To the Graduate Council:

I am submitting herewith a dissertation written by Steven W. Seagle entitled "Habitat Availability and Animal Community Characteristics." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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HABITAT AVAILABILITY AND ANIMAL COMMUNITY CHARACTERISTICS

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Degree

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ABSTRACT

The microhabitat utilization and niche characteristics of Peromyscus leucopus, Ochrotomys nuttalli, and Blarina brevicauda were examined within a pine plantation on the Oak Ridge National Environmental Research Park in East Tennessee. Although general microhabitat utilization was the same, niche parameters (such as niche breadth) for each species varied between two study grids, apparently in response to differing understory density. Specialization is thus proposed to be a function of local microhabitat structure. Removal of the generalist species, P. leucopus, from one grid while maintaining the other as a control elicited a significant microhabitat shift and increase in niche breadth by O. nuttalli. B. brevicauda displayed a slight but nonsignificant microhabitat shift and increased niche breadth. These results are a counter example to the hypothesis that generalist species are poor competitors. Spatial microhabitat heterogeneity created by plant secondary succession and extrinsic disturbances such as tree blow-down is suggested to allow coexistence of these species by altering competitive abilities or microhabitat selection at a small spatial scale.

Since interspecific competition affects small mammal niche characteristics, two hypotheses to explain the relative abundances of coexisting animal species are examined. The "niche breadth hypothesis" proposes that the more resources controlled by a species the greater will be its abundance. Alternatively, the "habitat availability hypothesis" explains species abundance by the availability of habitat comprising the realized niche. Analysis of the small mammal fauna of the Oak Ridge National

Environmental Research Park indicates that habitat availability, not niche breadth, is a good predictor of abundance. This result is discussed in the context of habitat dynamics and the evolutionary history of the species. Results of slug, salamander and bird community analyses also support the habitat availability hypothesis.

Having established the importance of available habitat to animal species abundance, a first-order Markov model is developed to simulate habitat dynamics on landscape islands of differing areal extent. Colonization of these islands is then allowed by animal species having different habitat requirements. The colonization process is modeled using a randomly generated species pool and a species pool adapted to the landscape dynamics regime. Model runs for each species pool were duplicated with the addition of interspecific competition thus totaling four species pool-competition scenarios. Results indicate that the succession/disturbance regime interacts with island area to promote more constant habitat diversity on larger islands. Colonization of the various sized dynamic landscapes resulted in species-area curves having slopes between 0.14 and 0.31, depending on species pool size. Balance between colonization and extinction due to habitat dynamics is the primary cause for this species-area relationship. The model also generates an approximately canonical distribution of species abundances. Patterns of species turnover vary due to species pool composition, competition and vegetation/habitat dynamics on different sized islands.

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CHAPTER I

INTRODUCTION

A great variety of faunal patterns can be seen in species range maps such as those compiled in Hall and Kelson's (1959) Mammals of North America. One striking observation is that some species ranges closely approximate vegetation type boundaries, such as the spruce-fir forest of northern North America and the chain of mountaintop islands extending southward along the crest of the Appalachians. Other species ranges do not follow any apparent plant association or topographic boundaries and may include such diverse geographic areas as eastern North America or the southeastern United States. Overlapping species ranges result in regionally characteristic groups of animals that are differentially adapted to the local mosaic of plant communities. This mosaic has been termed a landscape by Forman and Godron (1981). In a manner analogous to range maps, some species are found within many plant communities while others are patchily distributed within a few such landscape components. Those plant communities in which a particular species occurs may be defined as its habitat (Odum 1959). By analyzing the physiognomy of a species habitat, finer structural components or microhabitats integral to the ecology of the species may often be discerned. Thus a hierarchy of spatial scales exists at which the distribution of animal species or characteristics of animal communities may be studied (Appendix A). Because of this hierarchial arrangement a study at any one scale implicitly includes aspects of all smaller spatial scales.

This dissertation examines the utilization of this habitat spectrum by animals at the microhabitat, habitat and landscape scales (Appendix A) by first considering the effect of interspecific competition on microhabitat utilization within a single habitat type. Small mammals within a pine plantation habitat are the focal point of this study since competition has been assumed but often not demonstrated to be important within small mammal communities (Brown 1978, Dueser and Hallett 1981).

Abundance of species populations may be affected by competition through changes in niche breadth. Alternatively, abundance may be a function of the availability of resources comprising the niche of a species. Small mammals on the Oak Ridge National Environmental Research Park (NERP) in East Tennessee, along with data from several other taxonomic groups, are used to examine the effects of niche breadth and habitat availability on species abundance. Such studies present a picture of species abundances at a single point in time. However, animal habitats change through ecological time as a function of disturbance and plant succession. Therefore, the effects of such dynamics on animal community characteristics are explored by modeling habitat dynamics on landscape islands. Together, these three studies attempt to partially describe the role of habitat in the development of animal community characteristics.

CHAPTER II

COMPETITION AND COEXISTENCE OF SMALL MAMMALS IN AN EAST TENNESSEE PINE PLANTATION

A conventional ecological assumption is that interspecific competition is of major importance in structuring animal communities. From this assumption comes the hypothesis that resource generalists are poorer competitors than resource specialists (Case and Gilpin 1974, Morse 1974, Colwell and Fuentes 1975). Presumably, microhabitat specialists select their preferred microhabitat and by superior interspecific competitive ability maintain it against generalist species. This conjecture has not been tested in many ecological communities. Indeed, the entire premise of interspecific competition leading to niche differences has been questioned (Strong et al. 1979, Conner and Simberloff 1979).

One alternative to ongoing competition is that coexisting species intrinsically select different resources, such as habitat, and thereby avoid competitive exclusion. Habitat selection and competition have been distinguished by Crowell and Pimm (1976), Dueser and Hallett (1981), and Porter and Dueser (1982) through multiple regressions of species abundances and microhabitat parameters. By using regression techniques to partial out the effect of habitat selection, these authors estimate the effect of interspecific competition. Currently, this technique is the most plausible nonexperimental method for estimating competition coefficients. However, unequivocal distinction between between microhabitat selection and competition-enforced microhabitat segregation can only be

made through experimental manipulation of animal populations. In addition, these studies have also failed to elucidate what microhabitat characteristic or suite of characteristics comprise the limiting resource for which competition may occur. Lack of this information inhibits further study of the spatial and temporal dynamics of limiting resources. There is a related need to determine whether limiting resource availability is controlled intrinsically by the animal community or by extrinsic factors. This point questions whether interactions among species or external resource dynamics controls community structure, stability, etc.

This study uses an experimental manipulation and discriminant function analysis to examine microhabitat utilization and niche parameters of the small mammal fauna inhabiting a pine plantation in East Tennessee. These techniques can provide direct evidence of competition and allow identification of the contested resource. Potential problems with niche analysis in discriminant space have recently been debated (Dueser and Shugart 1979, Carnes and Slade 1982, Dueser and Shugart 1982, Van Horne and Ford 1982). Points of technical improvement suggested by Carnes and Slade (1982) are used here to extend this type of analysis to the experimental results. Specific questions addressed include the following: Is a small mammal species that is a generalist at geographic and regional scales necessarily a poor competitor at a local scale? If competition is demonstrated, what is the limiting microhabitat factor and how does it vary spatially and temporally? Can niche analysis by discriminant function analysis be used to detect microhabitat shifts elicited by removal experiments?

Methods

Two 80 m by 80 m live trap grids were established in a 27 year old loblolly pine (Pinus taeda) plantation on the Oak Ridge NERP in Roane County, Tennessee. Controlled burning and other management practices had not been applied to the plantation so that an understory of hardwood trees and honeysuckle thickets was present. The 64 traps in each grid were located at 10 m intervals, and sunflower seeds (Helianthus spp.) were used as bait. During a 13-week period from June to early September 1980, 3072 trap-nights were recorded for each grid. By confining the study to this short time interval, it was possible to eliminate the extraneous effect of seasonal microhabitat shifts by small mammals (Kitchings and Levy 1981).

Three species, Peromyscus leucopus (white footed mouse), Ochrotomys nuttalli (golden mouse), and Blarina brevicauda (short-tailed shrew), were captured on each study grid. P. leucopus and B. brevicauda are distributed over virtually the entire eastern United States while O. nuttalli is confined to the southeastern United States (Hall and Kelson 1959). On the Oak Ridge NERP, B. brevicauda is found in every habitat type, P. leucopus in all forest habitats, and O. nuttalli in only those forest habitats having dense, viney growth (Dunaway 1955, personal communication with J. T. Kitchings). During the first five weeks of the study (Trap Period 1), populations of the three species were sampled on each grid and an array of 22 microhabitat parameters (see Appendix B) measured at each capture site. These parameters were also measured at 30 trap sites, chosen randomly without replacement, on each grid. To examine the competitive effect of P. leucopus on the other two species, all marked

individuals of this species were removed from one grid by trapping during the sixth week of the study. The last seven weeks of the study (Trap Period 2) were used to monitor O. nuttalli and B. brevicauda on the experimental grid and all three species on the control grid. Eight unmarked P. leucopus immigrated to the experimental grid during Trap Period 2 and were removed when captured. Microhabitat parameters were also measured at capture sites during Trap Period 2.

Analysis of the species microhabitat data from Trap Period 1 consisted of one three-group discriminant analysis for both the control and experimental grids. The data for the analyses consisted of each capture for all three species and the array of microhabitat paramaters associated with each capture site. The SPSS (Nie et al. 1975) discriminant program was used with all variables entering the discriminant model simultaneously. The discriminant functions were interpreted by Pearson product-moment correlation (SAS Institute Inc. 1982a) of the discriminant function scores with the microhabitat parameters. By this method, species with strongly positive discriminant scores have large values for those variables positively correlated with the discriminant function and small values for those variables negatively correlated with the discriminant function. Species data from Trap Period 2 were then plotted into the corresponding two-dimensional discriminant space using the discriminant functions derived from the Trap Period 1 analysis. This method allows direct comparison of individual species microhabitats during the two trap periods both graphically and by calculations of niche metrics within a single geometric space. Microhabitat shifts caused by species removal should be manifested by each technique. Since the initial concept of using a

multivariate statistical space for calculating niche metrics (Fuji 1969, Shugart and Patten 1972, Dueser and Shugart 1979), many technical improvements have been made (Carnes and Slade 1982) and are used herein. Niche breadth was calculated for each species as the coefficient of variation for individual observation distances from the species centroid (Carnes and Slade 1982). A 95% prediction ellipse was drawn for each species by the principle axis technique (Sokal and Rohlf 1981) and used to calculate niche overlap as the percentage of a single species area overlapped by each other species. Finally, niche position, a measure of the likelihood of a species finding favorable microhabitat, was calculated as the distance of each species centroid from the origin of discriminant space (Shugart and Patten 1972). Since only capture sites were used in the analyses, this origin represents the average small mammal microhabitat sampled.

A comparison of the two study grids was made by a two-group discriminant analysis of microhabitat data collected at the 30 randomly chosen grid points. Correlation of the resulting single discriminant function with the microhabitat parameters allowed identification of structural differences between the two grids.

Results

Trapping Results and Study Grid Comparison

Table II-1 provides a systematic means of looking at the experimental design used in this study and, in addition, shows the number of captures for each species. Carnes and Slade (1982) have demonstrated that widely disparate sample sizes mechanistically affect the positioning of species

Table II-1. Experimental design, number of captures and number of individuals captured (in parentheses) for Trap Periods 1 and 2 on the control and experimental grids

Trap Period	Control Grid			Experimental Grid		
	P. leucopus	O. nuttalli	B. brevicauda	P. leucopus	O. nuttalli	B. brevicauda
1	31 (8)	29 (10)	15 (6)	88[a] (16)	14 (5)	22 (10)
2	43 (11)	38 (7)	24 (8)	Removed	47 (12)	16 (9)

[a]A random sample of 20 P. leucopus captures on the experimental grid were used in the analyses to avoid large sample size differences.

centroids in discriminant space and therefore adversely affect niche metrics calculated from a discriminant analysis. Preliminary analyses confirmed a strong sample size effect for the experimental grid data of Trap Period 1. Therefore, a sample of 20 P. leucopus captures were randomly chosen without replacement for inclusion in the experimental grid discriminant analysis. Sample sizes for Trap Period 2 are of no consequence for either grid as these data are not used in the actual discriminant function formulation. Except for the B. brevicauda of the experimental grid, there is a general increase in species sample sizes from Trap Period 1 to Trap Period 2 which reflects greater trapping effort. However, the increase in O. nuttalli captures on the experimental grid is exceptional and may be of biological significance since recruitment of unmarked individuals from surrounding habitat formed the basis of this increase.

A microhabitat comparison of the two study grids by discriminant analysis of the 30 randomly chosen grid sites showed a significant difference between the grids with an F-test at $\alpha = 0.001$. The structural differences between the two grids are shown by the variable-discriminant function correlations of Table II-2. Since the control and experimental grid mean discriminant scores were -1.37 and 1.37, respectively, a negative correlation for a variable indicates a higher value for the control grid while a positive correlation indicates a larger value of the variable for the experimental grid. Thus the control grid appears to have a more dense understory with thicker woody vegetation and more open canopy than the experimental grid. This difference in understory thickness is later shown to be of crucial importance to small mammal niche parameters.

Table II-2. Significant Pearson product-moment correlation coefficients of the original variables with the discriminant scores resulting from the control and experimental grid comparison

Variable	Correlation
Litter-soil compactability	-0.28[a]
Woody stem density	-0.34[b]
Understory tree dispersion	0.63[c]
Tree stump dispersion	0.28[a]
Fallen log size	-0.26[a]
Thickness of woody vegetation	-0.49[c]
Percent shrub cover	0.27[a]
Percent canopy closure	0.41[c]
Climbing vine density	0.59[c]

[a] = Significance at $\alpha = 0.05$.
[b] = Significance at $\alpha = 0.01$.
[c] = Significance at $\alpha = 0.001$.

