dependent variable categories as distinct populations, thereby losing any information on their relative order.

Polytomous logistic regression does assume that sample sizes are sufficiently large for the asymptotic results of maximum likelihood theory to hold (McCullagh and Nelder 1989). Even at small sample sizes, however, the maximum likelihood estimates are more consistent than the DFA estimates (Press and Wilson 1978, Choi 1986). For datasets where the independent variables are multivariate normally distributed and the dependent variable is dichotomous, DFA is a more powerful technique (Afifi and Clark 1984). Use of DFA, however, does require losing any information inherent in the ranking of the sites by use-intensity.

After the final, parsimonious PLR model is developed (see Hosmer and Lemeshow 1989 for a detailed discussion), an allocation method must be chosen. The allocation method determines which category of use-intensity to assign a site, based on the model's predictions. Though several methods have been proposed (Ashby et al. 1986) the most commonly used is the maximum probability method: the observed microhabitat measures for a site are entered into the final model, along with the estimated model parameters, to calculate the site's logit for each use-intensity class. The estimated probability of the site belonging to a particular use-intensity class can then be calculated from the logits:

$$F_i(X) = 1/(1 + \exp(-L_i(X)))$$

$$i = 1, \ldots, k$$

$$\Pi_1(X) = F_1(X) = 1/(1 + \exp(-L_i(X)))$$

$$\Pi_i(X) = F_i(X) - F_{i-1}(X)$$

$$i = 2, \ldots, k - 1$$

$$\Pi_k(X) = F_k(X)$$

For example: $\Pi_{low}(X) = F_{low}(X) = 1 / (1 + \exp(-L_{low}(X)))$, $\Pi_{medium}(X) = F_{medium}(X) - F_{low}(X)$.

The site is then assigned to the use-intensity class with the highest probability of membership.

Polytomous logistic regression is in SAS under the CATMOD procedure (SAS Inst. Inc. 1988) and in S-Plus (Stat. Sci. 1993) under ordinal logistic regression in the Design Library Functions (Harrell 1994).

Model Assessment

Whenever possible, microhabitat models should be tested to assess how well they can predict animal usage of different potential habitats. While some models are tested (Cook and Irwin 1985, Lancia et al. 1982, Laymon and Barrett 1986, Laymon and Reid 1986, Raphael and Marcot 1986), most are not because of cost and time constraints (Morrison et al. 1992). Testing microhabiat models reduces the risk of finding spurious correlations (Karr and Martin 1981, Rexstad et al. 1988) or failing to find significant relations (Armstrong 1967). The ability of microhabitat models to predict habitat usage from environmental variables will vary between species. Life history traits such as whether a species is migratory or territorial, a generalist or has a narrow niche, will likely influence the predictive power of a microhabitat model. Given these influences on habitat usage, models at best may account for only 50% of the variation in a species density or abundance at a particular site (Morrison et al. 1992). Before applying a microhabitat model, wildlife managers should know how well a model performs.

One measure of performance is to estimate the classification errors of the final model. This is done by estimating the probability that a site of use-intensity i is erroneously classified to be of use-intensity j (where $j \neq i$). Estimating these error probabilities from the same data used to estimate model parameters will give biased results (Efron and Gong 1983). Generally, time and cost preclude collecting a new dataset for evaluating a model's performance. A jackknife approach, however, can overcome this estimation bias using the existing dataset (Knoke 1986). A single observation is removed from the data, the remaining data are used to estimate the model parameters, and the fitted model is applied to this unused observation to predict its use-intensity class. This process is repeated for each observation in the dataset, giving an unbiased estimate of the classification error for each use-intensity group.

Technique Example

To provide an example of how these techniques can be applied, we analyzed a demonstration set of structural characteristics of northern spotted owl foraging microhabitat in Washington State. Due to the controversy surrounding old-growth forests and the spotted owl, studies have produced extensive multi-year radiotelemetry data for owl pairs. An additional benefit was that the selection of the demonstration set of microhabitat measures was aided by many studies of spotted owl ecology (Forsman et al. 1984, Gutierrez and Carey 1985, Hamer 1988, Solis and Gutierrez 1990, Thomas et al. 1990, Carey et al. 1992) and the distinctive structures of the owl's preferred macrohabitat, old-growth forests (Franklin et al. 1981, Franklin and Spies 1984, Spies and Franklin 1991).

