Ecological Niche Responses Of Small Mammals To Gypsy Moth Disturbance

by

David Christian Tomblin

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Master of Science

in

Biology

Approved:

Jack A. Cranford, Chairman

Jackson R. Webster

Eric P. Smith

May, 1994

Blacksburg, Virginia

Ecological Niche Responses Of Small Mammals To Gypsy Moth Disturbance

by

David Christian Tomblin

Committee Chairman: Jack A. Cranford

Zoology

(ABSTRACT)

The objective of this study was to determine differences in small mammal assemblage structure and population dynamics among four oak dominated sites at four different stages of gypsy moth disturbance: a high tree mortality site, a disturbance in process site, a disturbance recovery site, and an undisturbed reference site. More specifically, the study was designed to identify changes in habitat structure that would influence small mammal microdistributions and determine the quality of habitat created by gypsy moth herbivory using demographic structure of *Peromyscus* populations as an indicator of habitat quality.

Peromyscus leucopus, Peromyscus maniculatus, the Soricids, and *Clethrionomys gapperi* had greater abundances at the disturbed sites relative to the reference site. Gypsy moth disturbance increased the abundance of small mammals

and the number of coexisting species within a given area, which was attributed to several changes in habitat structure. The disturbed sites were characterized as having more fallen logs and standing dead snags, greater shrub and herbaceous cover, and higher invertebrate abundances relative to the reference site. These changes in habitat structure provided small mammals with increased cover from avian predators, more food resources, and potential nesting cavities.

P. leucopus populations at the high mortality site exhibited greater demographic stability than the reference site populations. This was marked by higher proportions of females, smaller density fluctuations, more fall recruitment of young, higher residency, and lower proportions of males. Strong evidence for density-dependent population regulation was observed for *P. leucopus* populations at the high mortality site and the *P. maniculatus* population at the recovery site. At high densities these populations exhibited extensive intraspecific microhabitat segregation. Female adults segregated from juveniles and male adults into more optimal microhabitats. Male adult microhabitat use significantly differed from male juvenile microhabitat use. The exclusion of young mice from optimal microhabitats by adults may be a mechanism by which adults limit over-exploitation of resources by subordinate members of the

population at high densities. The results of this study suggest that gypsy moth disturbance of areas dominated by chestnut oaks at least temporarily improves habitat quality for small mammals.

Acknowledgements

I would like to thank my committee members, Dr. Jack A. Cranford, Dr. Jackson R. Webster, and Dr. Eric P. Smith, for their constructive criticisms and insightful comments about my research. Dr. Jack Cranford extensively helped me with my writing skills and critical reviewing of the literature. Dr. Jackson R. Webster supplied me with endless amounts of computer money and asked many insightful questions at my committee meetings. Dr. Eric P. Smith gave helpful comments on statistical analysis of my data. Norman Brach, Jason Walker, Elizabeth Folis, and Erica Serabian provided exceptional assistance in the field and lab. Further, I would like to thank my most consistent field assistant, Josh, for his companionship. I would like to thank my parents, Robert and Pamela Tomblin, for providing a research vehicle and moral support. I would like to thank John Hutchens and Terry Ehrman for saving me when the Jeep broke down (actual mechanical problems will not be discussed). Walter Lee Daniels from the Soils Department provided the soil penetrometer for my soil compactibility analysis. Andy Roberts from the Department of Entomology provided gypsy moth egg mass and male moth data. James Hunt, Gary Peery, and Theresa Chittum of the George Washington National

Forest, Pedlar District provided logistical help in locating my sites, weather data, and use of national forest land. Funding for this research was provided by a Sigma Xi grant, a Virginia Academy of Science grant, the Biology Department of Virginia Polytechnical Institute and State University, and the Virginia Museum of Natural History.

Table of Contents

(Table of Contents Continued)

Thesis Introduction

Ecosystems are subject to disturbances at many different scales. Fires, tornadoes, hurricanes, animal movements, and herbivory are all disturbances that can create a mosaic of different sized habitat patches within an ecosystem. When large enough new habitat patches are created by a disturbance, the organisms within those patches have to either adapt or locally go extinct. Small mammals have been extensively investigated from the disturbance point of view; especially man induced disturbances such as clearcutting (e.g., Kirkland, 1990). Results from these studies often indicate increases in abundance and diversity of small mammals (Kirkland, 1990), but these increases are not interpreted as increases in habitat quality. Clearcuts are usually characterized as low quality habitat and serve as dispersal sinks for subordinate members of populations from undisturbed adjacent forest (Sullivan, 1979, Van Horne, 1983, Linzey, 1989). Another disturbance to forests that could potentially have important ecological consequences to small mammals is gypsy moth (*Lymantria dispar*) herbivory.

Gypsy moths were introduced in Medford, Massachusetts, in 1869. Since then gypsy moth populations have been a major

destructive force in eastern forests through extensive defoliation, which can eventually result in tree death (Campbell and Sloan, 1977a). Annual areas of defoliation can reach as much as 5 million hectares, and recent attempts to keep gypsy moth populations in check have been mostly unsuccessful (Grace, 1986).

Permanent alterations to forests by gypsy moth herbivory usually takes at least two years of heavy defoliation. After one year of heavy defoliation, the existing understory is enhanced due to increased light intensity, increased levels of soil moisture, and decreased leaf litter depth (Collins, 1961, Grace, 1986, Mconnell, 1988). If heavy defoliation occurs in successive years, tree mortality ensues and the understory becomes even more complex and dense (Campbell and Sloan, 1977a, Hix et al., 1991). Defoliation and the subsequent mortality of trees causes dramatic changes in the forest floor environment and plant assemblage structure. These changes should affect small mammal assemblage structure and population dynamics.

Gypsy moth defoliation alters habitat structure and resources available (i.e. mast crop, McConnell, 1988, Gottschalk, 1989) to small mammal populations thus altering small mammal assemblage structure, demography, and

population dynamics. If the habitat becomes more heterogeneous, thus making resources patchy, a small mammal population may respond by segregating by sex or age class (Morris, 1984a, Seagle, 1985, Adler and Wilson, 1987, Adler, 1987). Within a community, the number of species able to coexist (Kirkland, 1990, Chesson and Rosenzweig, 1991), small mammal population densities and demographics (Adler and Wilson, 1987, Adler, 1987), niche characteristics (Dueser and Shugart, 1979, Seagle et al., 1984), vulnerability to predation (Kotler, 1984), and the intensity of interspecific and intraspecific competition (Schoener, 1983, Chesson and Rosenzweig, 1991) have been shown to be altered by changes in resource availability. For example, interspecific competition may increase due to reduction in available resources producing a higher rate of interaction between species. Intraspecific competition may decrease because of reduced spatial limitations within a given area due to decreased population density. Different species will increase or decrease in numbers depending on how the gypsy moth affects their preferred resources and the resources of potential competitors.

This study focused on changes of available habitat to small mammal populations and the alteration of small mammal

assemblages and population structure as a consequence of gypsy moth disturbance. Chapter 1 focuses on changes in small mammal assemblages. Species niche characteristics, microhabitat use, and temporal changes of interactions between species were measured from habitats prior, during, and after disturbance. Chapter 2 presents detailed demographic changes in populations of *Peromyscus leucopus noveboracensis* (white-footed mouse) and *Peromyscus maniculatus nubiterrae* (cloudland deermouse) and relates these changes to quality of habitat resulting from gypsy moth disturbance.

Chapter 1

Niche Characteristics, Microhabitat Use, and Interactions within Small Mammal Assemblages affected by Gypsy Moth Disturbance

Through evolutionary time, organisms have been constantly subject to abiotic and biotic disturbances that either temporarily or permanently alter their habitat. If an organism's habitat is drastically changed, it either has to adapt or locally go extinct. After disturbance, small mammal assemblages exhibit species turnover as habitats change through successional time (Pearson, 1959, M'Closkey, 1975, Swihart and Slade, 1990, Fox, 1990). In order to facilitate this turnover, there must be intrinsic (density-dependent population regulation) and extrinsic (competition, predation, environmental factors) mechanisms operating on different species as habitats change. A change in habitat structure due to disturbance may negatively or positively affect a species depending upon how that change affects the species' food resources, potential competitors, susceptibility to predation, exposure to environmental extremes, and behavioral attributes that limit population size.

The effects of disturbances on small mammal

assemblage structure have been evaluated for fire (Ahlgren, 1966, Krefting and Ahlgren, 1974, Fox, 1990), strip mining (Sly, 1976, Kirkland, 1976), habitat alterations due to agricultural practices (Geier and Best, 1980), silviculture (reviewed by Kirkland, 1990), and tornado blowdowns (Powell and Brooks, 1981). In all these studies, small mammal assemblage structure was altered. Further, early successional stages after disturbance had higher small mammal species diversity and abundances relative to the predisturbed habitats (except for strip mining).

Microhabitat structure is an important factor in determining the distribution of small mammal species (e.g. Dueser and Shugart, 1978 and 1979, Dueser and Hallet, 1980, Vickery, 1981, Kithcings and Levy, 1981, Seagle et al., 1984). Several studies have reported differences in microhabitat use by different species of small mammals at different magnitudes of disturbance and different successional points after disturbance. Yahner (1986) found differences in small mammal microhabitat use between even-aged stands of mixed oak and aspen in Pennsylvania. Morris (1984b) compared small mammal microhabitat use within six macrohabitats in Alberta and Ontario, Canada, (including clearcut and transitional forests) and demonstrated differential microhabitat use that was dependent upon

macrohabitat type. Differential responses to opening sizes in the canopy by *P. maniculatus* and *P. leucopus* populations were demonstrated by Buckner and Shure (1985) in southern Appalachian forests. *P. maniculatus* densities were greatest in habitats with large canopy openings, but *P. maniculatus* were not present in habitat with small canopy openings. *P. leucopus* densities were highest within small canopy openings, but still had higher densities within large canopy openings relative to undisturbed forest habitat. These trends were attributed to greater shrub cover within openings relative to undisturbed forest habitat. The increased cover in the largest openings provided protection from predators and a more complex habitat which enabled the coexistence of the two *Peromyscus* species (Buckner and Shure, 1985). In an old field community on Butt Mountain, Virginia, a high diversity of small mammal species was found, and this was attributed to previous clearcutting and periodic clearing of land by fire (Cranford and Maly, 1986). It is clear from these studies that disturbance alters small mammal assemblage structure, population dynamics, and microhabitat use.

Microhabitat characteristics of small mammals in habitats of different susceptibilities to gypsy moth defoliation were evaluated by Yahner and Smith (1991). They

reported that habitats with high densities of small mammals had low susceptibility to defoliation and that habitats of high susceptibility to defoliation had lower densities of small mammals. The present study focused on habitats that have the potential for extensive defoliation and habitats that have been disturbed by gypsy moth defoliation in order to discern the impact gypsy moth disturbance has on small mammal assemblages.

The objective of this study was to compare differences in small mammal assemblage structure within four oak dominated sites at four different stages of gypsy moth disturbance: a high tree mortality site in which most of the trees have been dead for at least two years, a disturbance in process site where gypsy moths have been at high densities for two years, a recovery site where gypsy moths had an impact in the first year of the study but not in the second year, and an undisturbed reference site with comparable tree species composition to predisturbed tree species composition at the disturbed sites. The four sites were evaluated to discern if there were significant changes in small mammal assemblage structure due to gypsy moth defoliation. Four characteristics of small mammal assemblages were assayed at all sites: 1) species diversity and richness, 2) species specific microhabitat use, 3) niche

overlap between species and niche breadth of each species, and 4) seasonal changes of microhabitat use and niche characteristics.

Chapter 1

Study Methods

Site Selection - There is extensive variation in the susceptibility of tree stands to gypsy moth defoliation. There are several factors that influence a forest stands susceptibility to defoliation. The most important factor is the species composition of overstory trees, which is generally dependent upon topographical factors such as aspect and slope (Houston, 1981). In addition, the distribution and abundance of egg mass, larva, pupa, and moth predators may have an impact on a gypsy moth population's ability to extensively defoliate a stand of trees (Houston, 1981, Smith, 1985). The palatability of oak species to gypsy moths (Brown et al., 1979) and the relatively stressful xeric conditions on ridge tops and southwesterly facing slopes where oaks generally grow, make oak communities the most susceptible to extensive gypsy moth damage (Houston, 1981). Variation due to the above factors was limited by establishing all sites in areas that are now, or were prior to extensive defoliation, predominately composed of chestnut oak (*Quercus prinus*) and had southwesterly facing slopes at elevations between 850 and 1000 meters. The narrow elevation gradient was needed

because elevation can affect small mammal assemblage structure and densities.

Study Area - In the Pedlar District of George Washington National Forest, four sites at different stages of gypsy moth disturbance were established in the summer of 1992: a high tree mortality site in which most trees had been dead for at least two years, a defoliation in process site where gypsy moths had been at high densities for two years, a recovery site where gypsy moths had an impact in the first year but not in the second year, and an undisturbed site (reference).

The high mortality site was located in Nelson County, Virginia, (37° 52'N, 79° 00'W) at an elevation of 895 meters on a southwest facing slope. Gypsy moth egg mass densities in 1991 for the general area were 780 per hectare (egg mass data from the USFS APIM project). The understory was dominated by mountain laurel *(Kalmia latifolia)*, azaleas (*Rhododendron* spp.), black gum saplings (*Nyssa sylvatica)*, and blueberry shrubs (*Vaccinium* spp.).

The in process site, also in Nelson County (37° 50'N, 79° 07'W), was at an elevation of 990 meters and faces west. Gypsy moth egg mass densities in 1991 for the general area were 7440 per hectare. During the second year of the study

(1993), it was decided that this site should be divided into two sites due to significantly different responses of small mammals and the trees to gypsy moth defoliation. In the second year of the study one of the two grids was not impacted as extensively as it was in the prior year. This resulted in one grid being much more highly disturbed than the other. The least disturbed grid is now referred to as the recovery site.

The in process site understory was dominated by red maple saplings (*Acer rubrum),* chestnut and red oak seedlings and saplings (*Quercus prinus, Quercus rubra*), common aster (*Aster divaricatus*), golden rod (*Solidago* spp.), grass (*Poa* spp.), and blueberry shrubs (*Vaccinium* spp.). The recovery site had an overstory dominated by red oaks (*Q. rubra*) and pignut hickory (*Carya galabra*) and an understory dominated by striped maple (*Acer pennsylvanicum*) and variety of fern species.

The reference site was located in Rockbridge County (37° 18'N, 79° 18'W) at an elevation of 850 meters on a southwest facing slope. Gypsy moth densities in 1991 for the general area were zero per hectare. Gypsy moths were detected for the first time at this site at very low densities in 1993. In late summer caterpillars were found on the boles of trees, but there was no detectable defoliation

of the canopy. The understory was dominated by mountain laurels, chestnut oak seedlings and saplings, american chestnut saplings *(Castanea dentata)*, and blueberry shrubs.

Sampling Procedures - Small mammal trapping occurred at all sites in August and November 1992, and January, April, August, September, and November 1993. Supplemental trapping was conducted at the in process and recovery sites in June and July 1993 to study the small mammal populations at those sites in more detail. Two 90 by 90 meter grids were established at each study site. Each grid had 81 trap stations at which two Sherman live traps (1 large and 1 small) and one pitfall trap were used during census periods. Because of low densities in the second year, only one Sherman trap (large) was used at each trap station after April 1993. The live capture pitfall traps were constructed out of 2-liter plastic soda bottles with a diameter of 9.5 cm. The tops were cut off so that the pitfall would be 18 cm deep and holes were poked in the bottom to allow water drainage. The cut-off tops were used to close the pitfalls between trapping periods.

Traps were baited with crimped oats mixed with peanut butter (50 lbs of crimped oats were mixed with 18 ounces of peanut butter). During fall and winter trapping periods,

each trap was provided with a plastic zip-lock bag containing cotton and a couple grams of Crisco shortening. Traps were placed within a 1 meter radius of each trap station. Trapping periods lasted four days and nights. Traps were checked in the morning and evening and upon capture, each individual was identified to species, then data on body mass, age (adult, subadult, and juvenile; determined by pelage characteristics), sex, tail and body length, and reproductive condition (male testes: scrotal or non-scrotal; female: perforate or nonperforate, lactating, pregnant) were recorded. All individuals were ear tagged with serially numbered ear tags for later identification except shrews, which were uniquely toe clipped. Small mammal abundances are reported as number of individuals per hectare for each species.

Microhabitat Analysis - Microhabitat use by small mammals was measured by procedures developed by Dueser and Shugart (1978). These methods have been useful in many studies that characterize microhabitat use by small mammals (e.g. Geier and Best, 1980, Kitchings and Levy, 1981, Seagle et al., 1984, Seagle, 1985, Buckner and Shure, 1985, Yahner and Smith, 1991). Three independent sampling units were centered around each trap station; a 1.0 m^2 ring, two perpendicular

20 m^2 transects (1 meter wide), and a 14 meter radius circular plot (Fig. 1). The point quarter method was used at 25 random trap stations to determine the relative densities of tree species at each of the sites (Cottam and Curtis, 1956). Each trap station was characterized by 33 microhabitat variables that were thought to influence the distribution of small mammals (Table 1). Variables that seasonally vary (litter depth, herbaceous stem density, herbaceous profile, soil exposure, canopy cover, plant species richness) were measured again in the winter and in the second year of the study.

Statistical Analysis - Species diversity of small mammals and plants at each site was calculated with Hill's number which is the antilog of the Shannon-Weiner diversity index (Ludwig and Reynolds, 1988). Hill's number is a preferable measure of diversity because it weights species by their abundance thus putting less weight on rare species (Ludwig and Reynolds, 1988). Evenness of small mammal species at each site was calculated with the modified Hill's ratio. This evenness measure is preferred over others because it is unaffected by the number of species in the sample (Ludwig and Reynolds, 1988). Total number of small mammal individuals caught for each species by site was used to

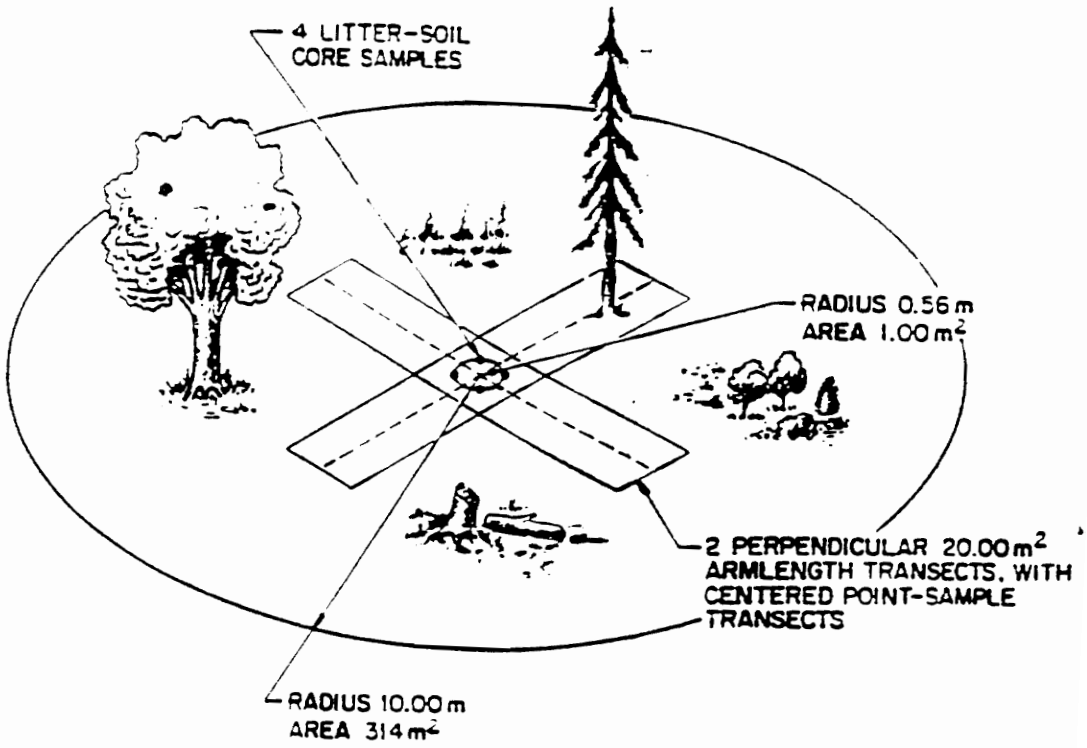


FIG. 1. Habitat variable sampling configuration.

Table 1 - A description of each microhabitat variable measured at each trap station. Abbreviations used to represent variables in other figures and tables are presented in parentheses. Variables with asterisks were measured both in the summer and fall.

Variable	Description
1) Percent Canopy Cover (CC)	Percentage of points with overstory vegetation from 20 vertical ocular tube sightings along the center lines of 2 perpendicular 20 m^2 transects centered on the trap. An ocular tube consists of a 11 cm long plastic pipe with a 4 cm diameter opening in which two cross threads that intersect at right angles are attached. A weight is attached to the center of the cross threads to aid in sighting straight up into the canopy. Presence or absence of canopy is determined by whether or not canopy leaves cover the intersection of the cross threads (James and Shugart, 1970).
2) Stem Densities at Breast Height (SDBH)	A measure of thickness of shrub canopy woody stems. Average number of contacts of woody vegetation at 1.5 m height along the 2 perpendicular transects centered on the trap station.
3) Shrub Cover (SC)	Percentage of points with shrub cover at 1 meter intervals along perpendicular transects centered on the trap station.
4) Overstory Tree Distance (TRD)	Distance (meters) from trap station to nearest overstory tree (DBH > 7.5 cm).
5) Overstory Tree Size (TRS)	Diameter at breast height (cm) of nearest overstory tree.
6) Understory Tree Distance (SAPD)	Same as (4); distance to nearest understory tree.

7) Woody Stem Density (WD)	Live woody stem count at ground level within a 1.0 m^2 ring centered on the trap station.
8) Short Woody Stem Density (SWD)	Same as (7) excluding stems > 0.4 meters tall.
9) Woody Profile Density (WP)	Average of counts of live woody contacts with a 0.8 cm plastic pipe rotated 360 degrees, representing a 1 m^2 ring centered on the trap station and parallel to the ground, at heights of 0.05, 0.1, 0.2. 0.4, 0.8, 1.0, 1.4, 1.8, and 2.0 meters above ground level.
10) Number of Woody Species (WS)	Number of woody species counted within a 1 m^2 ring centered on the trap station.
11) Herbaceous Stem Density (HD)*	Same as (7); herbaceous stem counts at ground level.
12) Short Herbaceous Stem Density (SHD)*	Same as (8) excluding herbaceous stems > 0.4 m tall.
13) Herbaceous Profile Density (HP)*	Same as (9) for herbaceous stem counts.
14) Number of Herbaceous Species (HS)*	Same as (10) for number of herbaceous species.
15) Evergreeness of Overstory (ECC)	Same as (1); percentage of points evergreen canopy cover.
16) Evergreeness of Shrubs (ESC)	Same as (3); percentage of points with evergreen shrub cover.
17) Evergreeness of Herb Stratum (EHC)	Percentage of points with evergreen herbaceous vegetation from 20 samples along the center lines of 2 perpendicular transects centered on the trap station.
18) Tree Stump Size (STUS)	Diameter (cm) of the nearest stump > 7.5 cm in diameter from the trap station.

19) Tree Stump Distance (STUD)	Distance (m) to the nearest stump > 7.5 cm in diameter from the trap station.
20) Log Size (LOGS)	Same as (18); diameter of nearest log.
21) Log Distance (LOGD)	Same as (19); distance to nearest log.
22) Litter Depth (LD)*	Depth of leaf litter layer (cm) as determined by a hand held ruler. The 1 m^2 ring was divided into four quarters and a sample was taken from each of those quarters. Litter depth at a trap station was the average of those four samples.
23) Soil Compactibility (SCOM)	Resistance of soil to a hand held soil penetrometer in pounds per square inch. The penetrometer was held perpendicular to the ground and pressed with equal pressure at four points around each trap station. Location of the four samples was determined the same way as litter depth (Paren and Capen, 1985).
24) Soil Surface Exposure (SOC)*	Same as (17); percentage of points with bare soil.
25) Rock Cover (RC)	Same as (17); percentage of points with rock.
26) Moss Cover (BRYC)	Same as (17); percentage of points with moss present.
27) Snag Size (SNS)	Diameter of nearest standing dead tree snag > 7.5 cm diameter from the trap station.
28) Snag Distance (SND)	Distance of nearest standing dead tree snag > 7.5 cm diameter from the trap station.

29) Plant Species Richness (SPD)	A combination of woody and herbaceous species richness within a 1 m^2 ring centered on the trap station.
30) Vertical Woody Heterogeneity (WHET)	Standard deviation of average stem counts estimated by woody profile density.
31) Blueberry Density (VAC)	Number of blueberry plants counted within a 1 m^2 ring centered on the trap station.
32) Seedling Density (SEED)	Same as (31); number of seedling plants counted.
33) Invertebrate	Number of forest floor invertebrates counted in 18 cm deep pitfalls at each trap station. This was only a sample of non-flying invertebrates.

calculate Hill's number and the modified Hill's ratio. Each plant species' site density was estimated by averaging the number of individuals counted at each trap station within a 1 m^2 ring, and these densities were used to calculate plant species diversity.

Means of microhabitat variables compared among sites within a season were analyzed using analysis of variance (ANOVA). Due to unequal sample sizes, Scheffe's test was used on multiple comparisons of means (Sokal and Rohlf, 1981).

Stepwise discriminant function analysis was used to select the microhabitat variables that would best describe differential microhabitat use by small mammals. This reduces the potential for confounding results with correlated variables. A p-value of 0.15 was used as the stopping rule for a variable to be entered into the model. This alpha level was used to limit the exclusion of variables which potentially exhibit ecologically meaningful trends. Variables were used in final analyses if they were interpreted as ecologically meaningful and accounted for significant amounts of variation in habitat use. The variables used in final statistical analyses of each site by season are listed in Appendix 1. The spring sample was omitted due to low sample sizes of small mammals.

Each capture of a species at a trap station represents one sample of that species' microhabitat use. Each species' captures were pooled by site and season for statistical analysis of a species' microhabitat use. If an animal was caught more than once at a trap station without visiting another trap station, only the first capture was used in the statistical analysis. A species' microhabitat use was always compared to the overall habitat structure in statistical analyses.

Canonical discriminant analysis (CDA) was used to determine significant differences in forest structure among sites and microhabitat use among small mammal species at each site by season. CDA is a multivariate statistical procedure that derives several canonical axes that explain among-class variation (i.e. species, sites) (Kleinbaum et al., 1988). Statistical differences among species and forest structure among sites were determined by F-statistic approximations derived from Mahalanobis multivariate distance measures (Kleinbaum et al., 1988). The relative contribution of each microhabitat variable to the distribution of small mammals was determined by CDA and each significant canonical axis was analyzed for ecologically meaningful relationships between species and microhabitat variables (Dueser and Shugart, 1978). Significance of

individual variables responsible for species separations were determined by univariate ANOVAs and overall significant differences in microhabitat use among small mammal species were determined by the F-approximations to Wilks' Lambda statistics.

Each species' relative preference to a stage of disturbance was determined by pooling each species' captures and each site's habitat characteristics into a single CDA. The Mahalanobis distances between each site and each species was used to determine site preference for each species.

Niche overlap and niche breadth were determined in multivariate statistical space by CDA (Shugart and Patten, 1972, Dueser and Shugart, 1979). Niche characteristics of each species were measured to ascertain if there were differences in small mammal abilities to exploit habitat that coordinate with changes in habitat structure induced by gypsy moth disturbance. All niche measurements were calculated in relation to overall habitat structure to alleviate potential problems with niche measurements due to varying abundances of small mammal species (Carnes and Slade, 1982).

Niche overlap is the amount of joint or shared use of a resource (i.e. habitat, food) by different species or individuals (Levins, 1968). Niche overlap was measured by

discriminant function analysis, which develops a discriminant criterion by which each observation (capture point) is classified into predetermined groups (species). The original data set containing all the captures of each species was used to determine what proportion of each species captures could be classified into its own class and the proportion of its captures that overlaps with other species' classes. The captures of a species classified into another species' microhabitat space was considered to be the degree of niche overlap of that species into another species' preferred microhabitat space. Niche breadth is the degree of exploitation by a single species of different resources such as microhabitat types or food (Schoener, 1968). As a species niche breadth increases, it is an indication that a species is exploiting more microhabitat types. Niche breadth was measured as the coefficient of variation of individual observation distances from the species centroid (class means) in CDA (Carnes and Slade, 1982). Canonical axes with a p-value < 0.1 were used in the calculation of niche breadth.

Habitat heterogeneity was measured at each site to demonstrate a sites potential for niche diversity. Habitat heterogeneity was calculated by multiplying the square root of the eigenvalue for each canonical axis by the coefficient

of variation of the discriminant scores for each canonical axis and then dividing the summed scores by the number of significant canonical axes. Calculating habitat heterogeneity with the eigenvalue of each significant canonical axis reduces the problem of differing accountability of variation among axes (Adler and Wilson, 1987).

In all comparisons an alpha level of 0.05 was used for minimal statistical significance, but at times alpha levels between 0.05 and 0.1 will be mentioned as tendencies towards significance.

