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MICROHABITAT PARTITIONING BY SMALL MAMMALS IN CEDAR GLADE AND DECIDUOUS FOREST HABITATS

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Steven W. Seagle

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DEDICATED TO

MY MOM AND DAD

whose encouragement and interest have made possible

both my undergraduate and graduate education

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ABSTRACT

Differential microhabitat use by the small mammal species found in deciduous forest and cedar glade habitats was investigated with discriminant function analysis. Blarina brevicauda and Peromyscus leucopus, the deciduous forest species, appear to be a microhabitat specialist and generalist, respectively. Blarina also appears to occupy a subset of the microhabitat utilized by Peromyscus. The cedar glade species include P. leucopus, again a microhabitat generalist, and Ochrotomys nuttalli, a microhabitat specialist. These two species appear to occupy slightly overlapping microhabitats. Analysis of trap sites at which no animals were captured indicates that portions of both these habitats are unsuitable for small mammal species. By including a randomly chosen group of grid sites in the analyses, the robustness of this multivariate technique was confirmed.

The Peromyscus sexes occupy different microhabitats in the deciduous forest and the same microhabitat in the cedar glade. Since the cedar glade is more heterogeneous than the deciduous forest, it is hypothesized that interspecific competition with Ochrotomys limits Peromyscus to more homogeneous portions of the cedar glade and thus allows neither Peromyscus sex the opportunity to gain a more favorable microhabitat through intraspecific competitive exclusion.

Differential microhabitat use by male and female Peromyscus in the deciduous forest probably increases the reproductive capacity of the individuals of this population, as females appear to occupy more favorable

microhabitats. This resource partitioning on the part of Peromyscus may explain the low diversity of rodent species in eastern deciduous forests and indicates the importance of considering intraspecific competitive regimes in the theory of species packing. It is postulated that intraspecific competition in heterogeneous habitats may serve as one basis for the evolution of kin and interdemic selection by selection for pseudo-altruistic males.

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CHAPTER I

INTRODUCTION

The Niche Concept and Competition Theory

Perhaps one of the few ecological tenets generally accepted by the scientific community is the concept of the niche. First proposed by Grinnell (1917, 1924), the concept stated that the niche is "the ultimate distributional unit, within which each species is held by both structural and instinctive limitations." Several aspects of this definition are notable. First of all, Grinnell placed emphasis on the distribution of species in space and, thus, placed habitat utilization in a position of primary importance for animal species. Secondly, this definition made no direct reference to the interaction of species. This prompted Vandermeer (1972) to refer to Grinnell's niche definition as the "preinteractive niche." A third point of consideration, which conflicts somewhat with the second, involves the "instinctive limitations" which bound the niche space of a species. This phrase connotes a genetic component that constrains a species actions and perceptions of the environment. Present knowledge of population genetics and the probability that interspecific competition leads to genetic selection suggest that, in order to limit competition, evolution should lead to different habitat preferences by sympatric species (Rosenzweig, 1974). If one considers habitat selection to be an instinctive process, then perhaps the dogma of Grinnell's "place niche" should be abolished.

Elton (1927) independently conceived of the niche in terms of the interaction between species. He stated that "the niche of an animal means its place in the biotic environment, its relations to food and enemies." This emphasis on the roles or functions of species within animal communities has led to the characterization of Elton's niche concept as the functional or "postinteractive niche" (Vandermeer, 1972). If one then accepts the genetic inference of Grinnell's definition, these two early definitions of the niche are not incompatible as suggested by Miller (1967) who touts only the distributional aspect of Grinnell's definition.

Obviously, the definitions of Grinnell and Elton were far too vague to allow quantification of niche dimensions. Hutchinson (1957) redefined the niche, using aspects of both the pre and postinteractive niche concepts, as an n-dimensional hypervolume with the distribution of a species along some biotic or abiotic factor forming each dimension. Since it is impossible to even recognize all n dimensions of the niche for a given species, this definition is certainly an abstraction. However, this definition does provide a conceptual framework for the measurement of the niche space of a species.

Intricately linked to the niche concept is the theory of competition and competitive exclusion or coexistence. Gause (1934), in experimental studies of competition between two Paramecium species, found evidence that two species cannot occupy the same ecological niche. With the emergence of Gause's principle, an era of investigation began that has demonstrated time after time that closely related sympatric species avoid

competitive exclusion by partitioning available resources. Pianka (1973), in his review of lizard community structure, has identified three loosely defined categories of resources that can be partitioned by competing species. These are food, space, and time. It seems reasonable, however, to look upon time not as a resource in itself but as a mechanism by which competing species can partition food or space. Colwell and Fuentes (1975) have reviewed the vast literature concerning experimental studies of niche relations between competing species and categorized the results as (1) niche inclusion, which is the containment of the niche of one species within that of another species (for a theoretical treatment see Case and Gilpin, 1975), (2) reciprocal niche overlap in which two species have overlapping niches but also possess an exclusive area of niche space, and (3) coextensive niches where the fundamental niches of two species overlap completely.

How similar two species can be and still coexist is often referred to as the question of "limiting similarity." This amounts to asking how many niche dimensions must be adequately quantified to define the coexistence of sympatric species. Cody (1968) stated that the number of coexisting species, the differences in their feeding ecology, and the relative habitat separation of the species in grassland bird communities can be predicted using only vegetation height and its standard deviation. In generalizing about lizard communities, Pianka (1973) found that, as the number of effective niche dimensions increases, the number of immediate neighbors in niche space decreases. It thus appears that just a few important niche dimensions must be known to define sympatric species niches but

an increase in the effective dimensions quantified allows a more distinct delineation of each niche. It is generally believed than the allowable degree of similarity between species is lower in communities having intense competitive interactions that in communities whose members are less competitive (Pianka, 1972). This indicates that either more resources are in short supply in communities with intense competition or that there are more species competing for relatively fewer limiting resources. The evolutionary results of such competitive interactions could be either competitive exclusion of the poorer competitor(s) or character displacement whereby one species evolves to exploit different resources and thus reduce competition with a superior competitor. Implicit in the concept of competition is the idea that competition is potentially most intense between closely related species and that intra-specific competition is more intense than interspecific competition. Ecologists are also becoming increasingly aware that competition may occur not only between conspecifics, or congeners, but also between members of radically different taxonomic groups (Brown, 1978). For example, Brown and Davidson (1977) cite evidence of competition between desert rodents and ants for food in the form of seeds.

Several methods have been devised for quantifying niche overlap, which is the ecological similarity between species, and niche breadth, a measure positively correlated with the generalist nature of resource utilization by a species. Levins (1968) adapted the Shannon-Wiener formula for species diversity to describe the niche in nature by using the proportions of a species population occurring in different habitat

types in the formula. Most methods used to quantify niche breadth and overlap have since been based on some arbitrary interpretation of resource utilization spectra (for examples see Colwell and Futuyma, 1971 and Pielou, 1972) often with the assumption that these resources are equally available. A measure of niche breadth based on the standard deviation of individual discriminant scores from a discriminant analysis of habitat data was proposed by M'Closkey (1976). Similarly, Dueser and Shugart (1979) approached the question of niche metrics through multivariate analysis of microhabitat data and thereby derived intuitively and biologically pleasing measures of niche breadth and overlap. Recently, Petraitis (1979) discussed problems associated with various measures of niche breadth and overlap, especially the assumption of equal resource availability. He then proposed alternative measures based on the likelihood of a species encountering needed resources.

In addition to the focus on limiting similarity between species, some interest has been expressed in whether the dimensions quantified most often by ecologists are the actual dimensions separating species and allowing coexistence. Schoener (1975) stated that niche differences would exist for species even if their niches were arranged randomly. This certainly indicates the need for manipulative experiments to demonstrate the importance of niche dimensions that appear to allow species coexistence. However, manipulations often have several drawbacks. These include failure to disclose the actual mechanisms structuring communities, failure to explain the origin of niche differences, and, in many cases,

impracticality of manipulations (Schoener, 1975). In addition, experimental manipulations may simultaneously affect an unrecognized and highly correlated interspecific interaction, thus leading to inaccurate interpretation of experimental results. Therefore, a descriptive approach may sometimes be of greater practicality than manipulations if previous studies with a particular taxonomic group have demonstrated the importance of the particular niche dimension being described. An example seems to be the case of communities of small mammal species whose niches separate quite nicely on the basis of habitat and microhabitat parameters (Grant, 1972 and Schoener, 1975). This niche separation is not surprising because of the close reliance of small mammals on habitat structure for protection from predators, their relative immobility, and the correlation between food availability and habitat structure.

Although competition is most closely tied to niche theory and resource partitioning, a growing body of literature indicates that predation and disturbance, possibly in the form of environmental fluctuations, may act to keep population levels low enough so that resources do not become limiting. Strong competition and possible competitive exclusion thus do not occur. Connell (1961), Paine (1966), and Dayton (1971) have demonstrated the predominant roles of predation and disturbance in keeping populations of intertidal invertebrates below their carrying capacity and thereby limiting competition. Predation has also been Suggested as the factor structuring a community of streambank dwelling Desmognathus salamanders (Hairston, 1980).

Multivariate Analysis of the Niche

The multivariate nature of the Hutchinsonian niche is explicit in its n-dimensionality and thus lends itself to quantitative investigation through the use of multivariate statistics. This fact appears to have first been recognized by Maguire (1967) who suggested the use of discriminant function analysis for the quantification of niche dimensions. Because of the perfect analogy between discriminant analysis and the n-dimensional niche, it is ideal for this purpose. Subsequent utilizations of this technique by Cody (1968), Hespenheide (1971), and Shugart and Patten (1972) in the analysis of breeding bird habitats, and by Green (1971) in a niche analysis of bivalve molluscs have borne out its appropriateness through the ecological interpretability of the results. Price (1978) combined discriminant analysis of microhabitat variables with manipulation of the microhabitat itself to demonstrate the role of habitat structure in the coexistence of heteromyid rodents. Dueser and Shugart (1978, 1979) also used discriminant analysis to define the microhabitats of the members of a forest floor small mammal community and to derive measures of niche breadth and overlap for Peromyscus leucopus, Ochrotomys nuttalli, Tamias striatus, and Blarina brevicauda.

Discriminant analysis forms those n-1 linear combinations of p microhabitat variables that best discriminate between the n groups utilized in the analysis (Tatsuoka, 1971). Although the variables measured are determined by the investigator, this analytical technique is unique in that the animal species themselves actually define their own

microhabitat by their activity and subsequent capture within a particular microhabitat. If a trapping technique is used, the assumption is made that traps are placed randomly within the available microhabitats. Except for the placement of the first trap in a trapping grid, this assumption is valid since all other grid sites are determined without previewing by the investigator.

Green (1971) discussed the assumptions on which discriminant analysis is based. These include a priori definition of groups or species, multivariate normality, and homogeneity of within-group variance-covariance matrices. With ecological data it seems that the assumptions of multivariate normality and homogeneity of variance-covariance matrices are the most difficult to meet. An additional qualification to test the assumptions of discriminant analysis is that a minimum of $p + 1$ characterizations of the p variables must be made for each group in the analysis.

As noted by Green (1971), the discrimination between groups is based on an analysis of parameters associated with the presence of an individual belonging to one of the groups to be analyzed and, thus, ignores species absences. Concerning the absence of a species from a sample, he stated that the species might not be biologically able to occupy that point in niche space, zoogeographical reasons have prohibited the species from inhabiting that particular area, or that by chance the sampling procedure failed to include an individual of that species. Thus far no studies have been devised to include information about the absence of a species from an area.

Habitat, Microhabitat and Small Mammals

The spatial relations of small mammals have been intensively studied over the last 20 years. Most studies, however, have dealt with species differences on the scale of whole habitats defined by obvious vegetative or physical differences. Sheppe (1961), working in British Columbia, found Peromyscus oreas only on ravine floors while P. maniculatus inhabited the sides of the ravines. After P. oreas was removed from the ravine floor, P. maniculatus apparently shifted into the habitat formerly occupied by P. oreas. Microtus montanus was found by Koplin and Hoffmann (1968) to occupy xeric habitats and M. pennsylvanicus more mesic habitats. Upon removal of M. pennsylvanicus, M. montanus shifted its habitat utilization to occupy both mesic and xeric sites. Various natural experiments consisting mainly of comparisons between island and adjacent mainland faunas have noted habitat shifts for many species on islands when their mainland competitors were not present (Grant, 1972).