The Northern Spotted Owl

The northern spotted owl is found from northern California to southern British Colombia in forest conditions that range from moist coastal redwood (*Sequoia sempervirens*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*) to more mesic Douglas-fir (*Pseudotsuga menziesii*) and mixed-conifer forests. Throughout its geographic range, the owl's preferred habitat is older forests (Thomas et al. 1990). Several hypotheses have been proposed to explain this preference (Forsman et al. 1977, 1984; Carey 1985, Carey et al. 1992). Two of these hypotheses focus on the owl's foraging success: (1) prey species are more abundant in older forests (Carey et al. 1992); and (2) prey capture is higher in older forests due to favorable foraging conditions (Carey et al. 1992, Rosenberg et al. 1994). The owl's prey base changes in different areas and appears to rely on woodrats (*Neotoma* spp.) in drier areas and northern flying squirrels (*Glaucomys sabrinus*) in more mesic forests. Over the owl's geographic range, changes in forest structure and owl prey base indicate preferred microhabitat conditions may also vary among regions. While foraging microhabitat conditions for the northern spotted owl have been examined in northern California (Solis and Gutierrez 1990), they have not been well-studied in the northern extent of the owl's range, where home range size reaches its maximum (Hamer 1988) (see Mills et al. [1993] for a study of roost sites). To demonstrate the proposed microhabitat analysis methods, we examined 5 structural characteristics of owl foraging sites on the Olympic Peninsula and in the North Cascades. The principal prey in these areas of Washington State are northern flying squirrels (Forsman et al. 1991). The areas' old-growth forests are mesic, multi-layered stands of western hemlocks and Douglas-fir.

Radiotelemetry Data Analysis

We selected radiotelemetry data collected on spotted owls which met the following criteria: data collection lasted 2 years or longer; observed owl pairs had produced offspring; and the time, date, bird's sex and estimated error of each telemetry location had been recorded.

Multi-year telemetry data were preferred because the home range size and extent of older forests used by spotted owls may not stabilize in 1 year of study (Carey et al. 1992). Larger, long-term telemetry data were preferred as the increase in sample size of locations probably is more representative of the owl's use preferences.

We included only telemetry for reproducing spotted owl pairs to reduce the chance of sampling sub-optimal habitat. As the extent of old-growth forests has diminished in the Pacific

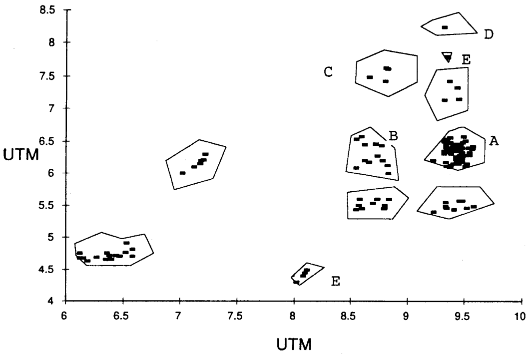

Fig. 1. A map of 162 selected telemetry locations for an owl pair plotted by universal transverse mercator (UTM) coordinates. Lines indicate stand boundaries where forest structure changes due to clearcut harvesting or disturbance. Unmarked areas between use areas are clearcuts or young forest (age ≤50 yr). Stands with different use-intensity levels are: "A" a high-use stand (36% of the owl pair's total telemetry locations), "B" a medium-use stand (7%), "C" a low-use stand (2%), "D" a stand with less than 3 locations which was excluded from the analysis, and "E" 2 stands excluded because of their small size.

Northwest, spotted owls sometimes pack into sub-optimal habitat where they survive, but rarely reproduce (Thomas et al. 1990, Carey et al. 1992). Because owl reproduction is highly variable year-to-year, and telemetry devices may affect reproductive success (Thomas et al. 1990, Paton et al. 1991) we required only that owl pairs had been observed to produce offspring either before, during, or after the telemetry collection.