Chapter 1

RESULTS

Forest Structure - All four sites had significantly different forest structure (df=63, 1380, F=52.37, $p<0.0001$, Fig. 2). From the positive to negative end of the first canonical axis, there was a gradient of greater rock cover, higher herbaceous species richness and seedling densities, larger tree size, shorter tree and stump distance, less evergreen shrub cover, and lower woody species richness. The recovery and in process sites were associated with the positive end of the axis, the reference site was intermediate, and the high mortality site was associated with the negative end of the axis. Along the second canonical axis the reference site separated from the other three sites by having higher blueberry and woody stem densities, greater evergreen canopy cover, greater snag and log distance, lower soil compactibility and invertebrate abundances, and smaller stumps. The third canonical axis discriminated between the in process site and the other sites. The in process site had greater evergreen herbaceous (mostly *Poa*, *Solidago* spp., and *Aster* spp.) and moss cover, more soil exposure, smaller trees and stumps, and shorter snag and tree distances relative to the other sites.

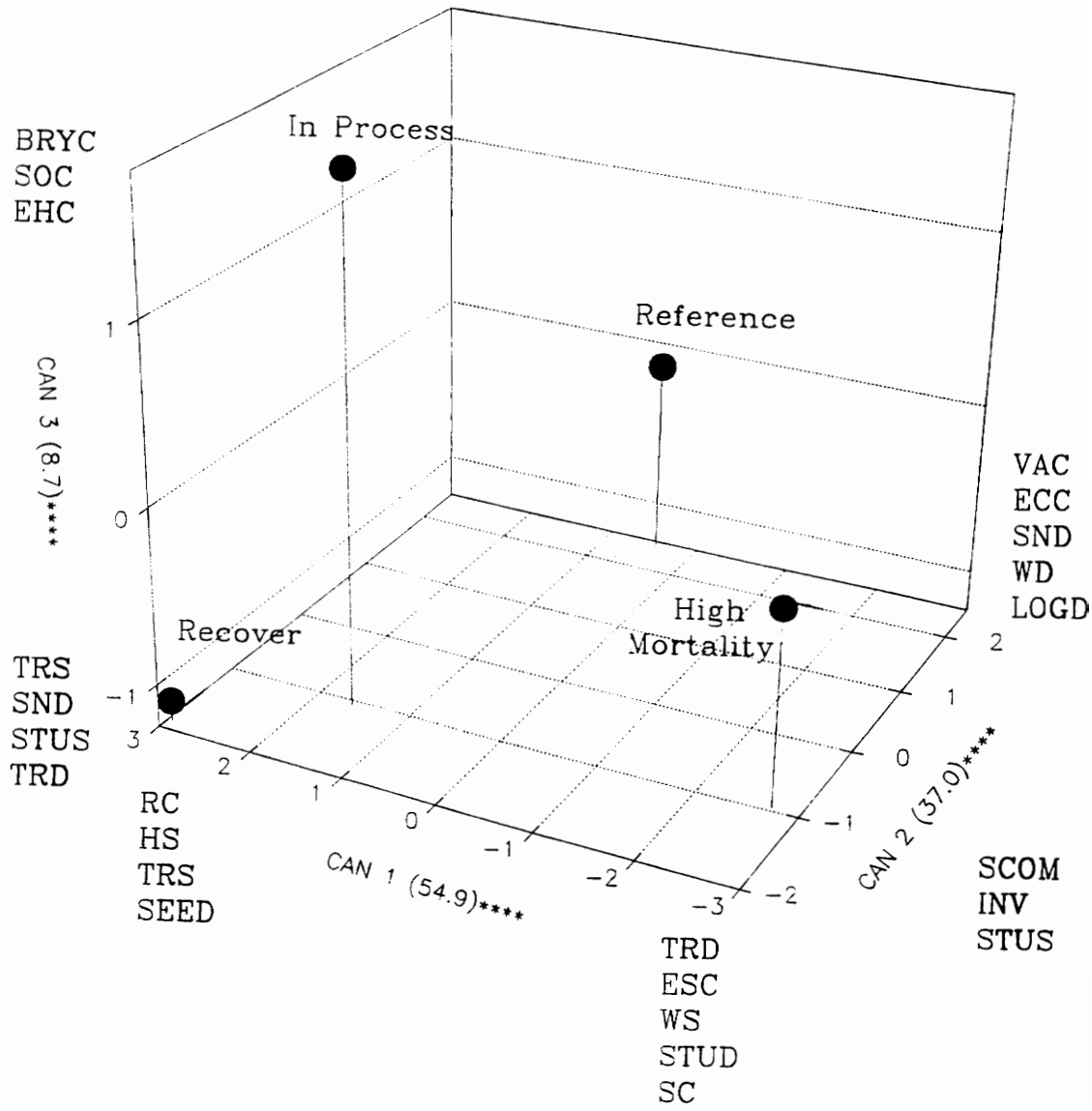


Fig. 2 - Canonical discriminant analysis (CDA) comparing forest structure among the high mortality, in process, recovery, and reference sites. The proportion of the analysis each canonical variate explains is in parentheses along each axis. Variables that significantly contribute to forest habitat structure differences are listed along axes with which they most correlate (all variables are significant, df=3, 482, $p<0.0001$). Each axis represents a gradient of habitat characteristics that describe forest structure differences among sites. Overall forest structure among sites was significantly different (Wilks' Lambda multivariate F approximation, df=63, 1380, F=52.37, $p<0.0001$).

Canopy cover was measured in late summer after the gypsy moths were dead and the trees had refoliated. After defoliation events, surviving trees will refoliate with leaves of reduced size in order to continue photosynthesis (Houston, 1981). Measurements taken at this time were thought to be the best indicator of the gypsy moth's impact for the year. Canopy cover measured after refoliation was significantly different among sites each year (1992 - $df=3, 482, F=288.88, p<0.0001$, 1993 - $df=3, 482, F=299.42, p<0.0001$). The high mortality and in process sites had significantly less canopy cover than the other two sites, but the recovery and reference sites canopy cover did not differ significantly from each other in canopy cover in either year (Fig. 3). Recovery site canopy cover went from a mean of 79.5 ± 1.0 % to 85.3 ± 1.1 % from 1992 to 1993. The recovery site was heavily defoliated in 1992, but exhibited greater refoliation than the in process site (personal observation). There was very little defoliation at the recovery site in 1992.

The reference site had the greatest structural heterogeneity among sites, while the recovery site had the least (Fig. 4). Heterogeneity at the reference site was a consequence of many interdispersed patches of blueberry shrubs, mountain laurel, evergreen canopy cover, and

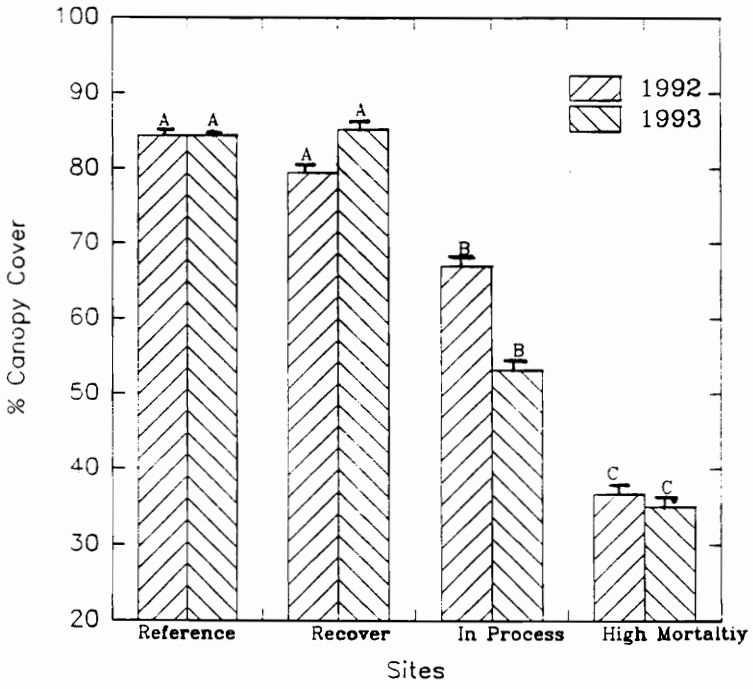


Fig. 3 - Percent canopy cover at each of the sites for 1992 and 1993. Different letters indicate significant differences in canopy cover between sites within years as determined by Scheffe's test for multiple comparisons.

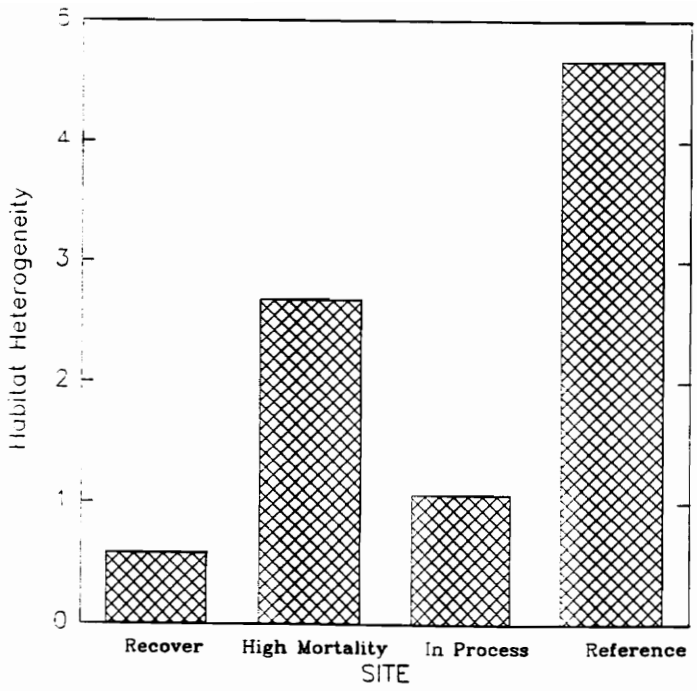


Fig. 4 - Habitat heterogeneity at each of the four sites. Habitat heterogeneity was calculated as the coefficient of variation of sample point distances from each sites centroid (class means) in discriminant space as determined by CDA. Axes that significantly contributed (Fig. 2) to site discrimination were used in the analysis.

herbaceous cover. The in process site was characterized by large patches of herbaceous cover amongst living and dead trees. The recovery site was characterized by evenly distributed cover of striped maple trees and herbaceous ground cover largely comprised of several species of ferns (*Pteridium aquilinum, Osmunda cinnamomea, Polystichum acrostichoides)*. The high mortality site was characterized by a homogeneous cover of mountain laurel interdispersed with patches of blueberry, azaleas, black gum saplings, and one large patch (90 m^2) of bracken fern (*Pteridium aquilinum*).

Plant species diversity was greatest at the in process and recovery sites and least at the reference and high mortality sites (Fig. 5A). Herbaceous species that thrived in canopy openings accounted for most of the increased diversity at the in process and recovery sites. Plant species diversity was equally split between woody and herbaceous species at the reference site and dominated by woody species at the high mortality site (Fig. 5B).

Small Mammal Abundances - A total of 13 small mammal species were caught during the study. All sites had a species richness of 9 except for the in process site which had 10. Diversity and evenness of small mammal assemblages varied

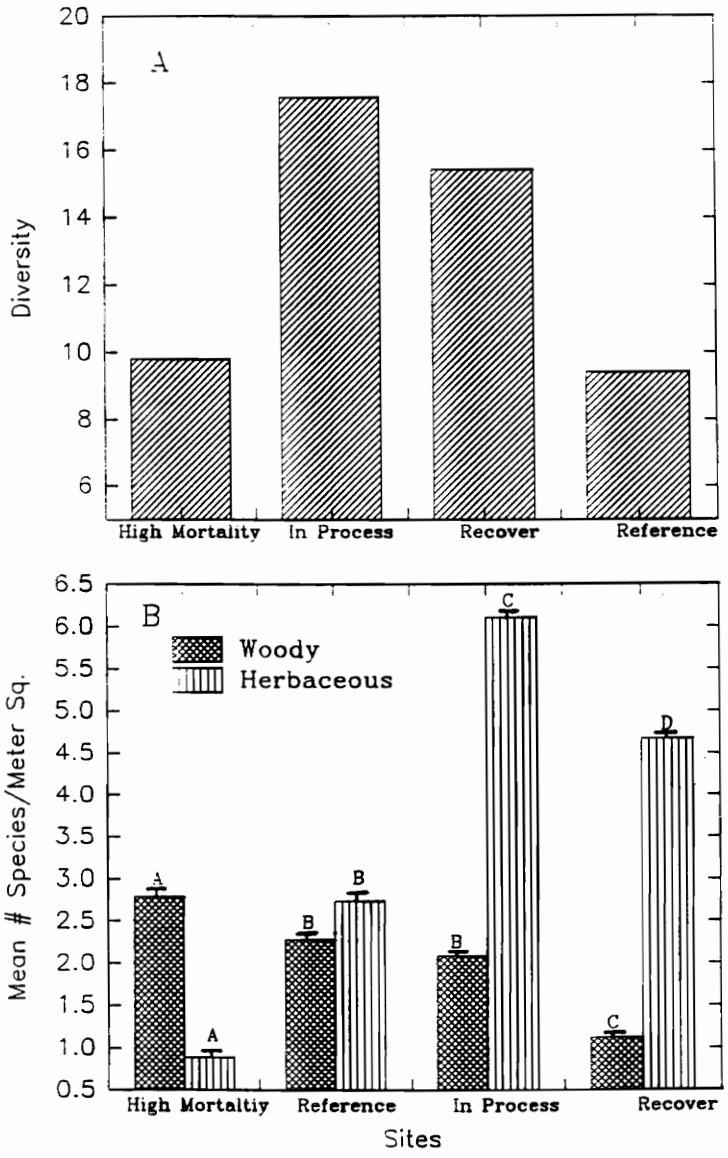


Fig. 5 - (A) Plant species diversity at each site in 1992 as determined by Hill's number. (B) Mean number of herbaceous and woody species counted within a 1 meter squared ring centered on each trap station at each site in 1992. Different letters indicate significant differences between sites as determined by Tukey's studentized range test for multiple comparisons.

among sites (Fig. 6). Species abundances varied among sites (Table 2, 3 and 4), but *P. leucopus* were the most abundant species except at the recovery site where it disappeared in the spring of 1993 (Table 2). At the in process site, *P. maniculatus* abundances were slightly lower than *P. leucopus* abundances in all samples except for fall 1993 (Table 2). At the reference site, *P. leucopus* was the only species to reach high abundances, but at times were very scarce (winter and spring 1993, Table 2). Soricids (*Blarina brevicauda, Sorex* spp.) were most abundant at the recovery and high mortality sites (Table 2). *Clethrionomys gapperi* were most abundant at the recovery and high mortality sites (Table 2) but had their greatest number of captures at the high mortality site (Table 3). *Tamias striatus* abundances varied greatly between seasons and years and among sites. They were most abundant at the recovery site, but were at similar abundances at the in process, high mortality, and reference sites during different seasons and years. In general, the high mortality site had the greatest shifts in species assemblages during the study (Table 2).

Habitat Use - Canonical discriminant analysis (CDA) was performed on small mammal assemblages at each site by season to describe microhabitat use of each species in relation to

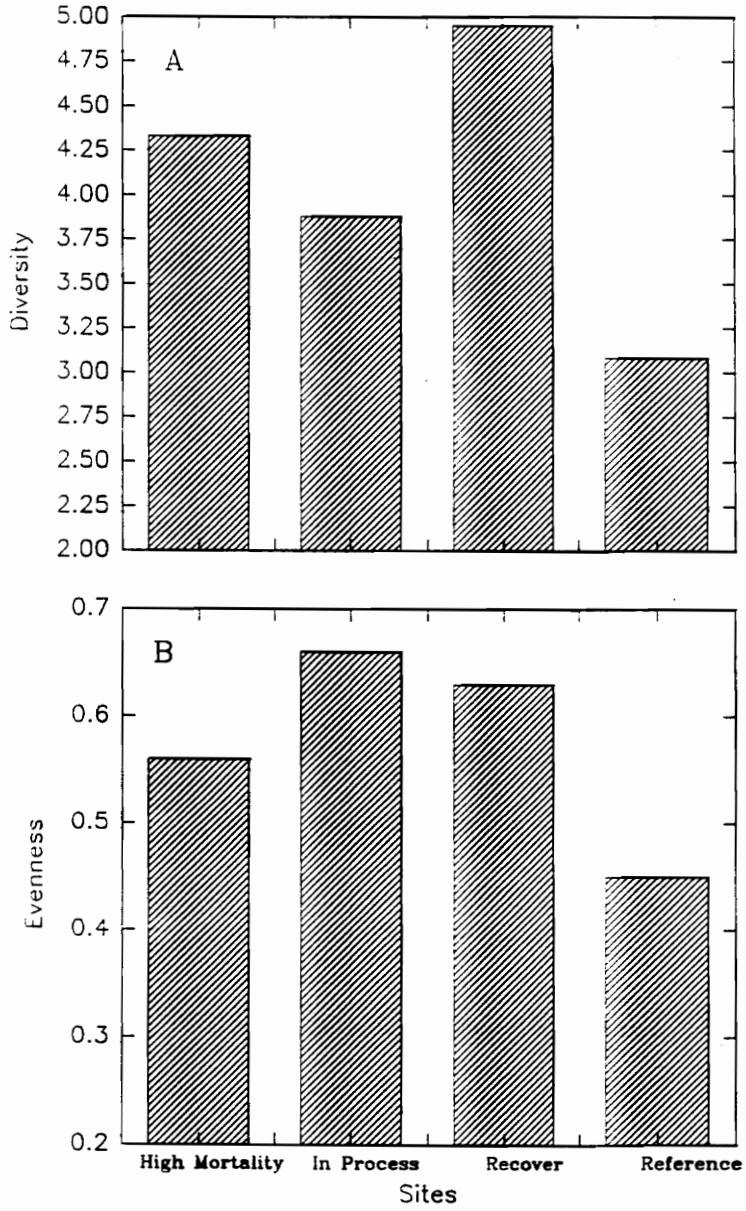


Fig. 6 - Small mammal species diversity and evenness at each site as determined by (A) Hill's number and (B) the modified Hill's evenness ratio. These indexes are derived from pooled small mammal abundances over the entire study.

Table 2 - Small mammal mean abundance at each site by season expressed as individuals per hectare. Dashes represent absence of species due to torpor.

Site/Species	Sum92	Fall92	Win93	Spr93	Sum93	Fall93
High Mortality						
P. leucopus	20.3	40.5	20.3	5.9	5.4	8.9
P. maniculatus	0.0	0.0	1.2	1.5	1.5	4.2
T. striatus	2.4	3.6	-	0.0	0.0	0.0
C. gapperi	2.4	3.6	3.6	0.6	0.0	3.6
B. brevicauda	3.0	10.1	0.6	1.2	3.6	7.7
G. volans	0.0	2.4	3.0	0.0	0.0	0.0
Sorex spp.	1.5	0.6	0.0	0.6	4.2	10.5
In Process						
P. leucopus	15.5	34.5	8.3	3.6	13.1	10.8
P. maniculatus	10.8	7.1	6.0	2.4	7.1	16.7
T. striatus	1.2	2.4	-	0.0	3.6	0.0
B. brevicauda	2.4	7.1	0.0	0.0	2.4	3.6
Sorex spp.	1.2	0.0	0.0	0.0	2.4	3.6
G. volans	0.0	0.0	1.2	0.0	0.0	0.0
C. gapperi	0.0	0.0	0.0	0.0	1.2	0.0
N. insignis	0.0	-	-	0.0	2.4	-
Recover						
P. leucopus	7.1	25.0	7.1	0.0	0.0	2.4
P. maniculatus	12.0	26.2	9.5	16.6	7.1	29.8
T. striatus	4.8	3.6	-	0.0	3.6	0.0
C. gapperi	3.6	4.8	1.2	0.0	3.6	2.4
B. brevicauda	8.3	17.9	0.0	0.0	8.3	8.3
N. insignis	1.2	-	-	0.0	4.5	-
Sorex spp.	6.0	6.0	0.0	0.0	3.6	7.1
Reference						
P. leucopus	48.8	19.6	2.4	0.6	4.8	6.0
P. maniculatus	5.4	1.2	0.0	0.0	0.0	0.0
T. striatus	0.0	0.6	-	0.0	2.4	1.2
G. volans	1.2	2.4	3.0	0.0	0.0	1.2
B. brevicauda	2.4	1.5	0.6	2.4	1.2	1.2
Sorex spp.	0.0	0.0	0.0	0.0	0.6	0.6
N. insignis	0.0	-	-	0.0	1.2	-
M. pinetorum	0.6	0.0	0.0	0.0	0.0	0.0

Table 3 - Number of captures for each species by site and season.

Site/Species	Sum92	Fall92	Win93	Spr93	Sum93	Fall93
High Mortality						
P. leucopus	59	97	51	32	20	27
T. striatus	10	8	0	0	0	0
C. gapperi	4	8	8	3	0	10
B. brevicauda	5	17	1	2	12	13
G. volans	0	4	6	0	0	0
P. maniculatus	0	0	2	3	4	10
Sorex spp.	3	1	0	1	7	17
In Process						
P. leucopus	29	47	16	6	65	11
P. maniculatus	15	9	5	4	23	18
T. striatus	1	5	0	0	9	0
B. brevicauda	2	6	0	0	2	3
Sorex spp.	1	0	0	0	2	3
G. volans	0	0	1	0	0	0
C. gapperi	0	0	0	0	1	0
N. insignis	0	0	0	0	2	0
Recover						
P. leucopus	11	38	9	0	0	2
P. maniculatus	11	32	16	21	32	42
T. striatus	13	6	0	0	9	0
C. gapperi	3	6	1	0	4	3
B. brevicauda	8	15	0	0	7	7
N. insignis	1	0	0	0	4	0
Sorex spp.	5	5	0	0	3	6
Reference						
P. leucopus	164	43	8	1	20	16
P. maniculatus	15	1	0	0	0	0
T. striatus	0	4	0	0	8	2
G. volans	3	4	7	0	0	2
B. brevicauda	4	3	2	4	2	2
Sorex spp.	0	0	0	0	1	1
N. insignis	0	0	0	0	3	0
M. pinetorum	1	0	0	0	0	0

Table 4 - Total number of captures for each species by site in 1992 and 1993.

Species	High Mortality	In Process	Recovery	Reference	Total
P. leucopus	286	174	60	252	772
P. maniculatus	19	74	154	16	263
T. striatus	18	15	28	14	75
B. brevicauda	50	13	37	17	117
Sorex spp.	29	6	19	2	56
G. volans	10	1	0	16	27
C. gapperi	33	1	17	0	51
N. insignis	0	2	5	3	10

habitat structure at different stages of gypsy moth disturbance (Figs. 7-11). Tables 5 and 6 present p-values derived from Mahalanobis squared distances generated from CDA, which determine significant separations of each species from the habitat mean and significant pairwise differences of microhabitat use between species at each site by season.

Summer 1992 - At the high mortality site, *B. brevicauda* and *T. striatus* deviated significantly (df=7, 229, p=0.019, p=0.0001) from the habitat mean (Table 5). *T. striatus* used microhabitat with larger snag sizes (SNS), greater vertical woody heterogeneity (WHET) and tree distances (TRD), and higher stump densities (STUD) relative to the habitat mean, while *B. brevicauda* used microhabitat with less stumps and greater vertical woody heterogeneity relative to the habitat mean (Fig 7A). All pairwise interspecific microhabitat use was significantly different (df=7, 229, $p<0.05$) except for *B. brevicauda/C. gapperi* and *P. leucopus/C. gapperi* (Table 6).

At the in process site, distribution of *P. leucopus* and *P. maniculatus* tended towards significant deviations (df=5, 118, p=0.057; p=0.079) from the habitat mean (Table 5) and used significantly different (df=5, 118, p=0.003) microhabitat from each other (Table 6). Along the first canonical axis, *P. leucopus* discriminated from *P.*

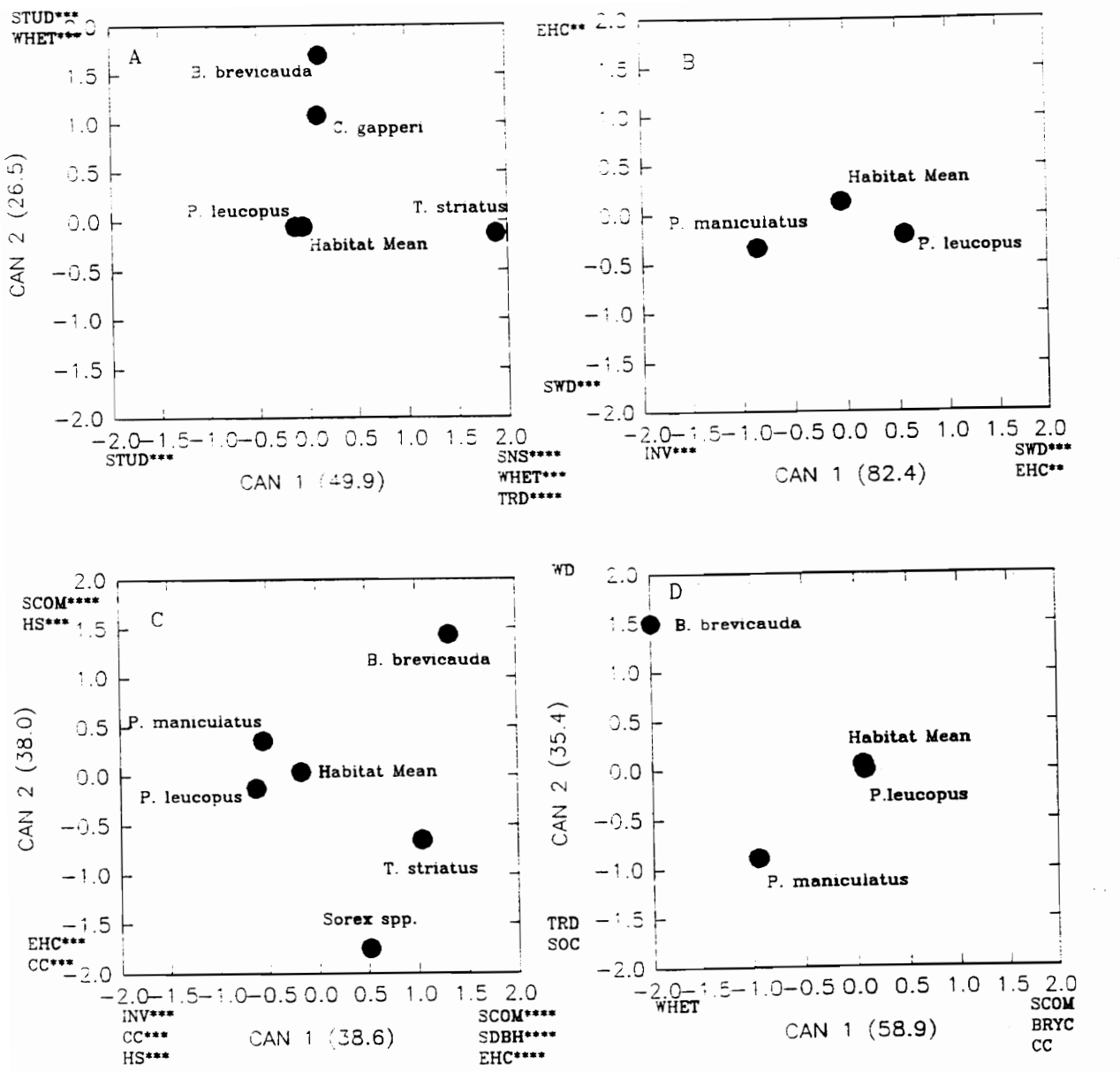


Fig. 7 - CDA of small mammal assemblages at the A) high mortality, B) in process, C) recovery and, D) reference sites for summer 1992. The proportion of the analysis each canonical variate explains is in parentheses along each axis. Variables that significantly contribute to species separation are listed along axes in which they most correlate ($p<0.15$ =*, $p<0.10$ =**, $p<0.05$ =***, $p<0.01$ =****). Each axis represents a gradient of habitat characteristics that correlates with each species habitat use (Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximation: High Mortality df=28, 827, F=2.59 $p<0.0001$, In Process df=10, 236, F=2.38, $p=0.011$, Recovery df=40, 508, F=2.36, $p<0.0001$, Reference df=27, 973, F=2.14, $p=0.0006$.