Microhabitats and Microhabitat Shifts

The control grid discriminant axes [Figure II-1(a)] can be interpreted using Table II-3 where, again, the sign and magnitude of each correlation coefficient indicates its direction and strength of correlation with the discriminant function. For example, discriminant function 1 accounts for 70.09% of the microhabitat variability between species. On this function, B. brevicauda has an average discriminant score of -1.86 and thus is found in areas having low litter-soil compactability, woody stem density, tree stump density, and thickness of woody vegetation and high herbaceous stem density and tree stump dispersion. P. leucopus, with an average score of 1.02, has the inverse relationship to these variables while O. nuttalli, with an average score of -0.13 is intermediate to these extremes. While this first discriminant function best separates B. brevicauda and P. leucopus, the second function of Figure II-1(a) accounts for the remaining 29.01% of among-species variance and best separates O. nuttalli from the other two species. On this function, O. nuttalli has a mean of 0.88 and is thus positively correlated with tree stump dispersion and fallen log dispersion while negatively correlated with herbaceous stem density, understory tree dispersion, fallen log size, and fallen log abundance. P. leucopus and B. brevicauda, with means of -0.53 and -0.61 respectively, have the inverse correlation with these variables. The first discriminant function of this analysis is apparently a gradient of understory development, while the second function is a gradient of ground structure in the form of fallen logs and stumps. P. leucopus thus occurs in areas with many fallen logs, stumps and thick understory, B. brevicauda in microhabitats with much ground structure and little

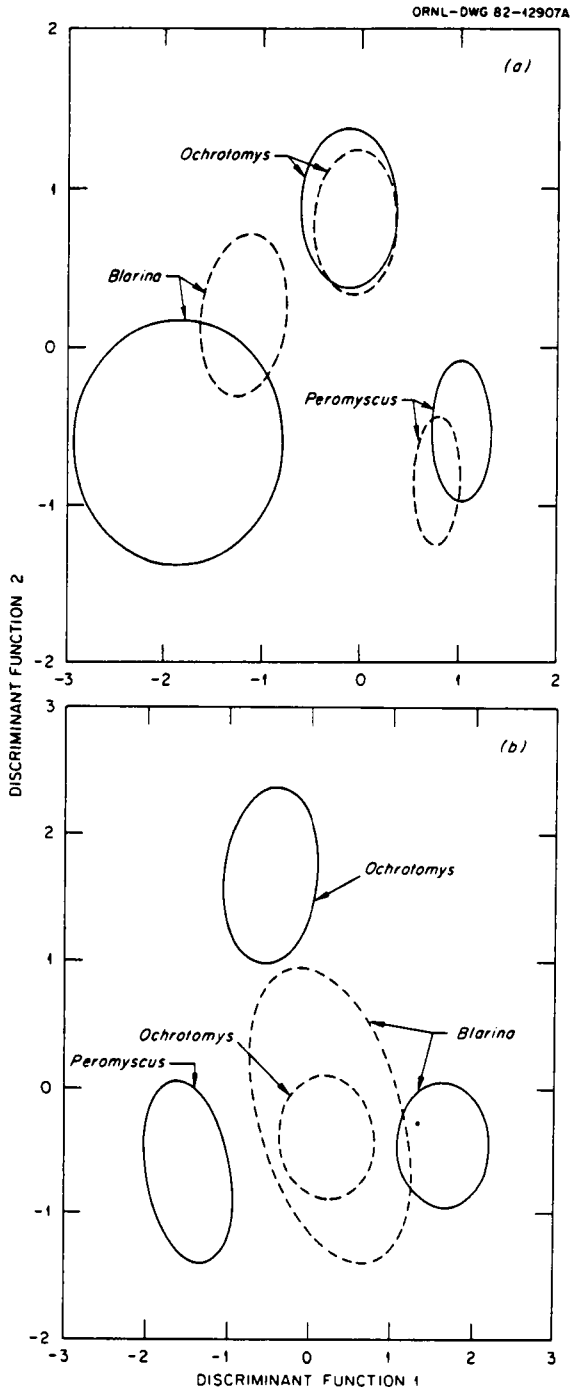

Figure II-1. The 95% confidence ellipses around species centroids for the control (a) and experimental (b) grids. Solid ellipses indicate baseline data collected before P. leucopus was removed from the experimental grid. Dashed ellipses represent data collected after the removal.

Table II-3. Significant Pearson product-moment correlation coefficients of the control and experimental grid discriminant scores with the original variables for the species microhabitat analyses where signs of the coefficients indicate the direction of the correlation

Variable	Control Grid Correlations		Experimental Grid Correlations	
	DF 1	DF 2	DF 1	DF 2
Litter-soil depth	0.06	-0.07	0.76[c]	-0.02
Woody stem density	0.24[a]	0.10	0.40[b]	-0.36[b]
Understory tree dispersion	-0.10	-0.38[c]	0.22	0.33[a]
Fallen log size	-0.06	-0.38[c]	0.54[c]	0.18
Fallen log dispersion	0.21	0.44[c]	0.42[b]	0.36[b]
Fallen log abundance	0.13	-0.36[b]	-0.60[c]	0.16
Litter-soil compactability	0.41[c]	0.05		
Herbaceous stem density	-0.70[c]	-0.31[b]		
Tree stump dispersion	-0.42[c]	0.50[c]		
Tree stump density	0.24[a]	-0.01		
Thickness of woody vegetation	0.56[c]	-0.13		
Overstory tree dispersion			0.21	0.38[b]
Climbing vine density			-0.67[c]	0.10

[a] = Significance at $\alpha = 0.05$.
[b] = Significance at $\alpha = 0.01$.
[c] = Significance at $\alpha = 0.001$.

understory development, and O. nuttalli in areas with less ground structure and moderate understory development.

Inspection of the solid 95% confidence ellipses (Sokal and Rohlf 1981) in Figure II-1(a) also indicates that all three small mammal species separate well in discriminant space. Indeed, all pairwise F-tests among the species are significant at $\alpha = 0.003$. The dashed ellipses, representing Trap Period 2 data, overlap extensively with the solid ellipses and indicate no significant microhabitat shifts by any of the species on this grid during the experiment. Therefore, any shifts noted on the experimental grid are explicable by the P. leucopus removal.

The experimental grid analysis can be interpreted in the same manner as the control grid analysis. Discriminant function 1 of Figure II-1(b) is positively correlated with litter-soil depth, woody stem density, fallen log size and fallen log dispersion while negatively correlated with fallen log abundance and climbing vine density (Table II-3). B. brevicauda, O. nuttalli, and P. leucopus have mean discriminant scores of 1.65, -0.48, and -1.48, respectively. This function, in accounting for 67.53% of the variation between species, is again primarily a gradient of fallen logs with strong components of litter-soil depth and climbing vine density. The second discriminant function is negatively correlated with woody stem density and positively correlated with overstory tree dispersion, understory tree dispersion, and fallen log dispersion (Table II-3). On this function the species averages are 1.67 for O. nuttalli, -0.45 for B. brevicauda, and -0.67 for P. leucopus. The remaining 32.47% of the species variation is explained by this function which is easily interpreted as a gradient of forest cover with the positive extreme of

the axis having highly dispersed trees and fallen logs. Thus, before the experimental treatment, B. brevicauda inhabits areas with moderate fallen log abundance but a deep litter-soil profile, P. leucopus is found in dense areas with abundant fallen logs and understory, and O. nuttalli in relatively open areas with little ground structure. All three pre-removal ellipses are widely separated in discriminant space [Figure II-1(b)] and F-tests indicate all are significantly different at α = 0.003. This general interpretation of species microhabitats is similar to that for the control grid indicating that, even though the two grids are significantly different in understory development, the species themselves do not drastically alter the microhabitats utilized. Trap Period 2 data for the experimental grid consists of O. nuttalli and B. brevicauda observations since removal of P. leucopus served as the experimental treatment. Plotting these data in discriminant space yielded the dashed confidence ellipses of Figure II-1(b). A nonsignificant microhabitat shift was displayed by B. brevicauda, however, a dramatic and significant shift in microhabitat use was shown by O. nuttalli parallel to the second discriminant function which originally separated this species from P. leucopus and B. brevicauda. Using the previous interpretation of this axis, it is apparent that O. nuttalli shifted its microhabitat use from open forest to areas with more fallen logs, better canopy development, and greater understory development. The composite effect of changes in microhabitat use by O. nuttalli and B. brevicauda is a nonsignificant difference between these two species microhabitats after the removal of P. leucopus.

Niche Characteristics

While the general descriptions of species microhabitats do not vary between the experimental and control grids, the differing understory characteristics of the two grids definitely affect niche characteristics of the species. The data of Table II-4 manifest this difference. Values of niche position for the control grid during Trap Period 1 (Table II-4) indicate O. nuttalli to be the best adapted species (in terms of finding suitable small mammal microhabitat) to the study area and B. brevicauda most poorly adapted. Alternatively, on the experimental grid, P. leucopus is best adapted while O. nuttalli is slightly less well adapted than B. brevicauda. Very little difference is found in niche position values for the control grid between Trap Periods 1 and 2. However, with the removal of the best adapted species (P. leucopus) on the experimental grid, there is a dramatic shift by both O. nuttalli and B. brevicauda toward a lower value for niche position. This shift indicates greater availability of suitable microhabitat.

The competitive effect of P. leucopus within this community is supported also by niche breadth used as an indicator of generalist/specialist tendencies (Table II-4). There is some variation between Trap Periods 1 and 2 in each species niche breadth on the control grid that may be indicative of dynamic interactions among the community members. However, this variation is not great for two of the three species. On the other hand, a very strong directional response to P. leucopus removal is apparent for the remaining species on the experimental grid. Both O. nuttalli and B. brevicauda show large increases in niche breadth, indicating increased generality of microhabitat use and complementing

Table II-4. Niche position and niche breadth for each species captured during each trap period on both the control and experimental grids

	Niche Position				Niche Breadth			
	Control Grid		Experimental Grid		Control Grid		Experimental Grid	
	Trap Period 1	Trap Period 2	Trap Period 1	Trap Period 2	Trap Period 1	Trap Period 2	Trap Period 1	Trap Period 2
O. nuttalli	0.89	0.79	1.74	0.45	81.75	89.41	72.34	95.14
P. leucopus	1.15	1.15	1.62	Removed	47.82	59.12	80.59	Removed
B. brevicauda	1.96	1.21	1.71	0.35	90.90	84.95	79.10	92.12

their concomittent decrease in niche position (Table II-4). Differences in generality of microhabitat use due to structural differences between the two study grids is apparent. On the control grid, B. brevicauda has the greatest niche breadth, followed by O. nuttalli which is much greater than P. leucopus (Table II-4, Trap Period 1). In comparison, P. leucopus has the greatest niche breadth on the experimental grid followed closely by B. brevicauda and less so by O. nuttalli.

Paired comparisons of niche overlap among community members over time should indicate the rigidity of any interspecific interactions. Table II-5 provides such information for two short adjacent periods in time, Trap Periods 1 and 2 on the control grid. The overlap for each pair of species is presented as the percent overlap of the first species by the second. Only the P. leucopus-O. nuttalli and O. nuttalli-P. leucopus pairs show virtually no variation between Trap Periods 1 and 2 and thus suggest strong interspecific interactions, that, considering the ecological release demonstrated by the removal experiment, can be interpreted as competition. The pairwise overlaps for the experimental grid (Table II-5) reinforce the interpretation from the control grid and show that B. brevicauda and O. nuttalli expanded their niche breadths to include microhabitat formerly used by P. leucopus.

To summarize the results, the control grid had greater understory development than the experimental grid. This difference apparently led to different niche characteristics for the species although the general microhabitats used by the species were very similar. Removal of P. leucopus from the experimental grid allowed O. nuttalli to shift into areas with more understory. After the removal, the niche characteristics

Table II-5. Niche overlap calculated as the percentage of a 95% prediction ellipse for the first species of each pair that is overlapped by the ellipse of the second species

	Control Grid Overlaps		Experimental Grid Overlaps	
	Trap Period 1	Trap Period 2	Trap Period 1	Trap Period 2
B. brevicauda-*O. nuttalli*	0.41	0.79	0.26	0.72
O. nuttalli-*B. brevicauda*	0.73	0.58	0.28	0.94
B. brevicauda-*P. leucopus*	0.27	0.28	0.28	0.39[a]
P. leucopus-*B. brevicauda*	0.83	0.36	0.23	0.88[a]
O. nuttalli-*P. leucopus*	0.40	0.39	0.50	0.52[a]
P. leucopus-*O. nuttalli*	0.69	0.69	0.37	0.90[a]

[a]The experimental grid Trap Period 2 caculations were made with *P. leucopus* data from Trap Period 1 to show microhabitat shifts by *O. nuttalli* and *B. brevicauda*.

of O. nuttalli more closely resembled this species characteristics on the control grid.

Discussion

Rosenzweig (1981) has theorized that competition itself may not be detectable although its effects may be documented in habitat selection. In addition to the example used by Rosenzweig (Schroder and Rosenzweig 1975), recent studies by Montgomery (1981) and Abramsky (1981) may also pose situations where competitive effects are not manifested overtly. On the other hand, work by Koplin and Hoffman (1968), Price (1978), and the present study indicate that competition does occur in nature and can be demonstrated. Competition, in this instance, has been demonstrated with certainty only between P. leucopus and O. nuttalli. This result is not unexpected since B. brevicauda differs greatly from the rodent species both morphologically and ecologically. However, with the experimental removal of P. leucopus, B. brevicauda did display shifts in niche breadth and niche position similar to those exhibited by O. nuttalli but of much lesser magnitude. Could competition for space be so pervasive among small mammals that shrews and rodents compete? This question remains unanswered, but if such interactions are real the presence of P. leucopus in this community apparently provides an ecological barrier to interactions between B. brevicauda and O. nuttalli. This observation is depicted graphically by Figure II-1(b), page 12.

I suggest that interference is the competitive mechanism since the microhabitat shift by O. nuttalli was immediate and the dramatic increase in O. nuttalli individuals with P. leucopus removal was due mainly to

recruitment of previously uncaptured individuals from surrounding habitat. Colwell and Fuentes (1975) state that when interference is shown to be the competitive mechanism, it is a specialist species that effectively interferes with a generalist. Morse (1974), after an extensive literature review, and Larson (1980) concur with Colwell and Fuentes (1975). There can be no doubt that P. leucopus is a generalist when compared with O. nuttalli since the species is more widely distributed geographically, occurs in more habitat types on the Oak Ridge NERP, and was found to have a greater niche breadth on the experimental grid. The experimental results presented thus provide a counter example to the widely accepted hypothesis that generalist species are poor competitors and that specialists should not increase their niche breadth with the removal of competitors. Whether these two species represent an exceptional case can only be determined by future studies, however, I would like to propose an alternative explanation.