In an effort to standardize telemetry locations, only data which identified the time, date, bird sex, and error of each location were selected. The recorded time of each telemetry location allowed us to select observations collected at night when the owl is predominantly foraging (Forsman et al. 1984, Guetterman et al. 1991), and to discard consecutive locations taken in less than 72 hours that might not be independent (Carey et al. 1989). Using each location's record of a bird's sex and date, we eliminated female locations during the breeding season that might be nesting locations. Acceptable error for each location was set at telemetry polygons of 5 ha or less. In the study areas, this selected size identified areas with a homogenous structure within a matrix of clearcuts and uncut forest. All locations that occurred at the edge between a clearcut and forest were discarded.

Using these criteria, we selected telemetry for 11 owl pairs. The number of locations for the 11 pairs ranged from 107 to 193 points. We plotted telemetry points on a 1:24,000 scale using the UTM (universal transverse mercator) coordinates for each location. We overlaid these plots on U.S. Geological Survey topographic maps and compared them with aerial photographs to identify use areas. Stands identified from the telemetry plots with only 1 or 2 telemetry locations were dropped from the analysis for having too few locations to establish an owl-use preference.

In this study, the experimental unit is the forest stand. The boundary of each area or stand containing telemetry points was defined by the adjacent borders of clearcuts or a distinct change in vegetation structure resulting from a disturbance (Fig. 1). In the study areas, logging and wind disturbance divided the landscape into discrete stands. Within each stand, the forest seral stage and disturbance history were relatively homogenous.

When using PLR, the study design and sampling scheme should be identified so that the appropriate likelihood functions can be selected (Hosmer and Lemeshow 1989). This example is a cohort study where observations (i.e. telemetry) are independent and data are collected from a sample of owl use stands (Chambless and Boyle 1985). All stands with radiotelemetry locations were stratified by size because the number of telemetry locations in a stand can be influenced by stand size as well as microhabitat quality. To minimize this confounding effect, only large stands between 40 and 80 ha in which prey populations could not be quickly depleted were included in the analysis.

Forty-one stands with 3 or more telemetry locations were identified. For each stand within an owl pair's home range, the percentage of total telemetry points occurring within the stand was calculated. This value gave a relative measure of each stand's use by the resident owl pair. For example, a stand with 10 telemetry locations used by an owl pair with 125 total locations would have an 8% value.

Classification of use-intensity levels was based on a frequency histogram of sample stands identified by their percentage of the total telemetry points within each owl pair's home range (Fig. 2). The frequency distribution displays patterns observed in each owl pair's map of telemetry locations (Fig. 1). Within each home range, owl use is concentrated in a few core stands (high-use stands), with lighter use of some stands further from the core area (medium-use stands) and infrequent but repeated use of several stands furthest from the core use areas (low-use stands). The histogram display was categorized into these 3 use-levels based on the clumping patterns in the frequency distribution. Stands with more than 2 telemetry locations and 1–2% of total owl pair telemetry points were assigned a low-use intensity (value 1). Stands with 3–10% of total telemetry points were given a medium-use intensity value (2) and stands with greater than 10% were assigned a high-use value (3).

Study Areas and Microhabitat Measurements

Sample stands were concentrated in 3 locales of Washington State: 2 areas on the west side of the Olympic Peninsula near Lake Quinnault and the town of Forks, and 1 in the North Cascade Range near Mt. Baker. The Olympic Peninsula sites are located in the *Picea sitchensis* and *Tsuga heterophylla* zones (Franklin and Dyrness 1988) at an elevation of 200 to 700 m. The North Cascade sites are at an elevation of 200 to 800 m and within the *Tsuga heterophylla* zone (Franklin and Dyrness 1988) found in the wet, western foothills of the Cascade Range. All stands were either old-growth (age ≥250 yr) or mature forests (age ≥70 yr) with a significant legacy of old-growth structure surviving from early century wind disturbance (Henderson et al. 1989).

Sixty-five measures of forest structure were collected in a 3-year study that measured 176 plots in 41 stands with different owl-use intensity levels (North 1993). For this demonstration, 1 microhabitat measurement was selected from each of 5 general categories of site characteristics: trees, snags, logs, canopy dimensions, and site physiognomy. Stand structures were selected that might influence the density of northern flying squirrels, or affect the owl's foraging success: the density of tall trees (*TALTRDE*) as it represents an increase in the height of the canopy environment and foliage layering, conditions which may influence owl movement and foraging success (Carey 1985); snag volume (*SNVOL*) because snags often provide cavities required by flying squirrels (Mowrey and Zasada 1984, Carey 1991); log volume (*LGVOL*) because large logs may provide runway structures for prey species (Maser and Trappe 1984); tree height class diversity (*HCLBP*) because multi-layer canopies may influence foraging success (Forsman et al. 1984); and the distance to water (*WATER*) which may influence forage site selection (Barrows and Barrows 1978, Solis and Gutierrez 1990).