Attention has begun to focus on the segregation of small mammal species not at the level of whole habitats, but at the level of microhabitats, which are described by subtle physical or vegetational differences within a habitat. M'Closkey and Fieldwick (1975) assessed food selection and habitat preferences for locally sympatric Peromyscus leucopus and Microtus pennsylvanicus. Significant structural habitat differences were found as well as dietary differences between these species. M'Closkey and Lajoie (1975), in a comparative habitat study, found P. leucopus densities to vary with foliage structure but not with floristic composition of the habitats. In a coastal sage scrub habitat

in Southern California, M'Closkey (1976) found microhabitat and body size differences for Peromyscus eremicus, Neotoma lepida, N. fuscipes, and Dipodomys agilis. Microhabitat differences were based on shrub structure and substrate patchiness. Three seasonal residents, P. maniculatus, P. californicus, and Reithrodontomys megalotis, overlapped resident species in both microhabitat utilization and body size distribution. The reliance of Dipodomys merriami on foliage height density and Perognathus penicillatus on the presence of bushes was demonstrated by Rosenzweig (1973) through experimental alteration of these microhabitats. Rosenzweig and Winakur (1969), in a study of desert rodent assemblages, found soil and vegetation characteristics to be the most important factors in determining rodent species diversity and constructed a model of these habitat characteristics to predict diversity. Holbrook (1979) used sequential removals of Neotoma stephensi, Peromyscus boylii, and P. maniculatus along with vegetative tailoring to examine the roles of microhabitat utilization and competition in structuring this rodent assemblage. She concluded that although interspecific competition is occurring, differential microhabitat use and morphological characteristics allow the coexistence of these species. Price (1978) demonstrated microhabitat differences between species in a heteromyid rodent community and based predictions of ecological interactions and niche shifts of the species on these results. Subsequent removal experiments and habitat manipulations confirmed the validity of these predictions. A forest floor small mammal fauna was analyzed by Dueser and Shugart (1978) using discriminant function analysis. They found three rodent species to utilize different

microhabitats. Peromyscus leucopus and Tamias striatus appeared to be microhabitat generalists, while Ochrotomys nuttalli occupied much more specialized microhabitats. Not only do rodent species themselves appear to segregate by differential utilization of microhabitat, but sexes of the same species may also inhabit different microhabitats. Bowers and Smith (1979) found that Peromyscus maniculatus females occupied more favorable moist microhabitat while males occurred in more xeric areas. They related this to the maximization of reproductive effort and increased survival of offspring.

Grant (1972), after reviewing the literature concerning competition between rodents, without considering microhabitat segregation, concluded that "competitive interaction for space is a general phenomenon among rodent species and is not restricted to the few species that have been studied in detail."

The Present Study

Considering the n-dimensionality of the niche and the probability that not all n dimensions can ever be known even for a single species, it is reasonable to focus on those dimensions which are of greatest utility in characterizing the individual niches of community members. Microhabitat parameters appear to compose the most important dimension for the study of small mammal communities.

Brown (1973) and Brown and Lieberman (1973) professed that the diverse assemblages of North American desert rodents coexist because they have evolved gradients of body size within communities and thus utilize different seed sizes for food. An amendment to this theory is the idea

that species with larger body sizes may be physically dominant and thus able to attain a more diverse diet. Smaller species, because of their ability to efficiently manipulate a smaller range of seed sizes, maintain more specialized diets. Brown (1973), however, proposed that seed size distribution is dependent on localized geography and habitat characteristics while Price (1978) and other workers have demonstrated the role of microhabitat in structuring desert rodent communities. The assertions of Brown and Lieberman seem to be soundly based, however, the predominant role of microhabitat cannot be disputed.

The present study seeks to characterize the microhabitats or structural niches (Dueser, Shugart, and Randolph, 1976) of two small mammal communities through the use of discriminant function analysis. The communities are defined by the gross nature of the habitats in which they occur, not by having radically different animal species assemblages. These habitats are a cedar glade, a relatively open evergreen forest composed of cedar, pine, and scattered hardwoods, and an eastern deciduous forest which is composed of various hardwood trees that form a high, closed canopy and patchy understory.

The small mammals captured in the cedar glade include the golden mouse, Ochrotomys nuttalli, and the white-footed mouse, Peromyscus leucopus. Ochrotomys is generally considered a semiarboreal, nocturnal species that is active year around. This species is most commonly associated with evergreen or mixed evergreen and deciduous forests (Linzey, 1968) which have heavy undergrowths of honeysuckle (Dunaway, 1955). Peromyscus is ubiquitous in North American forest habitats but

reaches highest densities in deciduous forests (Pearson, 1959 and Iverson et al., 1967). Nicholson (1941) has noted the semiarboreal nature of this species and Getz (1961) has demonstrated the necessity of ground structure, in the form of stumps, logs, and tree branches, in providing good P. leucopus habitat.

The deciduous forest mammal fauna also is composed of two species, P. leucopus and Blarina brevicauda, the short-tailed shrew. Blarina is a semifossorial insectivore that occurs in many habitat types (Burt and Grossenheider, 1976 and Linzey and Linzey, 1971). Morris (1955) noted the preference of this species for areas having fallen logs, stumps, and other ground structure.

The main questions to be answered by multivariate analysis of the structural niches of the small mammals found in the cedar glade and deciduous forest communities include the following.

1. Do species-specific microhabitats exist?
2. Are the microhabitats characterized valid representations in light of the difficulty in meeting the assumptions of discriminant analysis with ecological data?
3. Can microhabitat analysis be used to characterize unfavorable small mammal microhabitats?
4. Do the sexes of the small mammal species differ in their microhabitat utilization?

CHAPTER II

METHODS

Cedar glade and deciduous forest habitats on the Oak Ridge National Laboratory Reservation in Anderson County, Tennessee, were selected as study sites. These two habitats represent climax plant associations and are typical of many areas in East Tennessee. Red cedar (Juniperous virginiana), short-leafed pine (Pinus echinata), and sweetgum (Liquidambar styrachiflua) were the dominant plant species of the cedar glade with saplings of these species forming understory and shrub strata. Big bluestem (Andropogon spp.), little bluestem (A. scoporius), and broomsedge (A. virginiaus) composed the ground cover in the more open areas while honeysuckle (Lonicera japonica) was most abundant in the heavier wooded areas.

Chestnut oak (Quercus prinus), white oak (Q. alba), northern red oak (Q. rubra borealis), and occassional beech (Fagus grandifola) and tulip poplar trees (Liriodendron tulipifera) formed the overstory of the deciduous forest with dogwood (Cornus florida) and saplings of the overstory species as the main understory trees. Sparse herbaceous species of the forest floor included pipsissewa (Chimaphila umbellata), wild ginger (Asarum canadense), poison ivy (Rhus radicans), and wild grape (Vitis spp.).

Small mammal populations in the two habitats were sampled with Sherman live traps placed at 10 meter intervals in a 70 meter by 70 meter trap grid. Bait consisted of a mixture of peanut butter and rolled

oats. The traps were in operation six days per week from 1 July to 7 September, 1979, for a total of 3840 trap-nights in each habitat. All captured animals were sexed (except for juveniles and shrews), weighed, examined for reproductive condition, toe clipped for future identification, and released at the point of capture. Since prolonged trapping gradually yielded no unmarked animals, population densities were estimated from the minimum number of individuals known alive.

Microhabitats were characterized by measuring an array of 30 structural parameters around the capture sites. A 1 m^2 circle centered on the trap was used to characterize herbaceous and woody vegetation structure near the trap while a 10 m radius circle, again centered on the trap, was used to sample overstory and understory characteristics. All structural measurements were taken during the trapping period from July to September. These were many of the same parameters used by Dueser and Shugart (1978) and are listed in Table 1 along with a brief description of each. This same array of parameters was measured around 31 randomly chosen grid sites for inclusion in the analyses as a distinct group. Those randomly chosen grid sites at which no animals were captured were also established as a separate group for analysis.

In order to compare the structural diversity of the cedar glade and deciduous forest, some index of relative habitat heterogeneity must be derived. By totalling the standard deviations of all 30 variables for each group used in the discriminant analyses and dividing by the total number of variables, one arrives at a value indicative of the variability of the microhabitat for each group.

Table 1. List and description of the variables measured to characterize the cedar glade and deciduous forest microhabitats. (Adapted from Dueser, Shugart, and Randolph, 1976.)

Variable	Description
Litter-Soil Depth	Depth of penetration into litter-soil level of a hand-held core sampler with 1.00 cm radius barrel, measured in centimeters in each quarter of a 1 m^2 circle centered on the grid site
Litter-Soil Compactability	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 1.00 m^2 ring centered on the grid site
Short Herbaceous Stem Density	Count of live herbaceous stems < .4 m in height within a 1.00 m^2 ring centered on the grid site
Number of Herbaceous Species	Herbaceous species count within a 1.00 m^2 ring centered on the grid site
Woody Stem Density	Live woody stem count within a 1.00 m^2 ring centered on the grid site
Short Woody Stem Density	Count of live woody stems < .4 m in height within a 1.00 m^2 ring centered on the grid site
Number of Woody Species	Woody species count within a 1.00 m^2 ring centered on the grid site
Herbaceous Foliage Profile	Average of numbers of live herbaceous stem contacts with a .8 m rod rotated 360°, parallel to the ground, at heights of .05, .1, .2, .4, .6, .8, 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0 m above ground level

Table 1. (continued)

Variable	Description
Woody Foliage Profile	Average of numbers of live woody stem contacts with a .8 m rod rotated 360° parallel to the ground, at heights of .05, .1, .2, .4, .6, .8, 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0 m above ground level
Overstory Tree Size	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	Average of the distance in centimeters to the nearest overstory tree (> 7.5 cm) in each quarter of a 10 m radius circle centered on the grid site.
Understory Tree Size	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	Average of the distance in centimeters to the nearest understory tree (< 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	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

Table 1. (continued)

Variable	Description
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	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	Average of the total length in centimeters of all fallen logs (> 7.5 cm diameter) in each quarter of a 10 m radius circle centered on the grid site
Fallen Log Density	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	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
Evergreenness of Herb Stratum	Percentage of points with evergreen herbs along two 20 m perpendicular transects centered on the grid site, points counted at 1 m intervals along each transect
Soil Surface Exposure	Percentage of points with bare soil along two perpendicular 20 m transects centered on the grid site, points counted at 1 m intervals along each transect
Thickness of Woody Vegetation	Number of shoulder-height contacts with woody vegetation along two 20 m perpendicular arm-length transects centered on the grid site

Table 1. (continued)

Variable	Description
Shrub Cover	Percentage of points with shrub cover along two perpendicular 20 m transects centered on the grid site, points counted at 1 m intervals along each transect
Evergreenness of Shrubs	Percentage of points with evergreen shrubs along two perpendicular 20 m transects centered on the grid site, points counted at 1 m intervals along each transect
Evergreenness of Overstory	Percentage of vertical ocular tube sightings having evergreen overstory along two perpendicular 20 m transects centered on the grid site, sightings taken at 1 m intervals along each transect
Percent Canopy Closure	Percentage of vertical ocular tube sightings with closed canopy along two perpendicular 20 m transects centered on the grid site, sightings taken at 1 m intervals along the transects
Depth of Herbaceous Litter	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	Number of shoulder-height contacts with climbing vines along two perpendicular 20 m arm-length transects centered on the grid site

The data from each habitat were analyzed separately to focus on species relations within each habitat and avoid the difficulty in interpretation of higher multigroup discriminant analyses. Therefore, the discriminant functions derived by each analysis will not necessarily be identical. A univariate F-test was used to identify and remove parameters failing to differentiate between the species. The remaining variables were then subjected to discriminant function analysis using BMDP7M (Dixon and Brown, 1977) and SPSS (Nie et al., 1975) packaged programs. Four-group discriminant analyses were performed on the data from each habitat. These groups were the two species captured in each habitat, the grid sites at which no animals were captured, and the random selection of grid sites. A second discriminant analysis for each habitat included only the data for the two species captured in each habitat. This analysis amounts to an univariate test for species differences on each variable but allows the combining of the structural variables into a single discriminant function and subsequent ordering of the individuals for each species along that function. To investigate intraspecific microhabitat differences, the Peromyscus data for each habitat was broken down into male and female groups. This resulted in two three-group discriminant analyses composed of male Peromyscus, female Peromyscus, and either Blarina or Ochrotomys. Blarina and Ochrotomys were not divided into male and female groups due to the difficulty in sexing Blarina and the relatively small sample sizes of each species.

In this study, multivariate normality is assumed to exist for the data since, by the Central Limit Theorem, the derived discriminant

functions are more likely to be normally distributed than the original variables (Cooley and Lohnes, 1962). Tests for homogeneity of variance-covariance matrices were performed by an option contained in the Statistical Package for Social Sciences (SPSS) discriminant analysis program (Nie et al., 1975). Significant differences between matrices were found in several of the analyses. Therefore, to confirm the validity of any group differences and the robustness of discriminant analysis, predictions were made concerning the positioning of the random group in discriminant space. These predictions were:

1. The centroid of the random group should be centered near the origin of discriminant space since the origin represents the "average" microhabitat for the study site.
2. The random group should have a high variance along each discriminant function since, theoretically, all possible microhabitats are represented in this group.

Should these predictions prove true, then any differences between other groups may be considered valid even though the assumptions of discriminant analysis are not strictly followed.