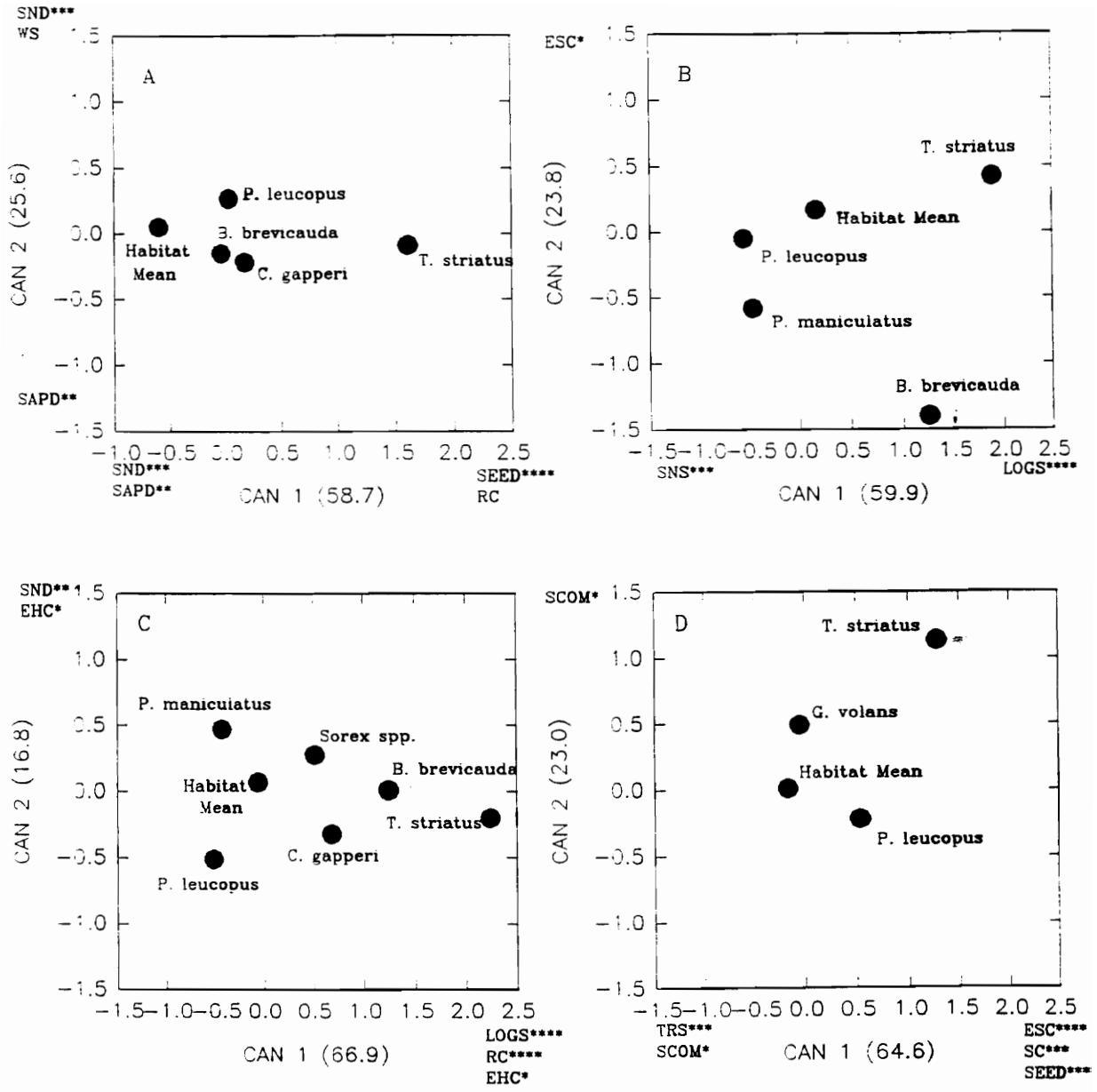


Fig. 8 - CDA of small mammal assemblages at the A) high mortality, B) in process, C) recovery and, D) reference sites for fall 1992. Refer to Figure 7 for interpretation of the plots. Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=24, 985, F=1.90, p=0.0058, In Process df=36, 508, F=1.97, p=0.0008, Recovery df=36, 754, F=2.81, p<0.0001, Reference df=24, 586, F=1.45, p=0.077.

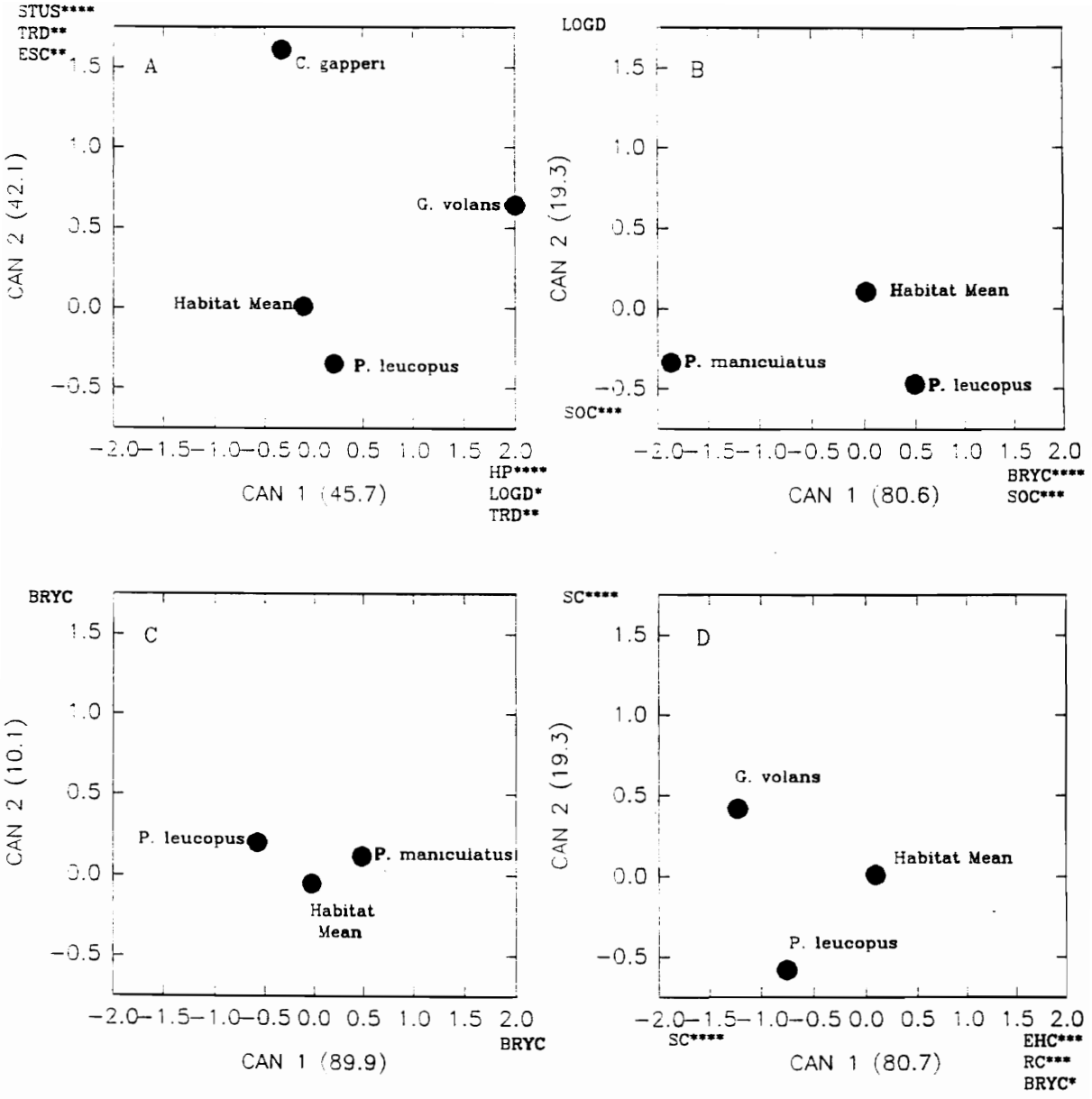


Fig. 9 - CDA of small mammal assemblages at the A) high mortality, B) in process, C) recovery and, D) reference sites for winter 1993. Refer to Figure 7 for interpretation of plots. Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximation: High Mortality df=33, 628, F=2.03 p=0.0007, In Process df=10, 190, F=2.53, p=0.007, Recovery df=10, 198, F=0.73, p=0.695, Reference df=10, 340, F=2.00, p=0.033.

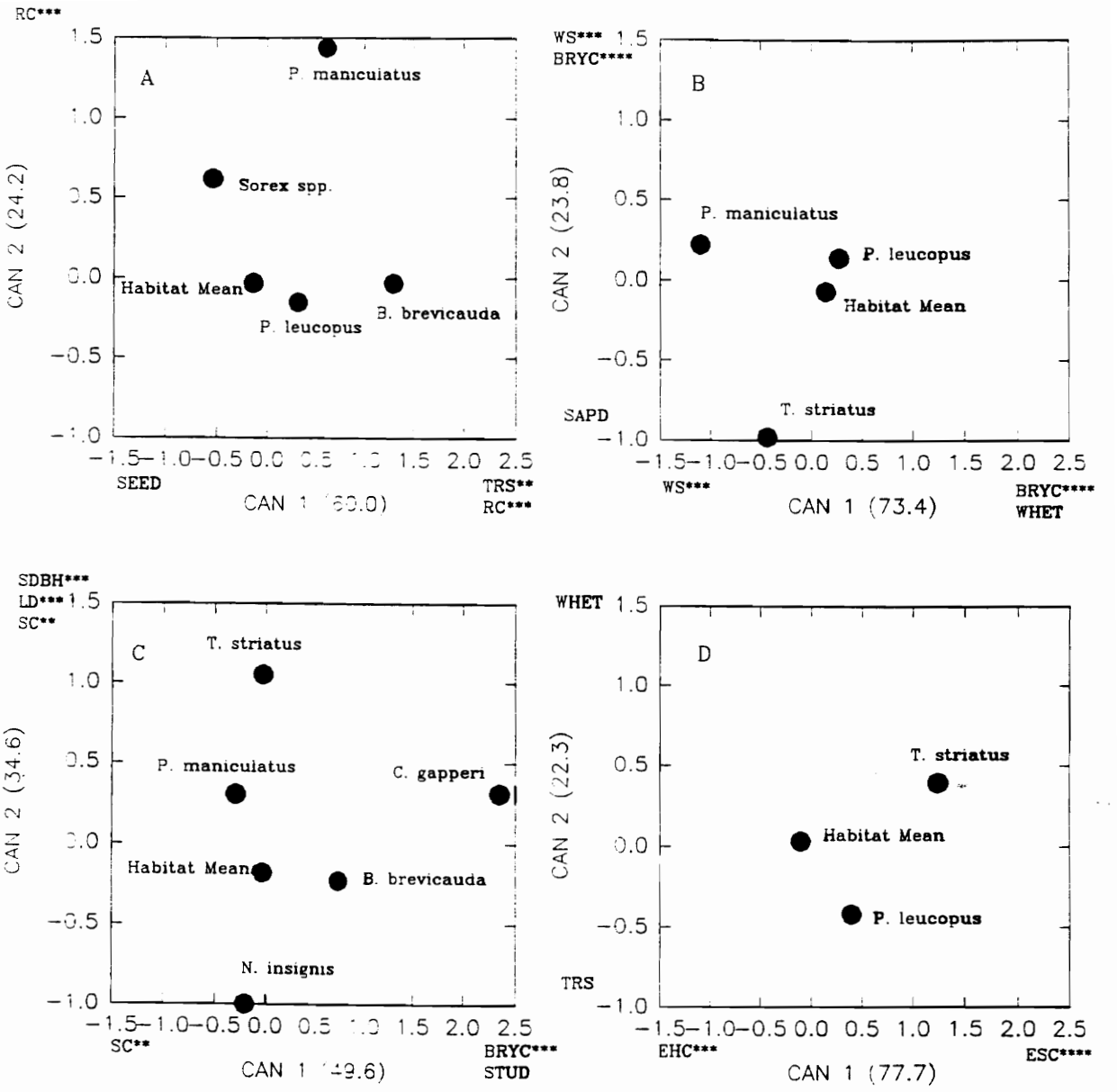


Fig. 10 - CDA of small mammal assemblages at the A) high mortality, B) in process, C) recovery and, D) reference sites for summer 1993. Refer to Figure 7 for interpretation of plots. Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximation: High Mortality df=32, 739, F=1.47, p=0.047, In Process df=12, 453, F=3.92, p<0.0001, Recovery df=35, 528, F=1.57, p=0.021, Reference df=12, 364, F=1.83, p=0.042.

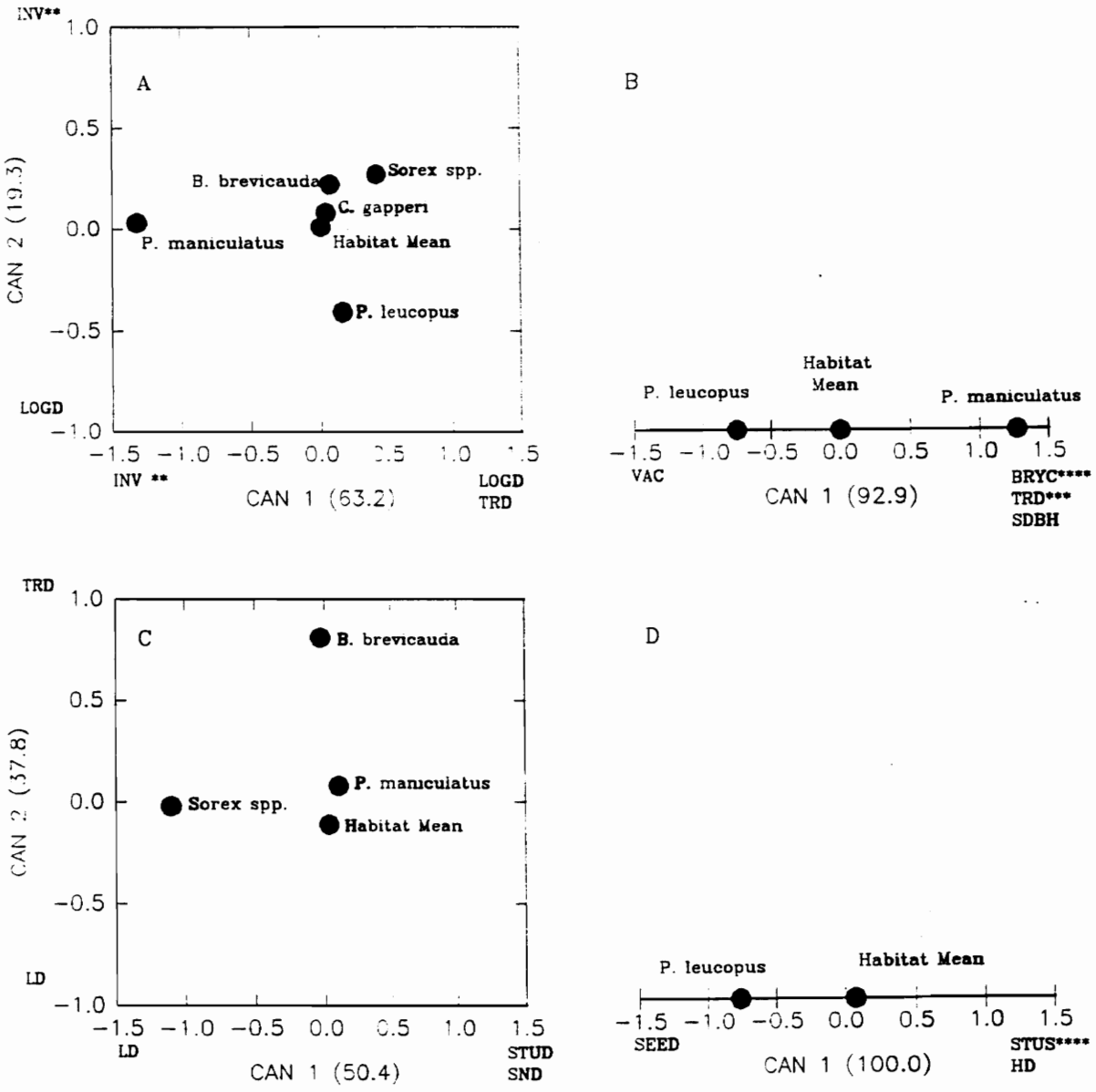


Fig. 11 - CDA of small mammal assemblages at the A) high mortality, B) in process, C) recovery and, D) reference sites for fall 1993. Refer to Figure 7 for interpretation of plots. Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximation: High Mortality df=25, 852, F=1.32, p=0.136, In Process df=8, 208, F=3.50, p=0.0008, Recovery df=12, 341, F=1.27, p=0.021, Reference df=4, 173, F=2.50, p=0.045.

Table 5 - Degree of seperation of each species from the overall habitat available at each site by season as determined by F-statistics derived from Mahalanobis squared distances. Numbers presented below are F-statistics from the analysis. Degrees of freedom for each analysis are in parentheses. Asterisks denote a a tendency towards or a significant deviation from the habitat mean (P<0.1*, P<0.05**, P<0.01***).

Species/Site	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality	(7, 229)	(6, 282)	(11, 213)	(8, 200)	(5, 229)
B. brevicauda	2.46**	1.19	-	2.95***	0.73
C. gapperi	1.85*	0.79	1.98**	-	0.21
P .leucopus	0.99	1.96*	0.39	0.37	0.95
P. maniculatus	-	-	-	3.02	3.27***
Sorex spp.	-	-	-	0.84	0.98
T. striatus	5.03***	3.51***	-	-	-
G. volans	-	-	5.44***	-	-
In Process	(5, 118)	(9, 135)	(5, 95)	(4, 171)	(4, 104)
B. brevicauda	-	2.21**	-	-	-
P. leucopus	2.19*	2.19**	1.38	0.86	4.08***
P. maniculatus	2.02*	1.29	3.94***	7.20***	2.35*
T. striatus	-	2.05**	-	2.45**	-
Recovery	(8, 116)	(6, 171)	(5, 99)	(7, 125)	(4, 129)
B. brevicauda	3.81***	3.77***	-	0.97	1.37
C. gapperi	-	1.77	-	3.22***	-
P. leucopus	1.17	2.32**	0.57	-	-
P. maniculatus	0.61	1.38	0.75	1.00	0.64
Sorex spp.	2.63**	1.14	-	-	1.81
T. striatus	3.18***	5.42***	-	2.00*	-
N. insignis	-	-	-	0.73	-
Reference	(9, 333)	(8, 202)	(5, 170)	(6, 182)	(4, 173)
B. brevicauda	3.15***	-	-	-	-
P. leucopus	0.44	2.30**	1.60	1.36	2.50**
P. maniculatus	2.79***	-	-	-	-
T. striatus	-	1.62	-	2.42**	-
G. volans	-	0.59	2.53**	-	-

Table 6 - All possible pairwise interspecific microhabitat use differences at each site by season as determined by F-statistics derived from Mahalanobis squared distances. Numbers below are F-statistics (Bb = *B. brevicauda*, Cg = *C. gapperi*, Gv = *G. volans*, Ni = *N. insignis*, Pl = *P. leucopus*, Pm = *P. maniculatus*, So = *Sorex spp.*, Ts = *T. striatus*). Degrees of freedom for each analysis are in parentheses. Asterisks denote a tendency towards or a significant difference of microhabitat use between species (P<0.1*, P<0.05**, P<0.01***).

Species pairs	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality	(7, 229)	(6, 282)	(11, 213)	(8, 200)	(5, 229)
Bb vs. Cg	1.56	1.45	-	-	0.32
Bb vs. Pl	2.43**	1.41	-	1.47	1.11
Bb vs. Ts	3.25***	4.37***	-	-	-
Bb vs. Pm	-	-	-	1.23	2.62**
Bb vs. So	-	-	-	2.10**	1.07
Cg vs. Pl	1.79*	0.78	2.53***	-	0.36
Cg vs. Pm	-	-	-	-	2.02*
Cg vs. Gv	-	-	2.42**	-	-
Cg vs. So	-	-	-	-	0.44
Cg vs. Ts	2.66**	3.10*	-	-	-
Pl vs. Gv	-	-	2.32*	-	-
Pl vs. Ts	4.96***	2.72***	-	-	-
Pl vs. Pm	-	-	-	1.16	3.48***
Pl vs. So	-	-	-	1.25	0.62
Pm vs. So	-	-	-	0.91	3.14***
In Process	(5, 118)	(9, 135)	(5, 95)	(4, 171)	(4, 104)
Bb vs. Pl	-	2.94***	-	-	-
Bb vs. Pm	-	1.77*	-	-	-
Bb vs. Ts	-	1.49	-	-	-
Pl vs. Pm	3.88***	0.68	4.13***	7.96***	6.80***
Pl vs. Ts	-	3.27***	-	3.50***	-
Pm vs. Ts	-	2.48**	-	3.05**	-
Recover	(8, 116)	(6, 171)	(5, 99)	(7, 125)	(4, 129)
Bb vs. Ts	3.29***	1.53	-	1.27	-
Bb vs. Pl	3.71***	6.10***	-	-	-
Bb vs. Pm	3.10***	5.55***	-	1.56	1.00
Bb vs. So	4.08***	0.87	-	-	1.51

Species Pairs	Sum92	Fall92	Win93	Sum93	Fall93
Recovery					
Bb vs. Ni	-	-	-	0.68	-
Bb vs. Cg	-	1.32	-	1.45	-
Cg vs. So	-	1.10	-	-	-
Cg vs. Pl	-	1.97*	-	-	-
Cg vs. Ni	-	-	-	2.60**	-
Cg vs. Pm	-	2.09	-	3.50***	-
Cg vs. Ts	-	1.66	-	2.67**	-
Pm vs. Pl	1.23	2.87**	1.27	-	-
Pm vs. So	3.08***	1.82*	-	-	1.89
Pm vs. Ni	-	-	-	1.20	-
Pm vs. Ts	2.73***	6.50***	-	0.98	-
So vs. Ts	1.85*	2.88**	-	-	-
Pl vs. So	2.34**	2.09*	-	-	-
Pl vs. Ts	2.92***	6.97***	-	-	-
Ni vs. Ts	-	-	-	1.70	-
Reference	(9, 333)	(8, 202)	(5, 170)	(6, 182)	(4, 173)
Bb vs. Pl	3.09***	-	-	-	-
Bb vs. Pm	2.49***	-	-	-	-
Pl vs. Pm	2.87***	-	-	-	-
Pl vs. Gv	-	0.77	0.93	-	-
Pl vs. Ts	-	1.13	-	1.30	-
Gv vs. Ts	-	0.93	-	-	-

maniculatus by residing in microhabitats with greater short woody stem density (SWD) and evergreen herbaceous cover (EHC) and lower invertebrate abundances (INV). Relative to *P. leucopus, P. maniculatus* resided in microhabitat with less structurally complex ground cover (Fig. 7B).

At the recovery site, neither *P. leucopus* or *P. maniculatus* significantly differed (df=8, 116, p=0.328; p=0.779) from the habitat mean or used significantly different (df=8, 116, p=0.304) microhabitat from each other (Tables 5 and 6). All other species significantly deviated (df=8, 116, $p<0.05$) from the habitat mean (Table 5). *B. brevicauda, T. striatus,* and *Sorex* spp. all separated from the habitat mean along the first canonical axis by residing in microhabitats with more compact soils (SCOM), higher breast height stem densities (SDBH) and evergreen herbaceous cover, and fewer invertebrates and herbaceous species (HS), and less canopy cover (CC) (Fig. 7C). They differed from each other on the second canonical axis which represents a gradient of more herbaceous species and high soil compactibility (*B. brevicauda)* to more evergreen herbaceous cover and canopy cover (*T. striatus* and *Sorex* spp.) (Fig. 7C).

At the reference site, *P. leucopus* did not significantly differ (df=9, 333, p=0.914) from the habitat

mean. All other species' microhabitat use differed significantly (df=9, 333, $p<0.05$) from the habitat mean and from *P. leucopus* microhabitat use (Tables 5 and 6). Along the first canonical axis, *P. maniculatus* were associated with more vertical woody heterogeneity, moss cover (BRYC), and canopy cover and lower soil compaction relative to other species. Along the second canonical axis, *P. maniculatus* were associated with greater tree distance, more soil exposure (SOC), and lower ground woody density (WD) relative to other species (Fig. 7D). *P. maniculatus* generally resided in microhabitats with less complex ground cover.

Important variables common among sites that described small mammal microdistributions were understory cover variables (WHET, SDBH) except for *P. leucopus* (Fig. 7). *P. leucopus* used microhabitat in proportion to its availability at all sites except for the in process site where understory complexity was lowest among all sites (Fig. 2). At the in process site, complex ground structure (SWD, EHC) was important to *P. leucopus* (Fig. 7B). *T. striatus* were associated with high stump densities (STUD) at the high mortality site (Fig. 7A), however, at the recovery site where stumps occurred at highest abundances (Fig. 2), the stump variable was unimportant.

Fall 1992 - At the high mortality site, only *T.*

striatus microhabitat use significantly differed (df=6, 282, p=0.002) from the habitat mean (Table 5). The only pairwise significant different microhabitat use was between *T. striatus/B. brevicauda* and *T. striatus/P. leucopus* (df=6, 282, p<0.05, Table 6). *T. striatus* tended to reside in microhabitats consisting of high seedling densities and rock cover and short snag and sapling distances (Fig. 8A). *P. leucopus* tended towards significantly different (df=6, 282, p=0.07) microhabitat use from the habitat mean by residing in microhabitats with lower snag densities and higher sapling densities relative to the habitat mean (Fig. 8A, Table 5).

At the in process site, all species' microhabitat use, except *P. maniculatus,* significantly differed (df=9, 135, p<0.05) from the habitat mean (Table 5). Most pairwise comparisons of microhabitat use significantly differed (df=9, 135, p<0.05) except for *P. leucopus/P. maniculatus* and *T. striatus/B. brevicauda* (Table 6). *T. striatus* and *B. brevicauda* were associated with greater log size and smaller snag size relative to the *Peromyscus* species. *T. striatus* used microhabitat with greater evergreen shrub cover (ESC) than did *B. brevicauda* or *P. maniculatus* (Fig. 8B).

At the recovery site, *B. brevicauda, P. leucopus,* and *T. striatus* microhabitat use significantly differed (df=6,

171, $p<0.05$) from the habitat mean (Table 5). *P. leucopus* and *P. maniculatus* used significantly different (DF=6, 171, P=0.011) microhabitat, and this was the opposite of the outcome between these two species at the in process site (Table 6). *P. maniculatus* used microhabitat with greater evergreen herbaceous cover and fewer snags than *P. leucopus* (Second canonical axis, Fig. 8C). Most species separated on the first canonical axis, which has a gradient describing decreasing log size, rock cover, and evergreen herbaceous cover from the positive to negative end. *T. striatus* were highly associated with the positive end, *B. brevicauda, C. gapperi,* and *Sorex* spp., to a lesser degree, were associated with the positive end, and the *Peromyscus* species were associated with the negative end of the axis (Fig. 8C).

At the reference site, *P. leucopus* microhabitat use significantly differed (df=8, 202, p=0.022) from the habitat mean (Table 5). There were no significant pairwise differences (df=8, 202, $p>0.05$) in microhabitat use between species (Table 6). *P. leucopus* resided in microhabitats that had greater evergreen shrub cover, seedling densities, and less compact soil than the overall habitat mean (Fig. 8D).

Important variables common among sites describing the microdistribution of *T. striatus* were seedling densities at the high mortality and reference sites and log size at the

in process and recovery sites (Fig. 8). Snag distance, snag size, and log size were important variables to *P. leucopus* at all sites except for the reference site where soil compactibility became an important variable (Fig. 8). Shrub cover variables were important to *P. leucopus* at the reference site but not at any other site. *P. maniculatus* were more associated with less complex ground cover and understory cover than was *P. leucopus* (Fig. 8). *B. brevicauda* were associated with log size at the in process and recovery sites, but did not show the same preference at the high mortality site (Fig. 8).

Winter 1993 - At the high mortality site, *Glaucomys volans* and *C. gapperi* microhabitat use significantly differed ($df=11, 213, p<0.05$) from the habitat mean (Table 5). All pairwise comparisons of microhabitat use significantly differed ($df=11, 213, p<0.05$, Table 6). Along the first canonical axis, *G. volans* resided in microhabitats associated with fewer logs, higher herbaceous profile (HP), and more living trees relative to other species. Along the second canonical axis, *C. gapperi* resided in microhabitats associated with larger stumps, fewer live trees, and greater evergreen shrub cover relative to other species, especially *P. leucopus* (Fig 9A).

At the in process site, *P. maniculatus* deviated

significantly (df=5, 95, p=0.005) from the habitat mean (Table 5). *P. leucopus* and *P. maniculatus* used significantly different (df=5, 95, p=0.002) microhabitat (Table 6) with *P. leucopus* residing in microhabitats with more moss cover and soil exposure than *P. maniculatus* (Fig. 9B).

At the recovery site, neither *P. leucopus* or *P. maniculatus* microhabitat use deviated significantly from the habitat mean or from each other (df=5, 99, p>0.05, Tables 5 and 8). There were no significant microhabitat variables at the recovery site which suggests a high degree of spatial overlap between these two species (Fig. 9C).

At the reference site, only *G. volans* microhabitat use deviated significantly (df=8, 202, p=0.03) from the habitat mean (Table 5). *G. volans* microhabitat was associated with greater shrub cover (SC) and less evergreen herbaceous cover, rock cover, and moss cover relative to the habitat mean (Fig. 9D).

Due to low small mammal abundances, there were very few common important variables among sites in the winter 1993 sample. *G. volans* and *C. gapperi* were the only species other than *P. leucopus* and *P. maniculatus* with enough captures to analyze. *P. leucopus* used microhabitat in proportion to its availability at all sites (Table 5), while P. maniculatus deviated from the habitat mean at the in process site but

not at the recovery site (Table 5).

Summer 1993 - At the high mortality site, only *B. brevicauda* microhabitat use significantly deviated (df=8, 200, p=0.004) from the habitat mean (Table 5), and only *B. brevicauda* and *Sorex* spp. used significantly different (df=8, 200, p<0.05) microhabitat (Table 6). Along the first canonical axis, *B. brevicauda* discriminated from *Sorex* spp. and the habitat mean by residing in microhabitat with more rock cover, larger trees and fewer seedlings (Fig. 10A).

At the in process site, *P. maniculatus* and *T. striatus* microhabitat use significantly deviated (df=4, 171, p<0.05) from the habitat mean (Table 5) and all pairwise comparisons of microhabitat use significantly differed (df=4, 171, p<0.05, Table 6). Along the first canonical axis, *P. maniculatus* resided in microhabitat with higher woody species richness (WS) and less moss cover than *P. leucopus*. Along the second canonical axis, *T. striatus* resided in microhabitats with fewer saplings (SAPD) and woody species and less moss cover than *P. leucopus* and *P. maniculatus* (Fig. 10B). *P. maniculatus* and T. striatus used more open microhabitat than *P. leucopus*.

