USE OF MULTIPLE REGRESSION AND USE-AVAILABILITY ANALYSES IN DETERMINING HABITAT SELECTION BY GRAY SQUIRRELS (*SCIURUS CAROLINENSIS*)

JOHN W. EDWARDS, SUSAN C. LOEB, AND DAVID C. GUYNN, JR.

Department of Forest Resources, Clemson University, Clemson, SC 29634-1003. (JWE, DCG)
Southern Research Station, Department of Forest Resources, Clemson University, Clemson, SC 29634-1003. (SCL)

ABSTRACT.-Multiple regression and use-availability analyses are two methods for examining habitat selection. Use-availability analysis is commonly used to evaluate macrohabitat selection whereas multiple regression analysis can be used to determine microhabitat selection. We compared these techniques using behavioral observations (n = 5534) and telemetry locations (n = 2089) of gray squirrels (*Sciurus carolinensis*) on the Piedmont National Wildlife Refuge (PNWR) in Georgia. Use-availability analysis of stands classified according to their composition of pine and hardwood basal area produced inconsistent results; no pattern of selection was evident because similarly classified stands (e.g.. pine/ hardwood) received differing levels of use. In multiple regression analysis, tree species that predicted relative use by gray squirrels differed by season. Deciduous holly (*Ilex decidua*), sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), willow oak (Q. *phellos*), winged elm (*Ulmus alata*), and yellow-poplar (*Liriodendron tulipifera*) explained the most variation in seasonal stand use by gray squirrels; none of the 17 structural variables measured contributed significantly to predictive models. We found poor to moderate concordance (14.3 - 71.4%) between stand use predicted from multiple regression analysis and stand use determined by use-availability analysis. Our findings suggest that examinations of selection at different scales may result in differing interpretations of habitat use and erroneous inferences regarding habitat selection.

INTRODUCTION

Habitat selection is central to the study of animal ecology. Habitat is defined as an area with the resources and environmental conditions that promote occupancy by individuals of a given species and allows those individuals to survive and reproduce (Morrison et al., 1992). Animals may identify and select habitats by responding to composition of plant species, physiographic make-up, resource distribution, and structural attributes (Laundre and Keller, 1984). Factors such as interspecific and intraspecific competition and predation may further affect habitat selection. Selection is inferred when habitats are used disproportionately to their availability (Johnson, 1980). Johnson (1980) defines habitat selection using hierarchial orders of resolution; first-order selection is the geographic range of a species, second-order selection includes the habitats that make up an animal's home range, and third-order selection is the usage made of various habitats within the home range.

Determination of habitat selection is commonly done by comparing habitat use with habitat availability (hereafter referred to as use-availability). This analysis may be done at either the micro- or macrohabitat level, but is usually conducted at the macrohabitat scale (e.g., Neu et al., 1974; White and Garrot, 1990). Use-availability (UA) anaylses assume that a species selects and uses areas that are best able to satisfy its requirements, and as a result, animals use higher-quality habitats in

In M.A. Steele, J. F. Merritt, and D. A. Zegers (eds.). 1998. Ecology and Evolutionary Biology of Tree Squirrels. Special Publication, Virginia Museum of Natural History, 6: 320 pp

greater proportion than their availability (Schamberger and O'Neil, 1986). Reviews of several use-availability analyses found no superior method and suggest that the choice of analysis should be based on the biological question of interest and statistical assumptions (Thomas and Taylor, 1990; Alldredge and Ratti, 1992; Manly et al., 1993). Use of these analyses usually results in classification of habitat use as either greater than, proportional to, or less than that expected on the basis of availability. UA analysis, however, does not address the question of which habitat characteristics are most important in determining selection (Porter and Church, 1987). In UA analysis a habitat must be classified into an exclusive category (e.g., pine, hardwood, open field). This results in a loss of information and may ignore certain variables that may be important (e.g., structural variables or the presence of an important resource at low levels).

An alternative method for determining habitat selection is multiple regression (MR) analysis. MR analysis reveals habitat characteristics which are most associated with observed use and is helpful in assessing both macro- and microhabitat selection, but is particularly effective in determining microhabitat selection. Further, MR models can be used to predict habitat use.

Because UA and MR analyses usually address different levels of selection (i.e., macro versus micro), it is often necessary to reconcile results among studies using different methods and scales. Using telemetry locations and behavioral observations, we tested whether the results and interpretations of gray squirrel habitat selection at the macrohabitat scale using UA were comparable to those using MR at the microhabitat scale.

METHODS

Study Area.-We conducted the study on the Piedmont National Wildlife Refuge (PNWR), located in central Georgia (Jasper and Jones counties). Much of the 14,000-ha PNWR was covered by pine (*Pinus*) and mixed pine-hardwood forests. Loblolly pine (P. *taeda*) was dominant on ridges and upper slopes. Oaks, hickories (*Carya*), sweetgum, yellow-poplar, and blackgum (*Nyssa sylvatica*) dominated lower slopes and along streams. Midstory species included dogwood (*Cornus florida*), persimmon *(Diospyros* virginiana), hornbeam (Ostyu *virginiana*), winged elm, hawthorn, and maple (*Acer*). Broomsedge *(Andropogon),* japanese honeysuckle *(Loniceru japonica*), muscadine *(Vitis rotundifolia*), smilax (*Smilax*), and blueberry *(Vaccinium)* were common understory species (Radford et al., 1968; Petrides, 1972).