CHAPTER III

RESULTS

Trapping Results

Table 2 summarizes the number of animals captured in each habitat, their densities, and the total number of microhabitat characterizations for each species or group. Peromyscus is the most abundant species in each habitat and, in addition, appears to be the most easily trapped species. The number of characterizations for the no-capture groups appears to be quite low; however, since these grid sites were determined by the activity and captures of the species, nothing could be done to increase the sample size for these groups. Table 3 presents the average weights and standard deviations of these weights for each sex of the species captured in the cedar glade and deciduous forest. Male and female Blarina are considered collectively due to the difficulty of determining the sex of these individuals in the field.

Cedar Glade Analyses

Figure 1 illustrates the results of a four-group discriminant analysis for the cedar glade habitat. The ellipses, which were drawn by the principle axes technique (Sokal and Rohlf, 1969), include 95% of the data points for Peromyscus, Ochrotomys, the no-capture trap sites, and the random sample of grid sites plotted on discriminant functions I and II. Variables of significance on these discriminant functions are given in Table 4. These two functions account for 99% of the variance caused

Table 2. Number of individuals captured, population estimates, and the number of microhabitat characterizations for each group used in analyses of the cedar glade and deciduous forest.

Cedar Glade

Group	No. Individuals	Density	Total Number Characterizations
Peromyscus leucopus	16	25/ha	63
Ochrotomys nuttalli	11	17/ha	24
Random	--	--	31
No-Capture	--	--	12

Deciduous Forest

Group	No. Individuals	Density	Total Number Characterizations
Peromyscus leucopus	23	36/ha	105
Blarina brevicauda	13	20/ha	21
Random	--	--	31
No-Capture	--	--	9

Table 3. Numbers of each sex captured, average weights of each sex, and standard deviation of the average weight for the two small mammal species captured in the cedar glade and deciduous forest.

Cedar Glade Sex and Species	n	Average Weight	Standard Deviation of Weight
Male *Peromyscus*	7	30.71 g	3.99
Female *Peromyscus*	9	28.11 g	2.76
Male *Ochrotomys*	7	28.80 g	1.64
Female *Ochrotomys*	4	33.25 g	.96
Deciduous Forest **Sex and Species**	**n**	**Average Weight**	**Standard Deviation of Weight**
Male *Peromyscus*	13	24.92 g	3.09
Female *Peromyscus*	10	24.70 g	2.58
Male and Female *Blarina*	13	18.15 g	1.68

Figure 1. Ellipses containing 95% of the observational points graphed on discriminant functions I and II for each group included in the cedar glade four-group analysis. Significant variables on discriminant function I include litter-soil compactability, fallen log density, and shrub cover, while thickness of climbing vines, depth of herbaceous litter, and litter-soil depth are significant on discriminant function II.

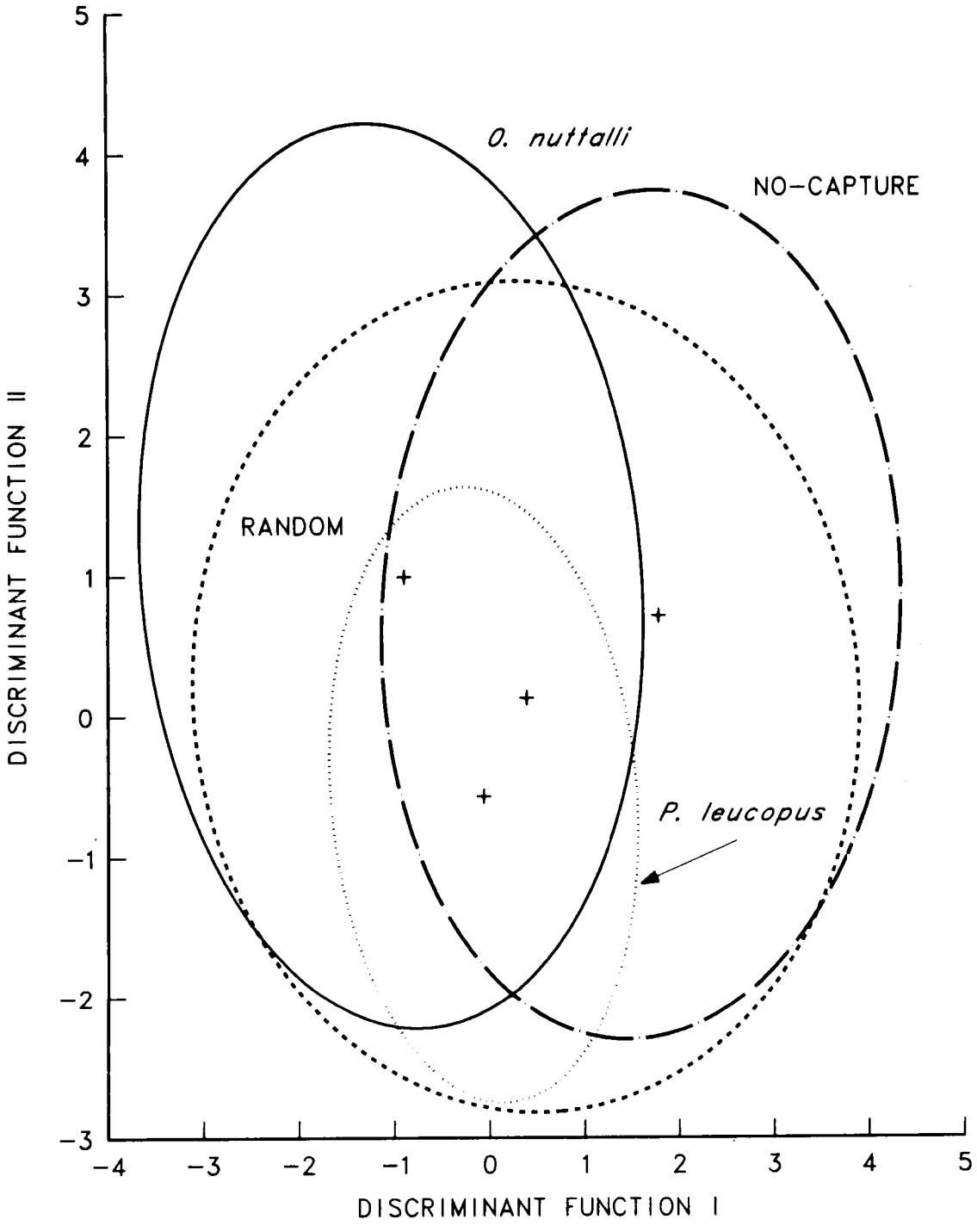

O. nuttalli
NO-CAPTURE
RANDOM
P. leucopus
DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
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Figure 1.

Table 4. Standardized discriminant function coefficients[1] for those variables that discriminate between groups in the cedar glade four-group analysis. (* indicates variables of greatest significance on a function.)

Variable	DF-I	DF-II	DF-III
Litter-Soil Compactability	.9872*	-.0982	- .1637
Fallen Log Density	-.4694*	.0725	.0737
Shrub Cover	.3247*	.0407	.1571
Thickness of Climbing Vines	-.1728	.7985*	.0755
Depth of Herbaceous Litter	.5782	.6302*	.2341
Litter-Soil Depth	-.0800	.5719*	.1336
Fallen Log Abundance	.6419	-.2522	-1.1332*
Tree Stump Density	.2166	.0269	.6541*
Herbaceous Stem Density	-.2445	.1725	- .4921*
Tree Stump Dispersion	.0100	.2157	.4274*
Evergreenness of Herb Stratum	.2029	.0547	.2034*

[1]Standardized discriminant function coefficients constitute weighting factors the absolute magnitudes of which are indicative of the significance of the variables on each discriminant function.

by species differences and, since very little information is contained in the third discriminant function, it will not be discussed. Graphing the first two discriminant functions allows the best possible two-dimensional view into the three-dimensional discriminant space derived by the analysis.

Table 5 (Cedar Glade Analysis) gives the discriminant scores for each group centroid and the distance of each centroid from the origin of discriminant space ($\overline{P}$) as calculated using the Pythagorean Theorem. The random points ellipse for the cedar glade is centered near the origin of discriminant space and, also, includes most portions of the other ellipses (Figure 1). Since the analysis substantiates these predictions about the random group, it would appear that any significant differences for the other groups in the analysis would be valid even though the assumptions of discriminant analysis are not met. The discriminant analysis thus appears to be quite robust and, therefore, pairwise F-tests for group differences will be presented.

Both Figure 1 and Table 5 indicate Peromyscus to be a microhabitat generalist and well adapted to the cedar glade since the Peromyscus group centroid is located near the origin of discriminant space. On the other hand, Ochrotomys is more restricted to specialized microhabitats within the cedar glade as indicated by the relatively great distance from the origin of the Ochrotomys centroid (Table 5, Figure 1).

Figure 2 depicts 95% confidence ellipses around the group centroids for the cedar glade analysis. It is obvious that Peromyscus and Ochrotomys are well separated in this discriminant space. The result of

Table 5. Discriminant scores of group centroids, distance from the origin of discriminant space of the group centroids ($\overline{P}$), and the percent variance accounted for by each discriminant function for deciduous forest and cedar glade groups in the four-group discriminant analyses.

Cedar Glade Analysis				
Group	DF-I	DF-II	DF-III	$\overline{P}$
Ochrotomys	-1.048	.947	-.958	1.722
Peromyscus	- .088	-.572	.533	.787
Random	.377	.132	-.330	.518
No-Capture	1.581	.715	-0.29	1.736
% Variance	63%	36%	1%	

Deciduous Forest Analysis				
Group	DF-I	DF-II	DF-III	$\overline{P}$
Blarina	- .866	-.134	-.346	.943
Peromyscus	- .029	-.127	.126	.182
Random	.265	.275	-.007	.382
No-Capture	.765	.854	-.639	1.312
% Variance	69%	30%	1%	

Figure 2. Ninety-five percent confidence ellipses around group centroids graphed on discriminant functions I and II from the cedar glade four-group analysis. Significant variables on discriminant function I include litter-soil compactability, fallen log density, and shrub cover, while thickness of climbing vines, depth of herbaceous litter, and litter-soil depth are significant on discriminant function II.

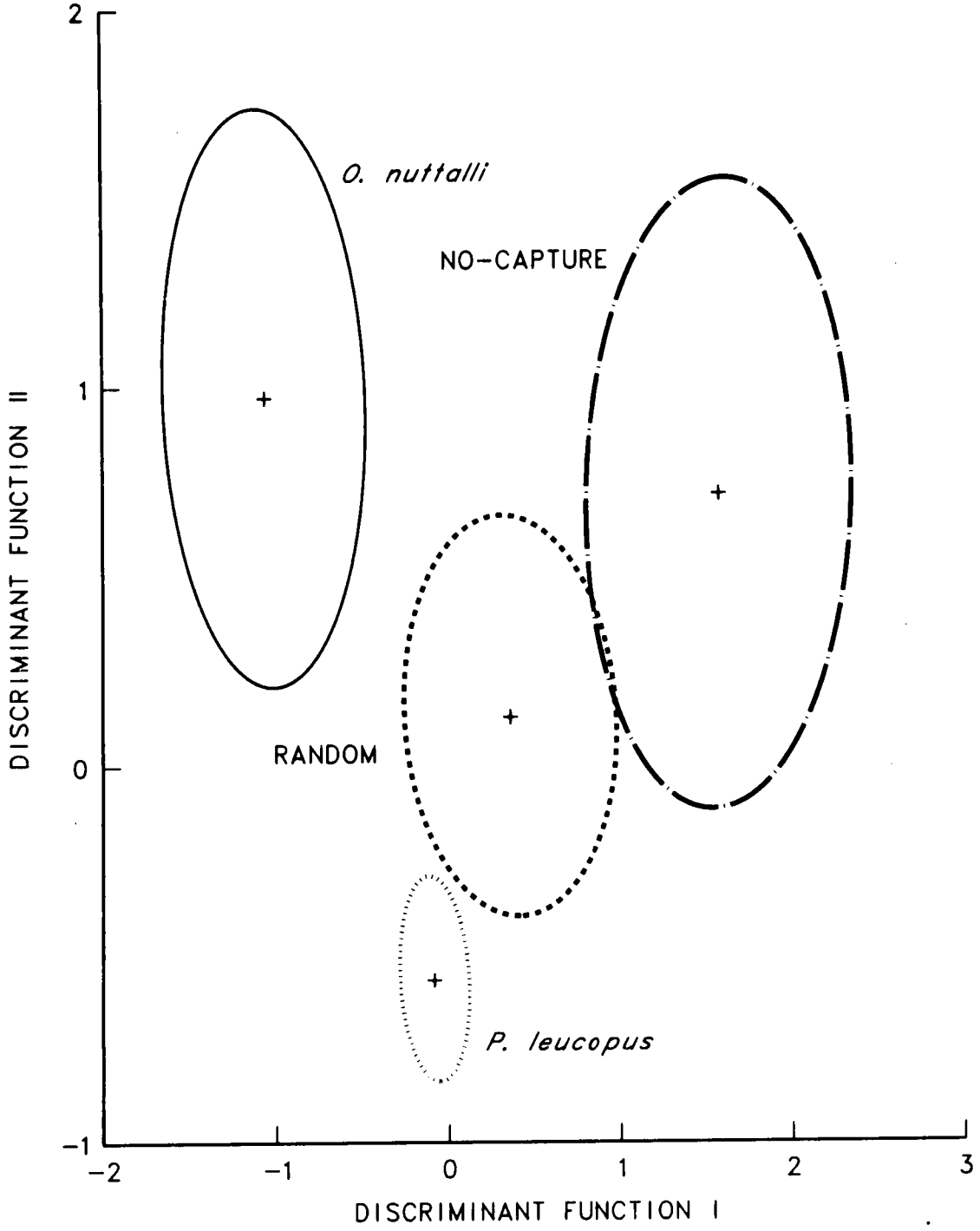

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DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
O. nuttalli
NO-CAPTURE
RANDOM
P. leucopus

Figure 2.

a pairwise F-test (Table 6, Four-Group Analysis) for these two species corroborates this result and leads to the conclusion that Peromyscus and Ochrotomys occupy different microhabitats. Peromyscus is not significantly different from the random group (Table 6) nor separated from the random group ellipse of Figure 2. This once again indicates microhabitat generality for Peromyscus. In contrast, Ochrotomys is well separated from the random group (Figure 2). The separation of the no-capture trap sites in discriminant space suggests that this group represents microhabitats unfavorable to either small mammal species. Significant pairwise F-tests between the no-capture group and both Peromyscus and Ochrotomys (Table 6, Four-Group Analysis) support this interpretation. Since the no-capture group is a subset of the random sample, a nonsignificant F-value is found in Table 6 for this comparison.