Miller (1967) states that analogous patterns of overlap occur at all levels of distribution and the P. leucopus-O. nuttalli pair certainly fit this observation geographically, regionally, and locally on the experimental grid. However, interspecific interactions such as interference must occur at very local levels and must also be influenced by the resource being contested. For small mammals it is likely that competition for space is a general phenomenon (Grant 1972) and that space is represented at the local scale by microhabitat. Therefore, subtle differences in microhabitat characteristics will affect the outcome of competitive interactions. Observations and experiments at scales larger than those actually contested by small mammals (such as habitats rather

than microhabitats) would be expected by chance to elicit niche shifts by microhabitat generalists rather than specialists, if such shifts are detectable at all (Dueser and Hallett 1981). The true nature of competition would thus be masked by ignoring the patchiness and dynamics of the contested resource, i.e., microhabitat. Considering this argument, it is not surprising that differences in niche breadth, overlap, and position were found for P. leucopus, O. nuttalli, and B. brevicauda on the control and experimental grids since microhabitat structure differed significantly between the two grids. Fox and Morrow (1981) came to virtually the same conclusion from their excellent review of herbivorous insects and state that "specialization is often a flexible attribute of a population that is responding to features of its particular community, rather than an attribute of a species throughout its geographical range." Fox and Morrow (1981) also conclude that the diversity of mechanisms that may lead to specialization leave no a priori reason to predict competitive advantages for specialists.

The spatial and temporal variation found in niche characteristics of small mammals can be attributed to spatial variation of the microhabitat, adjustment of niches to interspecific interactions or extrinsic factors such as weather patterns. Abramsky et al. (1979) noted seasonal changes in the niche overlap of a short grass prairie small mammal fauna and M'Closkey (1976) demonstrated shifts in niche breadth by the members of a seasonal chapperal fauna. Kitchings and Levy (1981) found seasonal microhabitat shifts by two of the species included in this study, P. leucopus and O. nuttalli, but made no quantitative niche measurements. Seasonal effects were minimized in this study to focus on spatial niche

differences and their causes. Data from Trap Period 1 for the control and experimental grids clearly indicate spatial differences in niche parameters for all three species even though each species selects the same general microhabitat on each grid. These niche differences are thus attributed to the understory microhabitat differences found between the two study grids. It is likely in this study that the different understory development of the two grids alter the relative competitive abilities of the species since the actual species microhabitats do not differ perceptably between grids and O. nuttalli moved to a microhabitat more similar to its control grid microhabitat when P. leucopus was removed from the experimental grid. This shift also led to greater similarity of niche parameters for control and experimental O. nuttalli.

With the proposition that resource variation provides the template for altered competitive or habitat selective abilities and therefore variation in niche characteristics, it becomes necessary to understand the dynamics of resource variation. Identification of the limiting resource being contested or the critical resource being selected by coexisting but noncompetitive species is the first criterion for studying such dynamics. Abramsky et al. (1979) and Gliwicz (1981) present examples of well executed, informative studies of small mammal competition that deny the opportunity to examine resource dynamics because the contested resource is not identified. In this study, understory thickness is the critical microhabitat characteristic that affects P. leucopus and O. nuttalli niche parameters in pine plantations. Understory thickness is a physical attribute of forest stands resulting from successional processes and disturbances. While succession in East Tennessee deciduous forests is

characterized by gap-phase tree replacement (Shugart and West 1977) which can easily lead to patchiness at the scale I have described for small mammals, pine plantations are less subject to such tree by tree replacement because of relatively uniform planting conditions and periodic clear cutting. However, the absence of management techniques such as controlled burning and thinning has allowed successional processes to develop a patchy hardwood understory in this particular plantation, especially where individual pines have been killed by disease or knocked down by windstorms. Such extrinsic disturbances imposed over an area uniform in slope, soil, and planting technique may be viewed as stochastic events that lead to a random mosaic of microhabitat characteristics. Given these conditions, the spatial variability of niche parameters for these small mammals are ultimately controlled by extrinsic stochastic processes which affect microhabitat selection and competitive abilities.

Price (1978), studying desert rodents, concluded that interspecific competition maintained microhabitat differences but the availability of appropriate microhabitat determined local species abundances. I suggest that this pine plantation represents a similar situation. This condition does not necessarily entail coexistence unless the microhabitat structure remains static. However, the dynamic nature of the pine plantation microhabitat may facilitate coexistence by altering relative competitive abilities and species adaptedness in different portions of the same plantation. In fact, it is not difficult to envision disturbance creating microhabitats with characteristics intermediate for the small mammal species and thus making the outcome of competition indeterminant (Grant 1972).

In summary, it has clearly been shown that niche characterization by multivariate statistical methods provides intuitively reasonable and sensitive results when used in experimental studies. The calculated measures of niche breadth and position indicate that variable microhabitats make specialization a local population phenomenon while facilitating species coexistence. Because specialization is shown to be a local phenomenon at the level of the contested resource, social dominance does not appear to be inherent with specialist species. Finally, both local coexistence and such community level properties as stability may ultimately be controlled by the creation of patchy microhabitats through stochastic extrinsic disturbances.

CHAPTER III

HABITAT AVAILABILITY AND SPECIES ABUNDANCE

Animal species are often found within certain habitat types as defined by characteristic floral associations. Recent studies have shown that species also respond differentially to small scale structural characteristics (e.g., tree density and log dispersion) or microhabitat within floristically defined habitats (Shugart and Patten 1972, M'Closkey 1976). These niche dimensions comprise an important resource for many animal species. The range of resources utilized by a species is a positive correlate of its niche breadth. When habitat is considered as a resource, niche breadth is a function of both the range of microhabitats utilized within a habitat type and the number of habitat types used by a species. This is especially true when one considers species distributions across habitat mosaics or landscapes (Forman and Godron 1981). Both intra-habitat and inter-habitat species distributions, however, may be subject to limitation by biotic factors such as interspecific competition. This limitation results in the realized (Hutchinson 1957) or post-interactive (Vandermeer 1972) niche. A second limitation on both types of distributions is the evolutionary history of a species that results in habitat selection such as that demonstrated for mice by Wecker (1963). Due to either or both of these limitations, virtually all taxonomic groups have some widespread species and others that are narrowly distributed at the landscape scale.

The roles of biotic interactions such as competition and predation in determining species distributions and niche breadths are difficult to assess. This fact, however, has not deterred ecologists from studying the realized niche and resulting species abundances. Theoretical ecologists often explain species abundance on the basis of characteristics intrinsic to the species themselves. In its most general form this intrinsic view of species abundances suggests that the more resources controlled by a species the greater its abundance (MacArthur 1957, Whittaker 1965). Realized niche breadth is the species-specific attribute that directly reflects these controlled resources with the understanding that greater niche breadth translates into more individuals (MacArthur 1957).

A second hypothesis to explain species abundance depends on factors extrinsic to the species and is commonly advocated by applied ecologists. For example, in modern wildlife management (Leopold 1933, Giles 1978), emphasis has been placed on habitat availability and manipulation to sustain harvestable yields of animals. Even a species having a narrow niche breadth may have a high abundance if its critical resources are abundant. Without human intervention, the natural dynamics of habitats and landscapes (Shugart et al. 1973, Pickett and Thompson 1978, Smith et al. 1981) may serve as the major determinant of abundance.

The goal of this chapter is to compare the contributions of the niche breadth hypothesis and habitat availability hypothesis in determining species abundances. Assessment of these hypotheses requires measures of niche breadth, habitat availability, and species abundance within taxonomically similar groups of species. In addition, niche breadth and

habitat availability should be calculated within a framework capable of integrating the various habitat/microhabitat scales within a landscape. In this chapter the scale of a landscape is defined by the species being considered. Therefore, a single woodlot may appear as a landscape mosaic to a slug species while hundreds of hectares may constitute a landscape for highly mobile bird species. For consistency and to avoid ambiguity, all examples should be calculated similarly. In this chapter, I develop in detail an example using small mammals found on the Oak Ridge NERP in Roane and Anderson Counties, Tennessee, and then extend the discussion to other taxonomic groups.

Methods

Since landscapes represent a habitat mosaic within which animal species may respond to both habitat and microhabitat scales, niche measurements may be made at several spatial scales. Structural habitat measurements taken at the finest scale are collectively capable of characterizing larger scales and also provide maximal detail on species abundance responses to habitat characteristics. The hierarchial nature of these spatial scales also lends itself to statistical compilation. For example, statistical techniques such as principal components analysis or factor analysis can differentiate between species or habitats through analysis of microhabitat characteristics. Each successive component or factor explains less variance in habitat structure so that a progression is developed from overt structural differences between habitats to fine resolution of microhabitat differences.

This line of reasoning was applied to small mammal sampling on the Oak Ridge NERP. Four common habitat types were recognized: deciduous forest (5070 ha), pine forest and plantation (3355 ha), old field (1283 ha), and cedar glade (497 ha). These habitats collectively comprise approximately 76% of the NERP with much of the remaining 24% being buildings, roadways, pastures and lawns (L. K. Mann and J. T. Kitchings, personal communication). Between May and mid-September of 1979-1981, small mammal species were sampled on 80 m by 80 m grids within these habitats using one Sherman live trap at 10 m intervals. In 1979, two grids were set up in old field, cedar glade, and deciduous forest habitats. Two different study grids were used in the old field, pine and deciduous habitats during 1980. Finally, five grids were placed in the pine habitats during 1981. These grids yielded only 30 animal caputures due to population collapses and are omitted from the analysis. At each capture site and at 30 randomly chosen sites in each grid, an array of 16 microhabitat variables (see Appendix B) were measured each trapping season. Thirty random sites were chosen througout the study to remain consistent with data compiled during 1979 as part of an earlier study. Also, by sampling over 46% of each study area, this random sample sufficiently describes the study areas.

Factor analysis (SAS Institute, Inc. 1982b), using an initial principal components analysis followed by a varimax rotation of these components, was used to integrate the random site microhabitat data to the landscape scale and thus form a multi-dimensional habitat space. Each small mammal observation was then plotted into the habitat space. By performing the factor analysis on the random sites, strong sample size

effects caused by inherent differences in species abundances were avoided (Carnes and Slade 1982). The representation of random sites in the factor analysis, however, was not unambiguous. Empirical observations have shown that the four habitat types are not equally abundant. These differences in area are known from management and mapping of the NERP and thus cannot be attributed to sampling error. The question thus becomes whether to weight the habitats proportional to their abundance and incorporate realistic sample size effects in the factor analysis or weight each habitat equally. Rather than make an arbitrary choice, both weightings were performed in separate analyses.

Having scored the small mammal observations in the habitat space, the scatter of the observations for a single species is a direct measure of niche breadth (Fuji 1969, Green 1971, Shugart and Patten 1972, Dueser and Shugart 1979). For consistency with earlier work (Dueser and Shugart 1979), the coefficient of variation of the distances of each observation from a species centroid was calculated as species niche breadth. Shugart and Patten (1972) and Dueser and Shugart (1979) correctly suggested that the center of a multivariate habitat space represents the average microhabitat sampled and that the distances of species centroids from this origin are relative measures of the likelihood of finding suitable habitat. By alleviating the sample size effects demonstrated by Carnes and Slade (1982) and using random sites from the four habitats representing 76% of the Oak Ridge NERP, these distances are relative measures of habitat availability on the 10,205 ha landscape represented by these habitats. This measure of habitat availability is referred to as niche position after Shugart and Patten (1972).

Since each patch of the four habitat types was not sampled, species abundances at the landscape scale had to be estimated. These estimates were made by multiplying the largest number of individuals for a species known to be alive on a grid of each habitat type by the proportion of that habitat type in the landscape and then summing across habitats. The estimation is thus maximal and assumes similar densities of a species in different patches of the same habitat. Linear regression with a semi-log transformation (SAS Institute, Inc. 1982b) was used to test the ability of niche breadth and niche position (habitat availability) to predict this abundance.

Results

Eight small mammal species wre captured in the four habitats for a total of 1,240 captures of 436 individuals (Table III-1). Multiple captures of an individual animal at a single trap site were discarded from this total number of captures. As expected in studies of species abundances (Preston 1948), some species (e.g., P. leucopus) were common and widespread while others (e.g., Tamias striatus) were very rare and specialized in their habitat affinity. Since the random habitat observations rather than the species observations were used in the factor analysis, sample size biases (Carnes and Slade 1982) were avoided.

Factor analyses with the four habitats weighted proportionally and equally produced similar results both qualitatively and quantitatively. Therefore only the former is discussed. The first six factors accounted for 99.99% of the variance among random habitat samples (Table III-2). Pearson product-moment correlation (SAS Institute, Inc. 1982a) of the

Table III-1. Small mammal species captured on the Oak Ridge NERP and number of captures for each species with values in parentheses indicating number of individuals captured

Species	Habitats				
	Old Field	Cedar Glade	Pine Forest/ Plantation	Deciduous Forest	Σ
Cryptotis parva	28(19)				28(19)
Microtus pinetorum	257(89)				257(89)
Reithrodontomys humulis	167(50)				167(50)
Sigmodon hispidus	15(9)				15(9)
Blarina brevicauda	23(18)		105(47)	37(26)	165(91)
Peromyscus leucopus		58(16)	148(46)	257(54)	463(116)
Ochrotomys nuttalli		24(11)	113(45)		137(56)
Tamias striatus				8(6)	8(6)
Σ	490(185)	82(27)	366(138)	302(86)	1,240(436)

Table III-2. Results of the factor analysis of Oak Ridge NERP habitats including percent variance and cumulative variance for each factor and significant Pearson product-moment correlations between the factors and original variables

	Factors					
	1	2	3	4	5	6
Percent variance	60.33	15.13	11.38	7.89	5.25	0.01
Cumulative percent variance	60.33	75.46	86.84	94.73	99.98	99.99
Overstory tree dispersion	0.93					
Herbaceous litter depth	0.43					
Percent canopy closure	-0.61					
Understory tree size	-0.62					
Percent shrub cover	-0.62					
Overstory tree size		0.76				
Litter-soil compactability		0.57				
Woody vegetation density		0.53				
Litter-soil depth		0.50				
Tree stump dispersion			0.98			
Tree stump density			-0.70			
Fallen log abundance				0.88		
Fallen log density				0.58		
Understory tree dispersion					0.84	
Climbing vine density						0.91

original variables with the rotated factors (Table III-2) resulted in two interpretable patterns. First, those variables highly correlated with a factor have some degree of homogeneity. For example, factor one is most highly correlated with overstory tree dispersion. There is an obvious positive relationship between overstory tree dispersion and herbaceous litter depth while the remaining three variables (percent canopy closure, understory tree size and percent shrub cover) are reasonable negative correlates with overstory tree dispersion. Similar relationships are apparent for the remaining five factors that are composed of more than one variable. The second pattern apparent in the correlations of Table III-2 is the decrease in spatial scale described by each successive factor. Factors one and two are composed of variables defining distinct habitats at the landscape scale while the other factors progress to fine microhabitat scales of resolution. This observation is supported by Figure III-1 which displays average small mammal species scores on each factor. Factor one separates forest species from old field species while factor six shows the dependence of O. nuttalli on climbing vines (Linzey 1968, Dunaway 1955). The factor analysis thus effectively combined the various spatial scales implicit in this study and needed to integrate small mammal habitat/ microhabitat responses.