Habitat patterns on the PNWR were influenced by aspect, slope, and forest management practices (Brender, 1973). Because of the topography, presence of several drainages, and small stand size, habitats were uniformly available over the study area.

Radiotelemetry.—We captured gray squirrels using Mosby-type box traps (Day et al., 1981) placed systematically (100 by 100 m) over 12 1 ha (Tappe, 1991; Tappe et al., 1993). Additional animals were captured using 88 nest boxes (modified from Barkalow and Soots, 1965) placed systematically (100 by 100 m) in trees at 8.5 to 9.8 m throughout a 73-ha portion of the study area. Adult animals were removed from traps or nest boxes, restrained in a soft-webbed handling cone (modified from Day et al., 198 1), anesthetized with ketamine hydrochloride, and fitted with a radio transmitter-collar unit (Telonics Inc., Mesa, AZ). These procedures were defined under Animal Use Protocol 348 of the Clemson University Animal Research Committee. Transmitters weighed 18-20 g and had an expected battery life of 9-11 months. We estimated squirrel locations by triangulating from 3 of 115 telemetry stations using a three-element Yagi antenna; the geometric center of the triangle formed by the three intersecting azimuths was used as the animal's location. During 1989 and 1990, we obtained locations on radio-collared squirrels every 2 hours between sunrise and sunset, 2 days each week. Sampling intensity was similar within diurnal periods and among seasons (spring = 148, summer = 216, fall = 19 1, winter = 207 locations). Activity was measured on 4-5 animals each season (n = 19), with 35-48 locations for each animal.

We assessed radiotelemetry accuracy by placing transmitters 5 cm above the ground at premapped locations. Azimuth readings were taken from 8-10 telemetry stations on transmitters placed at six locations unknown to the observer. We determined error arcs for each trial and calculated an average 90% confidence interval, error polygon (Springer, 1979). We conducted testing during August 1990 to simulate "worst-case" signal attenuation caused by maximum foliar coverage and high humidity (Lee et al., 1985; Chu et al., 1988).

Habitat delineation and characteristics.—We delineated stand boundaries using aerial photographs and ground reconnaissance. A stand was defined as a contiguous group of trees sufficiently uniform in species composition, arrangement of age classes, and condition to be a homogeneous and distinguishable unit (Smith, 1962). On a 10 by 40-m (0.04 ha) plot in each stand, we recorded diameter at breast height (dbh) and identified species of codominant and dominant stems (Smith, 1962). On a 5-m by 20-m plot, we recorded dbh and identified species of midstory stems >2.5 cm dbh and > 1.4 m in height. Plots were located centrally to typify stand characteristics. Structural measures included: aspect, slope, % overstory composed of pine, % overstory composed of hardwoods, % midstory composed of pine, % midstory composed of hardwoods, overstory hardwood stems per ha (OHSHA), overstory pine stems per ha (OPSHA), midstory hardwood stems per ha (MHSHA), midstory pine stems per ha (MPSHA), overstory basal area per ha, midstory basal area per ha, stand area, and stand perimeter. In addition, a vertical cover index was determined at the plot center using a 3.6-m pole divided into five equal sections and oriented horizontally at each cardinal direction (N,E,S,W). We recorded a hit if any vegetation contacted the pole in a specified segment. Index values were calculated using the ratio of recorded hits over possible hits (20), at heights of 30, 9 1, and 152 cm.

We assigned vegetation types on the basis of basal area (USDA Forest Service, 1988). Individual stands were assigned to 1 of 4 types: 1) pine (>69% pine), 2) pine/ hardwood (5 1-69% pine), 3) hardwood/pine (5 1-69% hardwood), and 4) hardwood (>69% hardwood) We further classified stands on the basis of slope position (top, upper mid, lower mid, and bottom).

Habitat use-availability.-We determined boundaries of seasonal home ranges for each squirrel with >39 locations per season using the harmonic mean method (Dixon and Chapman, 1980) for 95% (95HM) and 53-68% ($\bar{x}$ = 61%, CORE) of the animal's use distribution (Program HOMERANGE, Ackerman et al., 1990); the latter determination represents the core area (Kaufmann, 1962) and is defined as the maximum area where the observed utilization distribution exceeds a uniform utilization distribution (Ackerman et al., 1990). This model identifies areas of concentrated use within home-range areas (e.g., core areas) and thus provides a biological approach to analyzing utilization distributions. We also determined a seasonal home-range boundary with a 95% minimum convex polygon (MCP; Michener, 1979). We used the seasonal home-range boundaries of each squirrel to delineate their available habitats. Spatial analyses on animal locations, stand boundaries, home-range area, and availability of habitats were performed using Geographical Information Systems ARC/INFO (Environmental Systems Research Institute, Redlands, CA). We considered the area of available habitats to be known measures and not estimates (Thomas and Taylor, 1990).