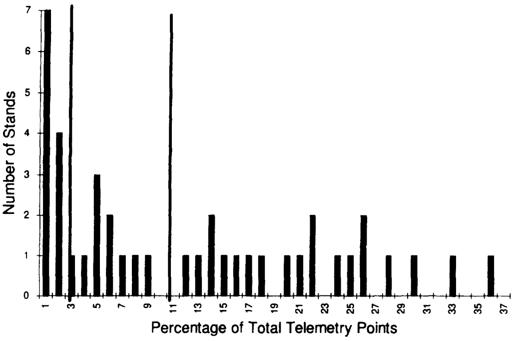

Fig. 2. A histogram of 41 stands used by spotted owls. Owl use is measured as the percentage of total telemetry locations of an owl pair that occur in the stand. A total of 11 owl pairs are represented. Stands with 1–2% of the total telemetry locations for their owl pair were classed as low-use, stands with 3–10% as medium-use, and more than 10% as high-use. The vertical lines indicate the boundaries for each use-intensity level.

RESULTS

Changes in the use-intensity levels for the 41 selected stands were analyzed against the 5 selected microhabitat measures to investigate their potential importance to owl site-selection. Model investigations used the lrm (ordinal logistic regression) function in the Design Library of Functions (Harrell 1994) in S-Plus (Stat. Sci. 1993). A forward approach was used in model selection. In the first step, use-intensity class was regressed against each of the 5 variables individually. The most important variable (i.e., with the highest change in deviance) was then included in the model if significant, and the procedure repeated (Table 1). Each variable or interaction term not already in the model was added individually and its importance measured by the change in deviance. With PLR, independent variables can appear nonlinearly (e.g., higher powers, logs), but graphical explorations of the microhabitat data indicated a linear model was appropriate for our data.

The final model selected was:

$$\text{logit (use-intensity level } i) = \alpha_i + \beta_1 \times SNVOL + \beta_2 \times HCLBP$$

Interaction among the selected variables, *SNVOL* and *HCLBP*, was explored with the likelihood-ratio test, but the model was not significantly improved.

Table 1. Forward Model Selection for the PLR model of northern spotted owl demonstration data.

Current model	*SNVOL*	*HCLBP*	*LGVOL*	*TALTRDE*	*WATER*
Intercepts only +	44.31[a]*[b]	35.37*	3.95*	0.07	0.83
Intercepts + *SNVOL*+		6.97*	2.18	0.09	0.24
Intercepts + *SNVOL* + *HCLBP* +			1.78	2.46	0.86

[a] Cells display the change in deviance, (−2·log likelihood), due to adding the selected term to the current model. All terms contribute 1 degree of freedom, therefore the change in deviance should follow a Chi-square distribution with 1 df under the null hypothesis that the selected coefficient is zero.

[b] A significance level of $\alpha = 0.10$ was used as the criterion for adding terms. Significant terms are denoted by *.

A graph of the sample stands by snag volume and height class diversity indicate a general increase in the level of owl use with the selected variables (Fig. 3).

Multicollinearity among the selected variables was a concern in model building as many forest structures, such as the size of trees, snags, and logs are highly correlated with stand age and disturbance history. Multicollinearity arises when independent variables are highly associated, making it impossible to accurately distinguish their individual contributions to the model. The final selected model's variance inflation factor (*VIF*) of 13.5 indicates that multicollinearity is a concern (Weisberg 1985, Wetherill et al. 1986) and may have affected the accuracy of the parameter estimates. However, the likelihood ratios from the model selection process (Table 1) support the model's variable selection.