At the recovery site, only *C. gapperi* microhabitat use significantly deviated (df=7, 125, p=0.004) from the habitat mean (Table 5). *T. striatus* tended towards a significant

deviation (df=7, 125, p=0.06) from the habitat mean (Table 5). Most pairwise comparisons of microhabitat use were not significantly different (df=7, 125, p>0.05) except for those between *C. gapperi and N. insiginis, P. maniculatus,* and *T. striatus* (df=7, 125, p<0.05, Table 6). *C. gapperi* used microhabitat with greater moss cover and fewer stumps relative to the habitat mean, and *T. striatus* used microhabitat with higher breast height stem densities, greater litter depth, and more shrub cover relative to the habitat mean (Fig. 10C). *N. insignis* tended to use microhabitat with a more open understory relative to the habitat mean (Fig. 10C).

At the reference site, *T. striatus* microhabitat use significantly deviated (df=6, 182, p=0.024) from the habitat mean, but *T. striatus* did not significantly deviate (df=6, 182, p=0.259) from *P. leucopus* microhabitat use (Tables 5 and 6). *T. striatus* used microhabitat with more dense understory cover (ESC, WHET) relative to the habitat mean and *P. leucopus* (Fig. 10D).

Important microhabitat characteristics common among sites for *T. striatus* were understory cover variables (EHC, SDBH, WHET) at the recovery and reference sites, but not at the in process site (Fig. 10). Microhabitat with less structurally complex ground cover was important to *P.*

maniculatus at the in process and recovery sites (Fig. 10). Soricids used microhabitats in proportion to their availability at sites where they were present, except for *B. brevicauda* at the high mortality site (Table 5) where they used microhabitat with more rock cover and larger live trees relative to the habitat mean (Fig. 10A). *P. leucopus* used microhabitats in proportion to their availability at all sites (Table 5). In contrast to small mammal microhabitat use in the summer 1992, small mammal assemblages in 1993 discriminated less from the habitat mean and from each other than in 1992 (Tables 5 and 6) despite their reduced abundances in summer 1993 (Table 2). The types of microhabitat variables that were important to each species microhabitat discrimination varied greatly between years (Figs. 7 and 10).

Fall 1993 - At the high mortality site, *P. maniculatus* microhabitat use significantly deviated ($df=5, 229, p<0.05$) from the habitat mean and all other species present (Tables 5 and 6). *P. maniculatus* microhabitat use was associated with greater invertebrate abundances and more logs and living trees relative to other species and the habitat mean (Fig. 11A). All other species at the site did not significantly deviate ($df=5, 229, p>0.05$) from the habitat mean or from each other, which suggests a high degree of

spatial overlap (Tables 5 and 6).

At the in process site, only one canonical axis was derived from the analysis (Fig. 11B). *P. leucopus* microhabitat use significantly deviated (df=4, 104, p=0.005) from the habitat mean, but *P. maniculatus* microhabitat use only tended towards a significant deviation (df=4, 104, p=0.059) from the habitat mean (Table 5). The microhabitats used by the two species significantly differed (df=4, 104, p<0.0001, Table 6). *P. leucopus* used microhabitats with more moss cover, higher breast height stem densities, and fewer living trees and blueberries (VAC) relative to *P. maniculatus* and the habitat mean (Fig. 11B).

At the recovery site, there were no significant deviations of microhabitat use from the habitat mean and no pairwise comparisons of microhabitat use were significantly different (df=4, 129, p>0.05, Tables 5 and 6, Fig. 11C).

At the reference site, only one canonical axis was derived from the analysis (Fig. 11D) with *P. leucopus* the only species at densities sufficient for an analysis (Table 2). *P. leucopus* microhabitat use significantly deviated (df=4, 173, p=0.047) from the habitat mean (Table 5) and was associated with higher seedling and herbaceous stem densities and smaller stumps relative to the habitat mean (Fig. 11D).

In general, the Soricids and *C. gapperi* showed very little microhabitat discrimination (Fig. 11). *P. maniculatus,* in the presence of *P. leucopus,* used different microhabitats than *P. leucopus* and the habitat mean. *P. maniculatus* microhabitats were generally associated with less tree distance (or more living trees) and less structurally complex understory (Fig. 11). At the high mortality site, *P. maniculatus* microhabitat use was associated with high log densities and invertebrate abundances (Fig. 11A), but this was not evident at the in process or recovery sites (Fig. 11A and B). At the in process site, *P. maniculatus* and *P. leucopus* showed greater microhabitat discrimination in fall 1993 than fall 1992. However, at the high mortality site in fall 1993, *P. leucopus* microhabitat use was less discriminating than in fall 1992. *P. leucopus* microhabitat use at the reference site and *P. maniculatus* microhabitat use at the recovery site in fall 1993 was similar to their respective microhabitat use in fall 1992 (Figs. 8 and 11, Table 5).

Niche Characteristics - Niche breadth and overlap are presented for each species at each site by season in Tables 7 and 8. Niche measures were derived from and related to the analyses presented in Figures 7 - 11.

Table 7 - Niche breadth of each small mammal species at each site by season.

Site/Species	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality					
P. leucopus	5.87	35.0	2.75	1.93	4.18
T. striatus	1.46	0.65	-	-	-
C. gapperi	1.05	3.71	0.98	-	13.3
B. brevicauda	1.49	1.42	-	0.61	10.7
G. volans	-	-	1.00	-	-
P. maniculatus	-	-	-	2.06	1.20
Sorex spp.	-	-	-	7.57	1.73
In Process					
P. leucopus	1.75	1.28	1.48	4.22	0.72
P. maniculatus	0.83	1.49	0.44	1.45	1.09
T. striatus	-	0.63	-	1.31	-
B. brevicauda	-	1.14	-	-	-
Recovery					
P. leucopus	1.72	1.39	1.50	-	-
P. maniculatus	1.72	2.07	1.93	2.06	11.0
T. striatus	0.63	1.87	-	25.6	-
C. gapperi	-	2.30	-	0.62	-
B. brevicauda	1.05	1.64	-	2.19	3.21
N. insignis	-	-	-	2.76	-
Sorex spp.	0.44	2.21	-	-	1.21
Reference					
P. leucopus	15.7	1.54	0.70	2.33	0.31
P. maniculatus	1.22	-	-	-	-
T. striatus	-	0.13	-	0.38	-
G. volans	-	24.2	0.12	-	-
B. brevicauda	0.92	-	-	-	-

Table 8 - Pairwise niche overlap of small mammals at the high mortality, in process, and recovery sites. Niche overlap is measured as the proportion of the first species (i.e P.leucopus/T.striatus) captures that are classified in the second species habitat space. Refer to Table 6 for abbreviation interpretations.

High Mortality	Sum92	Fall92	Win93	Sum93	Fall93
Bb vs. Cg	-	0.0	-	-	0.0
Cg vs. Bb	-	0.0	-	-	20.0
Bb vs. Pl	20.0	94.8	-	33.3	92.3
Pl vs. Bb	1.7	2.1	-	11.1	0.0
Bb vs. Ts	0.0	0.0	-	-	-
Ts vs. Bb	0.0	0.0	-	-	-
Pl vs. Ts	1.7	2.6	-	-	-
Ts vs. Pl	40.0	75.0	-	-	-
So vs. Bb	-	-	-	0.0	11.8
Bb vs. So	-	-	-	0.0	0.0
So vs. Pl	-	-	-	42.8	52.9
Pl vs. So	-	-	-	0.0	2.6
Cg vs. Pl	-	100.0	37.5	-	80.0
Pl vs. Cg	-	0.0	2.0	-	0.0
Ts vs. Cg	-	0.0	-	-	-
Cg vs. Ts	-	0.0	-	-	-
Pm vs. Bb	-	-	-	-	0.0
Bb vs. Pm	-	-	-	-	0.0
Pm vs. Cg	-	-	-	-	0.0
Cg vs. Pm	-	-	-	-	0.0
Pm vs. Pl	-	-	-	-	60.0
Pl vs. Pm	-	-	-	-	7.4
Pm vs. So	-	-	-	-	0.0
So vs. Pm	-	-	-	-	0.0
Gv vs. Pl	-	-	33.3	-	-
Pl vs. Gv	-	-	2.0	-	-
Gv vs. Cg	-	-	16.7	-	-
Cg vs. Gv	-	-	0.0	-	-
So vs. Cg	-	-	-	-	0.0
Cg vs. So	-	-	-	-	0.0
In Process					
Bb vs. Pl	-	33.3	-	-	-
Pl vs. Bb	-	0.0	-	-	-
Bb vs. Ts	-	16.7	-	-	-
Ts vs. Bb	-	0.0	-	-	-
Pl vs. Ts	-	0.0	-	1.5	-

(Table 8 continued) 60

In Process	Sum92	Fall92	Win93	Sum93	Fall93
Ts vs. Pl	-	20.0	-	66.7	-
Bb vs. Pm	-	0.0	-	-	-
Pm vs. Bb	-	11.1	-	-	-
Pm vs. Pl	33.3	77.8	0.0	47.8	11.1
Pl vs. Pm	17.4	0.0	6.7	6.2	18.8
Ts vs. Pm	-	0.0	-	22.2	-
Pm vs. Ts	-	0.0	-	4.4	-
Recovery					
Bb vs. Pl	-	33.3	-	-	-
Pl vs. Bb	-	0.0	-	-	-
Bb vs. Ts	-	16.7	-	-	-
Ts vs. Bb	-	0.0	-	-	-
Pl vs. Ts	-	0.0	-	-	-
Ts vs. Pl	-	20.0	-	-	-
So vs. Bb	0.0	40.0	-	-	0.0
Bb vs. So	0.0	0.0	-	-	0.0
So vs. Pl	0.0	0.0	-	-	-
Pl vs. So	0.0	2.6	-	-	-
Cg vs. Pl	-	66.7	-	-	-
Pl vs. Cg	-	0.0	-	-	-
Ts vs. Cg	-	0.0	-	0.0	-
Cg vs. Ts	-	16.7	-	0.0	-
Bb vs. Pm	25.0	6.7	-	71.4	85.7
Pm vs. Bb	0.0	0.0	-	0.0	0.0
Pm vs. Cg	0.0	0.0	-	0.0	-
Cg vs. Pm	-	0.0	-	25.0	-
Pm vs. Pl	18.2	40.6	0.0	-	-
Pl vs. Pm	27.3	15.8	33.3	-	-
Pm vs. So	0.0	0.0	-	-	0.0
So vs. Pm	0.0	40.0	-	-	100.0
So vs. Cg	-	0.0	-	-	-
Cg vs. So	-	16.7	-	-	-
Ts vs. Pm	5.4	0.0	-	44.4	-
Pm vs. Ts	9.1	0.0	-	6.3	-
Ni vs. Pm	-	-	-	75.0	-
Pm vs. Ni	-	-	-	3.1	-

High Mortality Site - *P. leucopus* niche breadths were high throughout the study and in general were highest in the fall. *C. gapperi* niche breadths were relatively high in the fall and, their niche breadths were greater than that of P. leucopus in fall 1993 (Table 7). Niche breadths for most species decreased from summer to fall, except for *B. brevicauda* in summer and fall 1993 when they exceeded the niche breadths of *P. leucopus* (Table 7). Niche overlap increased from summer to fall and decreased again in the winter (Table 8). *T. striatus, B. brevicauda,* and *C. gapperi* had a high degree of overlap into *P. leucopus* habitat space in fall 1992. The same trend followed in fall 1993 except that *P. maniculatus* and *Sorex* spp. were present instead of *T. striatus* (Table 8).

In Process Site - *P. leucopus* niche breadths remained constant throughout the study except for in summer 1993 (Table 7). *P. maniculatus* niche breadths were either less than or approximately equal to *P. leucopus* except in fall 1993 (Table 7). *P. maniculatus* had a high degree of overlap into *P. leucopus* habitat space in fall 1992, but there was little overlap between these species in fall 1993 (Table 8). *P. maniculatus* overlapped more into *P. leucopus* habitat space in the summer 1993 than in fall 1993 (Table 8).

Recovery Site - All species had an increase in niche

breadths in fall 1992 except *P. leucopus* (Table 7). This trend continued in fall 1993 when *P. leucopus* was absent from the site. In the absence of *P. leucopus,* all species had higher niche breadths in summer 1992 except for *P. maniculatus* (Table 8). *P. maniculatus* did not exhibit a marked change in niche breadth until fall 1993 when it increased five-fold from previous seasonal measures (Table 7).

There were moderate increases in niche overlap between summer and fall 1993 (Table 8). *P. leucopus* and *P. maniculatus* had moderate to little overlap into each others habitat space except in winter 1993 when *P. leucopus* overlapped *P. maniculatus* habitat space, but *P. maniculatus* did not overlap into *P. leucopus* habitat space (Table 8). This was the only season and site in this study where this relationship occurred and it preceded the disappearance of *P. leucopus* from the recovery site (Table 2). In the absence of *P. leucopus, B. brevicauda* and *Sorex* spp. had a high degree of overlap within *P. maniculatus* habitat space (Table 8).

Reference Site - In summer 1992, *P. leucopus* had extremely high niche breadths compared to other seasons. After summer 1992, *P. leucopus* niche breadths decreased and remained relatively low despite low abundances of

conspecifics (Table 7). The extremely high niche breadths of summer 1992 is related to the extremely high densities reached during this sample interval (Table 2). *P. leucopus* niche breadths were relatively low compared to those at the high mortality site and were generally lower than those at the in process and recovery sites where *P. leucopus* coexisted with substantial numbers of *P. maniculatus* (Table 7). There was very little niche overlap among species at the reference site.

Pooled CDA Analyses - Pooled CDA were performed on total capture data for each small mammal species at each site to get a general picture of overall habitat use (Fig. 12). Only variables not affected by season or which remained stable over the two year period of the study were used in the analyses.

At the high mortality site (Fig. 12A), *B. brevicauda, C. gapperi,* and *T. striatus* microhabitat use significantly deviated ($df=9, 590, p<0.05$) from the habitat mean and *P. maniculatus* and *G. volans* tended towards significant deviations ($df=9, 590, p<0.10$). *B. brevicauda* used microhabitat with greater evergreen shrub cover, higher ground woody stem densities, less rock and canopy cover, lower breast height stem densities relative to the habitat

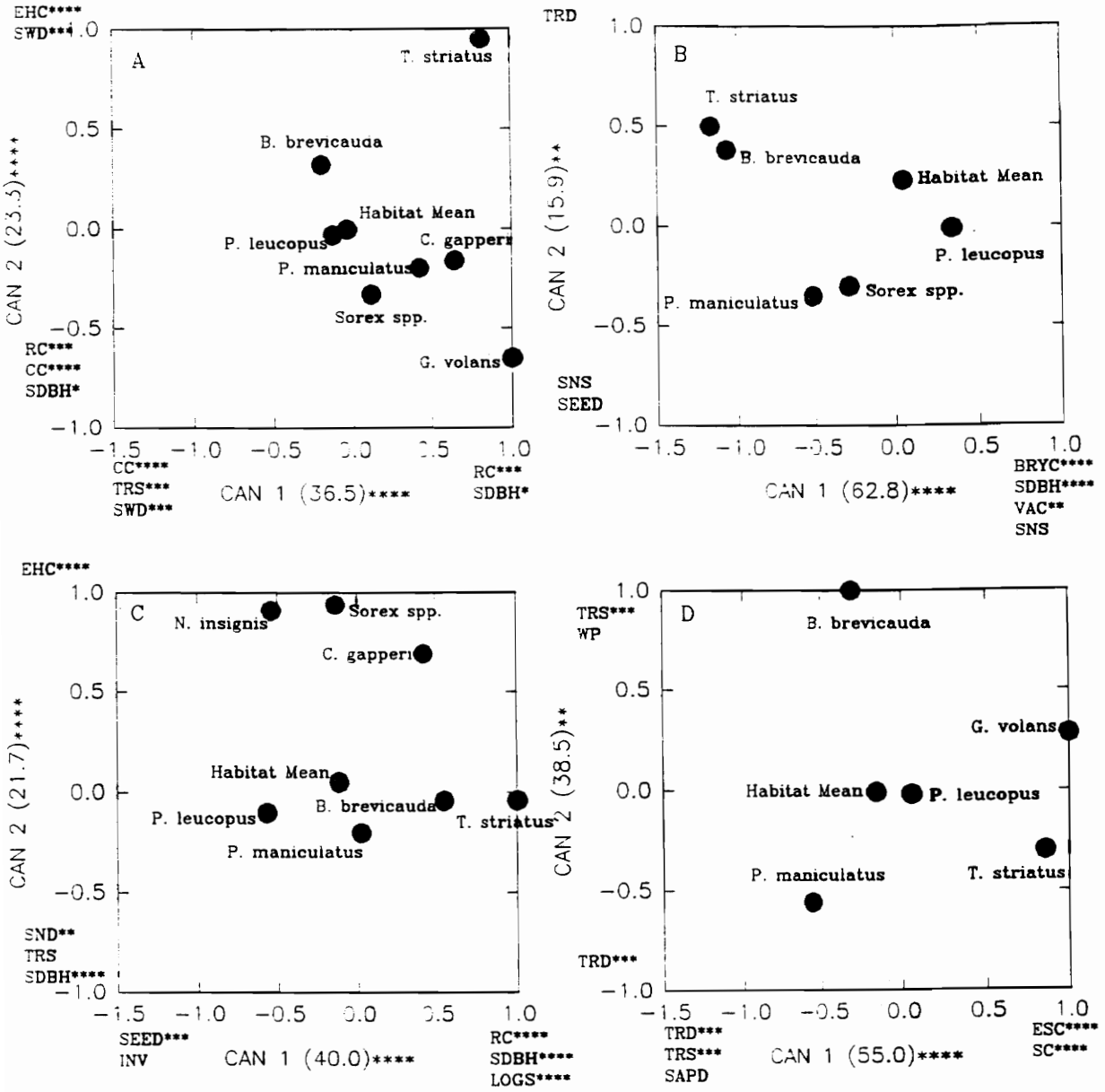


Fig. 12 - CDA of pooled capture data of small mammal assemblages throughout the study at the A) high mortality, B) in process, C) recovery and, D) reference sites. Only variable not affected seasonally were used in the analysis. Overall assemblage habitat segregation as determined by Wilks' Lambda multivariate F approximation: High Mortality df=63, 3329, F=2.01 p<0.0001, In Process df=45, 1622, F=2.63, p<0.0001, Recovery df=63, 2619, F=2.57, p<0.0001, Reference df=30, 1854, F=2.20, p=0.0002.

mean. *C. gapperi* used microhabitat with greater rock cover, less canopy cover, lower ground woody stem densities, and smaller living trees (DBH) relative to the habitat mean. To a lesser degree, *P. maniculatus* followed this same trend. *T. striatus* used microhabitat that had greater rock cover and evergreen shrub cover, less canopy cover, and smaller living trees (DBH) relative to the habitat mean. *G. volans* used microhabitat with greater canopy cover and rock cover, higher breast height stem densities, and less complex ground cover (SWD) relative to the habitat mean. *P. leucopus* and *Sorex* spp. used microhabitat in direct proportion to its availability.

At the in process site (Fig. 12B), *B. brevicauda, P. maniculatus,* and *T. striatus* microhabitat use significantly deviated ($df=9, 362, p<0.05$) from the habitat mean. *T. striatus* and *B. brevicauda* used microhabitat with less moss cover, lower breast height stem and blueberry densities, and smaller snags relative to the habitat mean. *P. maniculatus* exhibited the same tendency, except they resided in microhabitats with more living trees, greater snag size, and higher seedling densities relative to the habitat mean. *P. leucopus* and *Sorex* spp. used microhabitat in direct proportion to its availability.

At the recovery site (Fig. 12C), *T. striatus, B.*

brevicauda, and *C. gapperi* microhabitat use significantly deviated (df=9, 464, $p<0.05$) from the habitat mean, and *P. leucopus* and *Sorex* spp. tended towards significant deviations (df=9, 464, $p=0.056$; $p=0.062$). *T. striatus* used microhabitat with more rock cover, higher breast height stem densities, larger logs, and fewer seedlings and invertebrates relative to the habitat mean. *B. brevicauda* showed a similar trend. *P. leucopus* used microhabitat with more seedlings and invertebrates, smaller logs, less rock cover, and lower breast height stem densities relative to the habitat mean. This microhabitat was very open compared to the microhabitat they used at other sites. *C. gapperi* used microhabitat with greater rock cover, evergreen herbaceous cover, and log size relative to the habitat mean. *Sorex* spp. tended to use microhabitat with greater evergreen herbaceous cover relative to the habitat mean, while *P. maniculatus* and *N. insignis* used microhabitat in proportion to its availability.

At the reference site (Fig. 12D), *B. brevicauda*, *G. volans*, and *T. striatus* microhabitat use significantly deviated (df=6, 463, $p<0.05$) from the habitat mean. *B. brevicauda* used microhabitat with larger trees and a more dense understory relative to the habitat mean. *P. maniculatus* tended to use microhabitat with fewer trees and

less complex understory relative to the habitat mean. *G. volans* and *T. striatus* used microhabitat with greater evergreen shrub cover and smaller trees relative to the habitat mean. *G. volans* used microhabitat with larger trees relative to *T. striatus*. *P. leucopus* used microhabitat in proportion to its availability.

Figures 13 and 14 are three-dimensional representations of the in process and recovery sites. *P. leucopus* and *P. maniculatus* had large enough sample sizes to visually display spatial and microhabitat segregation. Overall pairwise comparisons of microhabitat use between *P. leucopus* and *P. maniculatus* were significantly different at the recovery ($df=9, 464, p=0.003$) and in process ($df=9, 362, p<0.0001$) sites. At the recovery site, *P. leucopus* captures (Fig. 13A) generally occurred in areas of lower breast height stem densities (Fig. 13C) and smaller logs (Fig. 13D), where *P. maniculatus* captures (Fig. 13B) occurred in areas with higher breast height stem densities and larger logs. At the in process site, *P. leucopus* captures (Fig. 14A) generally occurred in areas with greater moss cover (Fig. 14C) and higher blueberry densities (Fig. 14D), where *P. maniculatus* captures (Fig. 14B) occurred in areas of lower blueberry densities and less moss cover.

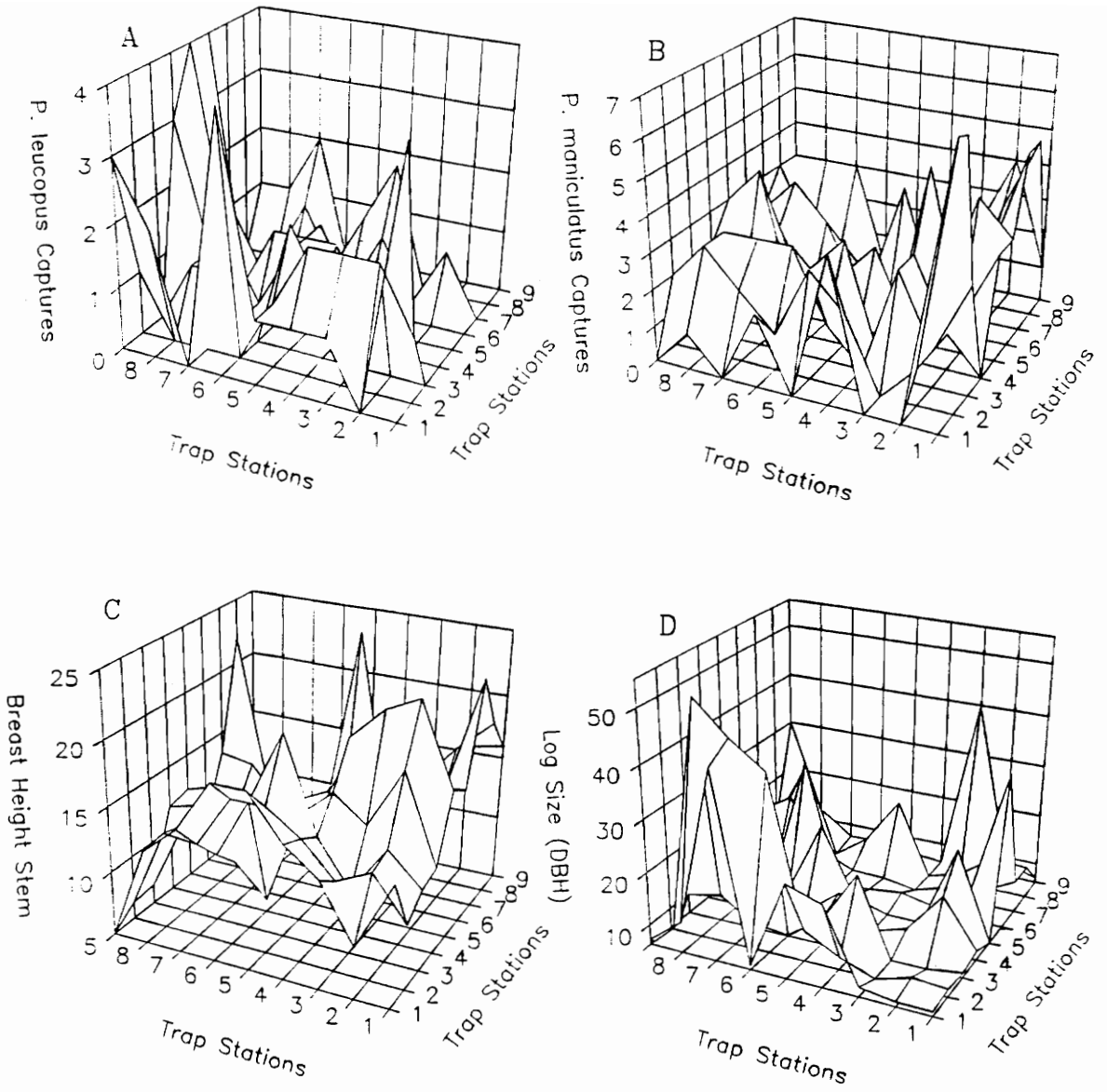


Fig 13 - Three-dimensional representation of (A) *P. leucopus* and (B) *P. maniculatus* habitat use and corresponding microhabitat for (C) breast height stem densities (SDBH) and (D) log size (LOGS) at the recovery site. The X and Y axis represent all sampling points on the recover site grid and the Z axis either represents capture abundances or habitat characteristics that correlate significantly with small mammal distributions.

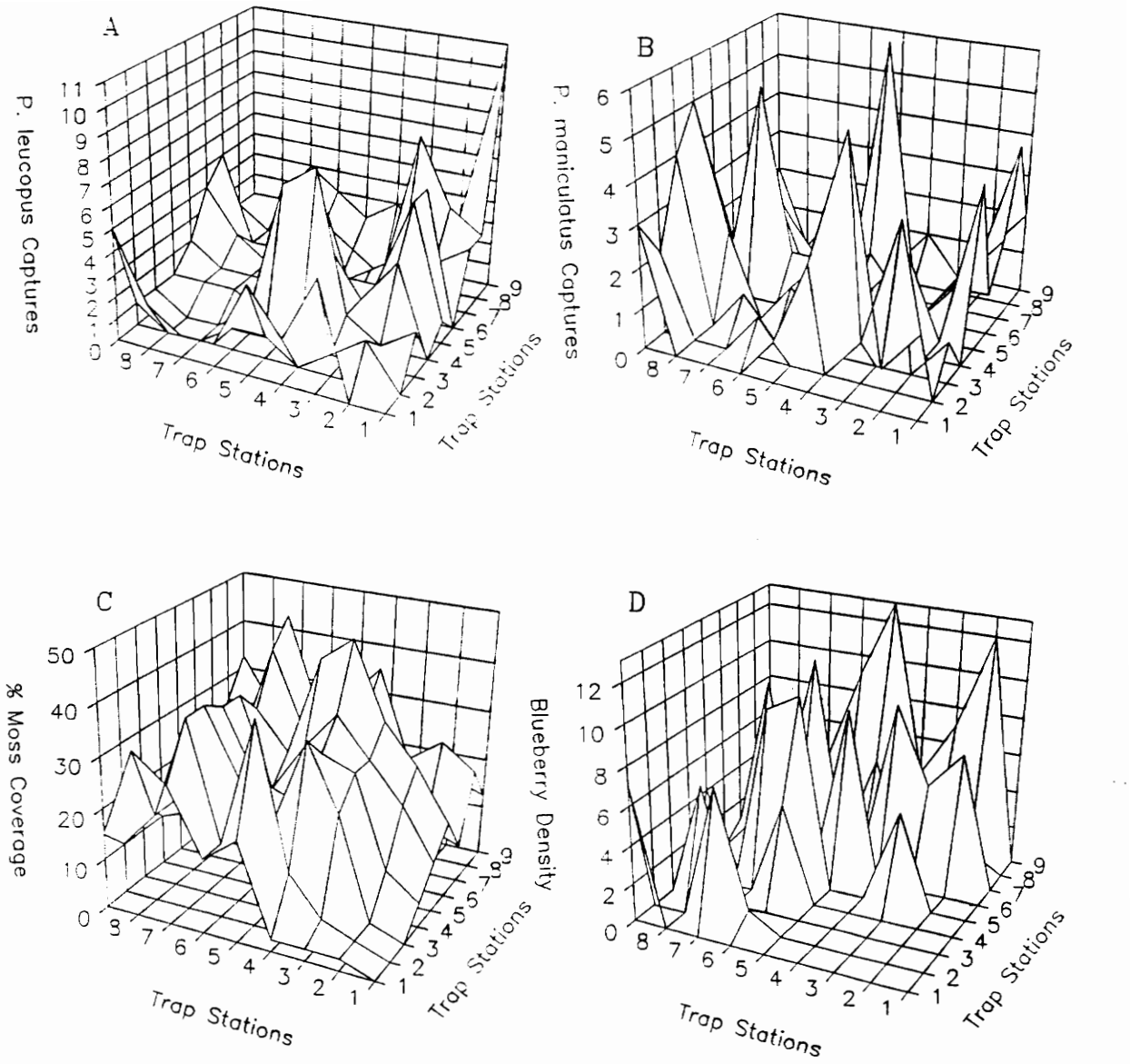


Fig 14 - Three-dimensional representation of (A) *P. leucopus* and (B) *P. maniculatus* habitat use and corresponding microhabitat for (C) moss coverage (BRYC) and (D) blueberry densities (VAC) at the in process site. The X and Y axis represent all sampling points on the recover site grid and the Z axis either represents capture abundances or habitat characteristics that correlate significantly with small mammal distributions.