We determined the UA of each stand within individual home ranges for each squirrel and then pooled across animals. This eliminated the assumption of equal availability of vegetation types for all individuals. Although pooling of data may mask individual variation in habitat selection (White and Garrot, 1990), we justified pooling because our objective was to examine group rather than individual patterns of habitat selection; and because sample size constraints prevented selection analyses of seasonal home ranges of individual squirrels. We assumed observations among individuals to be independent. Dependence among observations within individuals may result from insufficient time elapsing between observations or from biased spatial patterns of movements (Swihart and Slade, 1987). Time-to-independence for locational observations within animals, based on a mean body mass of 0.6 kg, is 138 min (Swihart et al., 1988); minimal time between successive locations in our study was 120 min.

Chi-square goodness-of-fit analyses were used to test the null hypothesis that vegetation type use was proportional to availability within seasonal home ranges of radio-collared squirrels (Neu et al., 1974; Byers et al., 1984). Categories were pooled so that at least one observation was expected in each, and no more than 20% of the categories contained <5 expected observations (Roscoe and Byars, 1971). We computed Bonferroni confidence intervals (95%) to infer selection of individual stands in those cases in which significant selection was detected (Neu et al., 1974; Byers et al., 1984). If expected frequencies were outside the confidence interval, then we considered the stand to be used greater than expected (+) or less than expected (-); expected frequencies within confidence intervals inferred stand use proportional (P) to availability. We examined levels of selection for each stand, vegetation type, and season.

Behavioral observations.-We conducted direct observations of randomly selected radio-collared individuals of both sexes, 1 day each month, during 1989 and 1990. Observations began 30 min before sunrise and continued until 30 min after sunset. Each day was subdivided into 3-hour sampling periods in which observations (instantaneous sampling) were recorded at 3-min intervals; sampling periods were staggered to avoid observer fatigue. Combined sampling periods conducted during 4 days each month comprised 2 observation days (i.e., 1 dawn-to-dusk observation for each sex). No individual was observed during consecutive sampling periods. Observations included stand number, strata occupied (e.g., canopy, bole, ground) and general behavior (e.g., resting and maintenance, feeding and foraging, vigilance, locomotion). Due to their wariness, we used precautions (e.g., camouflage clothing and/ or blinds) when observing the focal animal and each animal was located 30 min prior to the start of the observation period with the aid of telemetry and binoculars. If at any time during the sampling period the focal animal's behavior appeared affected by the observer's presence (e.g., extreme vigilance or barking directed towards the observer), we terminated the session.

Among the 142 stands comprising the study area, we recorded 5534 gray squirrel (n = 25) observations during the 2-year study. Relative use of stands was calculated, for each season as (number of observations within a stand / total number of observations) x 100. Due to a limited number of radio-collared animals, one individual squirrel contributed 23% of the winter observations; no individual contributed > 19% of the observations during other seasons. Observations on focal animals among months and sampling periods were considered independent whereas observations within sample periods were not assumed to be independent (Machlis et al., 1985). The 3-min sampling interval allowed the focal animal sufficient opportunity to change behavioral events; 3 min was not sufficient in most instances for an animal to move from one stand to another. We used a Wilcoxon paired-sample test (Mendenhall et al., 1990) to compare relative use in 3-min intervals with that in S-hour intervals. Relative use in 3-hour periods included only the first observation recorded in the sampling period and was therefore considered independent. We found no differences ($P > 0.10$) between measures of relative use in 3-min and S-hour intervals within seasons. Using the same test, we found no differences ($P > 0.10$) in patterns of stand use between males and females; and relative use of stands by gray squirrels did not differ ($P > 0.10$) between years. Comparisons within sexes and seasons between years were not possible because of limited paired samples of relative use. Therefore, analyses included all 3-min observations and combined male and female observations.

Regression analyses.-We used multiple stepwise regression (PROC STEPWISE, MAXR; SAS Institute, Inc, 1991) to model relative stand use. Eighty-four independent variables (17 structural, 25 overstory species, 42 midstory species) describing each stand were used to develop predictive models for each season. Structural variables OHSHA, OPSHA, MHSHA, and MPSHA were log10 transformed (Steel and Torrie, 1980). Importance values of overstory and midstory species ranged from 0 to 1. We calculated importance values by summing relative density with relative basal area and dividing by 2. We selected the five-variable model which explained the most variation in relative use by gray squirrels for each season. We used several diagnostic procedures to evaluate and determine that outliers and collinearity were not a problem in the data set (studentized residuals, Dffits, Dfbetas, pairwise correlation, VIF, condition number: SAS Institute, Inc, 1991). Partial regression coefficients were standardized using PROC REG, option STB (SAS Institute, Inc, 1991). Predicted values of relative use for all 142 stands were calculated for each season on the basis of MR models. We categorized the predicted use of stands within seasons as low (L), medium (M), or high (H), using first quartile, second and third quartiles, and fourth quartile of values of predicted use, respectively. We compared selection levels determined by UA analysis to predicted values of relative use by equating (-) with "L", (P) with "M", and (+) with "H". We determined the percent concordance between analyses for each method of home-range estimation and season.