By comparing the group means (Table 7) for the significant variables of each axis (Table 4, page 27) with the positions of the group centroids, one can visualize a gradient along the axis for each variable. The characteristics of these individual variables may then be considered collectively as a description of an overall gradient from one microhabitat type to another. For example, discriminant function I, which separates Ochrotomys and Peromyscus from the no-capture trap sites and accounts for 63% of the variance, is a gradient from areas with low litter compactability, higher density of fallen logs, and fewer shrubs to areas with higher litter compactability, lower density of fallen logs, and more shrubs. These variables appear to represent a gradient of understory and soil surface characteristics which indicates that the

Table 6. Pairwise F-tests for the cedar glade four-group, three-group, and two-group analyses. (** = significance at α = .01, *** = significance at α = .001.)

Four-Group Analysis (df = 11, 116)	
Pairwise Comparison	F-Value
Ochrotomys—Peromyscus	8.05***
Ochrotomys—Random	3.55***
Ochrotomys—No-Capture	5.25***
Peromyscus—Random	2.53**
Peromyscus—No-Capture	4.01***
Random—No-Capture	1.36
Three-Group Analysis (df = 30, 49)	
Pairwise Comparison	F-Value
Male Peromyscus—Female Peromyscus	.61
Male Peromyscus—Ochrotomys	5.10***
Female Peromyscus—Ochrotomys	5.75***
Two-Group Analysis (df = 11, 75)	
Pairwise Comparison	F-Value
Peromyscus—Ochrotomys	9.90***

Table 7. Ochrotomys, Peromyscus, random, and no-capture group means for those variables that discriminate between groups in the cedar glade four-group analysis.

Variable	Ochrotomys	Peromyscus	Random	No-Capture
Litter-Soil Depth	4.037	4.164	4.116	4.129
Litter-Soil Compactability	.255	.318	.377	.513
Herbaceous Stem Density	497.458	253.397	305.968	267.500
Tree Stump Dispersion	986.771	861.274	915.895	940.375
Fallen Log Abundance	251.417	85.198	208.635	167.623
Fallen Log Density	1.542	.635	1.097	.750
Tree Stump Density	.125	1.041	.675	.667
Evergreenness of Herb Stratum	.036	.102	.070	.059
Shrub Cover	.132	.182	.168	.168
Depth of Herbaceous Litter	3.281	1.874	5.592	3.378
Thickness of Climbing Vines	12.938	3.587	7.403	7.875

species avoid open areas with only shrubby cover. The second discriminant function, in accounting for 36% of the variance, separates Ochrotomys and Peromyscus in discriminant space. Peromyscus appears to inhabit more deeply wooded areas while Ochrotomys occurs in edge habitats as described by the gradients of litter-soil depth, depth of the herbaceous litter mat, and climbing vine density.

Since discriminant function analysis forms those linear combinations of the variables that best discriminant among all groups in the analysis, the true relationship between Peromyscus and Ochrotomys is somewhat obscured by the addition of artificial groups, such as the random and no-capture groups. Therefore, to focus on the species themselves, a two-group discriminant analysis was performed and the species ordered along the single discriminant function. Figure 3 shows a normalized frequency distribution of the two species along the resulting discriminant function. Peromyscus and Ochrotomys appear to occupy significantly different but slightly overlapping microhabitats. The single discriminant function can be interpreted as a gradient from heavily wooded microhabitat to edge microhabitat, with Peromyscus occupying the more wooded portion (Table 8).

Potential sex-specific microhabitat differences were sought in the population of Peromyscus found in the cedar glade by performing a three group discriminant analysis with male Peromyscus, female Peromyscus, and Ochrotomys. Figure 4 shows 95% confidence ellipses around the three-group centroids and indicates separation of all three in discriminant space. Results of the pairwise F-Tests (Table 6, Three-Group Analysis), however, indicate a nonsignificant difference between male and female

Figure 3. Frequency distribution of the cedar glade species on discriminant function I from the two-group analysis. Significant variables on this function include litter-soil depth, litter-soil compactability, herbaceous stem density, tree stump size, tree stump dispersion, fallen log abundance, fallen log density, evergreenness of the herb stratum, shrub cover, depth of the herbaceous litter, and thickness of climbing vines.

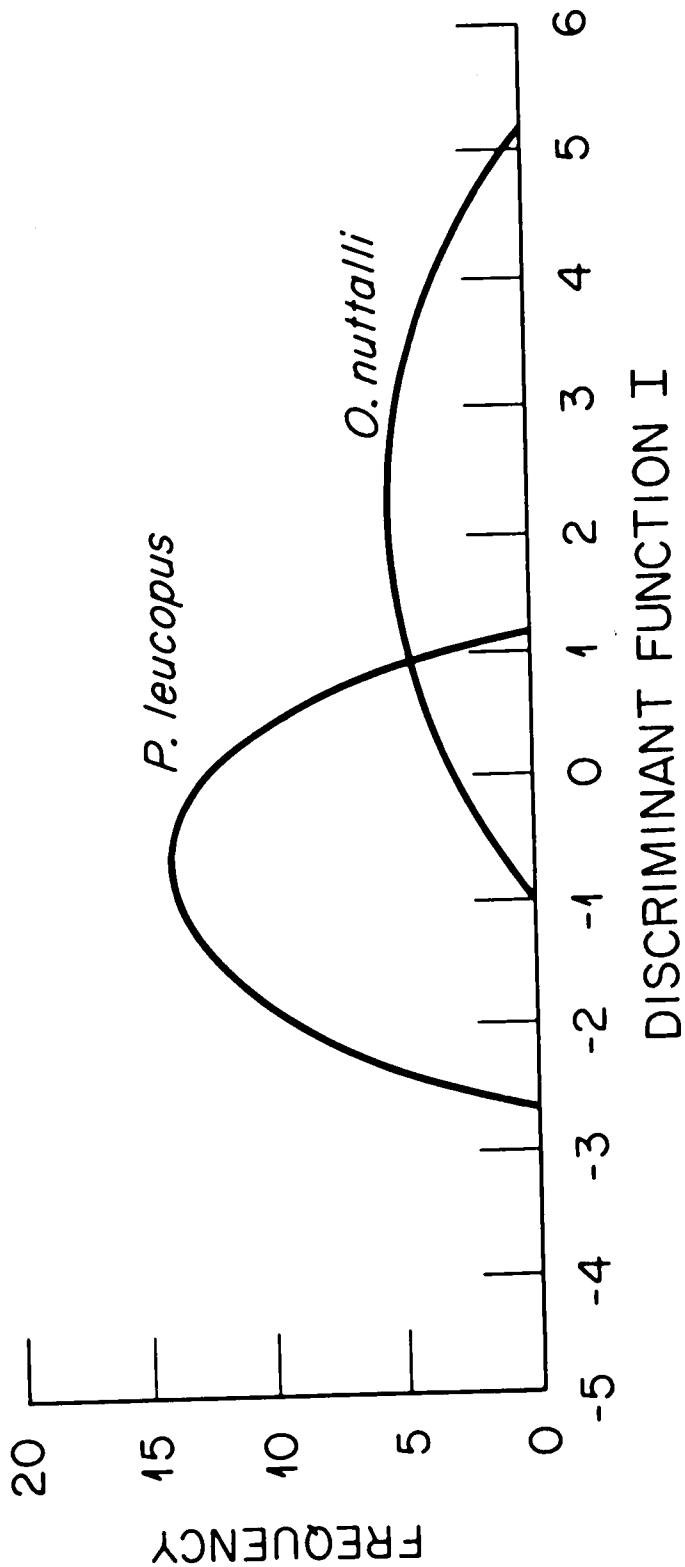

P. leucopus
O. nuttalli
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DISCRIMINANT FUNCTION I

Figure 3.

Table 8. Ochrotomys and Peromyscus group means for those variables that discriminate between groups in the cedar glade two-group analysis.

Variable	Ochrotomys	Peromyscus
Litter-Soil Depth	4.064	3.614
Litter-Soil Compactability	.255	.318
Herbaceous Stem Density	497.458	253.397
Tree Stump Size	7.183	12.201
Tree Stump Dispersion	986.771	861.274
Fallen Log Abundance	251.417	85.198
Fallen Log Density	1.542	.635
Evergreenness of Herb Stratum	.036	.102
Shrub Cover	.132	.182
Depth of Herbaceous Litter	3.281	1.874
Thickness of Climbing Vines	12.938	3.587

Figure 4. Ninety-five percent confidence ellipses around the group centroids graphed on discriminant functions I and II from the cedar glade three-group analysis. Variables significant on discriminant function I include herbaceous stem density, woody stem density, soil surface exposure, fallen log dispersion, and litter-soil depth. Tree stump size, thickness of woody vegetation, tree stump dispersion, fallen log size, and depth of the herbaceous litter are significant on discriminant function II.

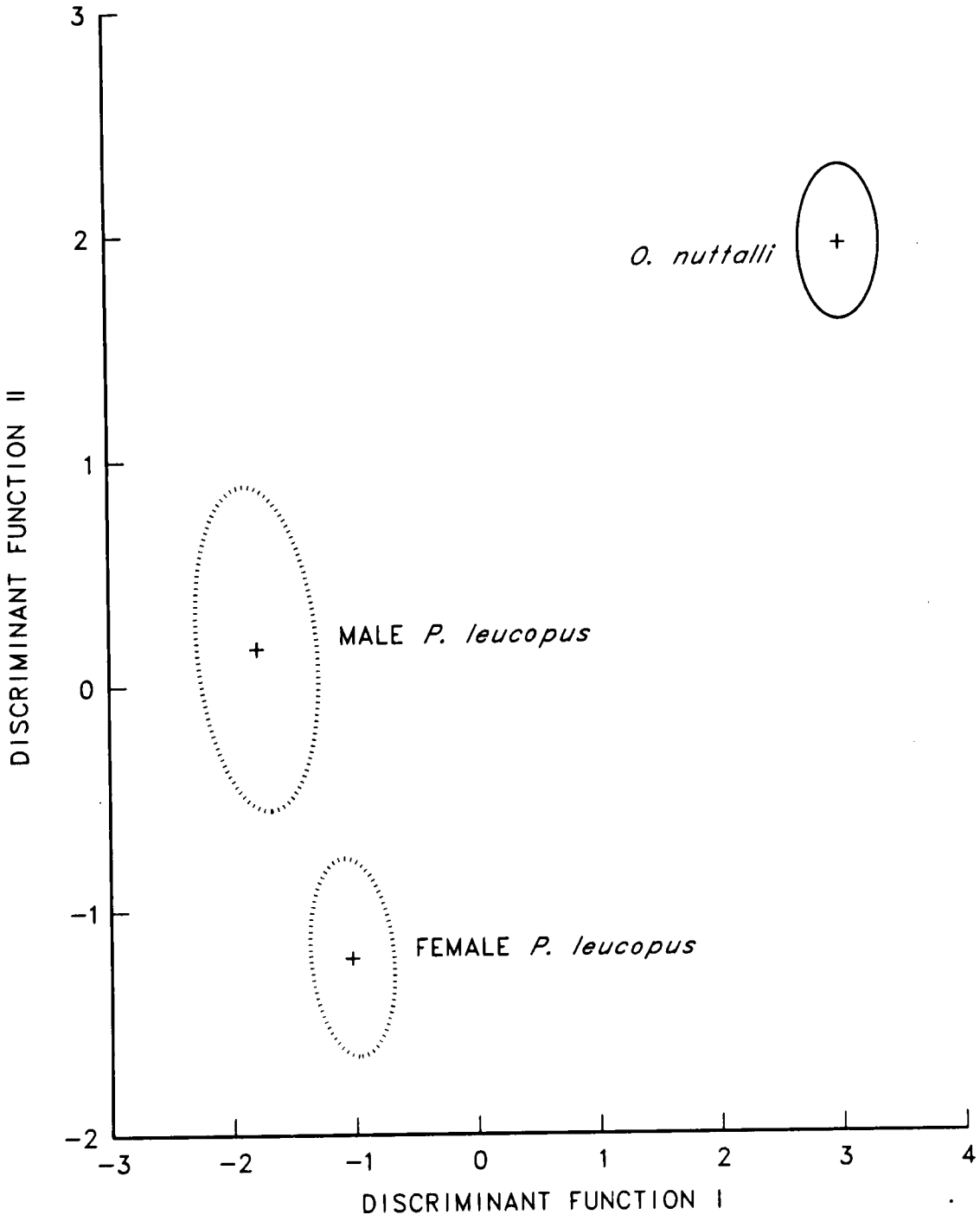

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DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
O. nuttalli
MALE P. leucopus
FEMALE P. leucopus

Figure 4.