Macroscale Analysis - A pooled CDA involving all species caught at all sites was performed to develop a general understanding of macroscale habitat characteristics of small mammal distributions. Species' captures pooled across all sites and each sites' habitat mean were included in the analysis. This analysis characterizes the associations of the small mammal species to a particular stage of disturbance (Fig. 15, Table 9).

B. brevicauda, C. gapperi, P. leucopus, Sorex Spp., and *T. striatus* all exhibited their highest associatins to the high mortality site (Table 9). *P. maniculatus* and *P. leucopus* were the only species that exhibited high associations to the in process site (Table 9). *P. maniculatus* exhibited the highest association of any species to any site to the recovery site, where as *B. brevicauda* and *T. striatus* also exhibited high associations to the recovery site (Table 9). *P. leucopus* exhibited a high association to the reference site, but this may be biased by the high densities they achieved during the summer of 1992 (Table 2).

The four sites were merged together into a three-dimensional construct which represents a contiguous landscape with a gradient from highly disturbed areas to undisturbed oak forest (Fig. 16 and 17). Along these gradients, habitat variables important to small mammal

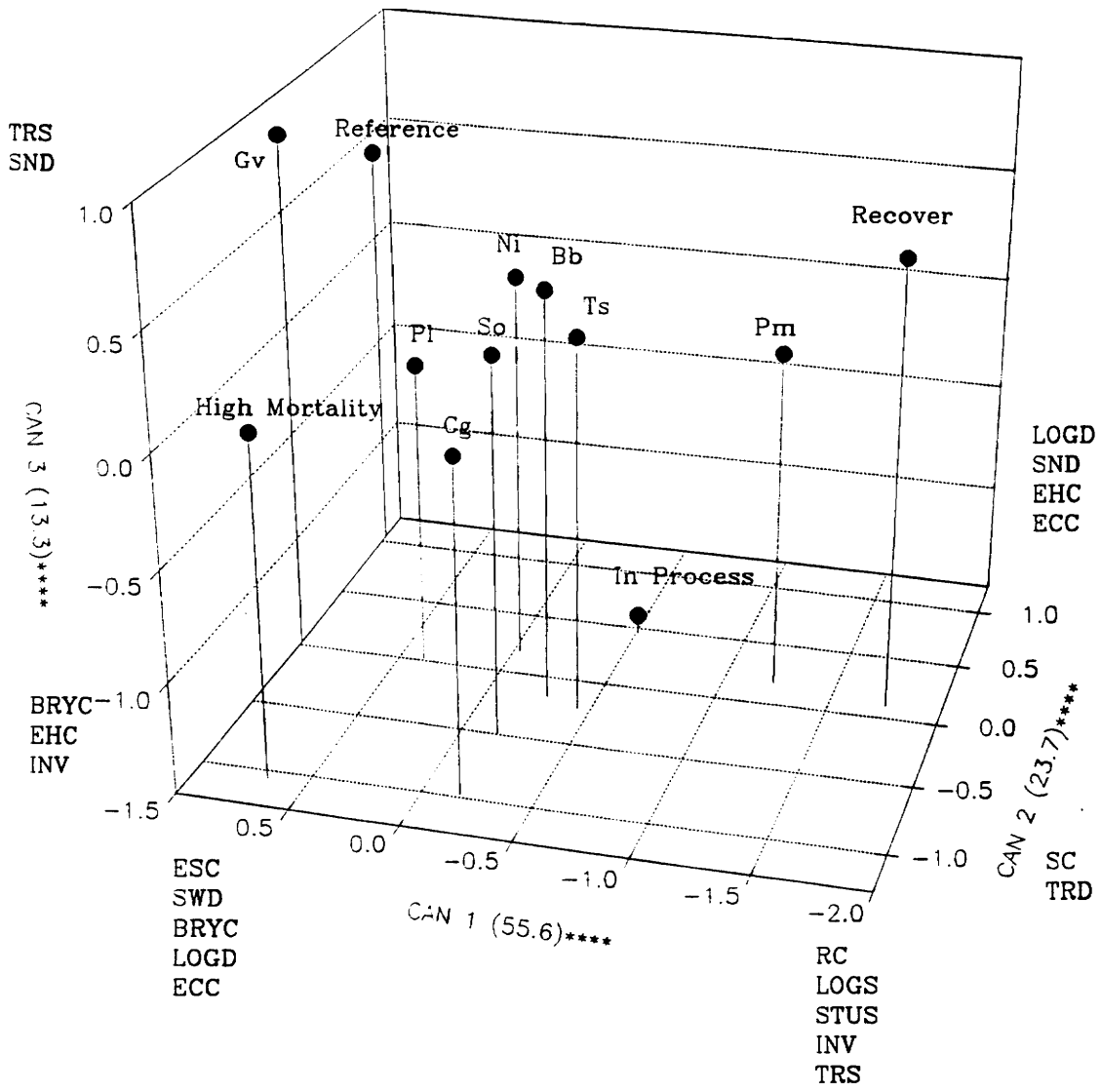


Fig 15 - CDA of all capture data of small mammal assemblages throughout the study. Only variables not affected seasonally were used in the analysis. All variables presented along axes significantly discriminated small mammal distributions (DF=11, 1843, P=0.0001). Overall small mammal habitat use was significantly different (Wilks' Lambda multivariate F approximation, df=154, 15974, F=11.82, p<0.0001). Sample sizes for species are presented in Table 4.

Table 9 - Species associations with different stages of disturbance. Numbers are Mahalanobis squared distances derived from CDA. Lower numbers indicate higher associations to sites (e.g. *B. brevicauda* has its highest association to the high mortality site). Assemblage association is the mean of all species habitat association scores at each site and is a measure of overall site preference for all species.

Species	High Mortality	In Process	Recover	Reference
B. brevicauda	1.98	3.64	2.51	3.30
C. gapperi	1.56	4.66	4.83	6.15
G. volans	3.34	8.77	9.23	2.73
N. insignis	2.74	3.77	3.84	2.45
P. leucopus	1.29	2.79	5.10	1.80
P. maniculatus	5.18	2.85	0.69	5.97
Sorex spp.	1.18	3.77	3.04	3.96
T. striatus	2.49	3.29	2.53	4.11
Assemblage Association	2.47	4.18	3.97	3.81

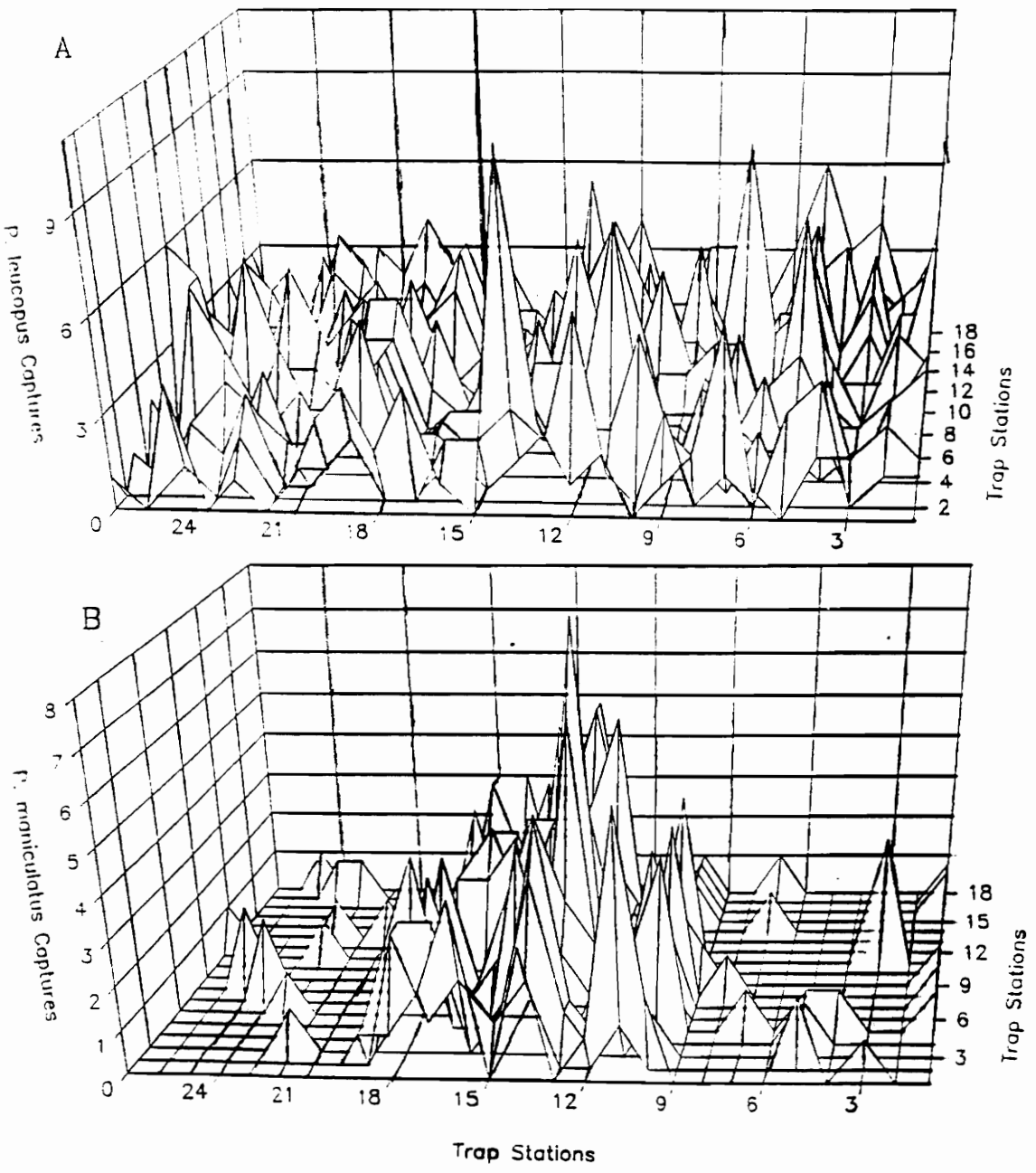
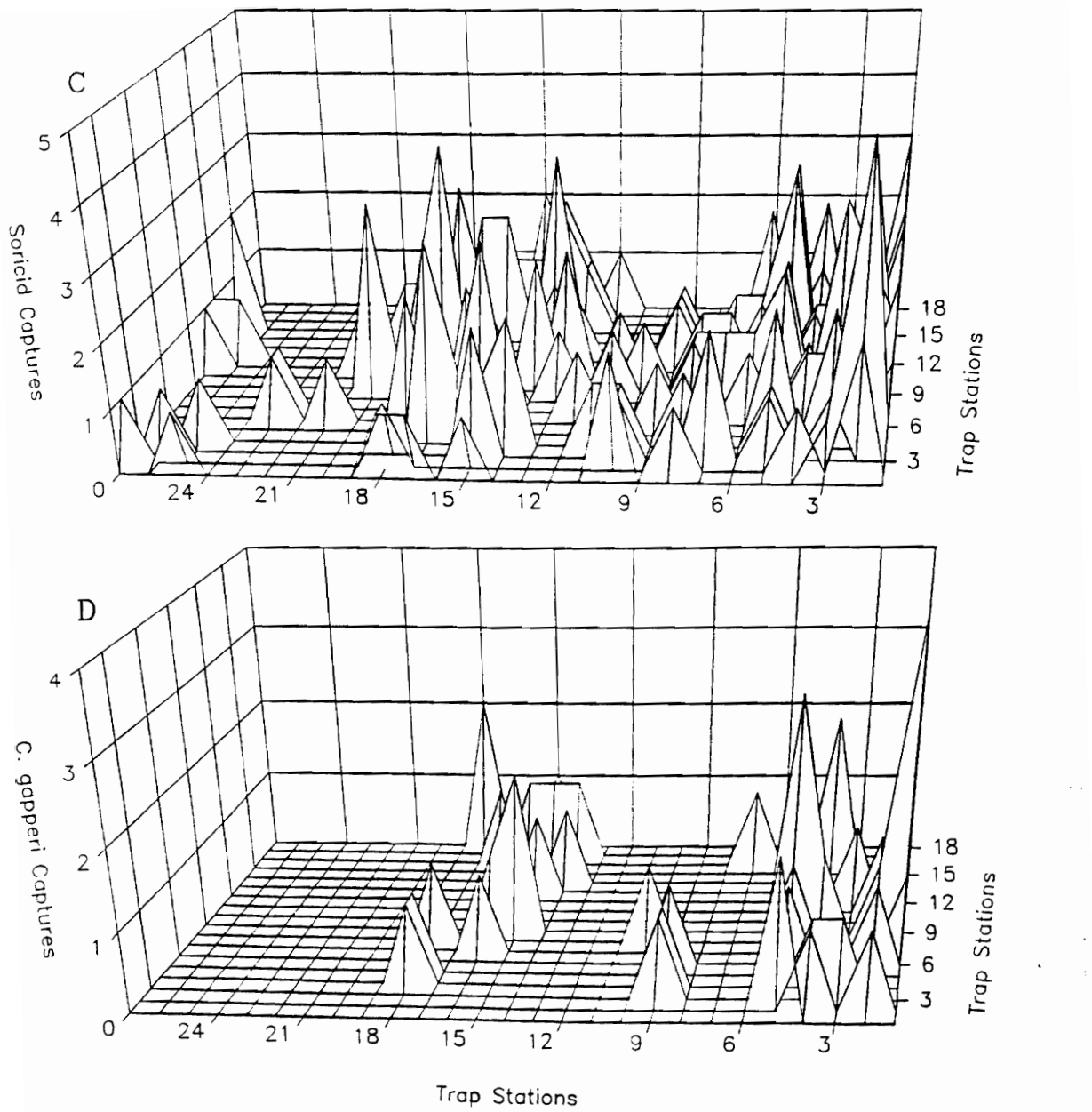


Fig 16 - Three-dimensional representation of (A) *P. leucopus*, (B) *P. maniculatus*, (C) Soricids and, (D) *C. gapperi* spatial use across all sites. The X and Y axis represent all sampling points at all sites and the Z axis represents capture abundances at each sampling point. Along the X axis from 0 to 9 represents the high mortality site, from 9 to 14 represents the in process site, from 14 to 19 represents the recover site, and from 19 to 27 represents the reference site. These figures correspond with the habitat mosaics depicted in figure 17.


C
Soricid Captures
0
1
2
3
4
5
24
21
18
15
12
9
6
3
Trap Stations
18
15
12
9
6
3
D
C. gapperi Captures
0
1
2
3
4
24
21
18
15
12
9
6
3
Trap Stations
18
15
12
9
6
3
Trap Stations

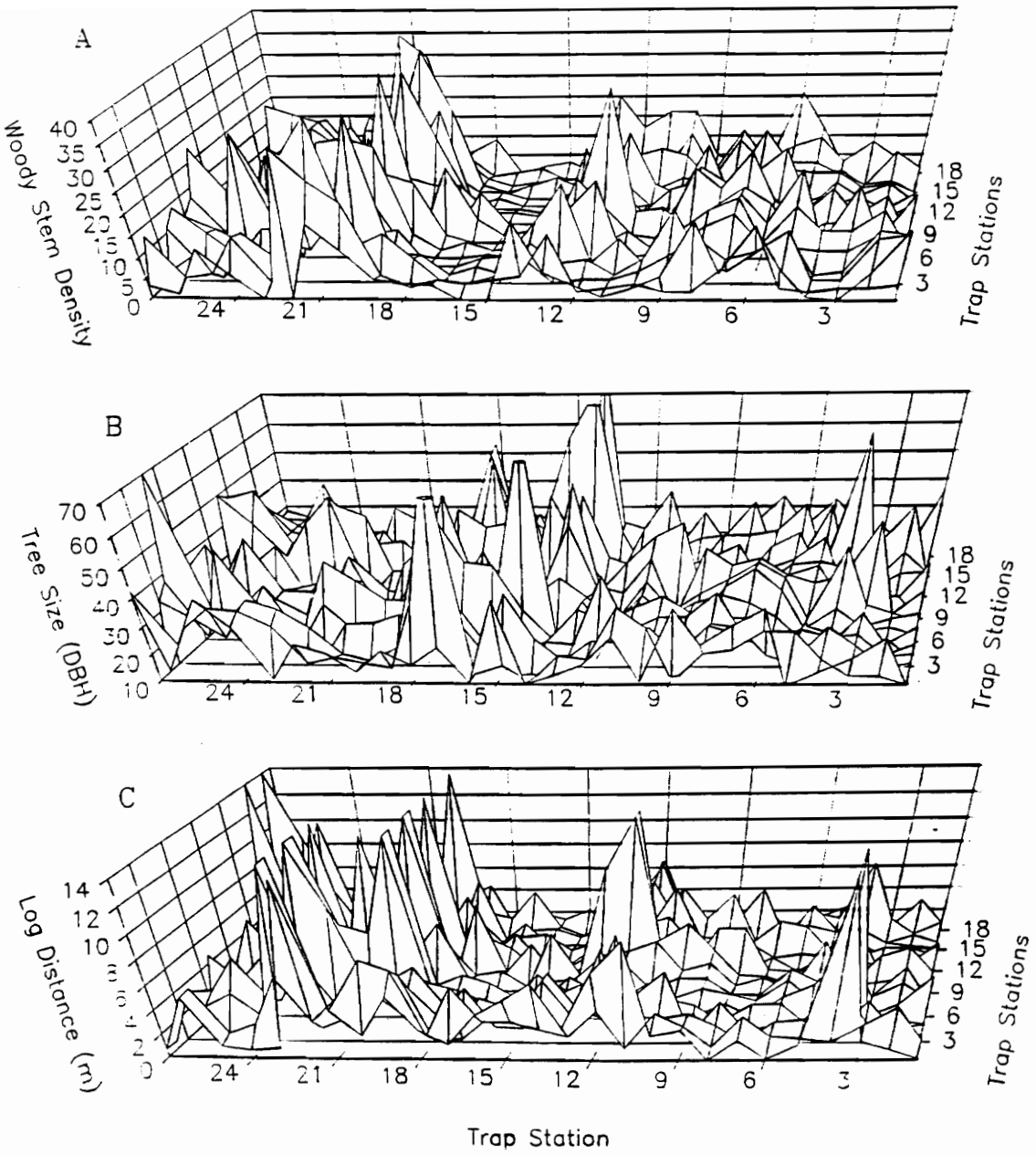
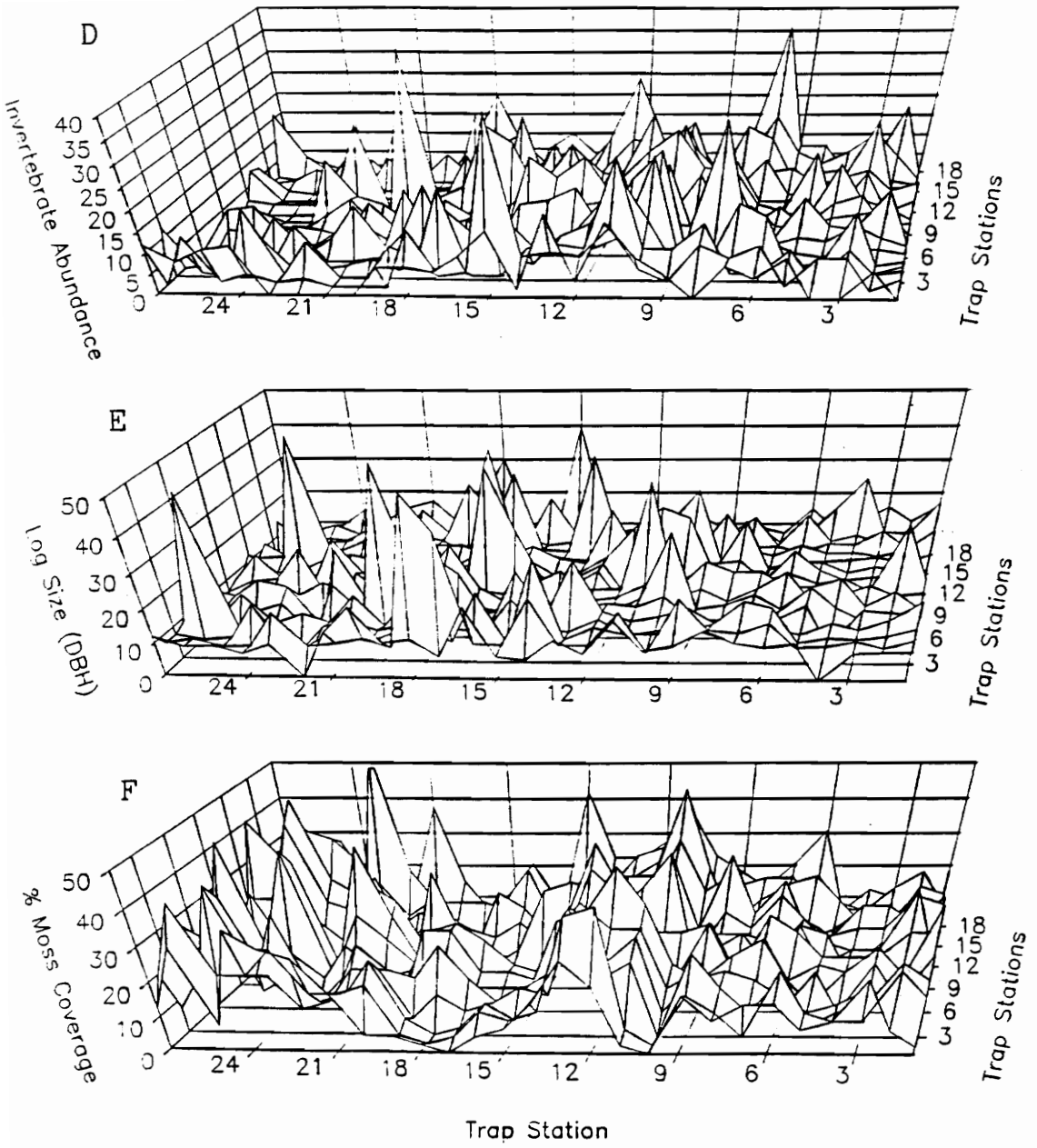


Fig 17 - Three-dimensional representation of a habitat mosaic of (A) woody stem density, (B) tree size, (C) log distance, (D) invertebrate abundance, (E) log size and, (F) moss coverage across all sites. The X and Y axis represent all sampling points at all sites and the Z axis represents habitat characteristics that correlate significantly with small mammal distributions. Along the X axis from 0 to 9 represents the high mortality site, from 9 to 14 represents the in process site, from 14 to 19 represents the recover site, and from 19 to 27 represents the reference site. These figures correspond with small mammal captures in figure 16.


D
Invertebrate Abundance
40
35
30
25
20
15
10
5
0
24
21
18
15
12
9
6
3
Trap Stations
18
15
12
9
6
3
E
Log Size (DBH)
50
40
30
20
10
0
F
% Moss Coverage
Trap Station

distributions were compared to capture frequencies at all the trap stations. *P. leucopus* had the most ubiquitous distribution of all the small mammals, but tended to have their greatest peaks at the high mortality site and to a lesser degree at the in process site (Fig 16A). Macrohabitat characteristics that coincide with their distributions were high log (Fig. 17C) and invertebrate abundances (Fig. 17D) and moderate ground woody stem densities (Fig. 17A). *P. maniculatus* exhibited strong associations with the in process and recovery sites (Fig. 16B), where macrohabitat characteristics were high abundances of large logs, large trees, and invertebrates and low ground woody stem densities (Fig. 17). The structure of the forest stands at the in process and recovery sites suggests that they were more mature than the reference site forest. Shrews (*B. brevicauda* and *Sorex* spp.) were pooled into an insectivore guild (Soricids) (Fig 16C) and were moderately associated with high ground invertebrate abundances and high abundances of large logs (Fig. 17). *C. gapperi* exhibited strong associations with the high mortality site and to a lesser degree with the recovery site (Fig. 16D). They were associated with high log and invertebrate abundances (Fig. 17).

Chapter 1

Discussion

The results of this study indicate that small mammals are influenced by gypsy moth disturbance of chestnut oak habitats. This comparative study demonstrated that a significant change in forest habitat occurs after successive defoliations. This change in forest structure was coincided with an increase in the diversity of favorable microhabitats and niches for small mammals, which in turn increased small mammal species diversity.

There were two scenarios of gypsy moth induced disturbance: 1) a habitat with dense understory prior to disturbance that became the high mortality site, and 2) a habitat with very little understory prior to disturbance that became the in process site. These sites represented different stages of disturbance, which were probably on different successional trajectories because of differences in the initial conditions of each sites' forest structure. The high mortality site probably did not have substantial numbers of herbaceous plants in its initial stages of disturbance because mountain laurel shading probably prevented herbaceous species from getting established. Due to its low abundance of mountain laurel, the in process site had no light limitations after canopy defoliation and

herbaceous plants were able to get established. These differences in initial conditions between the high mortality and in process sites were probably the reason for the observed differences in small mammal assemblages at these sites. At the high mortality and in process sites there was an increase in species diversity relative to the reference site, but the small mammal assemblage at each site was different. Differences in forest structure produced different small mammal assemblages after disturbance because different habitats have varying trajectories of succession in response to different initial environmental conditions (i.e. available light, soil nutrients, soil moisture for colonizing plants) and different sources of plant and animal colonization from immediate and adjacent habitats.

Most small mammal species increased in abundance in response to gypsy moth disturbance. This means that there were changes in habitat structure that increased the reproductive success of individuals colonizing or previously residing in the disturbed habitats. *P. leucopus* had their most stable abundances at the high mortality site, which had more snags, large logs, and shrub cover and greater ground invertebrate abundances relative to the reference site. Logs are important resources to *P. leucopus* because they provide quiet runways for avoidance of auditory predators such as

owls (Planz and Kirkland, 1992) and an abundance of invertebrates for food (Lovejoy, 1975). High shrub densities provide cover from potential avian predators (Kotler, 1984), while snags provide an abundance of potential nesting cavities (Dooley and Dueser, 1990), which could be an alternative to ground nests. In addition, the presence of gypsy moth larvae and pupae probably provided *P. leucopus* with additional food. It has been demonstrated that *P. leucopus* move into habitat with high abundances of gypsy moth larvae to exploit this food resource (McShea and Francq, 1984).

P. maniculatus had their highest abundance at the recovery site and their second highest abundance at the in process site. They were present at the high mortality site, but at low abundance. It was difficult to relate *P. maniculatus* occurrences at the recovery and in process sites to their occurrences at the high mortality site because these sites had different initial conditions prior to defoliation. It appears, relative to the reference site, that defoliation could benefit *P. maniculatus* at the in process and high mortality sites, but to different degrees. *P. maniculatus* were only present at the high mortality site when *P. leucopus* were at low abundances, but had their highest abundances in the last sample of the study. This

makes their future at the high mortality site unclear. *P. maniculatus* were not abundant at the reference site. They were present at the reference site in summer 1992 at low abundance, but disappeared by winter 1993. This coincided with the collapse of high abundance populations of *P. leucopus*.

The in process site was the only habitat where *P. maniculatus* and *P. leucopus* coexisted throughout the entire study. This habitat differed from other habitats by having more herbaceous and moss cover, greater invertebrate abundances, and patchy canopy cover. Most studies of microhabitat use between these species have demonstrated either little microhabitat separation on the basis of ground structure (Wolff and Dueser, 1986) or separation on the basis of rock cover (Parren and Capen, 1985, Barry et al., 1989). Other studies have suggested vertical stratification of microhabitat contributes to coexistence with *P. maniculatus* being more arboreal than *P. leucopus* (Barry et al., 1984, Harney and Dueser, 1987, Dooley and Dueser, 1990). At the in process site, *P. leucopus* used microhabitat with more moss cover, higher breast height stem densities, and more blueberry shrubs relative to *P. maniculatus*. In contrast, *P. maniculatus* used microhabitat that was relatively undisturbed and had simple ground cover structure

(low ground stem densities, less herbaceous cover). Neither species' use of snags, trees, or rock cover significantly differed from each other at the in process site. This differs markedly from previous studies on these species' microhabitat use (Parren and Capen, 1985, Barry et al., 1989, Dooley and Dueser, 1990). These differences were probably due to differences in habitat structure between previous studies and this study. The coexistence of *P. maniculatus* and *P. leucopus* populations have never before been investigated in this habitat type.