RESULTS

The angular error of 73 'trial azimuths, recorded from distances of 110 to 770 m, averaged 10.6" (SE = 0.87"). Most squirrel locations were determined from azimuths <300 m. The angular error of 16 trial azimuths between 200-300 m averaged 7.3" (*SE* = 1.41"); the 90% error polygon determined from two error arcs intersecting at 90" from a distance of 250 m was 0.78 ha. Mean stand size on the study area was 2.0 ha (*n* = 142, *SE* = 0.19 ha). All locations of squirrels were within 50 m of a stand boundary.

Macrohabitat selection (-, P, +) differed, within stands, depending on the method used to determine boundaries of home range (i.e., 95HM, MCP, CORE) and season (Fig. 1). All home-range methods resulted in concordant selection levels in >57% of stands. Mean percent concordance was highest (85.1%) between MCP and CORE estimates.

Macrohabitat selection within vegetation types differed by stands (Table 1). For example, pine and pine-hardwood types (overstory/midstory) received all levels (-, P, +) of selection in spring;

Table 1.-*Seasonal levels of selection of selected stands and vegetation types by gray squirrels on the Piedmont National* Wildlife *Refuge, Georgia, 1989-1990, on the basrs of use-availability analysis. Selection levels were determined on the basis of 95% harmonic mean home ranges; (+) = stand used more than expected; (-) = stand used less than expected; (P) = stand used in proportion to availability.*

Season	Stand	Selection	Vegetation type		Slope position
			Overstory	Midstory	
Spring	21	(+)	Pine	Pine	Upper mid
	50	(P)	Pine	Pine	Top
	66	(P)	Pine	Pine	Upper mid
	36	(-)	Pine	Pine	Lower mid
	72	(-)	Pine	Pine	Upper mid
	30	(+)	Pine	Hardwood	Bottom
	93	(P)	Pine	Hardwood	Lower mid
	99	(P)	Pine	Hardwood	Upper mid
	56	(-)	Pine	Hardwood	Upper mid
	57	(-)	Pine	Hardwood	Top
Summer	52	(+)	Hardwood	Hardwood	Upper mid
	35	(P)	Hardwood	Hardwood	Upper mid
	30	(P)	Pine	Hardwood	Bottom
	31	(P)	Pine	Hardwood	Bottom
	17	(-)	Pine	Hardwood	Upper mid
	18	(-)	Pine	Hardwood	Upper mid
Fall	15	(P)	Pine	Hardwood	Upper mid
	31	(P)	Pine	Hardwood	Bottom
	a4	(P)	Pine	Hardwood	Lower mid
Winter	30	(P)	Pine	Hardwood	Bottom
	58	(P)	Pine	Hardwood	Upper mid
	18	(-)	Pine	Hardwood	Upper mid
	32	(-)	Pine	Hardwood	Upper mid