Species responses to habitat structure and availability (Table III-3) are exceptional in one aspect: species utilizing more habitats do not display greater niche breadths. This dichotomy generally separates old field and forest species, suggesting that the old field habitat is more patchy than forest habitats in general. Application of the niche breadth metric to the random habitat samples supports this suggestion, resulting

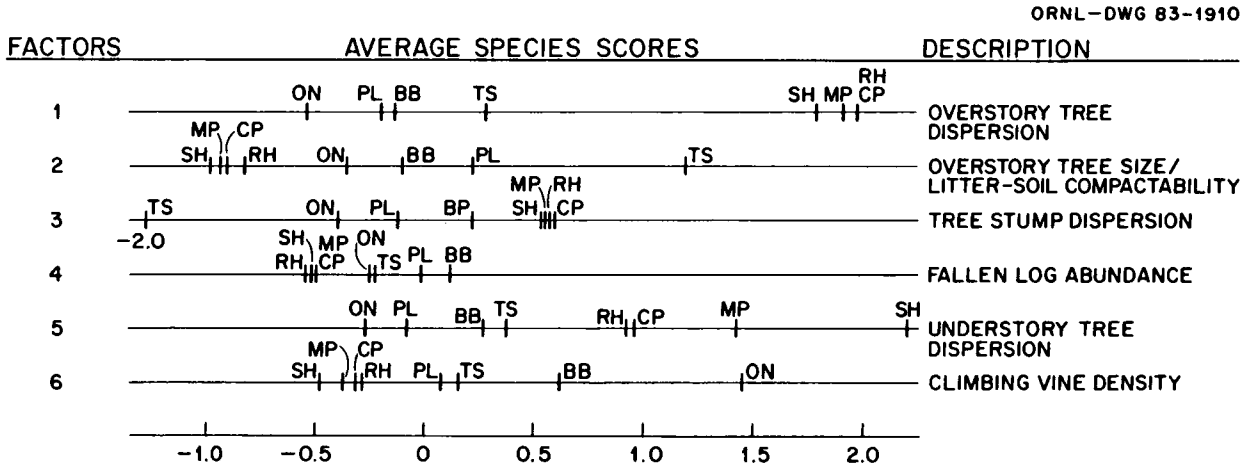

Figure III-1. Average factor scores for each small mammal species on the first six factors. Small mammal species abbreviations are as follows: CP = Cryptotis parva, MP = Microtus pinetorum, RH = Reithrodontomys humulis, SH = Sigmodon hispidus, BB = Blarina brevicauda, PL = Peromyscus leucopus, ON = Ochrotomys nuttalli, and TS = Tamias striatus.

Table III-3. Results of the niche analysis for the small mammal species along with abundance estimates and number of habitats in which they were captured

Species	Number of Habitats	Niche Breadth	Niche Position	Abundance
Cryptotis parva	1	113.11	2.51	33.8
Microtus pinetorum	1	117.86	2.68	111.8
Reithrodontomys humulis	1	176.81	2.47	65.0
Sigmodon hispidus	1	147.26	3.13	18.2
Blarina brevicauda	3	106.75	0.73	223.3
Peromyscus leucopus	3	106.95	0.32	353.9
Ochrotomys nuttalli	2	113.89	1.67	77.0
Tamias striatus	1	106.37	2.40	40.4

in values of 115.53, 118.48, 107.60 and 104.77 for the old field, cedar glade, deciduous and pine habitats, respectively. The regression of species abundance on niche breadth [Figure III-2(a)] was nonsignificant at the $\alpha = 0.05$ level and had a negative slope of -0.02. A positive slope would be expected if niche breadth were a reliable predictor of abundance. Alternatively, niche position was significantly correlated with species abundance [Figure III-2(b)] at $\alpha = 0.004$. The strong negative slope (-0.88) of this relationship is expected since niche position is inversely correlated with habitat availability.

Multivariate niche analysis has become commonly utilized and available examples represent a variety of taxonomic groups. McCracken and Seagle (personal communication), using data collected in McGowan's Woods in Ithaca, New York, found a significant negative relationship between slug species abundance and niche position [Figure III-3(a)] but no relationship between abundance and niche breadth. R. L. Jones (personal communication) found these same relationships for Appalachian stream cove salamanders in East Tennessee [Figure III-3(b)]. Figure III-4 provides an interesting contrast for avian species. D. L. Urban and W. D. Klimstra (personal communication) analyzed breeding bird habitats in southern Illinois by factor analysis. Their available data allowed calculation of niche position and the regression of abundance on this variable [Figure III-4(a)]. A significant negative correlation resulted. In contrast, Shugart and Patten (1972) analyzed wintering fringillids in northern Georgia. Regressions of their results gave nonsignificant relationships between abundance and niche breadth and abundance and niche position [Figure III-4(b)].

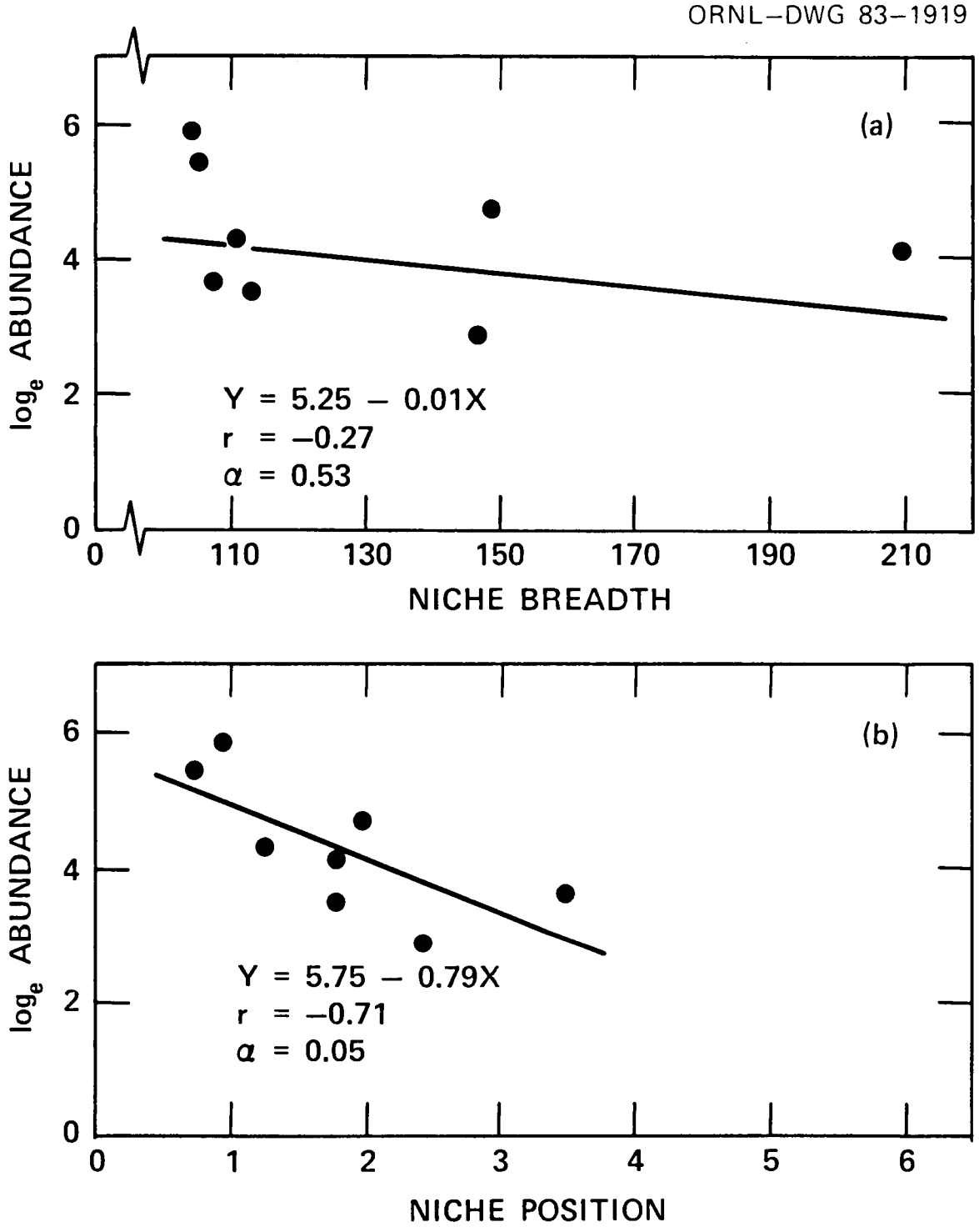

Figure III-2. Regressions of abundance on niche breadth (a) and niche position (b) for the small mammal species of the Oak Ridge NERP.

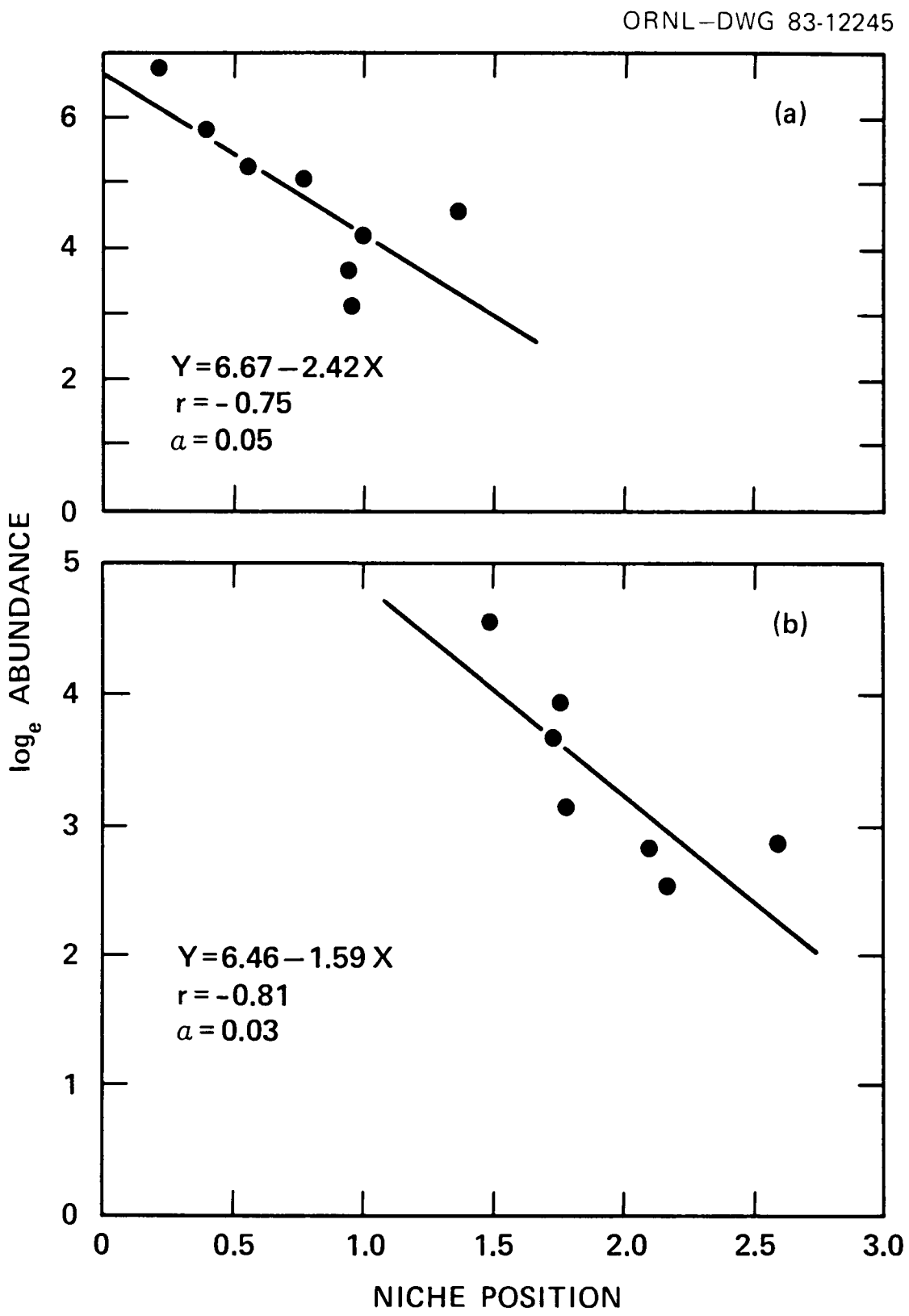

Figure III-3. Regressions of abundance on niche position for slugs (a) and salamanders (b).

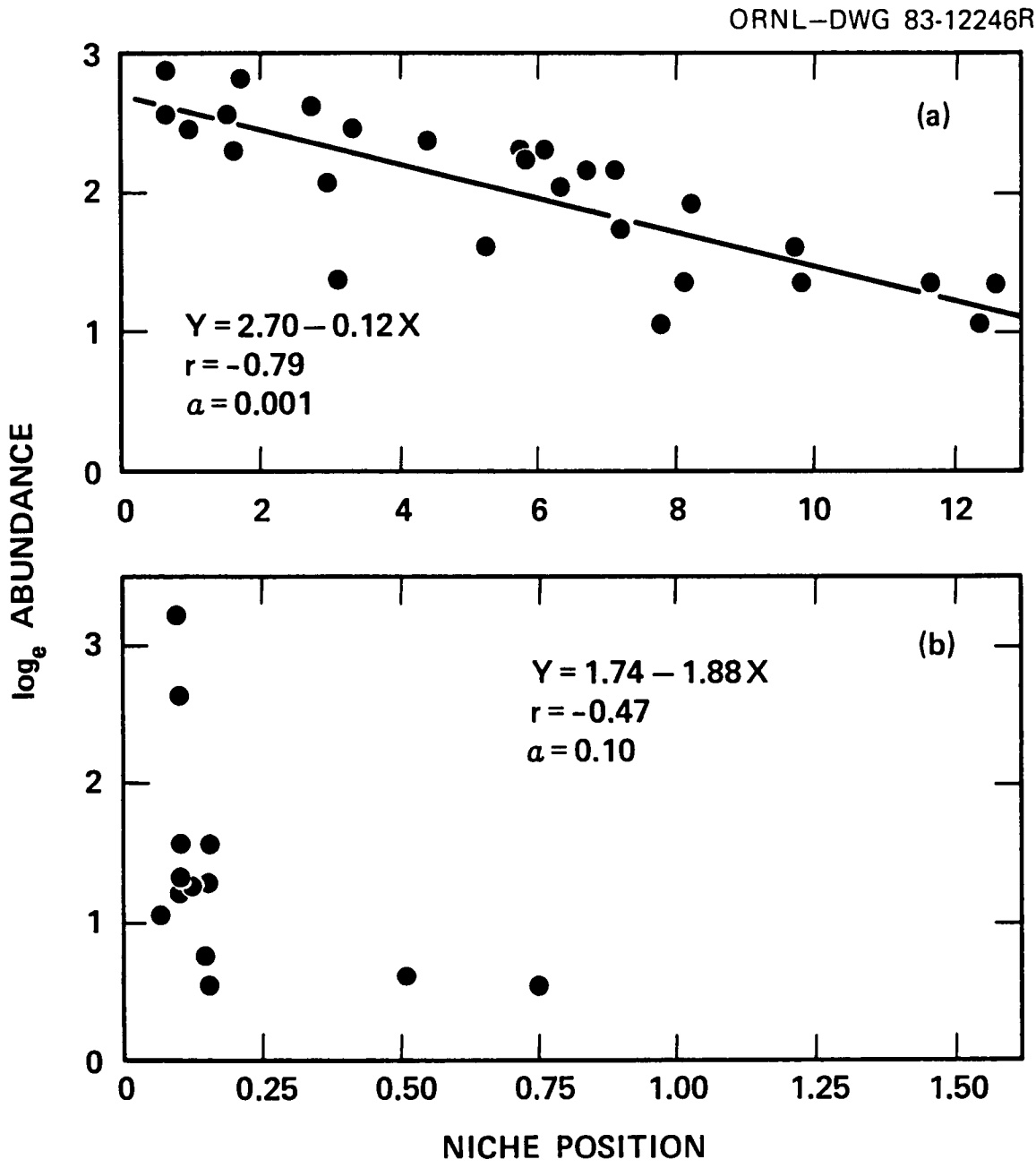

Figure III-4. Regressions of abundance on niche position for southern Illinois breeding birds (a) and northern Georgia winter birds (b).