At the in process site, the early successional nature of some patches of microhabitat interdispersed with undisturbed patches of microhabitat probably allowed for the coexistence of the *Peromyscus* species in this habitat. Even though these species have similar dietary requirements (Wolff et al., 1985), increased abundances of early successional flowering plants with large seed productions (Newell and Tramer, 1978), increased abundances of invertebrates associated with fallen logs (Lovejoy, 1975), and patches of blueberry shrubs probably adequately fulfilled both species' dietary requirements. The only time these species had significant microhabitat overlap at the in process site was at peak fall abundances in 1992. Despite the diversity of food resources at the in process site, *P.*

leucopus niche breadths were relatively low compared to their niche breadths at the high mortality site where *P. maniculatus* was either absent or in low abundances. This might be an indication that *P. maniculatus* and *P. leucopus* limited each other in some capacity at the in process site.

P. maniculatus was the numerically dominant species at the recovery site, which had the most rock cover and the largest trees and logs of any site. The recovery site was similar to habitats in which this species has been known to thrive (Parren and Capen, 1985, Wolff and Dueser, 1986, Krohne et al., 1988, Barry et al., 1989). *P. maniculatus* never significantly deviated from the mean habitat available at this site and always had high niche breadths relative to the in process site. High niche breadths suggest that this habitat was of high quality for *P. maniculatus*.

Interactions between *Peromyscus* species at the recovery site were different from those at the in process site. In the fall of 1992 at the recovery site, *Peromyscus* species microhabitat use significantly differed, which coincided with their combined peak abundance during this study. The significant separation of microhabitat use at high abundance between the *Peromyscus* species at the recovery site could indicate intense competition in the fall of 1992. This preceded the disappearance of *P. leucopus* after the winter

of 1993, which could indicate that *P. maniculatus* was better adapted to this habitat and thus competitively superior. The dramatic increase in *P. maniculatus* niche breadth in fall 1993 suggests that there was a competitive release due to the disappearance of *P. leucopus*. Given the circumstances, it probably means that subordinate members of the *P. maniculatus* population were not dispersing as far as they would in the presence of a potential competitor. Further, the delayed niche release may have been the result of drought conditions in the area (USFS George Washington National Forest, Pedlar District weather data).

Density-dependent aggression between these species has been documented (Wolff et al., 1983, Wolff, 1985b). Wolff (1985b) suggested that interspecific aggression occurs above a threshold of 25 to 30 mice/Ha (both species), and that home ranges would not constrict but begin to overlap. Interspecific home range overlap was not measured in this study, but niche overlap and the degree of microhabitat separation at the recovery site clearly show that these species were using distinctly different microhabitat in fall 1992. At this time, there were 53 mice/Ha (both species), which exceeds Wolff's (1985b) density-dependent threshold. Assuming that measures of interspecific home range and niche overlap are conceptually similar, the results of this study

are contrary to those reported by Wolff (1985b). This could be due to habitat structure differences between this study and Wolff's, but because no data is available from Wolff's study this can not be determined. Niche overlap measures were in concordance with Wolff's study (1985b) only at the in process site, but this habitat type was different from his study and abundances did not greatly exceed his threshold. It therefore seems plausible to consider habitat structure as a key factor in determining whether or not *P. leucopus* and *P. maniculatus* can coexist. If this is true, there will be differences in carrying capacity among habitat types where they coexist dependent upon habitat structure.

Soricids (*B. brevicauda, Sorex spp.*) were more abundant at the disturbed sites than the reference site. An increase in invertebrate abundances (esp. gypsy moth larvae and pupae) at the disturbed sites probably increased the available food resources for Soricids. Shrews along with many other small mammals are avid predators of gypsy moth larvae and pupae (Campbell and Sloan, 1976 and 1977b, Smith, 1985). Along with gypsy moth larvae, increases in fallen log and snag densities associated with invertebrates probably increased the potential resource base of Soricids (Lovejoy, 1975).

Interspecific interactions were variable for *B. Brevicauda* as they never used significantly different microhabitats from *C. gapperi* and rarely from the *Sorex* spp. Overlap of microhabitat space between *C. gapperi* and *B. brevicauda* can be attributed to similar microhabitat requirements in that they both have high moisture requirements (Getz, 1968, Wrigley et al., 1979). Even though they use similar microhabitat, they do not compete because shrews are secondary consumers while *C. gapperi* are primary consumers (Schloyer, 1977, Martell, 1981).

B. brevicauda overlap with *Sorex* spp. can be attributed to both similar microhabitat and dietary requirements. Overlap between these species occurred only in the fall when abundances of most small mammal species were highest. Fox and Kirkland (1992) presented a size-based species-assembly rule for Soricids that suggests larger shrew species will outcompete smaller shrew species for favorable food resources and displace smaller shrews into different foraging microhabitats. The resulting diversity of Soricids within a habitat type is dependent upon the availability of different foraging microhabitats. In this study, three different sizes of shrews were caught at the high mortality and recovery sites; *B. brevicauda* (10-15 g), *Sorex fumeus* (6-9 g), and *Sorex cinerus* and *Sorex hoyi* (2-7

g). Microhabitat discriminations among these species were not measured in this study, but based on Fox and Kirkland's assembly rule, the availability of different types of microhabitat must have increased to allow for the coexistence of Soricids.

At the high mortality site, *Sorex* spp. used microhabitat with higher breast height stem densities, more rock cover, less herbaceous cover, and lower ground stem densities relative to *B. brevicauda*. However, at the recovery site, *Sorex* spp. used microhabitat with more herbaceous cover, smaller logs, less rock cover, and lower breast height stem densities relative to *B. brevicauda*. At the high mortality site, invertebrate availability was probably very high, which could imply that there was no need for segregation of microhabitat on the basis of logs or snags and that there might have been subtle differences in the invertebrate fauna based on rock cover or the amount of herbaceous cover. At the recovery site, *B. brevicauda* exploited larger logs than *Sorex* spp. and displacement may have occurred.

A study at Land Between the Lakes in Kentucky and Tennessee revealed significant overlap of microhabitat use among a Soricid assemblage (Feldhamer et al., 1993). It was suggested that competition was alleviated among Soricids

through size differences, different timing of reproduction, and temporal differences of aboveground foraging activity (Feldhamer et al., 1993). Although sample sizes were small in the present study, a different seasonal pattern of aboveground activity between *Sorex cinerus* and *Sorex fumeus* was detected. At the recovery and high mortality sites, *S. cinerus* were caught during the summer, and *S. fumeus* were dominant in the fall.

Interactions between *P. leucopus* and *B. brevicauda* were complex. At the high mortality site, when *P. leucopus* abundance was high, *B. brevicauda* niche breadths were low (1992), but when *P. leucopus* abundance was low, *B. brevicauda* had higher niche breadths (summer and fall 1993). These two species used significantly different microhabitat only in the summer of 1992 at the high mortality site but separated significantly at all other sites. *P. leucopus* opportunistically exploits seasonally variable resources (i.e. seeds and berries), but their diets always have high proportions of invertebrates (Whitaker, 1963, Wolff et al., 1985). This suggests that *B. brevicauda* and *P. leucopus* can at times have very similar diets. Zegers and Ha (1981) claimed that potential competition for food resources may be alleviated as *P. leucopus* exploits the arboreal microhabitats. Yet another study described a high

microhabitat overlap between these species, but competition was ruled out because of ecological dissimilarity (Seagle, 1985). In this study, these species used different microhabitats at all sites except at the high mortality site, which can be attributed to site differences in habitat structure. At the recovery site, *B. brevicauda* were associated with large logs and high rock and shrub cover, and *P. leucopus* were associated with high densities of logs, but did not discriminate by log size. Niche overlap was high at the high mortality site because microhabitat variables that were important to the separation of *P. leucopus and B. brevicauda* at the recovery site were less prevalent at the high mortality site. There was less rock cover and variability of log size at the high mortality site relative to the recovery site. Therefore, at the high mortality site, *B. brevicauda* shared log microhabitat with *P. leucopus* because of low variability of log size and less rock cover. *B. brevicauda* niche breadths probably increased in the second year of the study because they were able to exploit a greater variety of microhabitats in response to the lower abundance of *P. leucopus*.

C. gapperi had their highest abundance at the high mortality site, but their abundance in this study was low relative to other studies (Wolff and Dueser, 1986, Barry et

al., 1989). *C. gapperi* are generally restricted to high moisture microhabitats (Getz, 1968) and are uncommon in dry oak forests (Kirkland, 1990), which would explain their absence at the reference site. Extensive defoliation increases the amount of moisture that reaches the forest floor (Grace, 1986, Mconnell, 1988), creating a more mesic microhabitat for *C. gapperi*. There were other factors that might have created a more mesic environment for C. gapperi. Because most of the trees at the high mortality site were dead, there was very little evapotranspiration, and this probably would have increased the amount of water in the soil. Further, the homogeneous shrub cover probably acted as a shield from higher temperatures due to less evapotranspiration, and thus decreased the amount of evaporation of water from the soil surface. Kirkland (1990) attributed increases in *C. gapperi* abundance at oak clearcuts to morning dew covering shrub and herbaceous ground cover, which increased the moisture potential of the ground level microhabitat relative to an uncut oak forest.

Low abundance of *C. gapperi* in this study can be explained by the absence of habitat characteristics that this species prefers at the sites where they were present. *C. gapperi* microhabitat use has been generally associated with rock cover (Wolff and Dueser, 1986, Barry et al., 1989,

Stewart, 1990), and rock cover may be a limiting factor for *C. gapperi* in this study. Barry et al. (1989) demonstrated that *C. gapperi* separates from *P. leucopus* by residing in microhabitat with high rock cover, which in turn facillitated a noncompetitive coexistence. Rock cover was low at the high mortality site relative to Barry et al's. study site. *C. gapperi* and *P. leucopus* did not use significantly different microhabitats in fall 1992 and 1993 when both species were at their peak abundance for the those years. When *P. leucopus* abundance was five times lower in fall 1993 than fall 1992, *C. gapperi* exhibited a dramatic increase in niche breadth relative to other seasons. It is possible that *P. leucopus* was limiting *C. gapperi* abundance because of the absence of microhabitat characteristics (rock cover) that would have otherwise facillitated a noncompetitive coexistence.

P. leucopus, P. maniculatus, the Soricids, and *C. gapperi* abundance increased in response to gypsy moth disturbance, but the extent to which the disturbance affected *T. striatus* and *G. volans* is unclear. *T. striatus* did not show a positive association with any site. Their niche breadths were always low and their microhabitat use usually significantly deviated from the mean habitat available at all sites. *T. striatus* used significantly

different microhabitat from all species except for the insectivorous Soricids.

At the disturbed sites, important spring and summer food items were abundant (Leptodopteran larvae, flowers, fungi), but important fall food items such as acorns (hard mast) were absent (Wrazen and Svendsen, 1978). Except at the recovery site in 1993 where hickory and oaks produced hard mast, the disturbed sites had no hard mast crops because of tree stress related to gypsy moth defoliation (Gottschalk, 1989). Because *T. striatus* have long bouts of torpor in the winter when they depend upon stored hard mast (i.e. acorns, hickory nuts) and fall fat reserves, absence of fall hard mast would be detrimental to their overwinter survival. Perhaps none of the sites were of sufficient quality for *T. striatus* and they were only opportunistically exploiting these habitats. *T. striatus* have not been known to establish populations in clearcuts, but they do opportunistically exploit oak clearcuts adjacent to uncut oak forests (Kirkland et al., 1985). *T. striatus* are common in deciduous forests with high evergreen shrub cover (Linzey and Linzey, 1971, Dueser and Shugart, 1978). The reference site habitat was similar to habitats that *T. striatus* generally inhabit, but they were not common at the reference site. Chestnut oaks were the only prevalent hard mast producer at this

site, which means that a good hard mast crop was only present every 3 to 4 years (Sork et al. 1993). Due to the monotypic nature of hard mast producers at the reference site and oaks having 3 to 4 year cycles of good mast crops (Sork et al., 1993), plentiful overwinter food resources were probably very intermittent.

Like *T. striatus*, *G. volans* extensively depend on acorn mast crops (Harlow and Doyle, 1990), but they do not have dormancy strategies to endure the hardships of winter (Stapp, 1992). *G. volans* were consistently present at the reference site, but not at high abundance. Although they were present at the high mortality site during winter 1993, it is conceivable that this species is very sensitive to changes in habitat structure. Life history traits such as no seasonal torpor, low metabolic rates, long periods of maternal investment, slow rate of growth and maturity, and low annual fecundity (Stapp, 1992) could make them more sensitive to habitat alterations than other species. Even though data were limited in this study on *G. volans*, the data suggest that changes in habitat structure and the food resource base negatively affect their populations. Like *T. striatus*, it was possible that the reference site was of low quality for *G. volans* and was only extensively exploited in years of good acorn crops.

Synthesis

Gypsy moth disturbance of chestnut oak habitat increased the abundance of small mammals and the number of potentially coexisting species within a given area. There were changes in habitat structure that increased the food resource base diversity, nesting sites, potentially decreased vulnerability to predators, and enhanced microenvironment for low moisture intolerant species. This suggests that gypsy moth disturbance at least temporarily improves habitat quality for small mammals of areas dominated by chestnut oaks. The longterm effects of gypsy moth disturbance on forest communities is not well documented (Campbell and Sloan, 1977, Hix et al., 1991), but general trends point to longterm reductions in hard mast production in areas of intense infestations. The reduction of hard mast producing trees will be the result of recruitment of more gypsy moth tolerant trees, such as birch (*Betula* spp.) and red maple (*Acer rubrum),* into oak forest communities (Gotschalk, 1989, Hix et al., 1991). This could possibly have a longterm impact on mammals that depend on hard masts.

Competition could be an important factor in determining the longterm outcome of small mammal assemblages after gypsy

moth disturbance. Competition is an important mechanism that partially determines species' local distributions (Schoener, 1982 and 1983, Rosenzweig and Abramsky, 1986, Dueser et al., 1989). Niche patterns demonstrated in this study suggest that competition could play an important role in the reorganization of small mammal assemblages after disturbance through successional time. The reference site had few species interactions, while the presence of more species at disturbed sites resulted in an increase of niche overlap among species. Direct evidence of competition would have to be resolved experimentally (Dueser et al., 1989), but an emphasis should be placed on the potential for competition at the disturbed sites.

In general, species niche breadths and niche overlaps increased in the fall when small mammal abundance was highest. This pattern is consistent with the seasonal dynamics of a small mammal assemblage on Asseteague Island, Virginia (Cranford and Maly, 1990). In addition, small mammal abundance was low in summer and fall 1993, but there was high niche overlap among small mammals. Even though high niche overlap might not be expected at low small mammal abundance, drought conditions existing at the study sites in summer 1993 could explain the high degree of overlap observed among small mammal species. These results indicate

that intensity of competition may have an inverse density-dependent relationship dependent upon the degree of environmental stress. Theoretically, intensity of competition should increase as population densities increase because all members of each species population will not be able to occupy a limited optimal habitat (Rosenzweig, 1981, Rosenzweig and Abramsky, 1986, Brown, 1989) and during times of resource scarcity induced by environmental stress (i.e. winter months, drought conditions)(Boag and Grant, 1981, Schoener, 1983, Chesson and Rosenzweig, 1991).

It is obvious from the results of this study that there are many abiotic and biotic factors that will influence small mammal assemblages after disturbance. The magnitude of the disturbance and forest habitat structure prior to disturbance will determine the initial impact that a disturbance will have on small mammal assemblages. On a longterm temporal scale, factors that influence successional processes after disturbance, such as frequency of weather disturbance and potential sources of colonization for plants, will ultimately drive the biotic mechanisms (e.g. predation vulnerability, competition) that determine small mammal assemblage structure.

Chapter 2

Quality of Habitat Created by Gypsy Moth Disturbance from the Perspective of *Peromyscus* spp.

Areas of gypsy moth (*Lymantria dispar*) defoliation in eastern deciduous forests can reach 5 million hectares annually and recent attempts to keep gypsy moth populations in check have been relatively unsuccessful (Grace, 1986). Gypsy moth disturbance can permanently alter forest habitat structure (Campbell and Sloan, 1977a, Hix et al. 1991). Due to differing susceptibilities of individual trees and stands of trees to defoliation and annual variations in the intensity of defoliation (Houston, 1981), gypsy moth disturbance creates a mosaic of habitat patches. These habitat patches will probably vary in quality and these changes in habitat quality will probably be reflected in the demographic characteristics of the animals that live there (Adler and Wilson, 1987). *Peromyscus leucopus* and *Peromyscus maniculatus* are small mammal species that are common in eastern deciduous forests. Due to extensive research on demographic properties of *Peromyscus leucopus* and *Peromyscus maniculatus* populations, specific criteria can be

established for assessing habitat quality relative to demography.

Demographic characteristics of populations of *P. leucopus* and *P. maniculatus* have been reported to vary by habitat type (Sullivan, 1979, Martell, 1983, Van Horne, 1982, Adler and Tamarin, 1984, Adler and Wilson, 1987, Linzey, 1989). Several studies have reported that disturbed habitats (usually clearcuts) are dispersal sinks for subordinate individuals of *Peromyscus* populations that reside in more optimal adjacent habitats (Sullivan, 1979, Martell, 1983, Linzey, 1989). Linzey (1989) found a difference in habitat quality between undisturbed forest habitat and clearcuts based on a experimental removal study of *P. leucopus* populations residing in an adjacent forest and clearcut. Forest residents never moved to the clearcut after the removal of clearcut residents, but after removal of forest residents, a large proportion of the clearcut residents colonized the forest. It was determined that the disturbed habitat served as a dispersal sink for behaviorally subordinate individuals (Linzey, 1989).

It has been suggested that *Peromyscus* populations exhibit more intrinsic regulation in high quality habitats than low quality habitats (Van Horne, 1983, Adler and Wilson, 1987). Many hypotheses have been proposed about the

intrinsic regulation of populations. Nadeau et al. (1981) hypothesized that at high densities aggressive behavior of adult males towards juveniles and subadults results in the dispersal of these age classes and regulates populations. Dispersal of juveniles has also been attributed to aggressive territoriality of adult females within high density populations (Metzgar, 1971, Hansen and Batzli, 1978, Bowers and Smith, 1979). Fretwell's (1972) ideal-despotic model proposes that over exploitation of resources in high density populations is limited by aggressive territoriality of dominant females, thereby excluding surplus subordinate members of a population from optimal microhabitat patches. It seems probable that both sexes play a role in population regulation. Microhabitat segregation among sex and age classes is a strategy to reduce resource overlap and thus intraspecific competition in high quality habitats.

Demographic structure of populations may exhibit shifts that reflect the immediate environmental conditions of a habitat. As environmental conditions improve, the populations' demographic structure will shift to reflect the good conditions and vice versa (Adler and Wilson, 1987). Linzey and Kesner (1991) suggested that a measure of habitat suitability can be derived from demographic characteristics of a population. Several studies have suggested that a

population tending towards K-selected demographic characteristics (i.e. stable densities, high proportions of adult females, stable age structure) (Pianka, 1970) is demonstrating good demographic performance and thus resides in suitable habitat (Adler and Tamarin, 1984, Adler and Wilson, 1987, Linzey and Kesner, 1991).

In this study, microhabitat use by sex and age classes and several demographic characteristics of *P. leucopus noveboracensis* (white-footed mouse) and *P. maniculatus nubiterrae* (cloudland deermouse) populations were used to assess the quality of habitat resulting from gypsy moth disturbance. If habitat quality is good in areas impacted by gypsy moth disturbance: 1) at high densities there should be microhabitat segregation among sex and age classes with adult females residing in the most optimal microhabitats, and 2) populations should exhibit K-selected demographic characteristics.

Chapter 2

Study Methods

General Methods - The study methods are the same as Chapter 1 except for some different statistical procedures. Refer to chapter 1 study methods for detailed information on the study areas, sampling protocols, and trapping procedures.

Statistical Analysis - Several demographic variables were created to analyze the demographic structure of populations in multivariate space (Adler and Wilson, 1987). This analysis was used to infer differences in demographic performance among populations at different stages of gypsy moth disturbance. Variables considered for each population in the analysis were proportion of male adults, proportion of female adults, proportion of juveniles, proportion of female juveniles, a residency index, abundance, proportion of reproductive female adults, proportion of reproductive male adults, an abundance fluctuation index, and a residency fluctuation index (Detailed descriptions of these variables are given in Table 10.). The residency index was used to infer a habitats potential for having permanent animal residents (e.g. animals with established home ranges). Proportional demographic variables were arcsine square-root transformed and abundance and residency related variables were log transformed to normalize the data (Sokal and Rohlf,

Table 10 - Demographic variables used in PCA to analyze population demographic structure in multivariate space.

Variables/Abbreviations	Description
Females (FEM)	Proportion of adult and juvenile females in the population.
Adult Females (ADFEM)	Proportion of adult females in the population.
Adult Males (AMAL)	Proportion of adult males in the population.
Juveniles (JUV)	Proportion of juveniles in the population.
Juvenile Females (FJUV)	Proportion of juvenile females in the population.
Reproductive Females (FRC)	Proportion of females in the population that are in reproductive condition.
Reproductive Males (MRC)	Proportion of males in the population that are in reproductive condition.
Residency Index (RES)	An index of residency calculated as total number of captures divided by total number of individuals in the population.
Residency Fluctuation (RF) Index	A measure of a habitat's residency stability. It is calculated as the magnitude of change in the residency index between seasons.
Abundance (DEN)	Individuals per hectare.
Abundance Fluctuation Index (DF)	A measure of population stability. It is calculated as the magnitude of abundance change in between seasons.

1981). In this analysis, each sites' grids were used as a seperate population to evaluate within site differences of demographic structure. These variables were used to develop a relative measure of differences in demographic structure among grid populations. Principal components analysis (PCA) was used to analyze these variables for each population by grid by season. Unlike canonical discriminant analysis (CDA), PCA does not need predetermined classes to analyze relationships and is considered to be a good exploratory analysis. Like CDA, PCA reduces the number of variables into a few explanatory dimensions (Pielou, 1984). The relative contribution of each demographic variable to a population's demographic structure was determined by PCA (Adler and Wilson, 1987). Each grid population was treated as a separate unit in the analysis to determine similarities in demographic structure within and among sites.

Canonical discriminant analysis (CDA) was used to determine significant differences in microhabitat use among sex and age classes at each site by season. Classes were created for adult males, adult females, juvenile males, and juvenile females for *P. leucopus* and *P. maniculatus* to determine potential microhabitat segregation among these classes. These classes were used in the same manner as species classes in chapter 1. Pairwise statistical

differences among classes were determined by Mahalanobis multivariate distance measures and F-statistic approximations (Kleinbaum et al., 1988). Redundancy of microhabitat variables was reduced by use of stepwise discriminant function analysis. Variables used in final analyses at each site by season are listed in Appendix 1. The relative contribution of each microhabitat variable to the distribution of each small mammal class type was determined by CDA and each significant canonical axis was analyzed for ecologically meaningful relationships among classes and microhabitat variables. The effects interspecific interactions between the *Peromyscus* species had on microhabitat segregation among sex and age classes of the *Peromyscus* species were examined by adding both species' sex and age classes into the CDA. Significance of individual variables responsible for interspecific and intraspecific separations were determined by univariate Anova's and overall significant differences in microhabitat use were determined by the F-approximations to Wilks' Lambda statistics.

In all comparisons a minimum alpha level of 0.05 was used for statistical significance, but at times alpha levels between 0.05 and 0.1 were mentioned as tendencies towards significance.

Chapter 2

Results

***Abundances* and Macrohabitat Use** - Between the two *Peromyscus* species, *P. leucopus* populations consistently had the highest abundances at all sites except at the recovery site where they disappeared after the winter of 1993 (Fig. 18). *P. leucopus* populations at the reference site in summer 1992 had the highest abundances of any *Peromyscus* species population, but these populations sharply declined in the following seasons and never recovered (Fig. 18A). *P. maniculatus* were present at the reference site in summer 1992, but disappeared by winter 1993. *P. maniculatus* were not present at the high mortality site until winter 1993 and reached their highest abundance in fall 1993 (Fig. 18B). At the in process site, *P. maniculatus* abundances were consistently lower than *P. leucopus* abundances except for fall 1993 (Fig. 18).

Figures 19 and 20 illustrate that each of the *P. leucopus* and *P. maniculatus* populations' habitat use significantly differed (summer-df=156, 1597, F=10.01, $p<0.0001$, fall-df=105, 1173, F=18.58, $p<0.0001$) among sites for summer and fall 1992. All four sites had distinctively different forest structure (Fig. 2, Ch. 1), which suggests

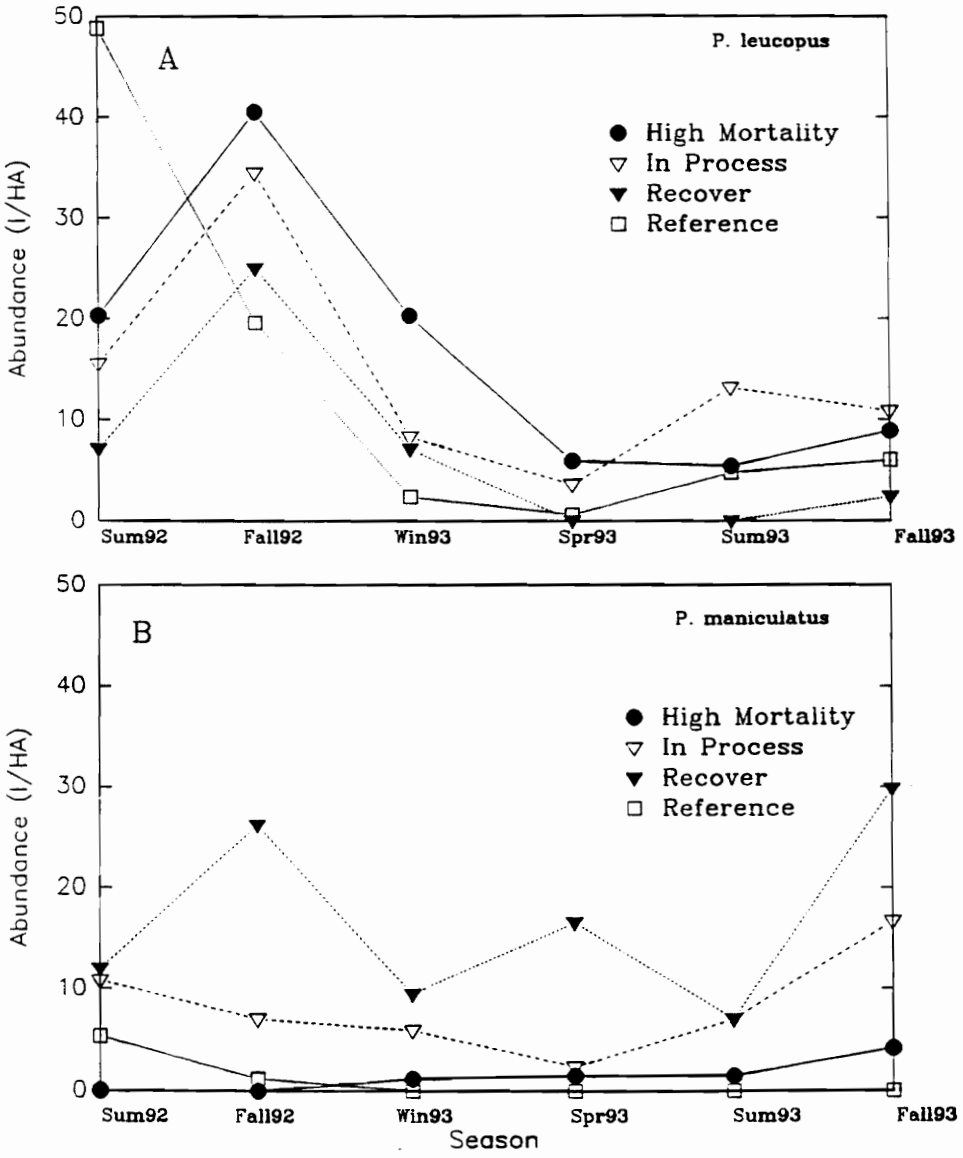


Fig 18 - Seasonal abundances of (A) *P. leucopus* and (B) *P. maniculatus* at each of the sites expressed as individuals per hectare (I/HA).