Peromyscus. The first discriminant function accounts for 94% of the variance caused by species differences and is obviously once again a gradient from wooded to edge habitat (Tables 9 and 10). Little information is contained in the second axis as confirmed by the small percentage of variance accounted for by this function (Table 11, Cedar Glade Analysis). This lack of information on the second discriminant function may indicate that the apparent graphical differences between male and female Peromyscus are only differences between the centroids while highly overlapping discriminant score dispersions indicate that the sexes do not actually occupy structurally distinct microhabitats. This interpretation and the previous test for robustness by inclusion of the random group in the analysis suggest that the insignificant F-test result is more indicative of the true relationship between male and female Peromyscus in the cedar glade. The data are certainly open to other interpretations and depend heavily on future statistical advances elucidating the robustness of discriminant analysis.

Deciduous Forest Analyses

A four-group discriminant analysis including Blarina, Peromyscus, no-capture trap sites, and the random points yielded the results found in Figure 5. The ellipses are drawn to include 95% of the observational points for each group on discriminant axes I and II. Discriminant function III was eliminated from consideration since it accounts for only 1% of the total variance (Table 5, Deciduous Forest Analysis, page 29). The random points ellipse is centered closely on the origin of the discriminant space (Table 5, Deciduous Forest Analysis) and includes high

Table 9. Standardized discriminant function coefficients[1] for those variables that discriminate between groups in the cedar glade three-group analysis. (* indicates variables of greatest significance on a function.)

Variable	DF-I	DF-II
Herbaceous Stem Density	14.461*	.176
Short Herbaceous Stem Density	-12.395*	.190
Woody Stem Density	5.080*	.912
Soil Surface Exposure	- 2.446*	-1.665
Fallen Log Dispersion	- 1.990*	-1.625
Short Woody Stem Density	- 1.792*	- .358
Litter-Soil Depth	1.661*	.314
Tree Stump Size	.982	1.775*
Thickness of Woody Vegetation	.039	-1.581*
Tree Stump Dispersion	1.339	1.453*
Fallen Log Size	.662	1.284*
Depth of Herbaceous Litter	.538	1.093*

[1]Standardized discriminant function coefficients constitute weighting factors the absolute magnitudes of which are indicative of the significance of the variables on each discriminant function.

Table 10. Ochrotomys, male Peromyscus, and female Peromyscus group means for those variables that discriminate between groups in the cedar glade three-group analysis.

Variable	Ochrotomys	Male Peromyscus	Female Peromyscus
Litter-Soil Depth	4.064	3.579	3.612
Herbaceous Stem Density	497.485	269.765	265.098
Short Herbaceous Stem Density	497.083	266.176	254.951
Woody Stem Density	3.083	2.647	4.049
Short Woody Stem Density	1.625	2.294	2.756
Number of Woody Species	1.333	1.118	1.756
Tree Stump Size	7.583	12.457	11.797
Tree Stump Dispersion	986.771	881.706	840.762
Fallen Log Size	6.142	5.729	6.278
Fallen Log Dispersion	859.323	907.912	824.646
Depth of Herbaceous Litter	3.281	2.492	1.842

Table 11. Discriminant scores of group centroids, distance from the origin of discriminant space of the group centroids ($\overline{P}$), and the percent variance accounted for by each discriminant function for cedar glade and deciduous forest groups in the three-group discriminant analyses.

Cedar Glade Analysis			
Group	DF-I	DF-II	$\overline{P}$
Male Peromyscus	-1.789	.163	1.796
Female Peromyscus	-1.026	-1.213	1.588
Ochrotomys	3.019	1.957	3.598
% Variance	94%	6%	

Deciduous Forest Analysis			
Group	DF-I	DF-II	$\overline{P}$
Male Peromyscus	1.271	.266	1.299
Female Peromyscus	- .689	.526	.867
Blarina	- .902	-1.785	2.000
% Variance	67%	33%	

Figure 5. Ellipses containing 95% of the observational points graphed on discriminant functions I and II for each group included in the deciduous forest four-group analysis. Significant variables on discriminant function I include thickness of woody vegetation and woody stem density. Fallen log dispersion and litter-soil compactability are significant on discriminant function II.

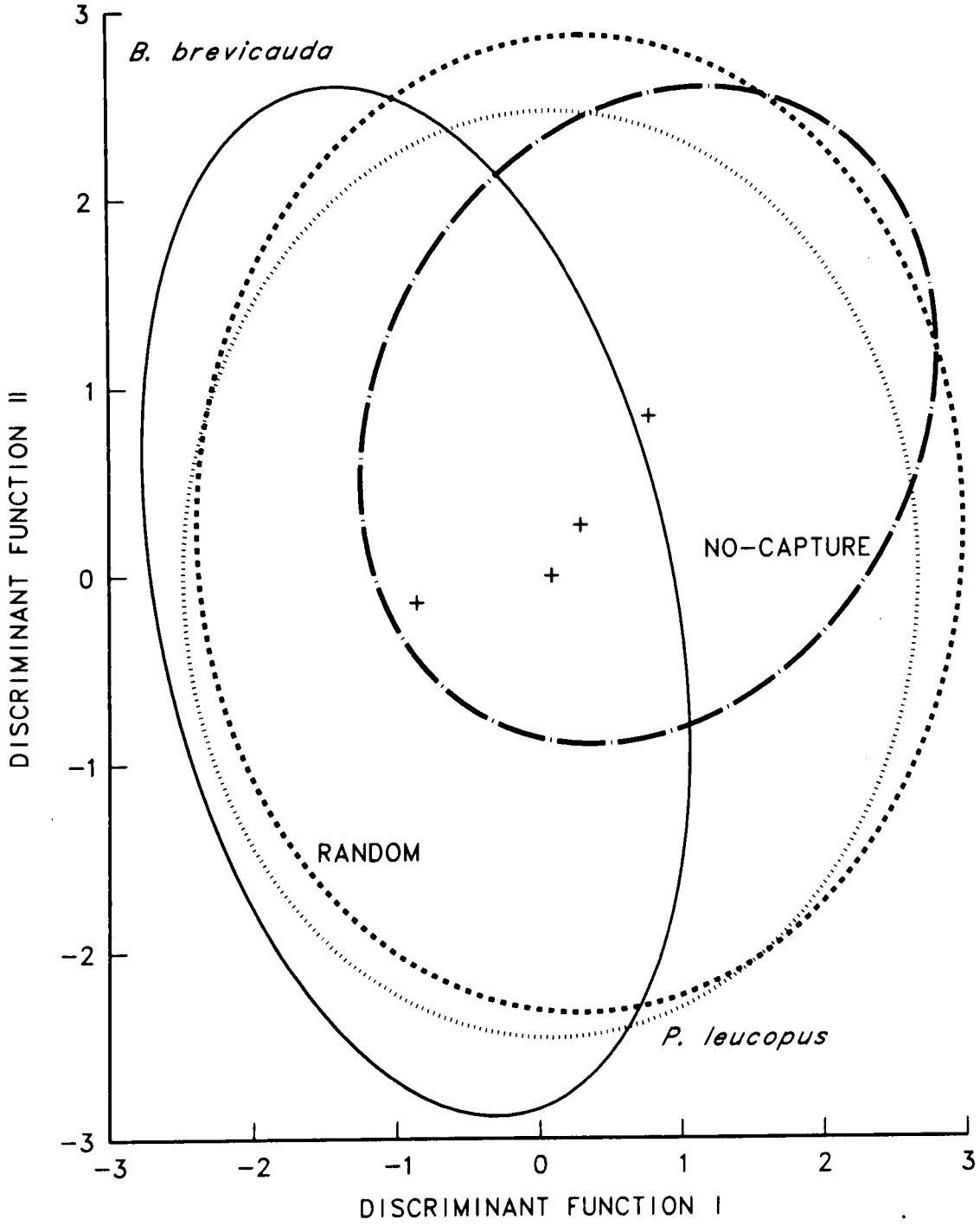

B. brevicauda
NO-CAPTURE
RANDOM
P. leucopus
DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
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Figure 5.

percentages of the other ellipses (Figure 5). Any differences among the remaining groups are therefore considered valid.

Figure 6 depicts 95% confidence ellipses around the group centroids and illustrates the separation of Blarina, Peromyscus, and the no-capture trap sites in discriminant space. These results are supported by significant pairwise F-tests among these three groups (Table 12, Four-Group Analysis). Peromyscus once again appears to be a microhabitat generalist since the group centroid is close to the discriminant space origin (Table 5, Deciduous Forest Analysis, page 29) and is not significantly different from the random group (Table 12, Four-Group Analysis). On the other hand, Blarina seems to be a microhabitat specialist with the group centroid located relatively far from the origin of discriminant space (Table 5, Deciduous Forest Analysis). The no-capture group appears to represent specialized microhabitats unsuitable to both small mammal species as indicated by the isolation of its ellipse in discriminant space (Figure 6) and the pairwise F-tests with Peromyscus and Blarina (Table 12, Four-Group Analysis). The nonsignificant difference between the no-capture and random groups (Table 12, Four-Group Analysis) is apparently due to the fact that the no-capture group is a subset of the random group.

Discriminant function I accounts for 69% of the variance caused by species differences and is interpreted as a gradient from thinner to thicker understory (Tables 13 and 14) with significant parameters being the thickness of woody vegetation and woody stem density. Blarina occurs in areas of thinner understory and Peromyscus in microhabitats of

Figure 6. Ninety-five percent confidence ellipses around the group centroids graphed on discriminant functions I and II from the deciduous forest four-group analysis. Significant variables on discriminant function I include thickness of woody vegetation and woody stem density. Fallen log dispersion and litter-soil compactability are significant on discriminant function II.

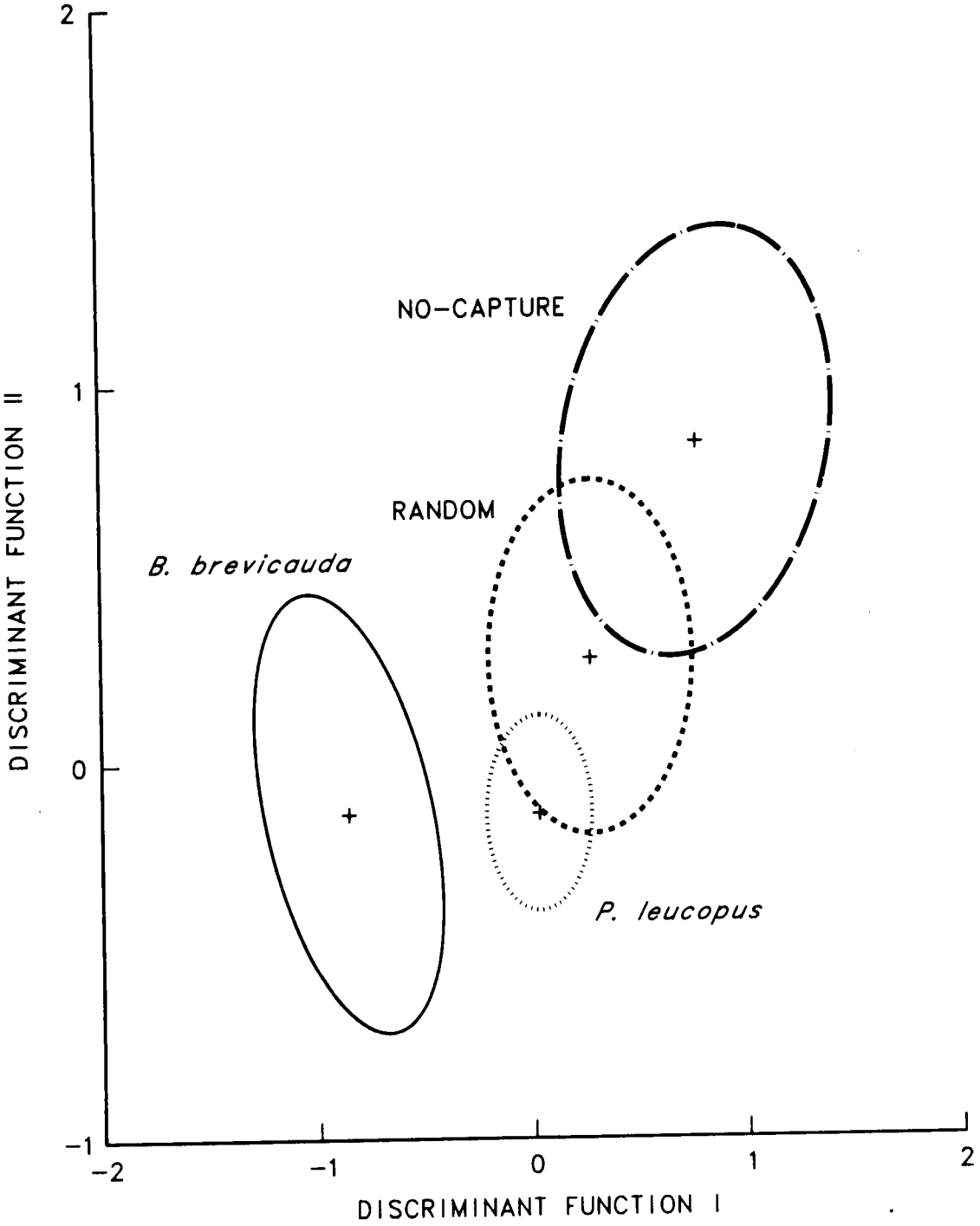

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DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
NO−CAPTURE
RANDOM
B. brevicauda
P. leucopus

Figure 6.