Discussion

One of the most basic ecological observations is that within any sample area some species have high abundances while relatively many others are rare (Preston 1948). Two potential hypotheses to explain this pattern have been examined here: the niche breadth hypothesis and the habitat availability hypothesis. A major obstacle to the evaluation of these alternatives, that of integrating microhabitat and habitat scales, was resolved by niche evaluation within a multivariate statistical space. A potential semantic problem remains, however, with the niche concept. The definition of "niche" varies within the ecological literature (Grinnell 1917, Elton 1927, Hutchinson 1957, Odum 1959, Whittaker et al. 1973, Pianka 1978, Patten and Auble 1981) not only with respect to a species function (Elton 1927) or resource use (Grinnell 1917) but also with respect to whether the niche is an attribute of an individual, a population or a species (Pianka 1978). The nebulous definition of "niche" leads to a similar uncertainty of the exact meaning of niche breadth. Fortunately, Hutchinson's (1957) definition of the niche as an n-dimensional hypervolume seems most commonly used and is analogous to multivariate statistical spaces such as those used by the examples in this study. Choice of individual, population or species level characterization basically translates to a choice of spatial scale. For the examples provided here, a niche was assumed to be characteristic of a species and questions of scale alleviated as previously discussed. Regardless of the exact definition of "niche," niche breadth has in practice always referred to a range of resource utilization. This basic characteristic makes all potential scales of measurement comparable when considering the contribution

of niche breadth in determining species abundance. This fact has been taken advantage of in order to draw on data sets representing a broad array of taxonomic groups all of which utilize habitat at different spatial scales.

Analysis of the Oak Ridge NERP small mammal fauna strongly supports the hypothesis that habitat availability is a better predictor of species abundance than niche breadth. Data from various taxonomic groups ranging from terrestrial molluscs to birds demonstrate the generality of these results with the exception of Shugart and Patten's (1972) winter bird analysis. This particular data set contrasts strongly with that of Urban and Klimstra's southern Illinois breeding birds. However, rather than limiting the generality of this study's conclusions, the contrast provides further insight to the applicability of the conclusions since the fringillids studied by Shugart and Patten (1972) are known to diversify their habitat use in winter, concentrating in old field and edge habitats. In fact, if the niche position outliers in Figure III-4(b) (which consist of extreme habitat specialists — the pine siskin and purple finch) are removed from the regression, an almost vertical relationship exists which indicates species abundance is independent of habitat availability. Such a result would be expected if the species utilized very similar habitats in winter but had abundances determined during the breeding season by segregation into habitats of differing availability.

Relative abundances of species have been used to investigate the factors producing structure in animal communities (Hairston 1959). For example, MacArthur (1957, 1960) developed several models to predict species abundances based on different assumptions about niche characteristics.

The results of these models were then compared to empirical species abundances. His empirical observations of birds best fit the model of contiguous, nonoverlapping niches within habitats, thus implying interspecific competition as a factor in structuring these communities. The regressions of the present study indicate that habitat availability is a good predictor of species abundances. The data of Table III-1 show that the small mammals of the Oak Ridge NERP overlap in their use of habitat types. In addition, previous studies (Dueser and Shugart 1979, Seagle 1980) have demonstrated that these small mammals overlap in their microhabitat utilization. The slug species (McCracken and Seagle, personal communication) also overlap in microhabitat use. These examples do not support MacArthur's (1957) simple model of competition either across habitats or within single habitat types. However, a second model proposed by MacArthur (1957, 1960) allows overlapping niches, implying that species abundances are determined independently of one another. This latter model is more consistent with the observations reported here and suggests the explanation of species abundances rests on species adaptations to use available habitat.

Pielou (1975) reviewed the models proposed to describe relative species abundances but emphasized that the interest of ecologists should focus on the ultimate evolutionary causes of such abundance distributions rather than the distributions themselves. For the several taxa considered in this study, species abundance is significantly related to availability of habitat comprising the species' realized niches. Therefore, to recognize the ultimate cause of abundances, an understanding of habitat dynamics and the intertwining evolutionary history of the species and

their habitats must be developed. A reasonable interpretation of these factors is possible for the Oak Ridge NERP small mammal fauna within the time-space domains described by Delcourt et al. (1983). Microhabitat dynamics affect small mammal abundances at the micro-scale ($<10^6$ m^2 and $<1.5 \times 10^3$ years after Delcourt et al. 1983) and, in forest habitats, are best described by gap-phase replacement of overstory trees (Shugart and West 1977, 1981). These localized disturbances would vary in areal extent and frequency among habitat types but in all situations are capable of producing the patchy microhabitat structure commonly described for Oak Ridge NERP small mammals (Dueser and Shugart 1978, Seagle 1980, Kitchings and Levy 1981). In open habitats such as the old field, growth of early successional tree species provide a patchy structure potentially analogous to forest gaps. At the macro-scale (10^6 - 10^{12} m^2 and 1.5×10^3 - 10^6 years), disturbances such as wildfire, a common natural component of many natural ecosystems drive the dynamics of landscape mosaics (Shugart and West 1981, Romme and Knight 1982) and thus control relative abundance of forest habitat types at any point in time. Forest management and silvicultural practices represent human interventions common on the NERP at the spatial macro-scale. Fossil small mammal records from a raptor roost in Baker Bluff Cave (Guilday et al. 1978) in northeast Tennessee are indicative of varying abundances of small mammal species in East Tennessee since 19,000 years B.P. These fluctuations are due to changing climate and forest type distributions in eastern North America since at least 40,000 years B.P. (Delcourt and Delcourt 1981) in addition to other microhabitat and habitat changes at the micro- and macro-scales.

In addition to forest dynamics, the roots of habitat selection for this small mammal fauna potentially extend to the mega-scale ($>10^{12}$ m^2 and $>10^6$ years) since, by the compilations of Webb (1974), all of the old field species except B. brevicauda have evolutionary origins in arid grassland habitats of southwestern North America. This species, along with P. leucopus and T. striatus, probably evolved in northern forests (Webb 1974). The evolutionary history of O. nuttalli is uncertain but fossil records indicate this species to be a recent (<800 years B.P.) addition to the Tennessee small mammal fauna (Guilday et al. 1969, Guilday et al. 1978). This information illustrates the intimate evolutionary adaptation of these small mammal species to specific habitats and associated microhabitats. The dynamic nature of these habitats, at all spatial and temporal scales, thus interacts with evolved habitat selection to produce species abundance distributions based on resource availability.

Unfortunately, detailed evolutionary history is not available for the remaining examples. However, slugs, salamanders and birds all represent strongly seasonal assemblages in terms of activity and/or breeding. Intuitively, immediate availability of appropriate habitat would seem more important than niche breadth to such assemblages. For example, Fretwell and Lucas (1972) present a model of habitat selection by breeding birds based on habitat availability and discuss the unlikeliness of breeding pairs in inferior habitat to raise a brood of young.

Uniformity of the results from these different examples lends generality to the conclusion that habitat availability better predicts abundance than niche breadth since a variety of landscape scales and taxonomic groups are represented. This conclusion, the observable

changes in habitat structure and the suggestion that landscapes themselves may be nonequilibrium ecosystems (Shugart and West 1981), support the possibility that animal populations and communities may themselves be nonequilibrium.

CHAPTER IV

LANDSCAPE DYNAMICS AND THE SPECIES-AREA CURVE

Preston (1962) provided a theoretical framework to unite the empirical observations that species abundances are distributed lognormally and that species-area curves from various communities or ecosystems have a common slope. The basis of Preston's hypothesis is that, on a log scale of abundance classes, the lognormal frequency distribution of species abundances becomes normal. This curve is referred to as the species curve. On the same scale, the frequency distribution of number of individuals per abundance class (individuals curve) has a terminal modal value that corresponds to the upper truncation point of the species curve. From this empirical observation, Preston (1962) reasoned that as the number of individuals increased the species curve must rise and proceeded to estimate the variables that described this "canonical" relationship. The resultant equation describing number of species as a function of number of individuals was

$$\log S = 0.263\ J/m + 0.317$$

where S is the number of species, J is the total number of individuals and m the number of individuals in the rarest species. Preston then assumed that the number of individuals was linearly related to the area under consideration:

$$J = \rho A$$

where A is area and ρ is density of individuals. Substituting this expression for J in the first equation gives

$$S = 1.83\ (\rho/m)A^{0.263}\ .$$

Combining constants, this equation becomes

$$S = CA^{0.263}\ ,$$

the common power function model for species-area relationships. In practice the theoretical exponent of 0.263 is referred to as z, and takes empirical values from 0.17 to 0.33 (Preston 1962) or 0.20 to 0.35 (MacArthur and Wilson 1967).

MacArthur and Wilson (1967) recognized the importance of Preston's (1962) findings for island species richness and focused further empirical investigations of the species-area relationship on islands, be they true oceanic islands or isolated woodlots in a matrix of agricultural land. Most researchers considered the theory of island biogeography to be a true principle of ecology (Gilbert 1980) and proceeded to seek biological explanations for its ubiquity. Subsequently, studies gave rise to several seemingly alternative hypotheses that explain the increase of species richness with area (Connor and McCoy 1979). The simplest explanation, that of passive sampling (Connor and McCoy 1979), is that larger islands receive larger samples from the source pool by passive dispersal and therefore gain more species. Preston (1960, 1962) and MacArthur and Wilson (1963, 1967) advanced the "area-per se hypothesis" and explained equilibrium species number as the balance of immigration and extinction rates which, in turn, vary with island size.

A final hypothesis, the "habitat-diversity hypothesis" (Williams 1964), is that larger areas have more habitat types and thereby are able to support a greater number of ecological strategies.

Ecologists have recognized the potential importance of the habitat-diversity hypothesis and attempted to account for habitat effects by regressions of species richness on independent variables such as island elevation, number of soil types, and number of vegetation types (e.g., Johnson and Simberloff 1974). Buckley (1982) considered islands to be composed of "habitat units" and calculated plant species number by summing equilibrium predictions from each unit. Buckley (1982) recognized that plant communities form a mosaic of community types potentially covering thousands of hectares. Such a mosaic has been called a landscape by Forman and Godron (1981). Only recently have ecologists begun to explicitly consider vegetation or habitat dynamics at the landscape scale and the interaction of such dynamics with area (Pickett and Thompson 1978). Vegetation dynamics are long term phenomena in most ecosystems and are thus tractable only through models validated by empirical observations of disturbance (Shugart and West 1977, Doyle 1980). The rationale for extending vegetation simulation models to the landscape scale has been developed (Shugart et al. 1973, Weinstein and Shugart 1983) but has not been applied to the theory of island biogeography, specifically the species-area relationship. The model presented here thus represents a quantitative attempt to demonstrate the relationship between area and vegetation dynamics and link these to hypotheses of animal species richness and abundance.

Methods

Forman and Godron (1981) defined a landscape as a kilometers-wide region of similar physiography and repetitious pattern of ecosystem components. Such components form a mosaic of vegetation patches with each patch belonging to a vegetation cover type. Succession and disturbance create a dynamic mosaic so that each patch has a probability of remaining in its current vegetation type as well as probabilities of changing to a patch of any other vegetation type. Although not modeling the details of successional processes, this view of landscape dynamics provides a shifting mosaic of vegetation patches that lends itself to simulation as a first-order Markov process. Manipulation of the number of vegetation patches effectively varies landscape island area while leaving the potential for all vegetation types to be present. Islands used in this model were 200, 800, 2,000, 8,000, and 20,000 patches in size. Different vegetation types were viewed as either suitable or unsuitable habitat by colonizing animal species. With these basic features the model was capable of simulating landscape islands of various sizes undergoing an identical succession/disturbance regime and interfacing the resulting habitat dynamics with the characteristics of colonizing animal species (Figure IV-1). Minor alterations of the species population growth equation also allowed interspecific competition among colonizing species. Further detail is now provided on some important aspects of the model flow diagram (Figure IV-1).