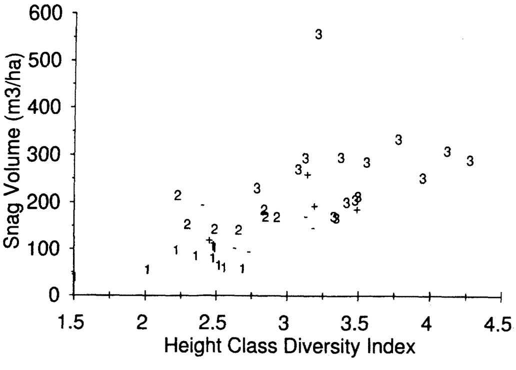

Fig. 3. Forty-one owl-use stands plotted against their measures of the variables selected by the PLR analysis. The graph also shows the jackknife allocation error for the stands by their use-intensity level: stands which the model correctly predict are shown by their use value (1 for low, 2 for medium, and 3 for high), under predictions by a "-" and over predictions by a "+". Note that although 1 stand has a high snag volume value, it is well within the high-use section and does not distort the PLR classification equations.

Model Goodness-of-Fit

The fit of a PLR model can be assessed with both summary measures and cross-validation techniques. The lrm function in S-Plus (Stat. Sci. 1993) calculated summary measures of the ordinal association of the final model: Somers $D_{xy} = 0.892$ and Goodman and Kruskal's Gamma = 0.914. Both statistics measure the rank correlation between the model-derived linear predictor portion of the logit, ($\beta 1 \times SNVOL + \beta 2 \times HCLBP$), for an observation and the actual use-intensity class (Agresti 1990, Harrell 1994). The D_{xy} and Gamma values, which can range from −1 to 1, indicate the model is a good fit for the data.

The final step in the analysis was an evaluation of the model's classification capabilities using a jackknife procedure. Each of the 41 stands was removed from the dataset, 1 at a time, and classified using PLR equations derived independently from the data on the remaining 40 stands. The process was repeated for all 41 stands.

The percentage of correct classifications ranges from 61.5 to 91 (Table 2). Although 15.4, 25.7, and 23.1 of the stands were misclassified in the low-, medium- and high-use categories, none of the misclassifications were off by more than 1 use-intensity level.

Although only a small set of variables were analyzed for the purpose of demonstration, the proposed technique developed a model with good predictors of the relative use of microhabitat sites. We believe the model's strong results are due to the careful selection of microhabitat measures and the technique's use of PLR analysis of use-only sites.

This demonstration of radiotelemetry data and PLR to analyze microhabitat provides a model of variables associated with spotted owl foraging in Washington State. We caution, however, that this demonstration used a limited number of microhabitat measures and does not attempt to explain the spotted owl's association with old-growth forests or explore factors other than the selected variables which may influence microhabitat selection.

DISCUSSION

Identifying important structures of an animal's microhabitat can be difficult because the preferred macrohabitat may differ in a variety of ways from available, but avoided, areas. For example, there are numerous, complex structural characteristics which distinguish old-growth from younger-age forests. These structural characteristics develop over time and in response to disturbances. Landscapes with a mosaic of seral stages and different disturbance histories will have an array of potential habitat sites, each with a different habitat value. In this situation, a microhabitat analysis that uses a presence/absence comparison simplifies the classification of suitability habitat sites. Furthermore, when use and nonuse sites substantially differ, the presence/absence comparison may not be able to tease apart the complex structure of the macrohabitat to identify the particular features which are important to the microhabitat.

While the use of radiotelemetry data avoids the problematic use of absence sites, it is still only an approximation of the relative habitat value of different sites to a study animal. The technique assumes that telemetry locations represent an animal's preference for different sites and by inference, reflect their microhabitat value. Assigning sites use values based on radiotelemetry points treats all locations with equal importance. However, some locations may be visited only briefly, yet be important to an animal's survival. Telemetry data will only be representative of use preferences for species with site fidelity and whose length of time at different sites reflects their relative habitat value. For instance, visitation time will not be a good measure of habitat suitability for animals that continue to forage in 1 area until prey populations are depleted.

The number of telemetry locations for each study animal should be large and of similar size. The probabilities of selecting any 1 stand will only be comparable between different animals with large, representative samples of use-intensity and fairly equal numbers of locations between animals. The method requires large telemetry datasets for several animals, as location screening can reduce the analysis sample to a few stands per animal. As the method models the use intensity of a sample population, sample size should include several animals, each with a range of use-intensity stands. Although the final number of stands may be small, high model classification accuracy can be attained as each stand's use-intensity is calculated from a large sample of the animal's use patterns (see Mladenoff et al. 1995 for a similar approach).