Table 12. Pairwise F-tests for deciduous forest four-group, three-group, and two-group analyses. (** = significance at α = .01, *** = significance at α = .001.)

Four-Group Analysis (df = 5, 158)	
Pairwise Comparison	F-Value
Blarina—*Peromyscus*	3.50**
Blarina—Random	3.81**
Blarina—No-Capture	4.57***
Peromyscus—Random	1.10
Peromyscus—No-Capture	3.38**
Random—No-Capture	1.34

Three-Group Analysis (df = 29, 82)	
Pairwise Comparison	F-Value
Male *Peromyscus*—Female *Peromyscus*	2.29**
Male *Peromyscus*—*Blarina*	3.21***
Female *Peromyscus*—*Blarina*	2.05**

Two-Group Analysis (df = 5, 120)	
Pairwise Comparison	F-Value
Peromyscus—*Blarina*	3.98**

Table 13. Standardized discriminant function coefficients[1] for those variables that discriminate between groups in the deciduous forest four-group analysis. (* indicates variables of greatest significance on a function.)

Variable	DF-I	DF-II	DF-III
Thickness of Woody Vegetation	.776*	-.045	-.146
Woody Stem Density	.617*	-.179	.222
Fallen Log Dispersion	-.086	.883*	.047
Litter-Soil Compactability	.142	.323*	-.017
Evergreenness of Herb Stratum	.046	.034	.888*

[1]Standardized discriminant function coefficients constitute weighting factors the absolute magnitudes of which are indicative of the significance of the variables on a discriminant function.

Table 14. Blarina, Peromyscus, random, and no-capture group means for those variables that discriminate between groups in the deciduous forest four-group analysis.

Variable	Blarina	Peromyscus	Random	No-Capture
Litter-Soil Compactability	.502	.526	.575	.671
Woody Stem Density	5.571	8.886	9.065	8.889
Fallen Log Dispersion	450.179	469.055	538.871	629.278
Evergreenness of Herb Stratum	.060	.088	.080	.042
Thickness of Woody Vegetation	9.667	11.457	12.290	14.333

relatively thicker understory. Neither species, however, is found in areas with very thick understories. Blarina and Peromyscus are separated quite well from the no-capture group by the second discriminant function, which accounts for 30% of the remaining 31% of the variance. Tables 13 and 14 indicate that ground structure in the form of fallen logs is important for both species. Overall, this analysis reveals the importance of understory vegetation and forest floor surface structure in providing favorable small mammal microhabitats in the deciduous forest.

In order to focus on the microhabitat relations between Peromyscus and Blarina, a two-group discriminant analysis was performed on the data for these species. Figure 7 illustrates the resulting frequency distribution of the species along the single discriminant function. It appears that Blarina occupies a subset of the microhabitat suitable for Peromyscus, although the two centroids apparently are significantly different as indicated by the separation of the Peromyscus and Blarina ellipses (Figure 6) and the significant pairwise F-test (Table 12, Two-Group Analysis). Table 15 permits interpretation of the discriminant function as a gradient from areas having little understory and abundant ground structure to areas having a thicker understory, again with ground structure as indicated by the significant parameters of woody stem density and thickness of woody vegetation. As in the four-group analysis for the deciduous forest, Peromyscus occurs in areas having a thicker understory as compared to Blarina.

A three-group discriminant analysis to investigate differential microhabitat utilization by male and female Peromyscus captured in the

Figure 7. Frequency distribution of the deciduous forest species along discriminant function I from the deciduous forest two-group analysis. Significant variables on the discriminant function are woody stem density, tree stump dispersion, evergreenness of the herb stratum, soil surface exposure, and thickness of the woody vegetation.

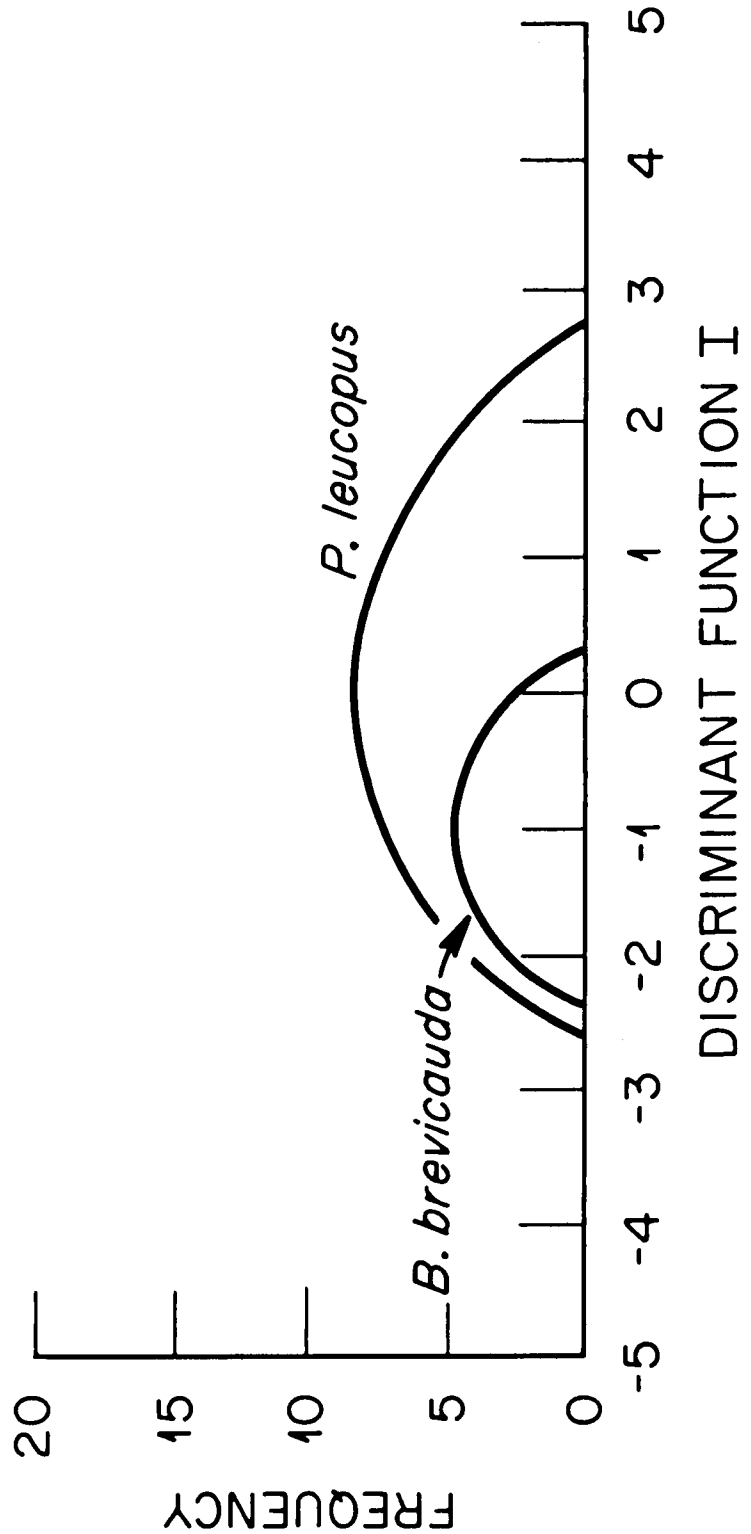

FREQUENCY
20
15
10
5
0
B. brevicauda
P. leucopus
-5
-4
-3
-2
-1
0
1
2
3
4
5
DISCRIMINANT FUNCTION I

Figure 7.

Table 15. *Blarina* and *Peromyscus* group means for those variables that discriminate between groups in the deciduous forest two-group analysis.

Variable	*Blarina*	*Peromyscus*
Woody Stem Density	5.571	8.886
Tree Stump Dispersion	738.262	808.421
Evergreenness of Herb Stratum	.060	.088
Soil Surface Exposure	.023	.011
Thickness of Woody Vegetation	9.667	11.457

deciduous forest yielded the results found in Figure 8 where 95% confidence ellipses are graphed around centroids for Blarina and the Peromyscus sexes. Blarina is segregated from the Peromyscus groups in discriminant space; however, male and female Peromyscus also display microhabitat differences. The separation of the Peromyscus ellipses in discriminant space is further confirmed by the significant pairwise F-test for these sexes (Table 12, Three-Group Analysis, page 50).

The first discriminant function, accounting for 67% of the variance, represents a gradient from thicker herbaceous vegetation and little ground structure to areas with more ground structure and fewer herbs (Tables 16 and 17). The distribution of the groups along this function indicates that male Peromyscus occur in more open areas, as indicated by the high herbaceous stem density and lack of ground structure. Blarina and female Peromyscus occupy areas of more ground structure and fewer herbaceous plants. Discriminant function II, which separates Blarina from both Peromyscus groups, accounts for 33% of the variance and represents a gradient from microhabitat characterized by thin understory and ground structure to areas with thicker understory vegetation and abundant ground structure (Tables 16 and 17).

Relative Habitat Heterogeneity

Table 18 lists the mean standard deviations of the structural variables for all four groups in each habitat. The mean standard deviation of the random group represents an index of heterogeneity for each habitat. When compared, these indices indicate that the cedar glade is more heterogeneous than the deciduous forest. Comparisons of the random

Figure 8. Ninety-five percent confidence ellipses around the group centroids graphed on discriminant functions I and II from the deciduous forest three-group analysis. Significant variables on discriminant function I include herbaceous stem density, litter-soil compactability, herbaceous foliage profile, short herbaceous stem density, and litter-soil depth. Overstory tree dispersion, woody stem density, and thickness of woody vegetation are of greatest significance on discriminant function II.