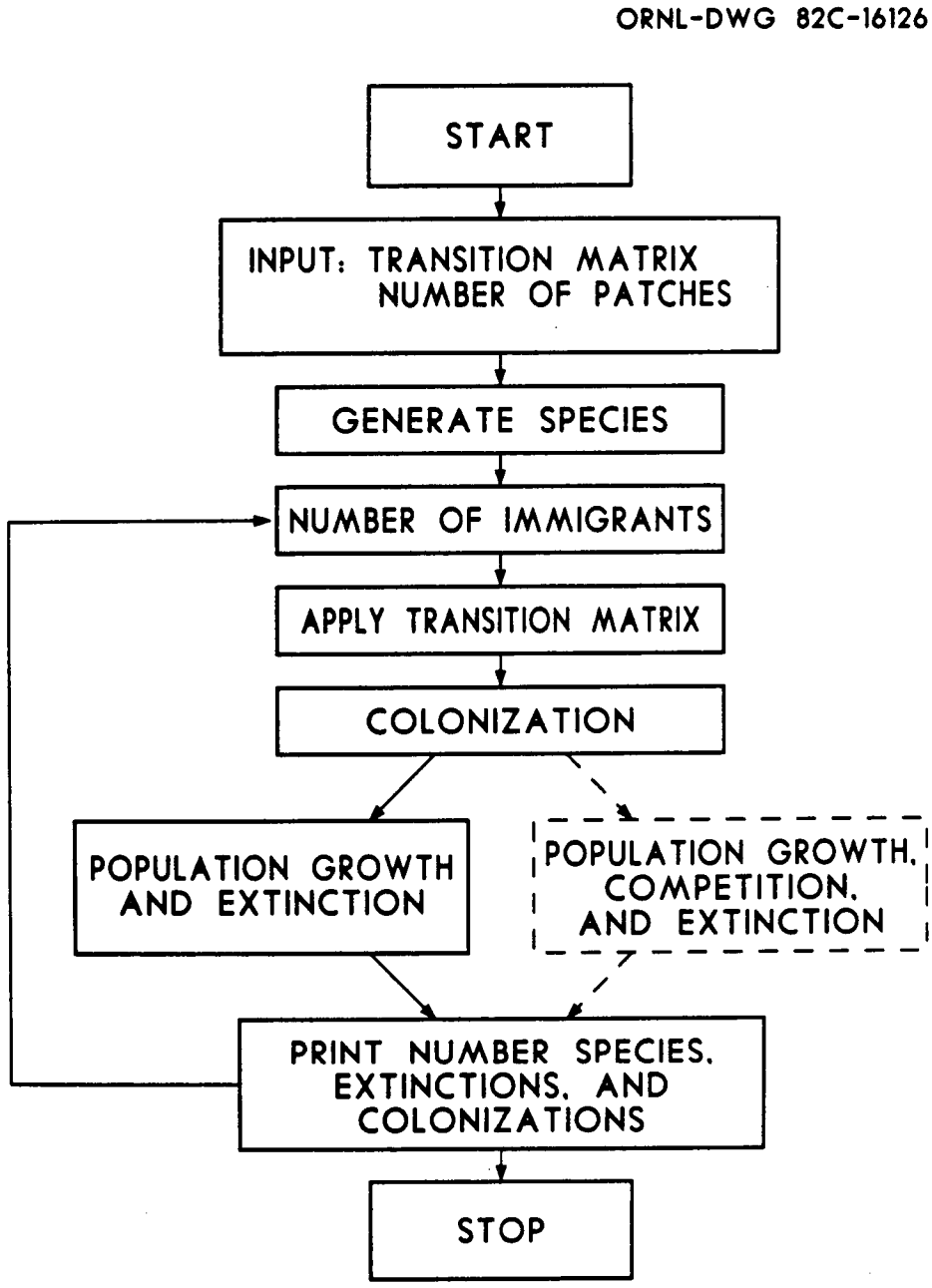

Figure IV-1. Flow diagram of the model interfacing landscape dynamics on various sized islands with colonization by animal species.

The Transition Matrix

The pattern of landscape change in the simulation model (Figure IV-1) is based on the vegetation dynamics of a Tasmanian wet sclerophyll-rainforest ecosystem (Noble and Slatyer 1980). Ten habitat types were recognized and a yearly probability of change from one habitat type to all others calculated as the reciprocal of the successional time between habitat types. The probabilities were tabulated as a 10 by 10 transition matrix that served to characterize the landscape dynamics as a first-order Markov process. During each year or iteration of the model, the appropriate elements of this matrix were used to determine whether each patch of habitat succeeded to another habitat type or simply aged one year. Three hundred interactions (simulated years) comprised each model run, and the results of the patch dynamics were tabulated as the number of patches in each element of a 10 habitat by 300 age class matrix. Starting conditions for each model run were uniform and consisted of the equilibrium configuration of habitat patches at the end of a model run made during model development.

The Species Pool

A pool of 150 hypothetical species was generated from uniform statistical distributions for different species-level characteristics. These characteristics included range of habitats utilized ($\bar{x}$ = 2, S.D. = 0.5), range of habitat ages utilized ($\bar{x}$ = 15, S.D. = 2), intrinsic rate of population increase ($\bar{x}$ = 3, S.D. = 0.05), home range in number of habitat patches ($\bar{x}$ = 20, S.D. = 5.0), and efficiency of habitat utilization ($\bar{x}$ = 5, S.D. = 1.5). The ranges of habitat and age defined each species niche and were positioned within the habitat-age matrix randomly.

Intrinsic rate of increase was used in calculations of population growth and home range size in determining colonization and carrying capacity. The efficiency of habitat utilization was used in determining competition coefficients. Details of these computations are provided below.

Colonization

Each model run began with no species occupying the landscape to mimic invasion of a defaunated island. The number of immigrant species during each model iteration was chosen from a uniform distribution with mean 12 and standard deviation 2.0. This number was chosen from the same distribution regardless of the landscape area under consideration. Thus no target effect (MacArthur and Wilson 1967) was included in the model. This aspect, approximately equal immigration to both large and small landscapes, removes the passive sampling theory of species-area relations from consideration. Colonization of each immigrant species was permitted only if the landscape had twice the number of patches per home range within the designated niche space of a species. If this criterion was met, a propagule of two was established. Established species were not allowed to colonize. Thus no "rescue effect" (Brown and Brown 1977) was incorporated, although a species could recolonize after extinction.

Population Growth and Extinction

During each year of a model run all established populations increased or decreased through the logistic growth model as a difference equation:

$$N(t + 1) = N(t) + r\, N(t)\, [1 - N(t)/K] .$$

In this equation, N(t) is the population size at time t, N(t + 1) is the population size at time t + 1, r is the species-specific intrinsic rate of increase, and K is the species-specific carrying capacity of the landscape. Carrying capacity was calculated by

$$K = \frac{\sum_{i=MINHAB}^{MAXHAB} \sum_{j=MINAGE}^{MAXAGE} (P_{ij})}{HR}$$

where HR is the number of habitat patches required by an individual, P is the number of patches within one element of the habitat-age matrix, and the subscripts on the summation symbols denote the position of a species niche within the habitat-age matrix. In the version of the model where species were allowed to compete, the equation

$$N(i,t+1) = N(i,t) + r_i\, N(i,t)\, \left(1 - \frac{N(i,t)}{K} - \frac{\sum_{j=1}^{n} (\alpha_j N_j)}{K}\right),$$

was used where α_j is the product of the proportion of patches species j shares with species i and the ratio of their resource utilization efficiencies, N_j is the population size of species j, and n is the number of species established on the landscape.

A single criterion based on population size was also used for species extinction. The expression

$$\frac{1}{2^{N-1}},$$

which gives the probability of all offspring in a single generation being of the same sex, was compared to a randomly generated probability to

determine whether extinction occurred. This probability rapidly decreases as population size (N) increases and therefore reflects the assumptions of MacArthur and Wilson (1967) and empirical results of Jones and Diamond (1976) concerning population size and extinction. For extinction to occur, then, population size must reach a low level. Depending on the growth equation utilized, such low population sizes may result from habitat loss or habitat loss combined with competition.

Model Procedures

To examine the interplay of landscape dynamics and area, the Shannon-Weiner Index (Pielou 1977) was used to calculate habitat diversity from the habitat-age matrix. Each element of this matrix was considered an independent observation for this calculation since the suitability of a landscape for any particular species depends on the distribution of patches with respect to both habitat type and age.

Species-area curves were derived from ten model runs at each island area for the random species pool both with and without competition. For each model run colonization and extinction equilibrated by approximately year 260 and thus yielded an equilibrium number of species. These numbers were averaged over the ten replicates for each area to get a mean and standard deviation for the equilibrium number of species. To examine the effect of a nonrandom species pool on the species-area curve, a subset of 29 species from the random pool was assembled. This subset consisted of those species colonizing a 20,000 patch landscape at the end of a single model run allowing competition among random pool species and was randomly chosen from the ten replicates. This second species pool is referred to as "adapted" since the species may be adapted to the landscape

dynamics regime, competition, or both. Species-area curves were also derived, both with and without competition, for the adapted pool. Slopes for the species-area curves were derived from log number of species-log area plots. Species turnover rates after equilibration were calculated in the same manner as equilibrium species number for each of the four species pool and competition combinations.

Results

The effect of a dynamic landscape on the success of colonizing species is best illustrated by plotting the number of species versus island area. With 150 species and no competition this species-area curve rises rapidly and plateaus at approximately 38 species (Figure IV-2). In contrast, when these species are allowed to compete, the curve plateaus at about 17 species (Figure IV-2). These results correspond to 25.3% and 11.3%, respectively, of the species pool. The fact that competition lowers the equilibrium number of species is not a surprising result. However, the slopes of 0.31 ($r = 0.86$) for the curve without competition and 0.29 ($r = 0.94$) for the curve with competition are within the empirically determined range of 0.20 to 0.35 (MacArthur and Wilson 1967). These results suggest that the shape of the species-area curve itself is controlled by the dynamics of the habitat interacting with island area. Figure IV-3 shows this conjecture to be true. This figure illustrates the change in habitat diversity through time by single representative model runs having areas of 200, 2,000, and 20,000 patches. The average diversity for these three areas does not differ greatly, however, the constancy of diversity varies dramatically due to landscape dynamics

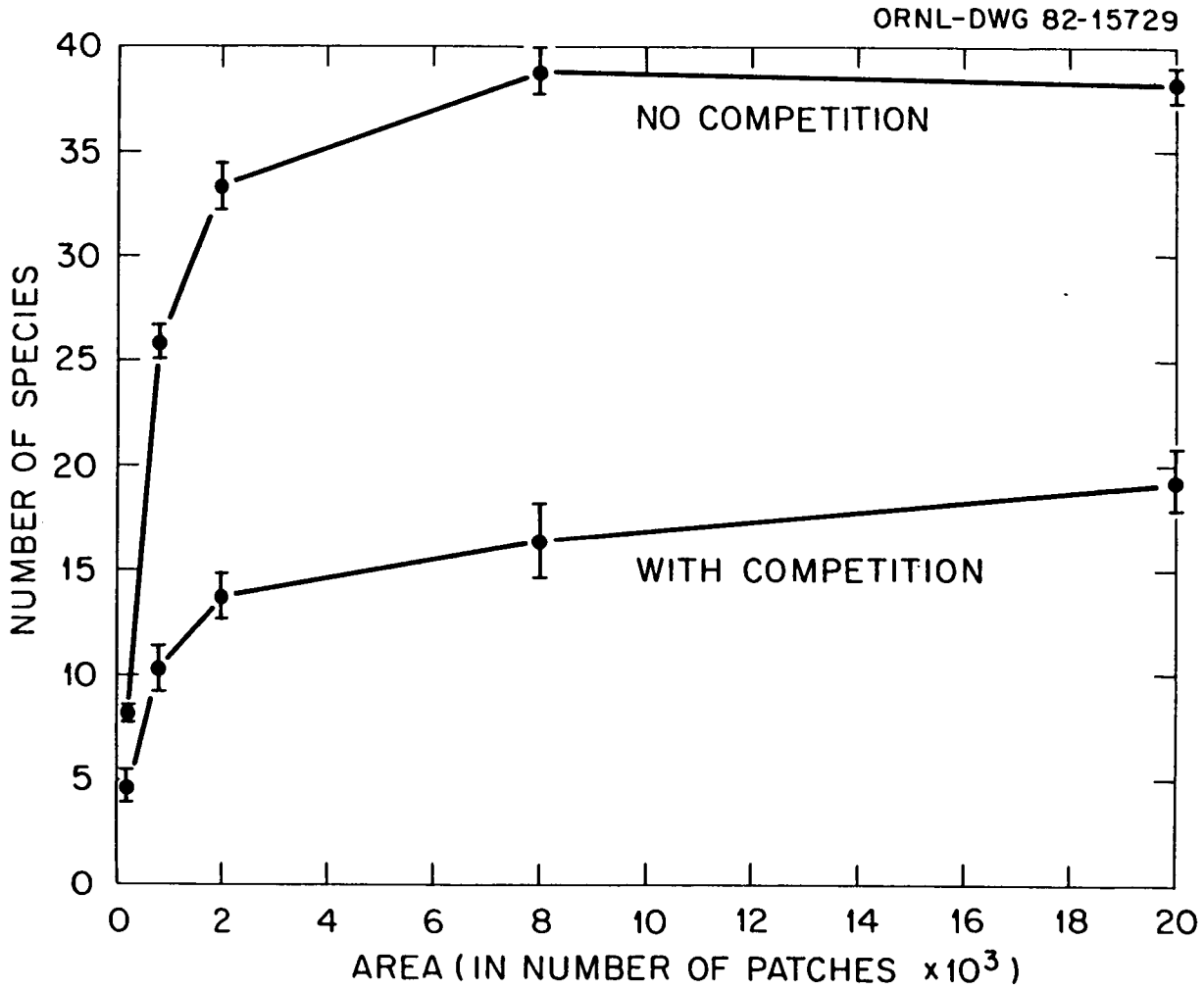

Figure IV-2. Species-area curves from model runs using a random species pool both with and without competition among colonizing species.