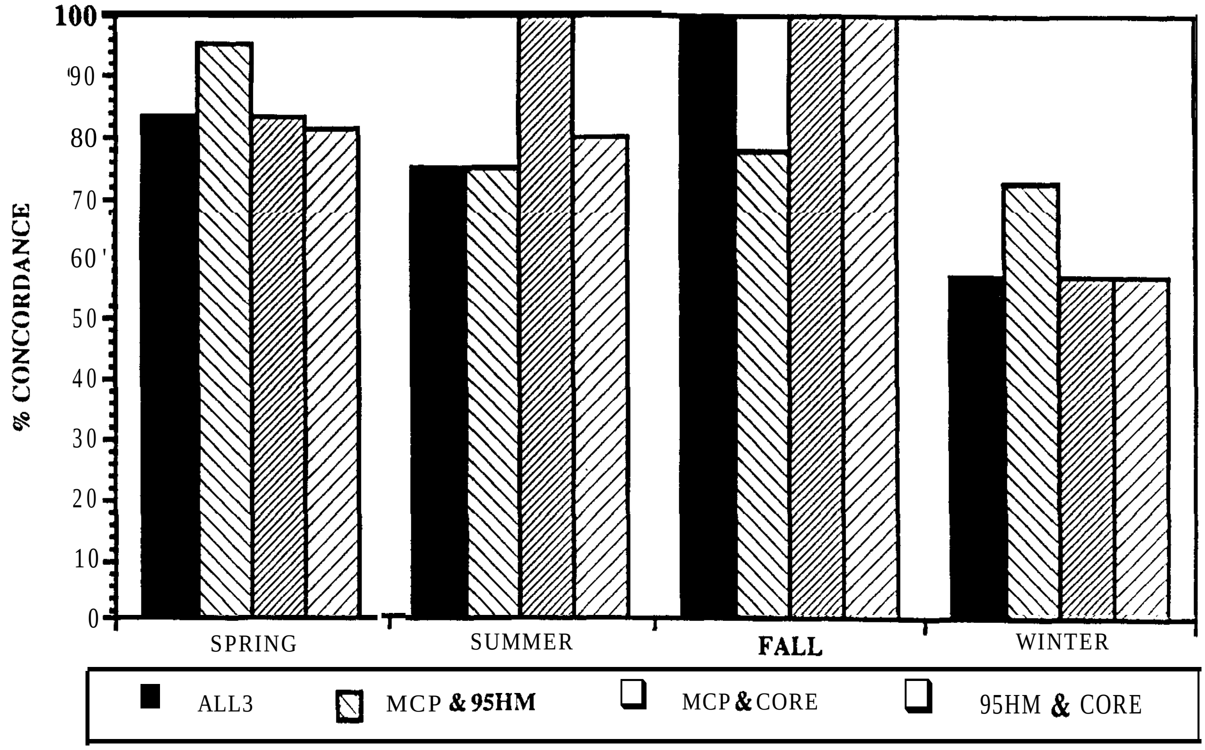

Fig. 1 .-Concordance (%) of macrohabitat levels of selection among home-range methods (95% minimum convex polygon [MCP], 95% harmonic mean [95HM], and core area [CORE]), on the basis of use of individual stands by gray squirrels on the Piedmont National Wildlife Refuge, Georgia, 1989-l 990.

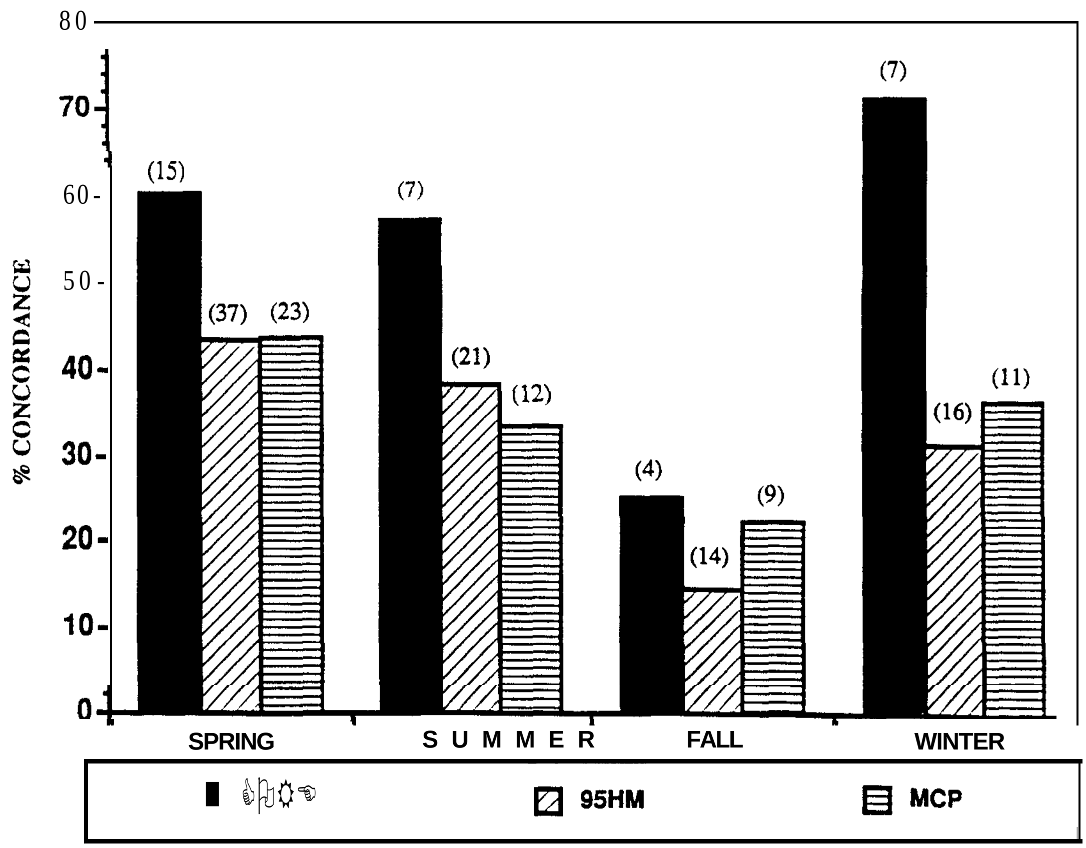

Fig. 2. -Concordance (%) of levels of selection determined by use-availability analysis and those predicted by multiple regression models on the basis of relative use by gray squirrels on the Piedmont National Wildlife Refuge, Georgia, 1989-1990; CORE = core area; 95HM = 95% harmonic mean: MCP = 95% minimum convex polygon. Values in parentheses are numbers of stands.