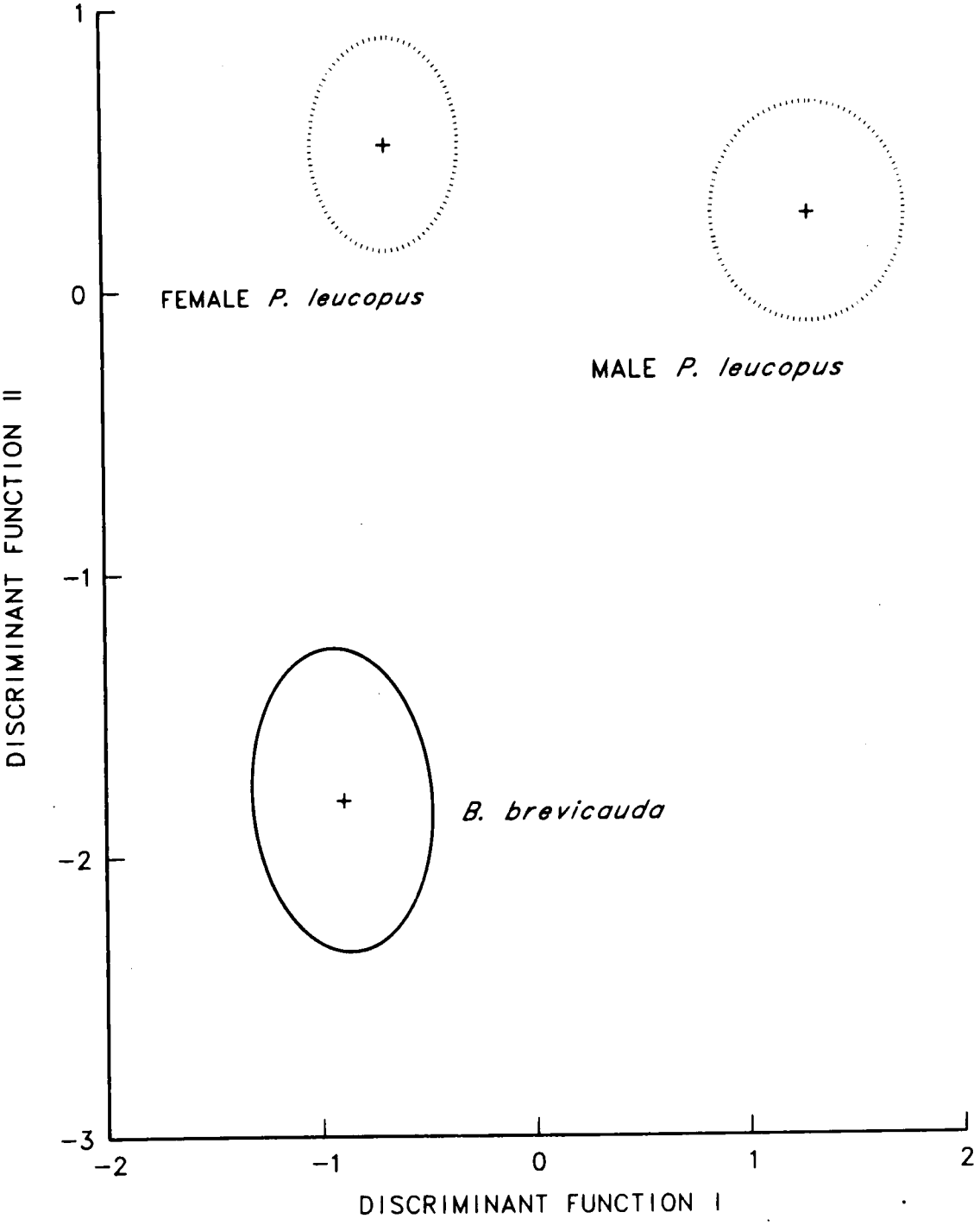

1
0
−1
−2
−3
−2
−1
0
1
2
DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
FEMALE P. leucopus
MALE P. leucopus
B. brevicauda

Figure 8.

Table 16. Standardized discriminant function coefficients[1] for those variables that discriminate between groups in the deciduous forest three-group analysis. (* indicates variables of greatest significance for a function.)

Variable	DF-I	DF-II
Short Herbaceous Stem Density	-4.350*	.054
Herbaceous Stem Density	2.146*	.396
Litter-Soil Compactability	1.784*	.311
Herbaceous Foliage Profile	1.771*	- .053
Litter-Soil Depth	-1.247*	- .283
Overstory Tree Dispersion	- .144	1.004*
Woody Stem Density	- .555	.762*
Thickness of Woody Vegetation	.218	.753*

[1]Standardized discriminant function coefficients constitute weighting factors the absolute value of which are indicative of the significance of the variables on each discriminant function.

Table 17. *Blarina*, male *Peromyscus*, and female *Peromyscus* group means for those variables that discriminate between groups in the deciduous forest three-group analysis.

Variable	*Blarina*	Male *Peromyscus*	Female *Peromyscus*
Litter-Soil Depth	5.530	5.746	5.743
Litter-Soil Compactability	.502	.516	.526
Herbaceous Stem Density	10.905	13.595	12.460
Short Herbaceous Stem Density	10.333	12.762	11.720
Woody Stem Density	5.571	8.024	9.340
Herbaceous Foliage Profile	6.215	7.993	6.869
Overstory Tree Dispersion	302.512	361.250	340.960
Thickness of Woody Vegetation	9.667	10.738	11.700

Table 18. Mean standard deviations[1] for each group in the cedar glade and deciduous forest.

Cedar Glade Group	Mean Standard Deviation
Ochrotomys	70.392
Peromyscus	45.654
Random	57.360
No-Capture	33.762

Deciduous Forest Group	Mean Standard Deviation
Blarina	27.818
Peromyscus	30.771
Random	28.247
No-Capture	25.494

[1]Calculated by averaging the standard deviations of all the variables.

group mean standard deviations with the species and no-capture group mean standard deviations within each habitat yield information about the relative heterogeneity and type of microhabitat occupied by each group. For example, the higher mean standard deviation of Ochrotomys (70.392) as compared to the cedar glade random group (57.360) is probably a result of the edge habitat that this species occupies. The microhabitat generalist nature of deciduous forest Peromyscus is reflected by the small difference in mean standard deviation for this species (30.771) when compared to the deciduous forest random group (28.247). A higher degree of microhabitat specificity is apparent for the cedar glade Peromyscus since the difference between the Peromyscus and cedar glade random group mean standard deviations (45.654 and 57.360 respectively) is quite large.

CHAPTER IV

DISCUSSION

Strong et al. (1979) reviewed the vast literature concerning gradients of body size and coexistence of island bird assemblages and tested ratios of culmen and wing length against random ratios generated by computer from the same data set. Their inability to reject the null hypothesis of no difference between the actual and random data sets led to the conjecture that much of the order described in nature by ecologists is perhaps due to a preconception on the part of the investigator that this order does indeed exist. Although the statistical techniques utilized by these authors are questionable (Hendrickson, manuscript), their idea of testing ecological patterns against the null hypothesis of randomness has merit.

The present study utilizes this same concept by including a random group in the initial discriminant analyses. In each case the random group centroid occurs near the origin of discriminant space and has a high variance on the discriminant function axes as would be predicted for such a data set. By meeting these predictions for the random group, the discriminant analysis appears to be revealing true differences between species-specific microhabitats even though the assumptions of discriminant analysis are not always met and sample sizes are relatively low.

Dueser and Shugart (1978, 1979), in a study of forest floor small mammals, included distinctly different forest types in a single

discriminant analysis. In the present study, the cedar glade and deciduous forest habitats were analyzed separately even though one species, P. leucopus, occurs in both. This presents a more rigorous examination of microhabitat segregation by the species in a particular habitat since the large degree of variance between the species which would be explained by forest type is dispensed with beforehand. This method of analysis also precludes a valid measure of niche breadth as quantified by Dueser and Shugart (1979) since the complete range of patch types occupied by a species is not represented in a single analysis. Calculations of structural niche overlap depend for their validity on the extent of genetic information exchange between the populations of Peromyscus in different habitats. If no migration occurs between habitat types, then niche overlap calculated within each habitat would be reliable. However, should migration occur, through some means such as juvenile dispersal, data from Peromyscus within each habitat should be pooled to calculate niche overlap. Although migration between these two particular study sites is highly unlikely because of their widespread (.75 miles) locations, the ubiquitous nature of Peromyscus makes it probable that genetic exchange does occur between these and more proximal forest habitats. Calculations of structural niche overlap are thus postponed until investigation of interhabitat gene flow in this ubiquitous species resolves the question of whether the structural niche is a property of the population or the species.

The generalist and specialist natures of the species in this study concur with the results of Dueser and Shugart (1978) who also found

Blarina and Ochrotomys to be relative microhabitat specialists and Peromyscus to be a microhabitat generalist. One slight exception is the degree to which Blarina appears to be a specialist in the deciduous forest. In the present study, Blarina does not appear quite as specialized in microhabitat characteristics. This discrepancy may be due to the small sample size of Blarina used by Dueser and Shugart and the inclusion of both deciduous and mixed pine and deciduous forest types in their analysis. A second point brought out by the present study is that Peromyscus is a relative microhabitat generalist even within the different forest types in which the species occurs. The resource exploitation ability of this species is thus apparent and future studies of the role of Peromyscus as a dominant exploitative competitor in small mammal communities may yield much information on animal community structure.

Results of the cedar glade two-group discriminant analysis indicate that Ochrotomys and Peromyscus utilize different and slightly overlapping microhabitats. This pattern could result from competitive exclusion or genetically determined microhabitat preferences on the part of each species. The choice between these alternatives depends on whether one considers competition to have occurred in the past with subsequent evolution of different microhabitat preferences by the two species or whether one considers competition an ongoing phenomenon. As indicated by Brown (1978), most investigations implicate the process of competition in structuring Eastern North American small mammal communities. Multiple regressions of capture frequencies and habitat variables (Dueser and Hallett, in press) predict ongoing competition, however, positive

identification of the reasons for microhabitat segregation by these species must await the results of manipulative experiments.

In contrast with the small overlap of structural niches by Ochrotomys and Peromyscus in the cedar glade, Blarina appears to occupy a subset of Peromyscus microhabitat in the deciduous forest. This overlap immediately suggests niche differences between these two species along some dimension other than space. This hypothesis presently cannot be ruled out. However, indications of an omnivorous diet by Peromyscus (M'Closkey and Fieldwick, 1975 and Burt and Grossenheider, 1976), observations by Nicholson (1941) of the semiarboreal nature of Peromyscus, and the semifossorial nature of Blarina suggest that three-dimensional use of space may allow coexistence of these two species. This could well explain the occurrence of Peromyscus in microhabitats with a heavier understory where arboreal adaptations would be advantageous. Still another explanation for the complete overlap of these species structural niches is that the niche of Blarina is truly included within the niche of Peromyscus. A theoretical treatment of the niche inclusion of a specialist within that of a generalist is found in Case and Gilpin (1975); it requires interference competition on the part of the specialist to maintain a portion of the limiting resources shared with the generalist. This possibility provides an hypothesis for future niche analysis of these two species, especially a comparative analysis of their food habits to delineate whether these species separate along this niche dimension.

The significant separation of the no-capture groups from both small mammal species in the cedar glade and deciduous forest points out the

unsuitable nature of some areas within each habitat for small mammals. It is unlikely that either of these results is due to small sample size because of the robustness of discriminant analysis as shown by analysis of the random groups, the biological interpretability of the discriminant axes for these areas, and the fact that both the cedar glade and deciduous forest habitats contain such areas. Also, no other forest floor small mammals are known to have been captured frequently in these habitat types except the eastern chipmunk, Tamias striatus. This species was characterized by Dueser and Shugart (1978) as a microhabitat generalist and is thus unlikely to fill this specialized microhabitat exclusively. Since no observations have been made of competitive exclusion of deciduous forest small mammals by any other animal taxa within these study areas, it seems most likely that the small mammal species simply avoid these microhabitats due to lack of cover and perhaps greater succeptability to predation. This lack of protection from predators also makes it unlikely that any other small mammals might occupy the microhabitat characterized by the no-capture groups with the possible exception of subterranean species.

Implications for the management of forests to provide favorable small mammal microhabitat are also suggested by the apparent dependence of the animals on forest floor characteristics. Obvious examples are the effects of slash left from logging operations and areas devoid of combustible deadfall around popular campsites in national parks and forests. Perhaps more attention should be given to small mammal management due to the lack of knowledge concerning their roles in ecosystems

(Chew, 1974 and Brown, 1978) and their position near the base of the food chain for many endangered carnivores.

Differential resource utilization by male and female conspecifics through sexual dimorphism is a well documented phenomenon in various taxa (Williamson, 1971 and Feduccia and Slaughter, 1974). Therefore, it seems likely that some means of resource division might occur within small mammal populations to decrease competitive pressure on reproductive females. The deciduous forest analysis indicates that the sexes of Peromyscus differentially use space in the form of microhabitat. Also, females apparently utilize microhabitats that have more abundant ground structure and thus provide greater protection from predators for themselves and their offspring. This result could conceivably be due to occupation of larger home ranges by breeding males and their traversing more microhabitat types. However, this explanation seems unlikely because the centroid of the males is further from the origin of discriminant space than that of the females (Table 11, Deciduous Forest Analysis, page 44), indicating that males are more microhabitat specialists than females. The exact mechanism by which the sexes segregate into different microhabitats can only be postulated. Due to obvious genetic similarities between conspecifics of the same population, though, intersexual aggression is perhaps the most feasible explanation. Garten (1976) found that female P. polionotus of larger body size are dominant over males of the same species. Bowers and Smith (1979) also suggest female dominance by larger body size to be the mechanism that enables female P. maniculatus to occupy more favorable habitats at the expense of male conspecifics. In

this study, the average body weights of the deciduous forest Peromyscus sexes were not significantly different ($t = .067$, $df = 21$, $P > .05$). This fact does not rule out female dominance, however, as factors other than body size may bear on this intraspecific relationship. Also, since the females occupy more favorable microhabitats and the female centroid is located closer to the origin of discriminant space, it thus appears that most of the habitat sampled is favorable for this species. Therefore, since prime microhabitat does not appear to be overly limiting in this habitat, there need not be a strong selective force for females of larger body size.