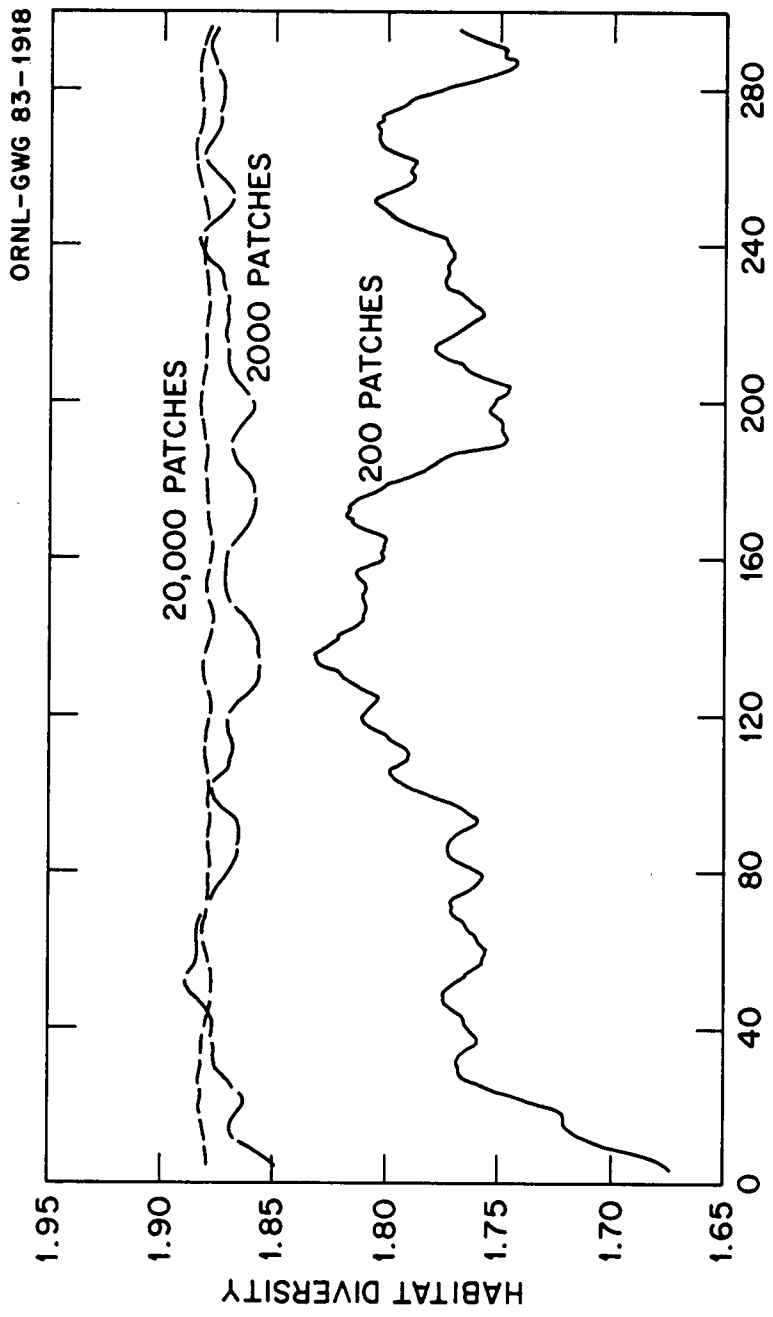

Figure IV-3. Habitat diversity through time for three different landscape island sizes.

interacting with island area. The lack of constancy on small islands thus decreases animal population size, leading to greater extinction probabilities and ultimately lower species richness.

Figure IV-2 illustrates the effect of competition among a randomly generated pool of species. In contrast, Figure IV-4 represents simulation results when the adapted species pool was utilized. The form of the two curves is similar to those of Figure IV-2, however, the equilibrium species richness is a much higher percentage of the species pool, 79.3% with no competition and 31.0% with competition. More importantly, the difference in equilibrium levels of the two curves (14 species) is less than the difference for the random pool curves (21 species), illustrating the potential effect of landscape dynamics and/or competition in creating complementary species assemblages. The slopes of these curves, $z = 0.14$ ($r = 0.80$) without competition and $z = 0.16$ ($r = 0.82$) with competition, are considerably lower than those calculated for the random pool and are below the empirical ranges identified by Preston (1962) and MacArthur and Wilson (1967).

An important indicator of how colonizing species interact with their environment and each other is species turnover. The turnover rates in number of species per year for the random pool (Table IV-1) manifests two patterns. First, the addition of interspecific competition to the model increases turnover dramatically. A less intuitive second result is that turnover rate increases until area reaches 2,000 patches and thereafter declines while area continues to increase. This pattern occurs for both competitive and noncompetitive scenarios. With the adapted species pool, the addition of competition to the model again increases turnover rates

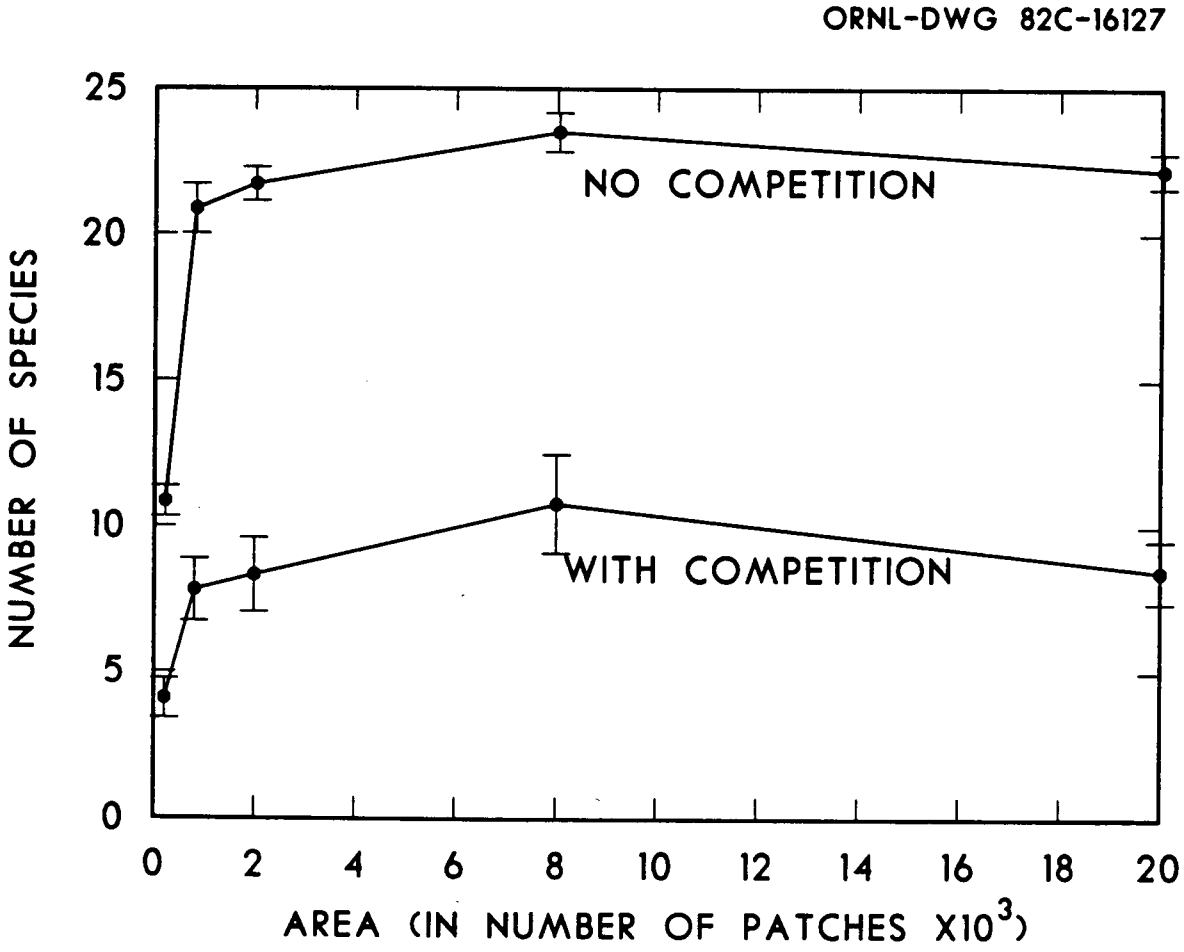

Figure IV-4. Species-area curves from model runs using an adapted species pool both with and without competition among colonizing species.

Table IV-1. Turnover rates in species per year for the random and adapted species pools both with and without interspecific competition where area is in number of habitat patches

Area	Random Pool		Adapted Pool	
	Without Competition	With Competition	Without Competition	With Competition
2×10^2	0.07	0.76	0.18	0.66
8×10^2	0.09	1.06	0.17	0.63
2×10^3	0.23	1.17	0.15	0.64
8×10^3	0.21	1.15	0.12	0.62
2×10^4	0.20	1.09	0.08	0.63

(Table IV-1). However, two new relationships between turnover and area appear. Without competition, turnover shows a steady decline from the smallest to the largest island area, a result consistent with the equilibrium theory of island biogeography (MacArthur and Wilson 1967). Alternatively, when the adapted species are allowed to compete, no clear pattern of turnover becomes apparent (Table IV-1).

Since the model does generate reasonable species-area curves having z scores within the range of empirical results, the distribution of species abundances produced by the model is examined. To insure an adequate sample size and examine a case with an empirically valid z score, only the noncompetitive scenario with a 150 species pool is considered (Figure IV-5). On a log scale of abundance classes, the species curve is approximately normal and the mode of the individuals curve is within one abundance class of the species curve's maximum class. This final abundance class includes only 3.19% of the species and 14.16% of the individuals, thus closely approximating Preston's (1962) canonical hypothesis. In addition, the average number of species for the ten model runs comprising this result is 40.1 species with a standard deviation of 3.17. Since a lognormal curve with this number of species would be expected to have a standard deviation of 3.11, the species curve is comparable to Preston's (1948) theory.

Discussion

Two assumptions form the basis of this model: (1) animal species colonize islands having appropriate habitat and (2) habitats form a dynamic landscape mosaic. The first of these is characteristic of all

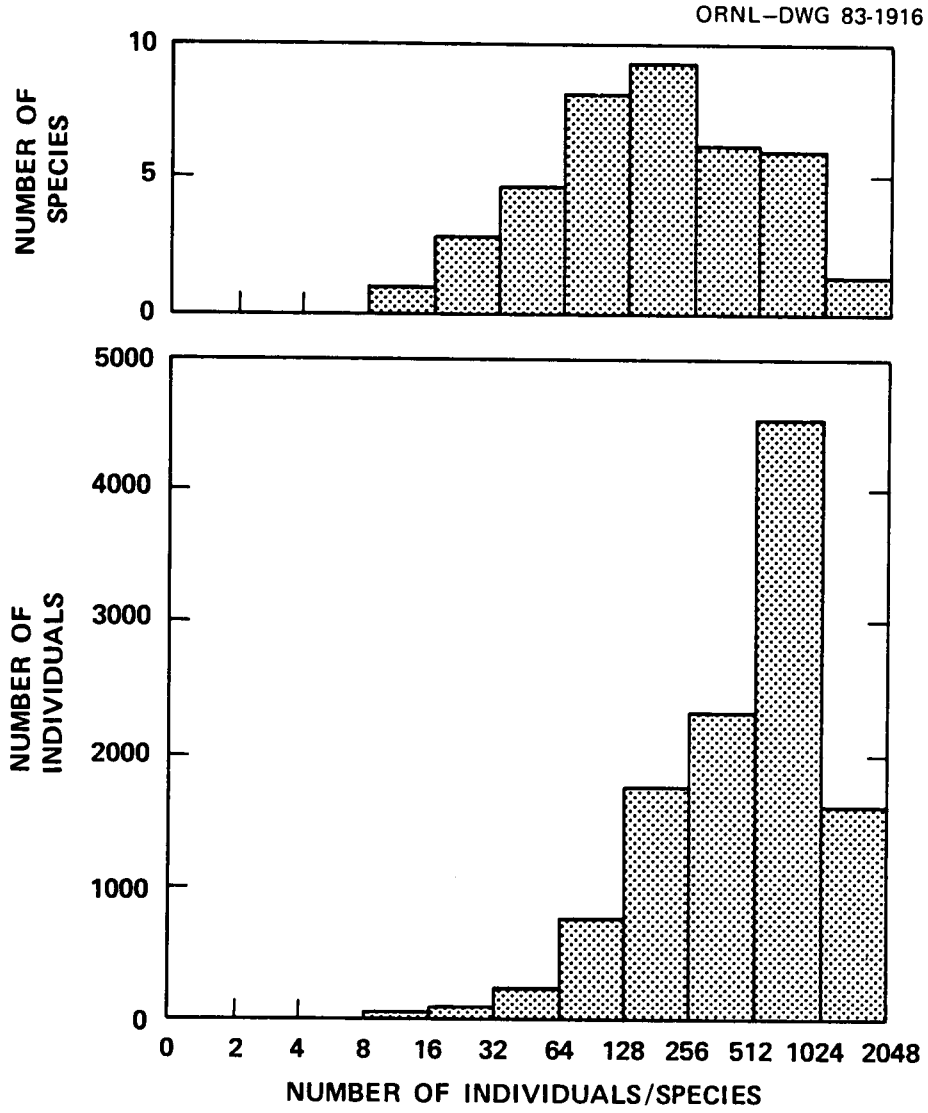

Figure IV-5. Frequency distributions of the number of species and number of individuals within a log series of abundance classes.

species-area hypotheses with the exception of such evoluntionary phenomena as taxon cycles (Ricklefs and Cox 1972). Colonization is also well documented by experimental island biogeography (Patrick 1967, Cairns et al. 1969, Simberloff and Wilson 1969, Schoener 1974). The effect of habitat dynamics resulting from succession and disturbance has rarely been considered in species-area hypotheses although the history of vegetational succession is long (MacIntosh 1980). Lynch and Johnson (1974) coined the term "successional turnover" to describe species turnover due to successional habitat changes and stated that species number "may not be controlled primarily by area-distance effects, but by the timing, extent, and nature of changes which may occur in the insular habitats." The emphasis of these authors is clearly on habitat dynamics but is aimed at turnover rather than species-area relations. Willis (1974) also recognized successional habitat changes as a factor in the extinction of birds on Barro Colorado Island. Karr (1982), in reevaluating avian extinctions on Barro Colorado Island, placed greater emphasis on the limited mosaic of habitats available to extinction prone species. However, none of these papers extended their observations to the interaction of area and succession/disturbance regimes called patch dynamics by Pickett and Thompson (1978). The results of this model reflect the insight of Pickett and Thompson (1978) and suspicions of Karr (1982) that mosaic habitats are affected differentially by area. Specifically, a successional/disturbance regime interacts with various areas to create different habitat patch dynamics. Within the present model these dynamics are reflected by variability in habitat diversity (Figure IV-3, page 58). Small landscapes are thus effectively nonequilibrium (Shugart and West 1981). The

meaning of the term nonequilibrium here should not be confused with that implied by Lynch and Johnson (1974) whose definition of nonequlibrium would include any landscape that did not remain constant.

Several hypotheses have been proposed to explain the increase of species richness with area (Connor and McCoy 1979). The model results presented here have ramifications for two: the area-per se hypothesis, and the habitat-diversity hypothesis. The first of these, deriving from MacArthur and Wilson's (1967) equilibrium theory of biogeography, emphasizes increased immigration and decreased extinction as island size increases while the habitat-diversity hypothesis stresses increased habitat diversity with greater area. Simulation results presented here demonstrate that elements of both hypotheses contribute to the species-area relationship through the interaction of area and landscape dynamics. Increased habitat diversity and especially the constancy of this diversity on larger islands increases species richness. However, immigration and extinction due to a dynamic landscape create a dynamic equilibrium of species richness on any particular island that accentuates the equilibrium theory. During their development of the equilibrium theory, MacArthur and Wilson (1963, 1967) recognized that smaller islands could have fewer habitats and thus fewer species. These authors gave miminal consideration to the causes of extinction other than small population size and the probability that smaller populations are more susceptible to extinction by environmental fluctuations. The results of the present model demonstrate how landscape dynamics can be viewed as an environmental fluctuation creating extinction prone small populations and may even be the ultimate cause of extinction.