Table 2.—*Independent variables found to predict microhabitat selection by gray squirrels on the Piedmont National Wildlife Refuge, Georgia, 1989- 1990. Relative use was determined on the basis of 1442 observations in spring, 1963 in summer, 920 in fall, and 986 in winter in 18, 29, 22, and 11 stands, respectively,*

Season	Canopy position[a]	Independent variable	Standardized coefficient[b]	*P*[c]	R^2[d]
Spring	Mid	Water oak (*Quercus nigra)*	0.66	co.01	0.78
	Over	Sweetgum (*Liquidambar styraciflua*)	0.52	0.03	
	Over	Willow oak (*Q. phellos*)	0.51	co.01	
	Over	*S.* red oak *(Q. falcata*)	0.27	0.07	
	Mid	Shagbark hickory (*Carya ovata*)	-0.72	co.01	
Summer	Over	Water oak	0.69	co.01	0.83
	Over	Willow oak	0.54	<0.01	
	Over	White oak (*Q. alba*)	0.40	co.01	
	Over	Winged elm (*Ulmus alata*)	0.34	co.01	
	Over	Overcup oak *(Q. lyrata*)	-0.35	co.01	
Fall	Mid	Winged elm	0.62	co.01	0.75
	Mid	Yellow-poplar (*Liriodendron tulipifera*)	0.50	co.01	
	Mid	Hornbeam (*Ostrya* virginiana)	0.31	0.03	
	Mid	Deciduous holly (*Ilex* decidua)	-0.26	0.06	
	Mid	Poison ivy (*Rhus radicans*)	-0.31	0.03	
Winter	Mid	Deciduous holly	0.84	<0.01	0.99
	Mid	Yellow-poplar	0.67	<0.01	
	Mid	Hawthorn *(Crataegus)*	0.18	<0.01	
	Over	Sweetgum	0.08	0.01	
	Mid	Willow oak	-0.15	<0.01	

[a] Over = overstory; Mid = midstory ; [b] Standardized partial regression coefficient ;

[c] Probability of > I t I ; [d] Coefficient of multiple determination

hardwood types (midstory) received all levels of selection in spring and summer. Stands further classified by slope position also received differing levels of selection,

Habitat variables that predicted gray squirrel microhabitat selection differed among seasons (Table 2). In spring and summer, stand use by gray squirrels was positively correlated with oaks (except overcup oak Q. *lyrata*) and negatively influenced by shagbark hickory (C. *ovata*) and overcup oak. In fall and winter, stand use by gray squirrels was positively correlated with deciduous holly, yellow-poplar, winged elm, and hornbeam, and negatively influence by poison ivy (*Rhus radicans*) and willow oak. Structural variables were unimportant in predicting relative use by gray squirrels in any season.

Concordance among selection levels of stands determined from UA analyses (-, P, +) and predicted levels of use (i.e., L, M, H) from MR models varied from poor to moderate (Fig. 2). Percent concordance differed by season and method of home-range estimation. Percent concordance was higher when the CORE home-range method was used (25.0% - 71.4%) than when the 95HM method (14.3% - 43.2%) or MCP method (22.2% - 43.5%) were used.

DISCUSSION

Studies of macrohabitat selection by radio-collared animals follow a common paradigm: 1) delineate study area boundaries, 2) identify spatial units (e.g., stands) within the study area, 3) classify spatial units into vegetation types on the basis of species composition and structural characteristics (e.g., pine/hardwood bottom), 4) determine availability of vegetation types, 5) quantify location data, and 6) perform UA analysis to determine selection.

One of the most critical aspects of UA analysis is the classification of stands into vegetation types. A problem in identifying vegetation types is the criteria on which they are based. The researcher must identify stand characteristics that best determine a species use (e.g., slope position, species composition, stand age, or sex-al stage) and then classify stands accordingly. If these criteria are different, too broad, or do not correlate with those of the animal under investigation, then UA analysis may lead to spurious conclusions. This process is made more complex when the different layers (e.g., overstory, herbaceous) of habitats are also considered. Further, stands are usually grouped by vegetation type before analyses are conducted. We found that similarly classified stands often received different levels of selection (see Table 1). Had we grouped stands into vegetation types prior to our analyses, as is commonly done, differences among stands of similar composition and structure would have been masked.

Boundary delineation and subsequent proportional availabilities of stands are also critical steps in UA analysis (Porter and Church, 1987). We restricted our analyses to within home ranges because these boundaries are biologically relevant to the animal and the animal has demonstrated access (availability) to these areas. However, we found macrohabitat selection differed within stands depending on the method of home-range analysis. The choice of which home-range estimate to use is subjective. Because there is no agreement as to which estimate is "best", researchers must choose on the basis of their knowledge of the animal under investigation and their understanding of home-range estimators. Therefore, results of UA analysis are likely to vary depending on which estimator is chosen.