Table 2. Jackknife classification errors for the PLR model of the northern spotted owl demonstration data.

Use-intensity level	Predicted level: 1	Predicted level: 2	Predicted level: 3
Observed level: 1[a]	91%[b]	9%	0%
Observed level: 2	15.4%	61.5%	23.1%
Observed level: 3	0%	16.7%	83.3%

[a] The dataset contained 11 stands classified as level 1 (low-use), 13 stands classified as level 2 (medium-use), and 18 stands classified as level 3 (high-use).

[b] Cells display the percentage of observations classified into each use-intensity level given the observed use-intensity level.

To improve the power of the predictive model, the distribution of telemetry location percentages should be categorized parsimoniously. For a given sample size and significance level, power is improved when the effect being modeled is easier to detect (Cohen 1988). Therefore as the number of use-intensity classes increases, the model will be less accurate at predicting subtle differences in microhabitat use.

Use-intensity classes can be defined by gaps or rapid declines in the number of stands for a range of consecutive telemetry percentages (Fig. 2). For some species, however, definition of use-intensity classes may be difficult when there is no pattern to the histogram of site frequencies by telemetry percentage or little is known about the species behavior. In these cases observations from field biologists or behavior patterns seen in long-term telemetry collections may help identify use-intensity classes. Within these conditions, we believe telemetry is the best approximation of animal use-intensity presently available as it provides a large temporal and spatial sample of use patterns.

The presented method may also have applications for forage selection studies. Although we have focused on microhabitat structure, forage patterns could be modeled using animal selection of different foraging items or areas. A use measure other than radiotelemetry, such as grazing intensity or pellet production, could be categorized into ordinal levels of selection and modeled with the PLR analysis. With a gradient analysis of selected items or areas only, this technique might improve the power and precision of foraging models used by wildlife managers and land managers.

The advantage of the proposed technique is its ability to establish a relative measure of use-intensity, eliminating the need to identify absence sites. Polytomous logistic regression can model the ranked order of the use sites, providing a finer analysis of microhabitat variables within the used macrohabitat. Ordinal PLR allows both continuous and categorical microhabitat measures, does not require a constant covariance structure across all use levels, and retains and incorporates the information in the ranking of the use-intensity levels. When radiotelemetry information for a species with site fidelity is available, this technique can improve on microhabitat analyses which use DFA or presence/absence sampling.

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A COMPARISON OF CONFIDENCE INTERVAL METHODS FOR HABITAT USE-AVAILABILITY STUDIES

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Abstract: Wildlife managers routinely compute sets of simultaneous confidence intervals to estimate the actual proportion of use of a set of k habitat types. Confidence intervals are determined by assuming that the counts of observed use are from k binomial populations. A set of k intervals is constructed from a large sample approximation for a confidence interval for a single binomial proportion. The simultaneous confidence level is controlled by use of the Bonferroni inequality. The coverage probability of these intervals can be less than the nominal $(1 - \alpha)$ 100% level. This paper presents results of a simulation study comparing the performance of these intervals with 3 alternatives; the usual method with a continuity correction factor, and 2 methods of computing confidence intervals for multinomial proportions. The 2 latter methods are superior and should be used in place of the binomial intervals.

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Key words: binomial, confidence intervals, habitat studies, multinomial, resource selection, use-availability studies.

Habitat use-availability studies are common in the wildlife sciences. The primary method of determining preference or avoidance of habitats by a species has been to count the number of times individuals used a particular habitat and compare observed counts with expected counts in a Chi-square goodness-of-fit test. Expected counts are computed under a null hypothesis of no difference between true proportions of use and actual proportions available of the habitat types. Rejection of the null hypothesis typically is followed by computation of a set of $100(1 - \alpha)\%$ simultaneous confidence intervals in an effort to estimate the true proportions of use. If the proportion available of a specific habitat lies below (above) the lower (upper) limit of its associated confidence interval then the conclusion is that the species is choosing (avoiding) that type.

If there are k habitat types, then a set of k