As noted earlier all four model scenarios examined here resulted in species-area slopes interpretable sensu MacArthur and Wilson (1967). Competition, while lowering species number, had little effect on this slope. A more interesting observation is that the model version with the adapted species pool exhibited a lower slope than that version with the random pool. MacArthur and Wilson (1967) suggested that slopes below Preston's (1962) canonical value of 0.263 were characteristic of continental areas where a large number of transient species could inflate species number on small areas. Preston (1960) had used a similar argument to explain lower slope values for nonisolated samples. Schoener (1976) proposed an alternative explanation when he suggested that smaller species pools may depress the slope of the species-area curve. Still another hypothesis, strongly related to the transient hypothesis, is that lower extinction or higher immigration rates may raise species numbers on small areas and thus decrease the value of z (MacArthur and Wilson 1967). Empirical studies have thus far not conclusively confirmed any of these hypotheses (Connor and McCoy 1979). In the simulations presented here, use of the smaller pool (adapted species) resulted in lower slope values than the larger pool (random species). This result supports Schoener's (1976) suggestion that species pool size controls the slope of the species area curve since the random pool, in addition to having species well adapted to this landscape regime, contained marginal species capable of transitory residence on a landscape due to brief periods of appropriate habitat. While this model does not include the distance effect of the equilibrium model, it is easy to envision the impoverished faunas of distant islands having a smaller species pool and lower species-area slope due to winnowing of immigrants by relative dispersal ability.

A slope within the range of 0.20 to 0.35 (MacArthur and Wilson 1967) or 0.17 to 0.33 (Preston 1962) is generally attributed to deriving the log species-log area relationship from an underlying lognormal distribution of species abundances (Preston 1962, Connor and McCoy 1979). This interpretation is not without dispute. May (1975) and Schoener (1976) suggest the characteristic range of slope values is a mathematical coincidence, and Connor and McCoy (1979) find the range of this parameter to be an artifact of its estimation by regression analysis. Sugihara (1981) disputes the result of Connor and McCoy (1979) and finds May's (1975) interpretation insufficient to explain the empirical regularity of slope values (Sugihara 1980). As an alternative Sugihara (1980) presents a model of sequential breakage of niche space that leads to a lognormal distribution of niche breadths. With the assumption that niche breadth is equivalent to number of individuals, he illustrates how this "minimal community structure" generates a canonical distribution of abundances and thus the characteristic slope values. Simulation results from the present model also indicate a simple type of community structure based on resource availability. Here the habitat dynamics of any particular landscape area presents to potential colonists a spectrum of available resources and thus selects those species whose niche characteristics are adapted to the dynamics. The ability of these dynamics to generate an approximately canonical lognormal distribution of abundances is well illustrated by Figure IV-5. While this figure shows the abundance distribution for large islands only, it is apparent that addition of smaller islands with smaller population sizes would exaggerate this lognormal relationship. This result shows how landscape dynamics can produce lognormal

species abundances not only on groups of various sized islands but on isolated islands or single sample plots on continents. Landscape dynamics (or the dynamics of any pertinent resource) thus provides a biological basis for the canonical distribution of species abundances and, by the canonical hypothesis of Preston (1962) and the contributions of Sugihara (1980, 1981), the regularity of species-area slopes.

Another characteristic of island ecosystems that is essential to the equilibrium theory of island biogeography (MacArthur and Wilson 1967) is species turnover while species number remains constant. According to this theory, one would also expect higher rates of turnover on smaller islands. Gilbert (1980) considered the evidence for turnover and found little support for its existence within the equilibrium theory context. Field studies of turnover are confounded by a myriad of complicating factors such as inadequate historical data, infrequent system perturbations (e.g., floods, fire, and succession), inadequate replication, and the roles of predation and competition. Model results do not resolve many of these problems and cannot replace well executed empirical studies of turnover. Models do, however, provide controlled conditions permitting the examination of such phenomena as turnover. The present simulations, having only area, competition, and species pool characteristics as factors, still result in several patterns of turnover. A clear result is that interspecific competition increases species turnover rates for both random and adapted species pools. With the random pool, turnover is not linearly related to island area. This result may be explained as follows. Smaller islands have fewer habitat patches and, due to disturbance, the chance of these patches reaching later successional stages is low.

However, some do succeed to later stages of maturity but are emphemeral since the chance of disturbance remains high. This process creates the erratic habitat diversity of small islands (Figure IV-3, page 58) and depresses colonization by later successional species. As island size increases, a larger number of patches reach later successional stages and are capable of supporting colonizing species. These species are subject to higher turnover due to disturbance of substantial proportions of their habitat. When area is large enough, a smaller number of late successional patches are disturbed yearly, and colonists requiring such habitat are subjected to lower extinction rates. This area is analogous to Pickett and Thompson's (1978) "minimal dynamic area." Turnover rates for the adapted species pool are generally lower than those for the random pool, simply reflecting the species adaptation to this landscape dynamic regime. Having taken this pool of species from the results of a large island model run where all stages of vegetation maturity were available, an inverse relationship between species turnover and area (without competition) is not surprising. This pattern of turnover is disrupted when competition is added to the model, resulting in little variation of turnover with landscape island size. Diamond (1969) found a similar lack of pattern for birds on the California Channel Islands. One can only interpret this result as an indication that this small pool of species was selected for adaptation to the landscape dynamics, not interspecific competition. Future simulations under different disturbance regimes may provide insight to the relative roles of resouce dynamics and competition in the development of animal communities. With the complex interactions of area, disturbance, and source pool characteristics revealed by this model,

it is not surprising that the study of faunal turnover is thus far inconclusive (Gilbert 1980).

As with most ecological models, the results in this paper are best viewed as hypotheses in need of empirical validation. The ability of the model to make predictions consistent with a large body of biogeographical data and theory constitutes a strong verification of its ability to generate such plausible hypotheses. I thus hope to have provided some insight to patterns of species turnover, variation in species-area slopes, and the relationship among hypotheses concerning the basis of the species-area relationship.

CHAPTER V

CONCLUSION

The theory of interspecific competition has come under close scrutiny in recent years, partially due to its acceptance as an ecological principle without proper testing (Connell 1980, Connor and Simberloff 1979) and also because other biological mechanisms such as predation (Paine 1966) have been shown to facilitate coexistence of similar species. Nonetheless, studies continue to accumulate that demonstrate competition to be a potent force in the organization of biological communities (Hairston 1980, Williams 1981). The species removal experiment described in Chapter II is exemplary of such studies. Perhaps a more important point made by this experiment is that some corollaries of competition theory (e.g., generalist species are poor competitors) are questionable. Future experiments may reveal that the true test of competition theory is not whether competition itself can be demonstrated conclusively, but whether its implicit corollaries are supported.

Using microhabitat as the potential limiting resource, the small mammal removal experiment indicated that interspecific competition may result in decreased niche breadth of the poorer competitor. This result empirically demonstrates that microhabitat is a critical niche dimension and thus merits further study. Consequently, the question is asked in Chapter III whether the abundance of species within a community is a function of niche breadth or habitat availability (as measured by niche position). The regression results unanimously confirm that resource

availability is a better predictor of abundance than niche breadth. Since these tests were made using data collected from a mosaic of habitats, the results are consistent with the suggestion in Chapter II that competition is a local phenomena. In addition, the diversity of taxonomic groups for which this relationship was demonstrated indicates it may be a general characteristic of animal communities.

The removal experiment and regressions of Chapters II and III, respectively, show that niche position is a species characteristic sensitive to interspecific competition and reflecting species abundance. Each investigation also implied habitat and landscape dynamics as important components of ecosystems. In effect, such dynamics create variable niche positions. The island landscape model of Chapter IV thus incorporates insight provided by the previous studies by allowing habitat availabiity to change through time. The ability of this model to generate empirically common phenomena such as species-area curves and the lognormal distribution of species abundances verifies its ability to mimic nature and gives landscape dynamics a promising future in the study of island biogeograhic pheonomena.

Collectively, Chapters II, III and IV indicate interspecific competition may occur over small spatial scales between similar species within a single habitat type. When a mosaic of habitat types is considered at a single point in time, the effect of interspecific competition as reflected by realized niche breadth is masked by dominant habitat dynamics within the landscape ecosystem. Depending upon disturbance intensity this masking may occur within habitats by gap-phase succession phenomena as suggested in Chapter II. However, when the interaction of

animal habitat selection with the dynamics of landscapes is considered, common animal community characteristics such as the lognormal distribution of abundances emerge as properties of the landscape ecosystem. Habitat utilization and dynamics are thus the common thread that binds these studies and potentially draws together several spatial scales of ecological phenomena. Perhaps Southwood (1977) was correct when he referred to habitat as the template for ecological strategies.

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APPENDICES

APPENDIX A

Definition of terms referring to levels of vegetation organization and spatial scales used by animal species.

Microhabitat — physical structure within a habitat to which animals respond ecologically.

Habitat — a characteristic association of plants such as forest types.

Landscape — a repetitious mosaic of habitat types and physiography.

Local — refers to species microhabitat distributions within a single habitat.

Regional — refers to large areas of homogeneous topography usually with a single landscape pattern.

Geographic — refers to very large areas or species ranges on a continental scale.

APPENDIX B

Variables measured to characterize small mammal habitats and microhabitats are found in Table B-1. The pine plantation study of Chapter II used all the variables while only those marked with the letter "a" were used in the study of Oak Ridge NERP small mammal abundance found in Chapter III. Each variable is accompanied by a brief description of the sampling technique and is patterned after the variables measured by Dueser and Shugart (1978).

Table B-1. Variables measured to characterize small mammal habitats and microhabitats

Variable	Description
Litter-soil depth[a]	Depth of penetration into litter-soil level of a hand-held core sampler with 1-cm radius barrel, measured in centimeters in each quarter of a 1-m^2 circle centered on the grid site.
Litter-soil compactability[a]	Percent compaction of the litter-soil core sample when maximum possible pressure was applied to the sample by means of a hand-held plunger.
Herbaceous stem density	Live herbaceous stem count within a 1-m^2 ring centered on the grid site.
Woody stem density	Live woody stem count within a 1-m^2 ring centered on the grid site.
Herbaceous foliage profile	Average of numbers of live herbaceous stem contacts with a 0.8-m rod rotated 360° parallel to the ground, at heights of 0.05, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0 m above ground level.
Woody foliage profile	Average of numbers of live woody stem contacts with a 0.8-m rod rotated 360° parallel to the ground, at heights of 0.05, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0 m above ground level.
Overstory tree size[a]	Average of diameters at breast height in centimeters of the overstory tree (>7.5 cm) nearest the grid site in each quarter of a 10-m-radius circle centered on the grid site.
Overstory tree dispersion[a]	Average of the distances in centimeters to the nearest overstory tree (>7.5 cm) in each quarter of 10-m-radius circle centered on the grid site.

Table B-1. (Continued)

Variable	Description
Understory tree size[a]	Average of diameters at breast height in centimeters of the understory tree (<7.5 cm) nearest the grid site in each quarter of a 10-m-radius circle centered on the grid site.
Understory tree dispersion[a]	Average of the distance in centimeters to the nearest understory trees (<7.5 cm) in each quarter of a 10-m-radius circle centered on the grid site.
Tree stump size	Average of diameters in centimeters of the tree stump (>7.5 cm) nearest the grid site in each quarter of a 10-m-radius circle centered on the grid site.
Tree stump dispersion[a]	Average of the distance in centimeters to the nearest tree stump (>7.5 cm) in each quarter of a 10-m-radius circle centered on the grid site.
Fallen log size	Average of diameters in centimeters of the nearest fallen log (>7.5 cm) in each quarter of a 10-m-radius circle centered on the grid site.
Fallen log dispersion[a]	Average of distances in centimeters to the nearest fallen log (>7.5-cm-diameter) in each quarter of a 10-m-radius circle centered on the grid site.
Fallen log abundance[a]	Average of the total length in centimeters of all fallen logs (>7.5-cm-diameter) in each quarter of 10-m-radius circle centered on the grid site.
Fallen log density[a]	Average of the total number of fallen logs (>7.5-cm-diameter) in each quarter of a 10-m-radius circle centered on the grid site.
Tree stump density[a]	Average of the total number of tree stumps (>7.5-cm-diameter) in each quarter of a 10-m-radius circle centered on the grid site.

Table B-1. (Continued)

Variable	Description
Thickness of woody vegetation[a]	Number of shoulder-height contacts with woody vegetation along two 20-m perpendicular arm-length transects centered on the grid site.
Shrub cover[a]	Percentage of points with shrub cover along two 20-m perpendicular transects centered on the grid site, points counted at 1-m intervals along each transect.
Percent canopy closure[a]	Percentage of vertical ocular tube sightings with closed canopy along two 20-m perpendicular transects centered on the grid site, sightings taken at 1-m intervals along the transects.
Depth of herbaceous litter[a]	Average depth in centimeters of the herbaceous litter mat taken in each quarter of a 1-m^2 ring centered on the grid site.
Thickness of climbing vines[a]	Number of shoulder-height contacts with climbing vines along two 20-m perpendicular arm-length transects centered on the grid site.

[a]Used in the study of Oak Ridge NERP small mammal abundance.

VITA

Steven Wyant Seagle was born on July 13, 1956, in Shelby, North Carolina, to Robert and Ethel Seagle of Vale, North Carolina. He attended Union Elementary School where, in fifth grade at the age of ten, he decided upon a future career as a biologist. After graduation from West Lincoln High School in 1974, he entered the University of North Carolina at Chapel Hill as a zoology major. Under the influence of Nelson G. Hairston, his interest in ecology heightened. He graduated with highest honors in zoology from "Carolina" in 1978 and began study toward the Master of Science degree at The University of Tennessee, Knoxville, under the supervision of Harrison W. Ambrose, III. In 1980, he received this degree with a major in ecology. During this year he also received the Association of Southeastern Biologists Research Award for his Master's research. For his doctoral work, he chose to remain at The University of Tennessee to study under H. H. Shugart on a research fellowship through the Environmental Sciences Division of Oak Ridge National Laboratory. The Doctor of Philosphy degree with a major in ecology was awarded in August 1983. Dr. Seagle, some eighteen years after deciding to be a biologist, then accepted a position as Assistant Professor of Biology at Lenoir-Rhyne College in Hickory, North Carolina.