The average weights of male and female Peromyscus captured in the cedar glade are also not significantly different ($t = 1.54$, $df = 14$, $P > .05$) and the sexes are interpreted to display no differential microhabitat use in the cedar glade. This evidence appears to contradict the theory that relatively heterogeneous habitats offer an advantage in resource use to females and differential use of space by the sexes may occur (Bowers and Smith, 1979). However, Bowers and Smith (1979) do not address the role of interspecific competition in intraspecific microhabitat partitioning. Although the cedar glade is more heterogeneous than the deciduous forest, Peromyscus seems limited to existence in only a portion of the habitat by interspecific competition with Ochrotomys. As indicated by the lower mean standard deviation of the microhabitat variables for Peromyscus as compared with the random group (Table 18, Cedar Glade Section, page 62), this portion of the microhabitat is relatively homogeneous and thus allows the Peromyscus females no energetic advantage in maintaining microhabitats segregated from the males.

The apparent pattern that emerges is that intraspecific competition may lead to differential microhabitat use by the sexes of a species that occurs in heterogeneous habitats. Interspecific competition, however, may act to restrict that species to more homogeneous portions of a heterogeneous habitat, thus decreasing the ability of the species to partition space intraspecifically. This, in turn, may limit the biotic potential of that species by prohibiting females from occupying relatively more favorable microhabitats. Interspecific competition may thus have a double payoff for some species by not only limiting access to resources by a competing species, but also by indirectly interrupting the social system of the competing species. If intraspecific habitat partitioning is important for a small mammal species to maintain a high biotic potential, then habitat specificity (if synonomous with habitat homogeneity) for that species should be selected against and genes promoting competitive tendencies and maintaining competitive ability should be preserved. Perhaps, therefore, coevolution of a community of species does not always procede to decrease competition. It is significant that intraspecific microhabitat partitioning by small mammals was first noted in two of the most widespread small mammal species in North America, P. maniculatus (Bowers and Smith, 1979) and P. leucopus. Both of these ubiquitous species occupy a broad spectrum of microhabitats and the above argument may explain why these regionally sympatric species are seldom locally sympatric.

Should differential microhabitat preferences by the sexes become fixed in the genome of a species with males actually preferring the less

hospitable microhabitats, then intraspecific competition and resource partitioning may serve as a basis for the evolution of kin selection. Behaviorally, males would be allowing nearby, probably closely related females to occupy more favorable microhabitats and by this pseudo-altruistic act (Pianka, 1978) be allowing related individuals to increase their reproductive output. Should the end result of genetically programmed male subordinance be kin selection within a breeding unit or deme which bestows that deme with demographic characteristics allowing greater exploitative competitive ability than other demes within the same population, then that deme with the pseudo-altruistic trait would have a selective advantage. Thus, group selection may be derived from a hierarchy of individual and kin selection which eventually leads to interdemic selection. The original pseudo-altruistic trait may enter this scheme as a result of individual selection which acts to reduce intraspecific competition. It is not difficult to visualize pseudo-altruism giving a selective advantage to any male dispersing to another deme without this trait since that male would only have to compete with nonaltruistic males already out-competed by dominant females. Also, barring catastrophic events, any demes with this trait should numerically overwhelm demes lacking pseudo-altruistic behavior. Therefore, interdemic selection of this nature must either be a terminal phenomenon or some force must select against the pseudo-altruistic trait. Population crashes by over-use of resources with subsequent recolonization by individuals occupying proximal habitats may occur and the sequences begin anew. Another possibility is that predation on pseudo-altruistic males

in suboptimal microhabitats or on dispersing males may keep the level of this behavior low and be analogous to the high extinction rates prominently mentioned in the writings of E. O. Wilson (1975) and Boorman and Levitt (1972).

An important question not addressed yet is why should a population undergoing intraspecific competition display female dominance which distributes females into more favorable microhabitats and thus probably increases reproductive output? Such a social system could evolve only if the end result were more efficient resource utilization at the expense of competing species. The commonly high population densities of Peromyscus in eastern deciduous forests as compared to other forest habitats indicate the ability of this species to thrive at high densities. With a social system that maintains these high densities in the forest, the interspecific, exploitative, competitive ability of this species is increased. This strong competitive ability on the part of Peromyscus may prevent invasion of these deciduous forests by other ecologically similar species, thus giving Peromyscus nearly exclusive use of the resources available to small rodents. The microhabitat generalist nature of Peromyscus, along with the omnivorous diet of this species, make it ideal for the role of a dominant, exploitative competitor. This increased resource utilization may not only explain the adaptive value to Peromyscus of maintaining a high reproductive output even at high population densities but also the extremely low diversity of rodents in eastern deciduous forests. Finally, the relatively homogeneous nature of desert ecosystems may preclude intraspecific microhabitat partitioning (Bowers

and Smith, 1979). If this is the case, then the present high diversity of rodent species in North American deserts may be partially explained by the inability of any of the species to effectively partition the homogeneous habitat intraspecifically. Subsequently, over evolutionary time, these communities have apparently coevolved to allow coexistence of many closely related species by gradients of body size and interspecific microhabitat partitioning. The theory of species packing may therefore need to be expanded to include aspects of the social systems of the species. In light of the differential use of space by deciduous forest small mammal species, the apparent absence of animals from portions of the available space, and the postulation that Peromyscus sexes utilize different microhabitats to maintain high reproductive output and competitive ability, it appears that these species are packed tightly and that the eastern deciduous forest is not depauperate in small mammal fauna relative to the resources it provides for the species.

LIST OF REFERENCES

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Boorman, S. A. and P. R. Levitt. 1972. Group selection on the boundary of a stable population. Proceedings of the National Academy of Sciences 69: 2711-2713.

Bowers, M. A. and H. D. Smith. 1979. Differential habitat utilization by sexes of the deer mouse, Peromyscus maniculatus. Ecology 60: 869-875.

Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology 54: 775-787.

Brown, J. H. 1978. Effects of mammalian competitors on the ecology and evolution of communities, p. 52-57. In D. P. Snyder, ed. Populations of small mammals under natural conditions, Pymatuning Symposia in Ecology, Vol. 5, University of Pittsburg, Pittsburg. 237p.

Brown, J. H. and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196: 880-882.

Brown, J. H. and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology 54: 788-797.

Burt, W. H. and R. P. Grossenheider. 1976. A Field Guide to the Mammals. 3rd ed., Houghton Mifflin Co., Boston. 289p.

Case, T. J. and M. E. Gilpin. 1975. Interference competition and niche theory. Proceedings of the National Academy of Sciences 71: 3073-3077.

Chew, R. M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio Journal of Science 74: 359-370.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. American Naturalist 102: 107-147.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Colwell, R. K. and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6: 281-310.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle, Chthalamus stellatus. Ecology 42: 710-723.

Cooley, W. W. and P. R. Lohnes. 1962. Multivariate Data Analysis. Wiley, New York. 364p.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389.

Dixon, W. J. and M. G. Brown, eds. 1977. Biomedical Computer Programs, P Series. University of California Press, Berkeley. 880p.

Dueser, R. D. and J. G. Hallett. 1980. Competition and habitat selection in a forest-floor small mammal fauna. Oikos (in press).

Dueser, R. D. and H. H. Shugart. 1978. Microhabitats in a forest-floor small-mammal fauna. Ecology 59: 89-98.

Dueser, R. D. and H. H. Shugart. 1979. Niche pattern in a forest-floor small-mammal fauna. Ecology 60: 108-118.

Dueser, R. D., H. H. Shugart, and J. C. Randolph. 1976. Structural niches in a forest floor small mammal community. ORNL/TM-5004. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Dunaway, P. B. 1955. Late fall home ranges of three golden mice, Peromyscus nuttalli. Journal of Mammalogy 36: 292-298.

Elton, C. S. 1927. Animal Ecology. Sidgwick and Jackson, London. 207p.

Feduccia, A. and B. H. Slaughter. 1974. Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. Evolution 28: 164-168.

Garten, C. T. 1976. Relationship between aggressive behavior and genic heterozygosity in the oldfield mouse, Peromyscus polionotus. Evolution 30: 59-72.

Gause, G. F. 1934. The Struggle for Existence. Reprinted., Hafner, New York, 1964. 163p.

Getz, L. L. 1961. Notes on the local distribution of Peromyscus leucopus and Zapus hudsonicus. American Midland Naturalist 65: 486-500.

Grant, P. R. 1972. Interspecific competition among rodents. Annual Review of Ecology and Systematics 3: 79-106.

Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of Central Canada. Ecology 52: 543-556.

Grinnell, J. 1917. The niche relationship of the California Thrasher. Auk 21: 364-382.

Grinnell, J. 1924. Geography and evolution. Ecology 5: 225-229.

Hairston, N. G. 1980. Species packing in the salamander genus Desmognathus: what are the interspecific interactions involved? American Naturalist 115: 354-366.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88: 61-74.

Holbrook, S. J. 1979. Habitat utilization, competitive interactions, and coexistence of three species of cricetine rodents in East-Central Arizona. Ecology 60: 758-769.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium in Quantitative Biology 22: 578-769.

Iverson, S. L., R. W. Sealbloom, and J. M. Hnatiuk. 1967. Small mammal distributions across the prairie-forest transition of Minnesota and North Dakota. American Midland Naturalist 78: 188-197.

Koplin, J. R. and R. S. Hoffmann. 1968. Habitat overlap and competitive exclusion in voles (Microtus). American Midland Naturalist 80: 494-507.

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton. 120p.

Linzey, A. V. and D. W. Linzey. 1971. Mammals of the Great Smoky Mountains National Park. University of Tennessee Press, Knoxville. 114p.

Linzey, D. W. 1968. An ecological study of the golden mouse, Ochrotomys nuttalli, in the Great Smoky Mountains National Park. American Midland Naturalist 79: 320-345.

Maguire, B. 1967. A partial analysis of the niche. American Naturalist 101: 515-523.

M'Closkey, R. T. 1976. Community structure in sympatric rodents. Ecology 57: 728-739.

M'Closkey, R. T. and B. Fieldwick. 1975. Ecological separation of sympatric rodents (Peromyscus and Microtus). Journal of Mammalogy 56: 119-129.

M'Closkey, R. T. and D. T. Lajoie. 1975. Determinants of local distribution and abundance in white-footed mice. Ecology 56: 467-472.

Miller, R. S. 1967. Pattern and process in competition. Advances in Ecological Research 4: 1-74.

Morris, F. F. 1955. Population studies of some small forest mammals in Eastern Canada. Journal of Mammalogy 36: 21-35.

Nicholson, A. J. 1941. The homes and social habits of the woodmouse (Peromyscus leucopus noveboracensis) in Southern Michigan. American Midland Naturalist 25: 196-223.

Nie, N. H. et al. 1975. Statistical Package for the Social Sciences. 2nd ed., McGraw-Hill, New York. 675p.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100: 65-75.

Pearson, P. G. 1959. Small mammals and old field succession on the piedmont of New Jersey. Ecology 40: 249-255.

Petraitis, P. S. 1979. Likelihood measures of niche breadth and overlap. Ecology 60: 703-710.

Pianka, E. R. 1972. r and K selection or b and d selection? American Naturalist 106: 581-588.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

Pianka, E. R. 1978. Evolutionary Ecology. 2nd ed., Harper and Row, New York. 397p.

Pielou, E. C. 1972. Niche width and niche overlap: a method for measuring them. Ecology 53: 687-692.

Price, M. V. 1978. The role of microhabitat in structuring desert rodent communities. Ecology 59: 910-921.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54: 111-117.

Rosenzweig, M. L. 1974. On the evolution of habitat selection, p. 401-404. In Proceedings of the First International Congress of Ecology. Structure, functioning, and management of ecosystems. Centre for Agricultural Publishing and Documentation, Waginingen, The Netherlands. 414p.

Rosenzweig, M. L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitat and environment complexity. Ecology 50: 558-572.

Schoener, T. W. 1975. Resource partitioning in ecological communities. Science 185: 27-39.

Sheppe, W. 1961. Systematic and ecological relations of Peromyscus oreas and P. maniculatus. Proceedings of the American Philosophical Society 105: 421-446.

Shugart, H. H. and B. C. Patten. 1972. Niche quantification and the concept of niche pattern, p. 284-327. In B. C. Patten, ed. Systems Analysis and Simulation in Ecology, Vol. 2, Academic Press, New York. 592p.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman Co., San Francisco. 776p.

Strong, D. R., L. A. Szyska, and D. S. Simberloff. 1979. Tests of community-wide character displacement against null hypotheses. Evolution 33: 897-913.

Tatsuoka, M. M. 1971. Multivariate Analysis. John Wiley and Sons, New York. 310p.

Vandermeer, J. H. 1972. Niche theory. Annual Review of Ecology and Systematics 3: 107-132.

Williamson, P. 1971. Feeding ecology of the red-eyed vireo (Vireo olivaceus) and associated foliage-gleaning birds. Ecological Monographs 41: 129-152.

Wilson, E. O. 1975. Sociobiology. Belknap Press, Cambridge, Massachusets. 697p.

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