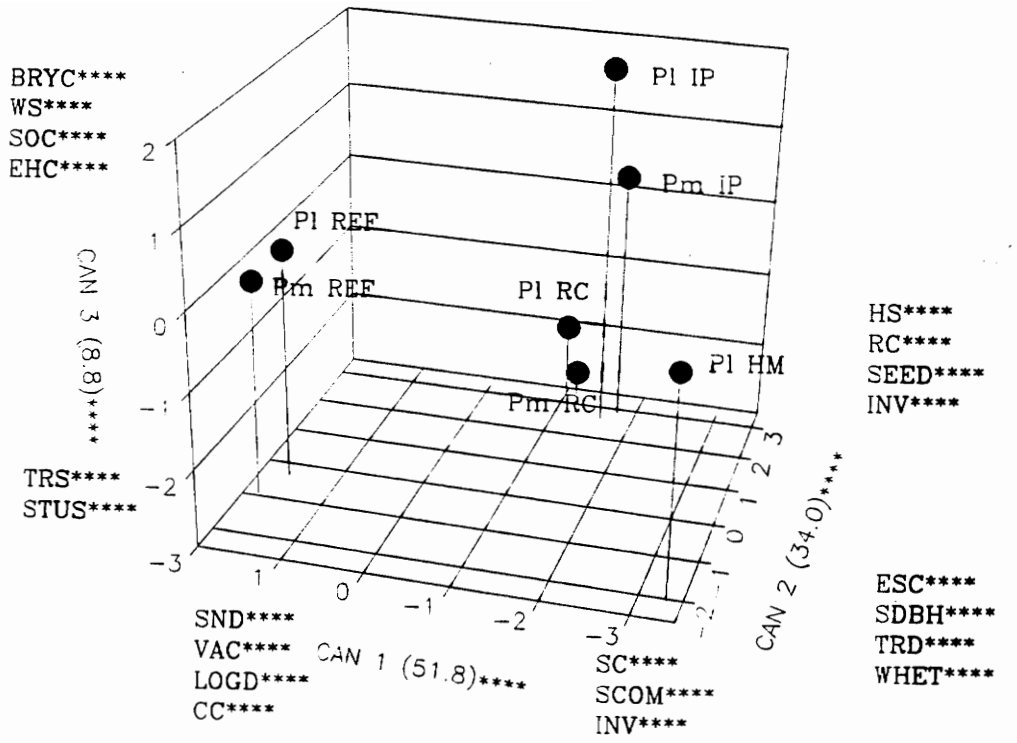


Fig. 19 - CDA comparing habitat use of *P. leucopus* (Pl) *and P. maniculatus* (Pm) populations at the high mortality (HM), in process (IP), recovery (RC) and, reference (REF) sites for summer 1992. The proportion of the analysis each canonical variate explains is in parentheses along each axis. Variables that significantly contributed to species separation are listed along axes in which they most correlate (df=6, 296, p<0.15 =*, p<0.10 =**, p<0.05 =***, p<0.01 =****). Each axis represents a gradient of habitat characteristics that correlates with each classes habitat use (Overall habitat use differences as determined by Wilks' Lambda multivariate F approximation: df=156, 1597, F=10.01 p<0.0001).

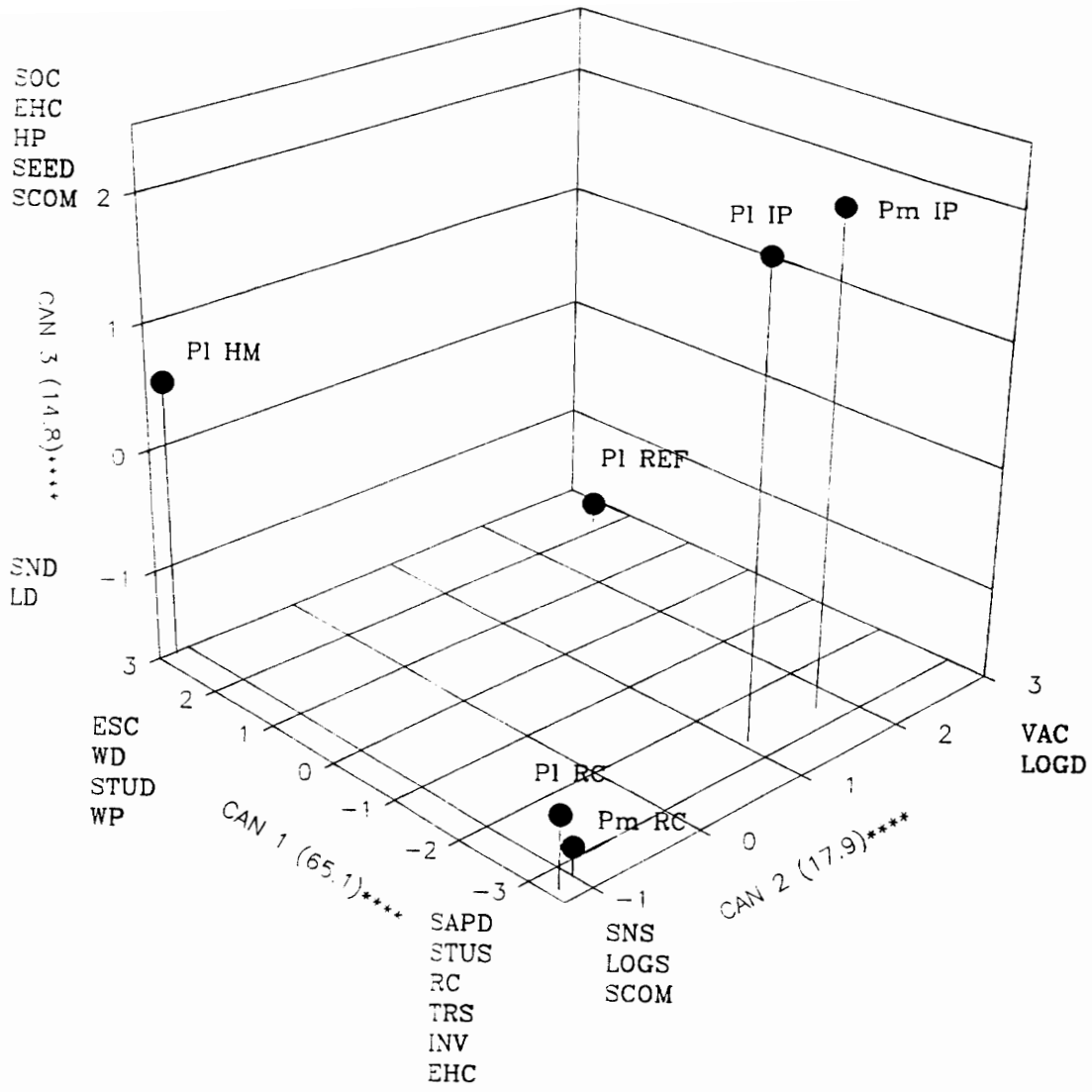


Fig. 20 - CDA comparing habitat use of *P. leucopus* (Pl) *and P. maniculatus* (Pm) populations at the high mortality (HM), in process (IP), recovery (RC) and, reference (REF) sites for fall 1992. The proportion of the analysis each canonical variate explains is in parentheses along each axis. All variables significantly contributed to species separation (df=5, 259, p<0.0001). Each axis represents a gradient of habitat characteristics that correlates with each classes habitat use (Overall habitat use differences as determined by Wilks' Lambda multivariate F approximation: df=105, 1173, F=18.58 p=0.0001).

that the habitat available to each of these populations was very different.

Demographic Structure - Demographic structure of *P. leucopus* populations varied among sites. Female adults (ADFEM) and total females (FEM) were at their highest proportions at the high mortality site and lowest proportions at the reference site (Table 11). Female juveniles (FJUV) were at their highest proportions at the in process and high mortality site and lowest proportions at the recovery and reference sites (Table 11). Juveniles (JUV) were at there highest proportions at the in process site, but differed little among sites. The recovery site and reference grid two had higher coefficients of variation for juvenile proportions relative to all other populations (Table 11). The in process site had the highest proportion of adults in reproductive condition (MRC, FRC) and the lowest coefficients of variation among all grids (Table 11). Proportions of male adults (AMAL) were similar among sites, but this variable had higher coefficients of variation at the recovery and reference sites (Table 11). Density fluctuations were greatest at the reference site and lowest at the in process site and high mortality grid two (Table 11).

As indicated by the coefficients of variation of demographic characteristics, the reference and recovery site

populations had more variation in their demographic structure than the other sites (Table 11). The recovery site population's demographic variation can be attributed to their disappearance after winter 1993 and their reappearance in small numbers in fall 1993. The reference site populations had an extremely productive summer in 1992, which was followed by no juvenile recruitment in fall 1992 and then a population crash in winter and spring 1993 (Fig. 18).

Demographic structure of the two persisting populations of *P. maniculatus* was similar, but the in process site population persisted at lower abundances than the recovery site population (Figure 18). In contrast to the recovery site population, the in process site population shared microhabitat with *P. leucopus* throughout the study.

Principal components analysis (PCA) was performed on the demographic variables (Table 11) of each population to discern demographic structure differences among populations in multivariate space (Fig. 21). Along the first principal component, there was a gradient of higher proportions of female adults and juveniles, higher abundance, smaller abundance and residency fluctuations, and lower proportions of male adults from the positive to the negative end of the component (Fig. 21). The *P. leucopus* high mortality and in

Table 11 - (A) Demographic characteristics of each *P. leucopus* and *P. maniculatus* population. The numbers are means of the six seasons for each grid population (N = 6, coefficients of variation are in italics below the means). All variables are proportions except for DEN, DF, RES, RF. Refer to table 10 for variable interpretations (HM = High Mortality, RC = Recover, IP = In Process, REF = Reference).

	P. leucopus						*P. maniculatus*	
Variable	HM1	HM2	RC	IP	REF1	REF2	RC	IP
ADFEM	0.44	0.38	0.21	0.27	0.26	0.22	0.31	0.30
	0.22	*0.32*	*1.14*	*0.48*	*0.88*	*1.09*	*0.29*	*0.76*
FEM	0.53	0.42	0.23	0.44	0.32	0.28	0.43	0.45
	0.24	*0.57*	*1.17*	*0.39*	*0.88*	*1.00*	*0.37*	*0.62*
JUV	0.15	0.19	0.22	0.27	0.21	0.22	0.33	0.39
	0.86	*1.05*	*1.77*	*1.00*	*1.05*	*1.55*	*0.70*	*0.74*
FJUV	0.12	0.13	0.02	0.16	0.06	0.06	0.13	0.23
	1.08	*1.38*	*1.50*	*1.06*	*1.67*	*2.50*	*1.07*	*0.78*
FRC	0.37	0.39	0.05	0.66	0.38	0.48	0.47	0.50
	1.35	*1.23*	*2.60*	*0.79*	*1.11*	*1.10*	*1.10*	*0.92*
MRC	0.40	0.33	0.08	0.45	0.32	0.17	0.29	0.28
	1.23	*1.24*	*2.50*	*1.16*	*1.25*	*2.41*	*0.74*	*1.57*
AMAL	0.41	0.42	0.22	0.43	0.53	0.39	0.33	0.32
	0.37	*0.48*	*1.22*	*0.60*	*0.72*	*1.05*	*0.67*	*0.78*
DEN	12.5	14.8	5.8	12.0	13.1	9.8	14.2	7.0
	1.04	*0.64*	*1.36*	*0.75*	*1.22*	*1.59*	*0.54*	*0.58*
DF	3.0	1.7	3.4	1.9	4.9	4.3	1.7	1.8
	0.60	*0.41*	*0.65*	*0.58*	*0.90*	*0.70*	*0.23*	*0.50*
RES	2.1	2.1	1.4	2.1	1.9	1.5	1.6	1.5
	0.38	*0.33*	*0.36*	*0.52*	*0.37*	*0.20*	*0.19*	*0.27*
RF	1.4	1.3	1.3	1.1	1.4	1.2	1.3	1.2
	0.14	*0.08*	*0.08*	*0.09*	*0.21*	*0.17*	*0.23*	*0.17*

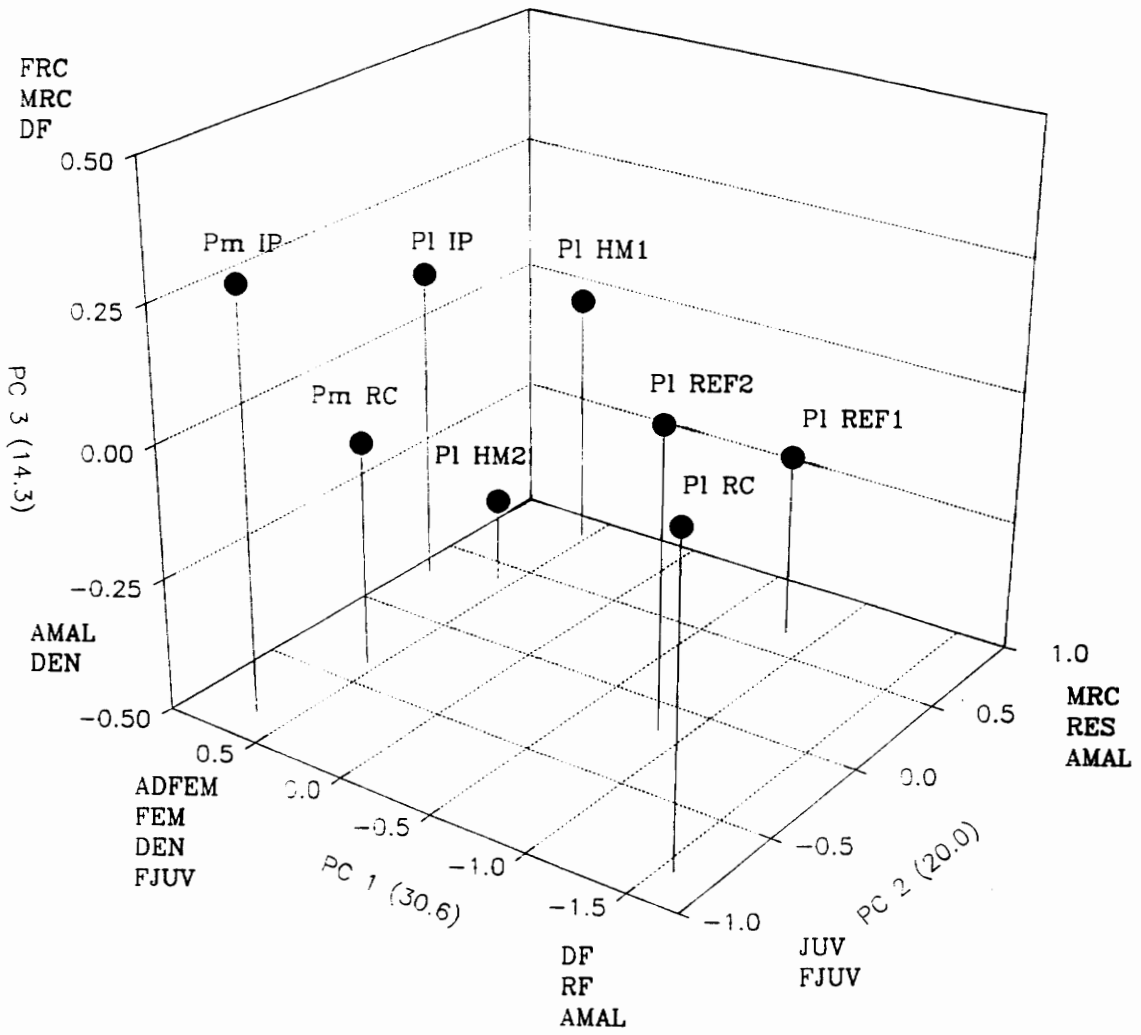


Fig 21 - Means of demographic PCA scores from each population plotted in three-dimensional space. Each axis represents a gradient of demographic characteristics that correlates with each populations demographic structure (Pm = *P. maniculatus*, Pl = *P. leucopus*, HM = High Mortality, IP = In Process, RC = Recover, REF = Reference). Demographic variable interpretations are presented in Table 10.

process site populations and the *P. maniculatus* recovery site populations were associated with the positive end of the first component. The *P. leucopus* reference and recovery site populations were associated with the negative end of the component with the recovery site population associating with the extreme negative end (Fig. 21). Along the second principal component, the *P. maniculatus* populations were associated with higher proportions of juveniles and female juveniles relative to *P. leucopus* populations. The *P. leucopus* recovery site population did not have high proportions of juveniles, but their position along the second component can be attributed to low proportions of male adults and reproductive males and a low residency index (Table 11, Fig. 21). The third principal component reflects minor secondary differences between populations. For example, the *P. maniculatus* population at the in process site had lower abundance and higher abundance fluctuations than the *P. maniculatus* population at the recovery site (Fig. 21).

Intraspecific Microhabitat Segregation - Canonical discriminant analysis (CDA) was performed on sex and age classes of *P. leucopus* and *P. maniculatus* populations at each site by season (Figs. 22-26) to determine potential

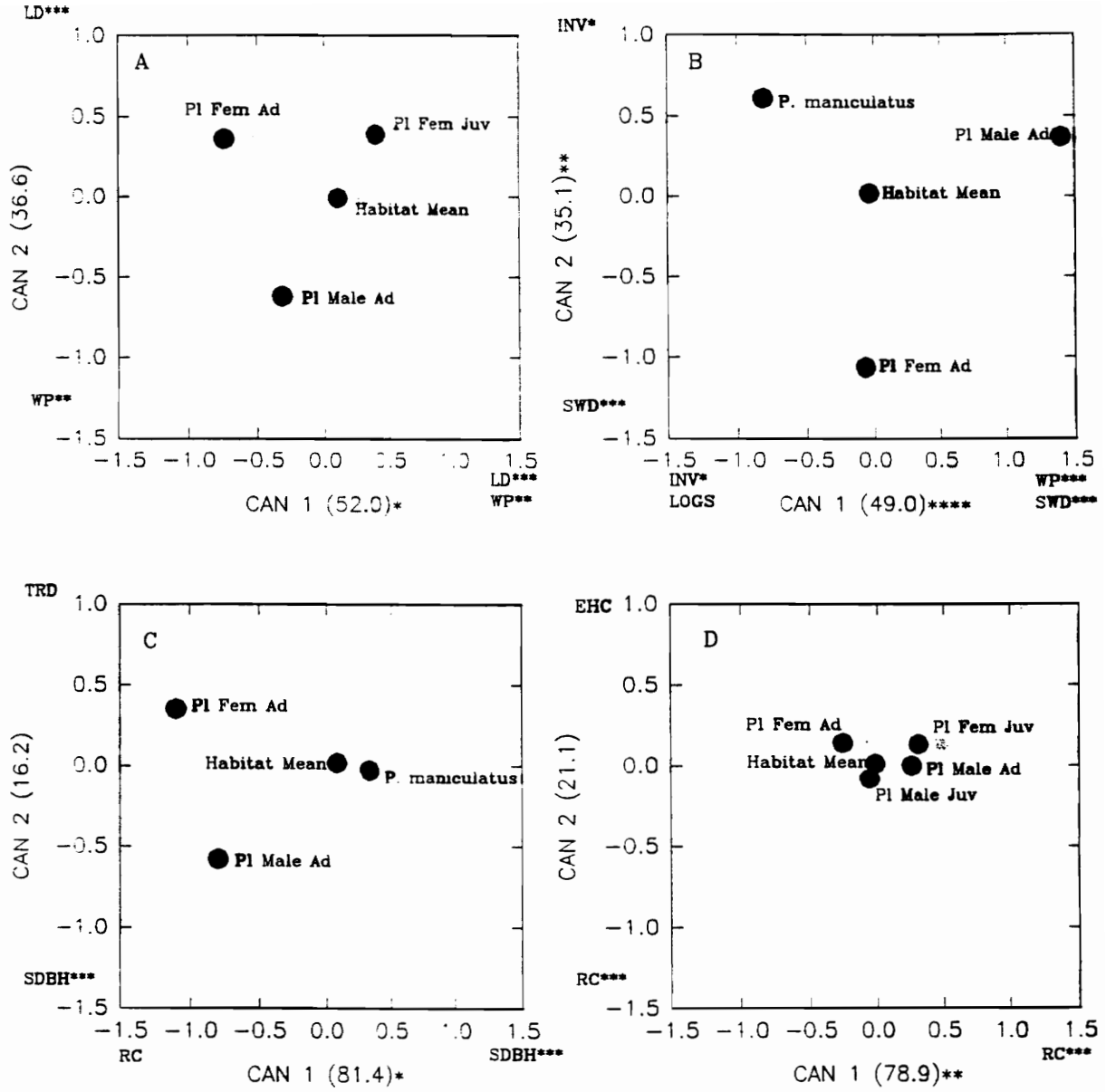


Fig. 22 - CDA of sex and age classes of *P. leucopus and P. maniculatus* populations at the A) high mortality, B) in process, C) recovery and, D) reference sites for summer 1992. Refer to Figure 19 for the interpretation of the plots. Overall class habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=24, 592, F=1.33 p=0.135, In Process df=36, 320, F=1.74, p=0.007, Recovery df=9, 236, F=1.62, p=0.111, Reference df=8, 624, F=1.73, p=0.09.

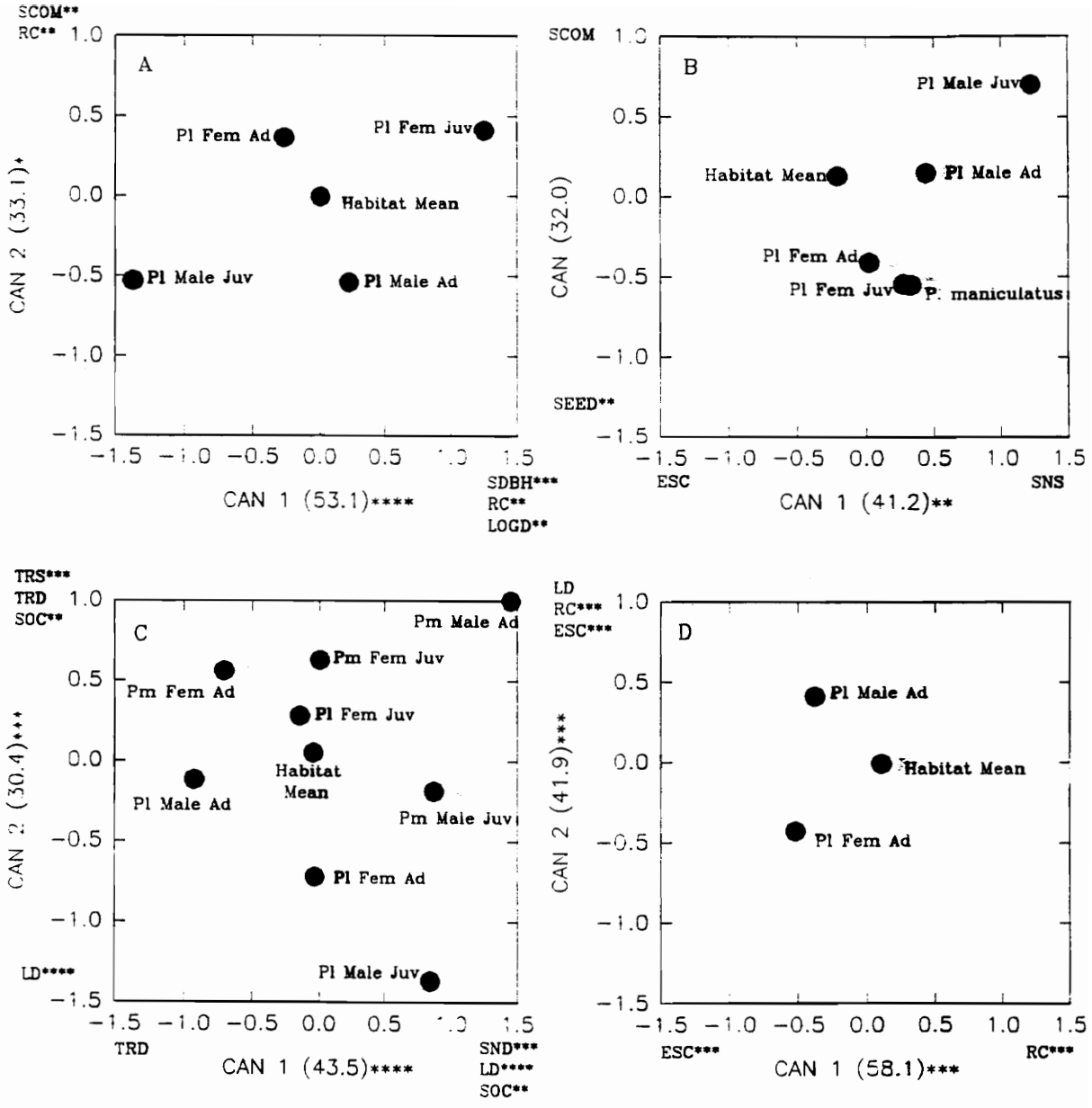


Fig. 23 - CDA of sex and age classes of *P. leucopus and P. maniculatus* populations at the A) high mortality, B) in process, C) recovery and, D) reference sites for fall 1992. Refer to Figure 19 for the interpretation of the plots. Overall class habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=28, 863, F=1.83 p=0.006, In Process df=25, 462, F=1.46, p=0.07, Recovery df=40, 587, F=1.98, p=0.0004, Reference df=6, 394, F=2.83, p=0.01.

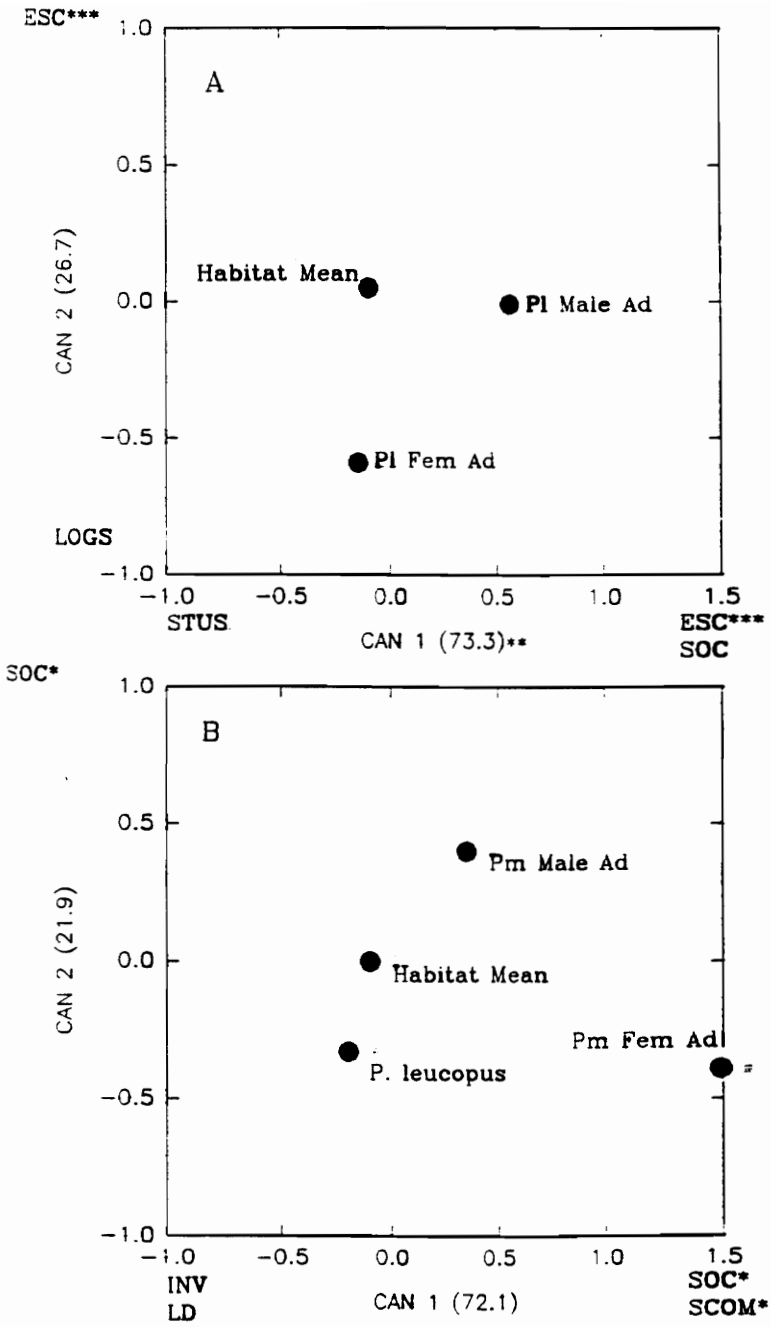


Fig. 24 - CDA of sex and age classes of *P. leucopus and P. maniculatus* populations at the A) high mortality and B) recovery sites for winter 1993. Refer to Figure 19 for the intrepretation of the plot. Overall class habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=10, 400, F=1.69 p=0.082, Recover df=12, 262, F=1.30, p=0.219.