MR analysis is commonly used in wildlife studies to determine which characteristics are most important in predicting animal use (Brown and Batzli, 1984; Bull and Holthausen. 1993; Kotler et al., 1993; Pauley et al., 1993). We found microhabitat selection by gray squirrels most correlated with oak species in spring and summer; sweetgum and shagbark hickory were also important in spring. Midstory, winged elm and yellow-poplar, and deciduous holly and yellow-poplar, were most correlated with squirrel use in fall and winter, respectively. Causal relationships between stand use and species associations are uncertain, however, because occurrences of individual plant species and their contributions in predictive models vary seasonally. On the basis of silvical characteristics (USDA Forest Service, 1990), stand use by gray squirrels was greatest in mesic habitats on lower slopes in all seasons. Because of the mesic conditions in these habitats, midstory hardwoods were abundant in stands used in spring, fall, and winter. We observed squirrels feeding on oak flowers during spring and early summer. Yellow-poplar, hornbeam, and deciduous holly, although providing a food resource in fall and winter, also are indicators of moister stand conditions. These stands on lower slopes provide the greatest availability of oak mast on the PNWR (Edwards et al., 1993). Cavity availability (Edwards and Guynn, 1995), interspecific competition (Edwards, 1995), and predator avoidance also influence stand use and thus, may correlate with stand characteristics. Interpretation of model variables is subjective and based on the researcher's knowledge of the biology and ecology of a species.

UA and MR analyses examine habitat selection at different levels of resolution (vegetation types versus vegetative characteristics). UA analysis provides information concerning selection of vegetation types. Because habitat units (e.g., stands) must be classified into exclusive categories, much information about the vegetative characteristics (composition and structure) as well as other habitat features are lost. In contrast, MR analysis reveals characteristics which are important features in determining habitat use. Our comparisions of these two methods found only poor to moderate concordance between macrohabitat and microhabitat selection in assessing levels of stand use. UA analysis of core areas of use resulted in the highest concordance with MR predictive models. Because core areas represent areas used more intensively than other portions of an animal's home range (Kaufmann, 1962), vegetative characteristics of these areas may be particularly important in determining habitat selection. In our study, both MR models and delineation of core areas and subsequent UA analysis were determined on the basis of intensity of stand use. This similarity, may in part, explain the higher concordance when using boundaries of core area as compared to other methods of home-range determination.

Our findings suggest that examinations of selection at different spatial scales and levels of resolution, although informative, may result in differing interpretations of habitat use and subsequent inferences regarding habitat selection. Where the ecology of a species is well known and the examination of traditional habitat types (e.g., USDA Forest Service, 1988) is important for management decisions, UA analysis (macrohabitat selection) may be a more pragmatic approach. If the goal. however, is to determine which characteristics are most correlated with a species' habitat use, then MR analysis (microhabitat selection) offers a more rigorous approach. We are confident that our MR models more accurately depict stand use by gray squirrels on the PNWR. Interpretation of these models is difficult, however, and their translation into practical guidelines for habitat management is premature. Further research is necessary to test the application of these models.

ACKNOWLEDGMENTS

Support for our study was provided by the USDA Forest Service, Southeastern Forest Experiment Station (Cooperative Agreement 18-409, # 110) and the Department of Forest Resources, Clemson University. We thank the staff of the Piedmont National Wildlife Refuge for cooperation in this study. M. L. Morrison and an anonymous reviewer provided many helpful comments.

LITERATURE CITED

ACKERMAN, B., F. LEBAN, M. SAMUEL, AND E. GARTON. 1990. User's Manual for Program Home Range. Forestry, Wildlife and Range Experiment Station Technical Report 15. University of Idaho, Moscow, 80 pp.

ALLDREDGE, J. R., AND J. T. RATTI. 1992. Further comparison of some statistical techniques for analysis of resource selection. The Journal of Wildlife Management, 56: 1-9.

BARKALOW, F. S., AND R. F. SOOTS. 1965. An analysis of the effect of artificial nest boxes on a gray squirrel population. Transactions North American Wildlife and Natural Resource Conference, 30:351-359.

BRENDER, E. V. 1973. Silviculture of loblolly pine in the Georgia Piedmont. Georgia Forest Research Council. Report 33, Southeast Forest Experiment Station, Macon, Georgia, 74 pp.

BROWN, B. W., AND G. 0. BATZLI. 1984. Habitat selection by fox and gray squirrels: a multivariate analysis. The Journal of Wildlife Management, 48:6 16-62 1.

BULL, E. L., AND R. S. HOLTHAUSEN. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. The Journal of Wildlife Management, 57:335-345.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. The Journal of Wildlife Management, 48:1050-1053.

CHU, D. S., B. A. HOOVER, M. R. FULLER, AND P. H. GEISSLER. 1988. Telemetry location error in a forested habitat. Pp. 188-194, in Biotelemetry X: Proceedings of the Tenth Intemationai Symposium on Biotelemetry. (C. J. Amlander, Jr., ed.). University of Arkansas, Fayetteville, 733 pp.

DAY, G. I., S. D. SCHEMNITZ, AND R. D. TABER. 198 1. Capturing and marking wild animals. Pp. 6 l-98, in Wildlife Management Techniques Manual. (S. D. Schemnitz, ed.). The Wildlife Society, Washington, DC, 686 pp.

DIXON, K. R., AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. Ecology, 61:1040-1044.

EDWARDS, J. W. 1995. Resource use by sympatric populations of fox and gray squirrels. Ph.D. dissertation, Clemson University, South Carolina, 66 pp.

EDWARDS, J.W., D. C. GUYNN, JR., AND S. C. LOEB. 1993. Seasonal mast availability for wildlife in the Piedmont Region of Georgia. Research PaperSE-287, Asheville, North Carolina: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, 13 pp.

EDWARDS, J. W., AND D. C. GUYNN, JR. 1995. Nest characteristics of sympatric populations of fox and gray squirrels. The Journal of Wildlife Management, 59: 103-l 10.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 6 1:65-7 1.

KAUFMANN, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorada Island, Panama. University of California, Publications in Zoology, 60:95-222.

KOTLER, B. P., J. S. BROWN, AND W. A. MITCHELL. 1993. Environmental factors affecting patch use in two species of Gerbilline rodents. Journal of Mammalogy, 74:614-620.

LAUNDRE, J. W., AND B. L. KELLER. 1984. Home-range size of coyotes: a critical review. The Journal of Wildlife Management, 48: 127-139.

LEE, J. E., G. C. WHITE, R. A. GARROT, R. M. BARTMANN, AND A. W. ALLDREDGE 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. The Journal of Wildlife Management, 49:658-663.

MACHLIS, L., P. W. D. DODD, AND J. C. FENTRESS. 1985. The pooling fallacy: problemsarising when individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie, 68:201-214.

MANLY, B. F. J., L. L. MCDONALD, AND D. L. THOMAS. 1993. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Chapman and Hall, New York, 177 pp.

MENDENHALL, W., D. D. WACKERLY, AND R. L. SCHEAFFER. 1990. Mathematical Statistics with Applications, 4th edition. PWS-Kent, Boston, Massachusetts, 818 pp.

MICHENER, G. R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian Journal of Zoology, *57:* 125-139.

MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN. 1992. Wildlife-habitat Relationships: concepts and applications. University of Wisconsin Press, Madison, 343 pp.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. The Journal of Wildlife Management, 38:541-545.

PAULEY, G. R., J. M. PEEK, AND P. ZAGER. 1993. Predicting white-tailed deer habitat use in northern Idaho. The Journal of Wildlife Management, 57:904-9 13.

PETRIDES, G. A. 1972. Afield guide to trees and shrubs. Easton Press, Norwalk, Connecticut, 428 pp.

PORTER, W. F., AND K. E. CHURCH. 1987. Effects of environmental pattern on habitat preference analysis. The Journal of Wildlife Management, 51:681-685.

RADFORD, A. E., H. E. AHLES, AND C. L. BELL. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, 1183 pp.

ROSCOE, J. T., AND J. A. BYARS. 1971. An investigation of the restraints with respect to sample size commonly imposed on the use of the Chi-square statistic. Journal American Statisticians Association, 66:755-759.

SAS INSTITUTE. INC. 199 1. SAS User's Guide, version 6. SAS Institute Inc. Cary, North Carolina, 890 pp.

SCHAMBERGER, M. L., AND L. J. O'NEIL. 1986. Concepts and constraints of habitat-model testing. Pp. 5-10, in Wildlife 2000; Modelling habitat relationships of terrestrial vertebrates. (J. Verner, M. L. Morrison, and C. J. Ralph, eds.). University of Wisconsin Press, Madison, *470* pp.

SMITH, D. M. 1962. The practice of silviculture, 7th edition. John Wiley & Sons, New York, 578 pp.

SPRINGER, J. T. 1979. Some sources of bias and sampling error in radio triangulation. The Journal of Wildlife Management, 43:926-935.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and Procedures of Statistics: A Biometrical Approach. McGraw-Hill, New York. 633 pp.

SWIHART, R. K., AND N. A. SLADE. 1987. A test for independence of movements as shown by live trapping. The American Midland Naturalist, 117:203-207.

SWIHART, R.K., N. A. SLADE, AND B. J. BERGSTROM. 1988. Relating body size to the rate of home range use in mammals. Ecology, 69:393-399.

TAPPE, P. A. 199 1. Capture-recapture methods for estimating southern fox squirrel abundance. Ph.D. dissertation, Clemson University, Clemson, South Carolina, 92 pp.

TAPPE, P.A., J. W. EDWARDS, AND D. C. GUYNN, JR. 1993. Capture methodology and density estimates of southeastern fox squirrels *(Sciurus niger)*. Pp. 7 l-77, *in* Proceedings of the Second Symposium on

Southeastern Fox Squirrels, *Sciurus niger* (N. D. Moncrief, J. W. Edwards, and P. A. Tappe, eds.). Virginia Museum of Natural Histor,y Special Publication, 1: l-84.

THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. The Journal of Wildlife Management, 54:322-330.

U.S. DEPARTMENT OF AGRICULTURE. 1988. Silvicultural examination and prescription field book. Atlanta, Georgia, USDA, Forest Service, Southern Region, 35 pp.

———. 1990 Silvics of North America. conifers volume 1 (675 pp.) and hardwoods volume 2 (875pp.). USDA Forest Service Agriculture Handbook 654, Washington. DC.

WHITE, G. C., AND R. A. GARROT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, New York, 382 pp.