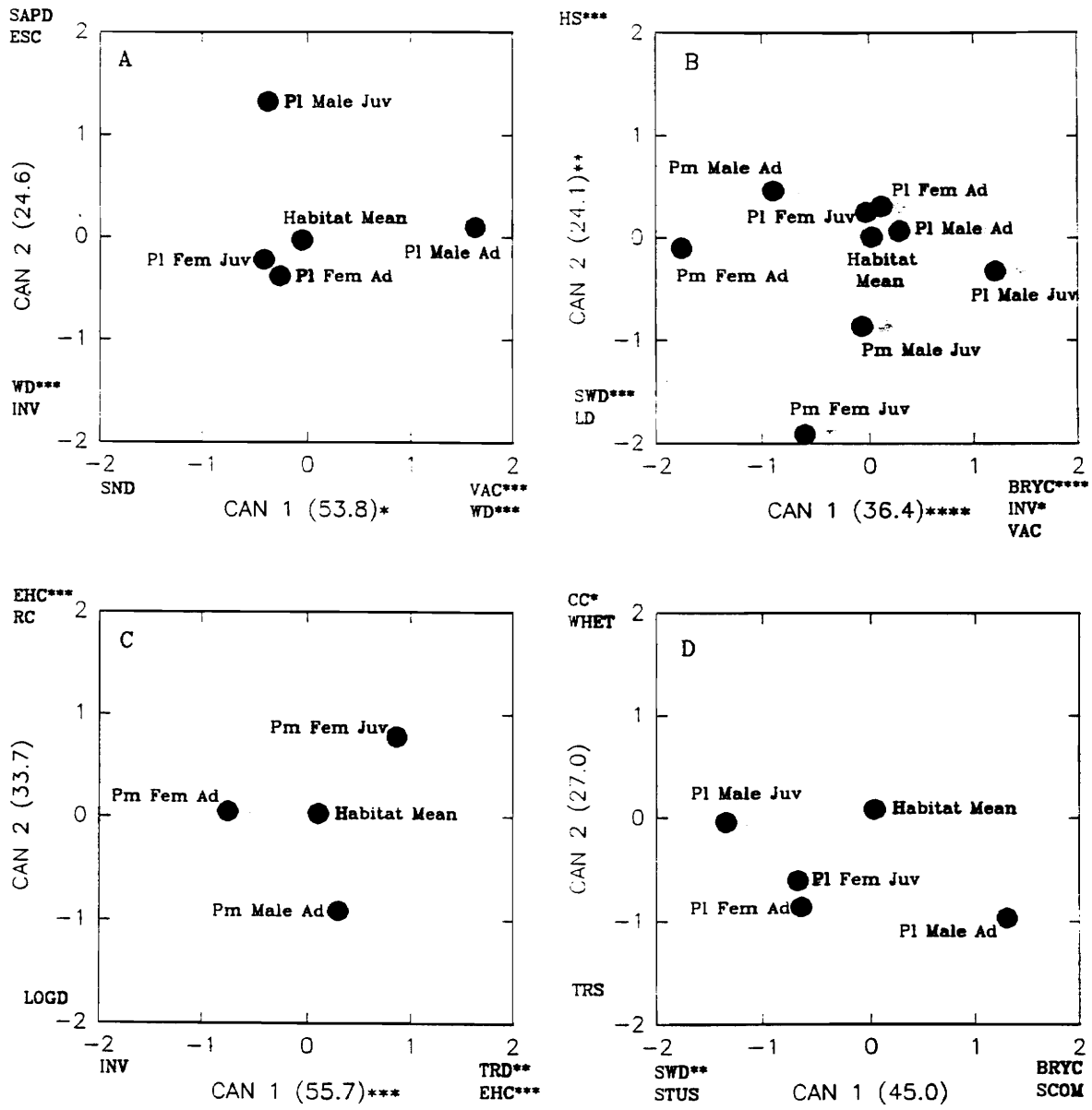


Fig. 25 - CDA of sex and age classes of *P. leucopus and P. maniculatus* populations at the A) high mortality, B) in process, C) recovery and, D) reference sites for summer 1993. Refer to Figure 19 for the interpretation of the plots. Overall class habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=36, 657, F=1.29 p=0.121, In Process df=64, 889, F=1.59, p=0.003, Recovery df=15, 287, F=1.76, p=0.04, Reference df=44, 641, F=1.00, p=0.48.

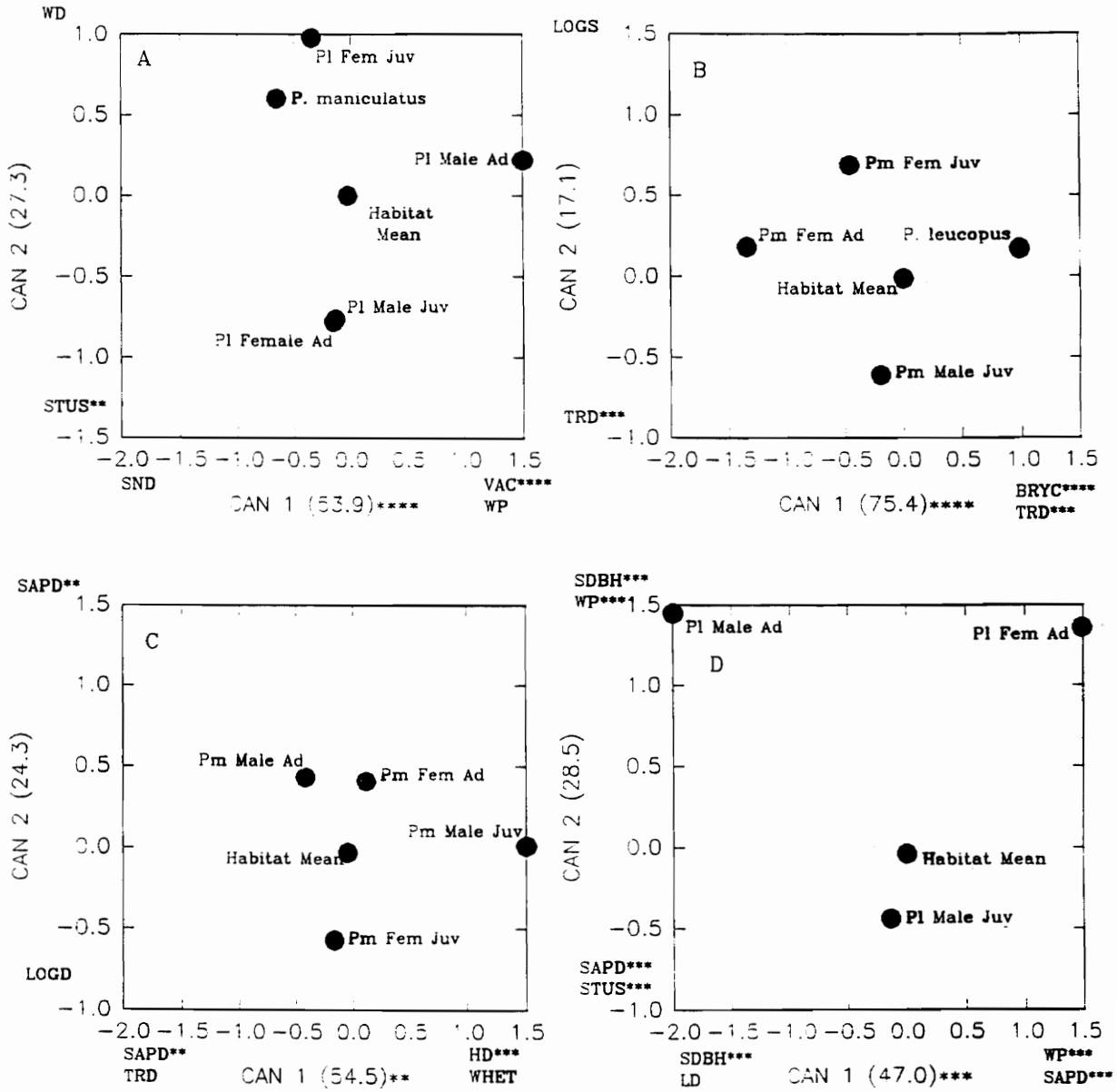


Fig. 26 - CDA of sex and age classes of *P. leucopus and P. maniculatus* populations at the A) high mortality, B) in process, C) recovery and, D) reference sites for fall 1993. Refer to Figure 19 for the interpretation of the plots. Overall class habitat segregation as determined by Wilks' Lambda multivariate F approximations: High Mortality df=30, 750, F=1.80 p=0.006, In Process df=12, 270, F=2.39, p=0.006, Recover df=20, 376, F=1.59, p=0.052, Reference df=39, 480, F=1.47, p=0.035.

Table 12 - Number of captures of each sex by age class for *P. leucopus* and *P. maniculatus*.

Site/ Sex-Age Class	Sum92	Fall92	Win93	Spr93	Sum93	Fall93
High Mortlaity						
P. leucopus						
Female Adult	23	46	11	11	5	7
Female Juvenile	14	9	0	0	4	3
Male Adult	18	30	24	14	15	9
Male Juvenile	1	4	0	0	4	6
P. maniculatus	0	0	2	2	4	10
In Process						
P. leucopus						
Female Adult	15	18	1	2	22	1
Female Juvenile	1	8	0	0	7	6
Male Adult	12	14	15	4	24	3
Male Juvenile	1	4	0	0	10	1
P. maniculatus						
Female Adult	11	4	2	0	6	6
Female Juvenile	1	2	0	2	4	4
Male Adult	3	0	3	2	10	1
Male Juvenile	0	2	0	0	5	7
Recovery						
P. leucopus						
Female Adult	5	17	2	0	0	0
Female Juvenile	1	6	0	0	0	0
Male Adult	3	13	7	0	0	0
Male Juvenile	1	3	0	0	0	0
P. maniculatus						
Female Adult	5	5	4	12	19	12
Female Juvenile	3	6	0	0	4	11
Male Adult	2	4	12	6	8	11
Male Juvenile	0	15	0	3	1	7
Reference						
P. leucopus						
Female Adult	59	17	0	0	7	5
Female Juvenile	35	0	0	0	4	0
Male Adult	29	24	8	1	5	3
Male Juvenile	25	0	0	0	4	8
P. maniculatus	15	1	0	0	0	0

Table 13 - Degree of separation of each sex and age class from the overall habitat available at each site by season for *P. leucopus* and *P. maniculatus* as determined by F-statistics derived from Mahalanobis squared distances (DF in parentheses, P<0.1*, P<0.05**, P<0.01***).

Site/ Sex-Age Class	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality	(8, 204)	(7, 239)	(5, 200)	(9, 175)	(6, 187)
P. leucopus					
Female Adult	1.91*	1.37	0.91	0.50	1.08
Female Juvenile	0.74	2.51**	-	0.77	0.77
Male Adult	1.25	1.39	2.44**	2.63***	4.13***
Male Juvenile	-	1.53	-	1.22	1.13
In Process	(12, 108)	(5, 124)		(8, 153)	(3, 102)
P. leucopus					
Female Adult	1.46	1.21	-	1.10	-
Female Juvenile	-	1.51	-	0.43	-
Male Adult	2.02**	1.07	-	0.91	-
Male Juvenile	-	2.27*	-	1.84*	-
P. maniculatus					
Female Adult	-	-	-	2.28**	3.84**
Female Juvenile	-	-	-	2.16**	0.96
Male Adult	-	-	-	2.40**	-
Male Juvenile	-	-	-	1.22	0.88
Recovery	(3, 97)	(5, 134)	(4, 99)	(5, 104)	(5, 113)
P. leucopus					
Female Adult	1.52**	1.58	-	-	-
Female Juvenile	-	0.88	-	-	-
Male Adult	1.14	1.72	-	-	-
Male Juvenile	-	3.11**	-	-	-
P. maniculatus					
Female Adult	-	1.21	2.51**	2.33**	0.79
Female Juvenile	-	0.68	-	1.19	0.75
Male Adult	-	3.12**	1.03	1.47	1.33
Male Juvenile	-	2.86**	-	-	3.10**
Reference	(2, 312)	(3, 197)		(11, 167)	(13, 162)
P. leucopus					
Female Adult	2.06	2.94**	-	1.02	1.55
Female Juvenile	2.57*	-	-	0.84	1.75
Male Adult	1.57	2.84**	-	1.22	2.10*
Male Juvenile	0.99	-	-	0.52	-

Table 14 - Interspecific and intraspecific pairwise comparisons of sex and age classes of *P. leucopus* and *P. maniculatus* habitat use differences with F-statistics derived from Mahalanobis squared distances. Degrees of freedom for each analysis are in parentheses. Asterisks denote degree of significance (P<0.1*, P<0.05**, P<0.01***). In some seasons sample sizes were too small to segregate a population into sex and age classes, in which its population was pooled (FA = female adult, FJ = female juvenile, MA = male adult, MJ = male juvenile, Pl = *P. leucopus*, Pm = *P. maniculatus*).

Site/ Class	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality	(8, 204)	(7, 239)	(5, 200)	(9, 175)	(6, 187)
P. leucopus					
FA vs. FJ	1.49	2.86***	-	0.80	1.58
FA vs. MJ	-	1.42	-	1.14	0.77
FA vs. MA	1.42	2.66**	1.47	1.88*	3.14***
MA vs. FJ	1.60	2.24**	-	1.51	2.02*
MA vs. MJ	-	1.67	-	2.11**	2.80**
FJ vs. MJ	-	3.19***	-	0.99	1.26
Interspecific					
PlFA vs. Pm					1.75
PlFJ vs. Pm					0.68
PlMA vs. Pm					4.38***
PlMJ vs. Pm					1.78
In Process	(12, 108)	(5, 124)	(ND)	(8, 153)	(3, 102)
P. leucopus					
FA vs. FJ	-	0.43		0.31	-
FA vs. MJ	-	2.04*		1.79*	-
FA vs. MA	2.16**	1.00		1.49	-
MA vs. FJ	-	1.10		0.64	-
MA vs. MJ	-	0.80		1.19	-
FJ vs. MJ	-	1.55		1.16	-
P. maniculatus					
FA vs. FJ				1.77	1.17
FA vs. MJ				2.17**	2.18*
FA vs. MA				1.66	-
MA vs. FJ				2.27**	-
MA vs. MJ				1.53	-
FJ vs. MJ				0.79	1.57

(Table 14 continued) 122

In Process	Sum92	Fall92	Win93	Sum92	Fall93
Interspecific					
PmFa vs. PlFA				2.83***	
PmMA vs. PlMA				2.48**	
PmFJ vs. PlFJ				1.79*	
PmMJ vs. PlMJ				1.33	
PmFA vs. PlMA				2.36**	
PmFA vs. PlFJ				1.72*	
PmFA vs. PlMJ				3.75***	
PmMA vs. PlFA				1.65	
PmMA vs. PlFJ				0.80	
PmMA vs. PlMJ				2.97***	
PmFJ vs. PlFA				2.29**	
PmFJ vs. PlMA				2.34**	
PmFJ vs. PlMJ				2.13**	
PmMJ vs. PlFA				1.37	
PmMJ vs. PlMA				1.48	
PmMJ vs. PlFJ				0.65	
Pl vs. PmFA					6.92***
Pl vs. PmFJ					2.51*
Pl vs. PmMJ					2.89**
Pm vs. PlFA	1.92**	1.14			
Pm vs. PlFJ	-	1.51			
Pm vs. PlMA	2.54***	0.91			
Pm vs. PlMJ	-	2.06*			
Recovery	(3, 97)	(5, 134)	(4, 99)	(5, 104)	(5, 113)
P. leucopus					
FA vs. FJ	-	1.59			
FA vs. MJ	-	1.56			
FA vs. MA	0.85	1.70			
MA vs. FJ	-	0.99			
MA vs. MJ	-	3.35***			
FJ vs. MJ	-	2.47**			
P. maniculatus					
FA vs. FJ		0.55	-	2.14*	1.52
FA vs. MJ		3.28***	-	-	2.26*
FA vs. MA		2.50**	1.45	2.24*	1.35
MA vs. FJ		1.26	-	1.71	1.41
MA vs. MJ		2.31**	-	-	3.25***
FJ vs. MJ		2.00*	-	-	2.76**

(Table 14 continued) 123

Recover	Sum92	Fall92	Win93	Sum93	Fall93
Interspecific					
PmFA vs. PlFA		2.02			
PmMA vs. PlMA		4.71***			
PmFJ vs. PlFJ		0.90			
PmMJ vs. PlMJ		2.62**			
PmFA vs. PlMA		0.61			
PmFA vs. PlFJ		0.46			
PmFA vs. PlMJ		2.88**			
PmMA vs. PlFA		3.92***			
PmMA vs. PlFJ		2.20*			
PmMA vs. PlMJ		2.74**			
PmFJ vs. PlFA		1.59			
PmFJ vs. PlMA		1.37			
PmFJ vs. PlMJ		2.61**			
PmMJ vs. PlFA		2.16*			
PmMJ vs. PlMA		4.55***			
PmMJ vs. PlFJ		1.58			
Pl vs. PmFA			2.02*		
Pl vs. PmMA			1.08		
Pm vs. PlFA	2.82**				
Pm vs. PlMA	1.81				
Reference	(2, 312)	(3, 197)	(ND)	(11, 167)	(13, 162)
P. leucopus					
FA vs. FJ	3.81**	-		0.70	-
FA vs. MJ	0.80	-		0.63	1.46
FA vs. MA	3.51**	2.40*		1.21	2.08**
MA vs. FJ	0.83	-		1.10	-
MA vs. MJ	0.95	-		1.55	1.56
FJ vs. MJ	1.43	-		0.60	-

microhabitat separation among these groups. CDA were not performed on populations at the in process and reference sites in winter 1993 and all sites in spring 1993 due to low *Peromyscus* sample sizes (Fig. 18, Table 12). Tables 13 and 14 present F-statistics derived from Mahalanobis squared distances generated by CDA which determine significant separations of sex and age classes from the habitat mean and significant pairwise differences between species and among sex and age classes at each site by season. Refer to Table 12 for sample sizes used in the analyses.

Summer 1992 - At the high mortality site, there were no significant deviations of microhabitat use from the habitat mean, but *P. leucopus* female adults tended towards significant deviation (df=8, 204, p=0.059, Table 13). There were no pairwise significant differences in microhabitat use among sex and age classes (Table 14). Along the first canonical axis, female adults tended to use microhabitat with less woody profile (WP) relative to the habitat mean, male adults, and female juveniles (Fig. 22A).

At the in process site, *P. leucopus* male adult microhabitat use significantly deviated (df=12, 108, p=0.029) from the habitat mean, and male and female adult microhabitat use significantly differed (df=12, 108, p=0.018) from each other (Tables 13 and 14). Additionally,

male and female adult microhabitat use significantly differed (df=12, 108, p=0.005, p=0.039) from that of *P. maniculatus* microhabitat (Table 14). *P. leucopus* female adults used microhabitat with less cover relative to male adults but used more cover relative to *P. maniculatus* (Fig. 22B). In general, *P. maniculatus* resided in a more open microhabitat with higher invertebrate abundances (Fig. 22B).

At the recovery site, *P. leucopus* female adult microhabitat use significantly deviated (df=3, 97, p=0.045) from the habitat mean, but male and female adults microhabitat use did not significantly differ (Tables 13 and 14). Only *P. leucopus* female adults microhabitat use significantly differed (df=3, 97, p=0.043) from that of *P. maniculatus* (Table 14). *P. leucopus* female adults used microhabitats with less cover (SDBH) relative to the habitat mean, male adults, and *P. maniculatus* (Fig. 22C).

At the reference site, none of the *P. leucopus* sex and age class microhabitat use significantly deviated from the habitat mean, but female juveniles tended towards a deviation (df=2, 312, p=0.078, Table 13). The only pairwise comparisons of microhabitat use that significantly differed were between female adults/female juveniles and female adults/male adults (df=2, 312, $p<0.05$) and these separations were based on rock cover (Table 14, Fig. 22D). At high

abundances (Fig. 18), *P. leucopus* had very little intraspecific microhabitat separation.

Fall 1992 - At the high mortality site, *P. leucopus* female juvenile microhabitat use significantly deviated from the habitat mean (Table 13). All pairwise comparisons of microhabitat use significantly differed ($df=7, 239, p<0.05$) except for female adults/male juveniles and male adults/male juveniles (Table 14). Along the first canonical axis, female adults used microhabitat with less rock cover (RC) and breast height stem densities, and more logs relative to male adults and female juveniles. Along the second canonical axis, female adults used microhabitat with a combination of more compact soil and higher rock cover relative to male adults (Fig. 23A).

At the in process site, *P. leucopus* male juvenile microhabitat use tended to deviate ($df=5, 124, p=0.052$) from the habitat mean (Table 13). None of the pairwise intraspecific comparisons of microhabitat use significantly differed nor were there any significant microhabitat use differences from *P. maniculatus* (Table 14). *P. leucopus* male juveniles tended to use significantly different ($df=5, 124, p=0.075$) microhabitats from *P. maniculatus* (Table 14). *P. leucopus* male juveniles used microhabitats with larger snags and more compact soil relative to the habitat mean and *P.*

maniculatus (Fig. 23B).

At the recovery site, only *P. leucopus* male juvenile and *P. maniculatus* female juvenile and male juvenile microhabitat use significantly deviated ($df=5, 134, p<0.05$) from the habitat mean (Table 13). *P. maniculatus* had more intraspecific pairwise separation of microhabitat use than *P. leucopus* (Table 14). Most sex and age classes had significant ($df=5, 134, p<0.05$) or tendencies towards significant ($P<0.1$) interspecific pairwise differences in microhabitat use (10/16 comparisons) except for *P. maniculatus* female juveniles/*P. leucopus* female juveniles, male adults, and female adults, *P. maniculatus* female adults/*P. leucopus* male adults and female juveniles, and *P. maniculatus* male juveniles/*P. leucopus* female juveniles (Table 14). Microhabitat separations between and within species were very complex, but in general, along the first canonical axis from the positive to negative end there was a gradient of higher tree densities, deeper litter depth, more soil exposure, and lower snag densities (Fig. 23C). *P. maniculatus* male adults and juveniles and *P. leucopus* male juveniles were associated with the positive end, while *P. maniculatus* female adults and *P. leucopus* male adults were associated with the negative end. The rest of the sex and age classes were intermediate along this gradient (Fig.

23C). Along the second canonical axis from the positive to negative end there was a gradient of larger well spaced trees, more soil exposure, and shallower litter depth (Fig. 23C). *P. maniculatus* male adults, female adults, and female juveniles were associated with the positive end while *P. leucopus* male juveniles and female adults were associated with the negative end (Fig. 23C).

At the reference site, *P. leucopus* male and female adult microhabitat use significantly deviated (df=3, 197, p=0.034, p=0.039) from the habitat mean (Table 13) and tended towards using significantly different (df=3, 197, p=0.069) microhabitats from each other (Table 14). They both used microhabitat with more evergreen shrub cover relative to the habitat mean while male adults used microhabitats with greater evergreen shrub cover relative to female adults (Fig. 23D).

Winter 1993 - At the high mortality site, *P. leucopus* male adult microhabitat use significantly deviated (df=5, 200, p=0.035) from the habitat mean (Table 13). There was no significant microhabitat use differences between male and female adults (Table 14). Male adults used microhabitat with more evergreen shrub cover and soil exposure relative to the habitat mean (Fig. 24A).

At the recovery site, *P. maniculatus* female adult

microhabitat use significantly deviated (df=4, 99, p=0.046) from the habitat mean (Table 13), but *P. maniculatus* male and female adults did not use significantly different microhabitat from each other (Table 14). *P. maniculatus* female adults used microhabitat with more soil exposure and greater soil compactibility relative to the habitat mean and *P. leucopus,* while *P. maniculatus* male adults used microhabitat with more soil exposure relative to *P. leucopus* (Fig. 24B).

Summer 1993 - At the high mortality site, only *P. leucopus* male adult microhabitat use significantly deviated (df=9, 175, p=0.007) from the habitat mean (Table 13). Among pairwise comparisons of intraspecific microhabitat use, male adults used significantly different (df=9, 175, p=0.031) microhabitats from male juveniles and tended towards a difference (p=0.057) from female adults (Table 14). Male adults used microhabitat with higher blueberry, snag and woody stem densities relative to the habitat mean, male juveniles, and female adults (Fig. 25A).

At the in process site, *P. maniculatus* female and male adult and female juvenile microhabitat use significantly deviated (df=8, 153, p<0.05) from the habitat mean, but none of the *P. leucopus* sex and age classes significantly deviated from the habitat mean (Table 13). *P. leucopus* had

no significant intraspecific microhabitat segregation, but *P. maniculatus* female adults/male juveniles and male adults/female juveniles used significantly different (df=8, 153, $p<0.05$) microhabitats from each other (Table 14). *P. maniculatus* male adults did not use significantly different microhabitat from *P. leucopus* female adults and juveniles and *P. maniculatus* male juveniles did not use significantly different microhabitat from *P. leucopus* female adults, male adults, and female juveniles (Table 14). The rest of the comparisons (10/16) either significantly differed (df=8, 153, $p<0.05$) or tended towards significance ($p<0.1$). Along the first canonical axis from the positive to negative end, there was a gradient of more moss coverage and higher invertebrate abundances and blueberry stem densities (Fig. 25B). *P. leucopus* male juveniles were associated with the positive end and *P. maniculatus* female adults, male adults, and female juveniles were associated with the negative end (Fig. 25B). Along the second canonical axis, *P. maniculatus* female and male juveniles were associated with higher short woody stem densities and lower herbaceous species richness relative to the habitat mean and the other sex and age classes (Fig. 25B).

At the recovery site, *P. maniculatus* female adult microhabitat use significantly deviated (df=5, 104, $p=0.047$)

from the habitat mean (Table 13) and female adult/female juvenile and female adult/male adult microhabitat use comparisons significantly differed (df=5, 104, $p<0.05$, Table 14). Female adults used microhabitat with higher invertebrate abundances, more trees, and less evergreen herbaceous cover relative to the habitat mean, male adults, and female juveniles (Fig. 25C).

At the reference site, there were no significant deviations from the habitat mean or significant differences of microhabitat use among sex and age classes (Tables 13 and 14, Fig. 25D).

Fall 1993 - At the high mortality site, only *P. leucopus* male adult microhabitat use significantly deviated (df=6, 187, $p<0.001$) from the habitat mean (Table 13) and male adults used significantly different (df=6, 187, $p<0.05$) microhabitat from female adults and male juveniles (Table 14). *P. leucopus* male adult microhabitat use significantly differed (df=6, 187, $p=0.0001$) from that of *P. maniculatus* (Table 14). *P. leucopus* male adults used microhabitat with more blueberries, snags, and woody profile density relative to the habitat mean, *P. maniculatus,* and the rest of the *P. leucopus* sex and age classes (Fig. 26A).

At the in process site, only *P. maniculatus* female adult microhabitat use significantly deviated (df=3, 102,

p=0.012) from the habitat mean (Table 13) and there was no intraspecific microhabitat segregation (Table 14). All *P. maniculatus* sex and age class microhabitat use either tended towards (df=3, 102, p<0.10) or were significantly different (p<0.05) from *P. leucopus* microhabitat use (Table 14). *P. maniculatus* female adults used microhabitat with less moss cover and more trees relative to the habitat mean and *P. leucopus* (Fig. 26B).

At the recovery site, only *P. maniculatus* male juvenile microhabitat use significantly deviated (df=5, 113, p=0.012) from the habitat mean (Table 13), but male juveniles used significantly different (df=5, 113, p<0.05) microhabitats from all other sex and age classes (Table 14). Male juveniles used microhabitat with greater herbaceous stem densities and vertical woody heterogeneity and more trees and saplings relative to the habitat mean and the other sex and age classes (Fig. 26C).

At the reference site, only *P. leucopus* male adult microhabitat use tended towards significant deviation (df=13, 162, p=0.054) from the habitat mean (Table 13), but male adults used significantly different (df=13, 162, p<0.05) microhabitats from female adults and juveniles (Table 14). Male adults used microhabitat with more woody stem densities at breast height, deeper litter depth, and

less saplings and woody profile relative to the habitat mean, female adults and female juveniles (Fig. 26D).

Synthesis - In general, *P. leucopus* populations at the high mortality site exhibited significant microhabitat segregation at high abundances but not at low abundances, and fall populations always exhibited greater separation than summer populations (Fig. 18, Table 14). At this site, female adults separated from male adults, and Male adults tended to always be highly separated from male juveniles. However, *P. leucopus* populations at the in process, recovery, and reference sites did not follow the same pattern as the high mortality site populations (Table 14). At the recovery and in process sites, *P. leucopus* were coexisting with *P. maniculatus* where they generally used significantly different microhabitats from *P. maniculatus* and had little intraspecific microhabitat segregation (Table 14). *P. maniculatus* populations tended to have more intraspecific microhabitat segregation than *P. leucopus* populations at the recovery and in process sites (Table 14). At the recovery site, *P. maniculatus* populations tended to show a high degree of intraspecific microhabitat segregation at high abundances but not at low abundances (Fig. 18, Table 14). At the reference site, *when P. leucopus* were at high abundances (summer 1992) there was little intraspecific

segregation of microhabitat, but at low (fall 1993) to moderate (fall 1992) abundances (Fig. 18), there was a tendency towards intraspecific segregation of microhabitat (Table 14).

Intraspecific Niche Breadths - At the high mortality site, niche breadths of sex and age classes generally increased from summer to fall except for female juveniles. Male juveniles had very low niche breadths except in fall 1993 (Table 15). When *P. maniculatus* were present, *P. leucopus* niche breadths decreased; especially male adults in the fall of 1992 (Table 15). Male adults were the only sex and age class to use significantly different microhabitat relative to *P. maniculatus* in fall 1993 (Table 14).

At the in process site, *P. leucopus* niche breadths were high relative to those of *P. leucopus* at the high mortality site (especially female adults and juveniles, Table 15). Niche breadths tended to increase from summer to fall in 1992, but this trend did not continue in 1993 (Table 15). Male juveniles consistently had low niche breadths compared to all other sex and age classes (Table 15). *P. maniculatus* niche breadths were low relative to *P. leucopus* niche breadths, but *P. maniculatus* male juveniles had high niche

Table 15 - Niche breadths of each sex and age class for *P. leucopus* and *P. maniculatus*.

Site/ Sex-Age Class	Sum92	Fall92	Win93	Sum93	Fall93
High Mortality					
P. leucopus					
Female Adult	1.58	3.15	2.94	1.50	2.56
Female Juvenile	2.15	1.10	-	1.72	1.20
Male Adult	1.38	4.31	0.96	1.17	0.61
Male Juvenile	-	0.36	-	0.38	3.29
P. maniculatus	-	-	-	(2.06)	(1.20)
In Process					
P. leucopus			(1.48)		(0.72)
Female Adult	1.59	32.6		3.82	
Female Juvenile	-	2.67		6.87	
Male Adult	0.82	1.77		4.56	
Male Juvenile	-	0.65		0.97	
P. maniculatus (0.83)		(1.49)	(0.44)		
Female Adult				0.24	0.40
Female Juvenile				1.16	1.33
Male Adult				1.04	-
Male Juvenile				2.77	3.76
Recovery					
P. leucopus			(1.50)	-	-
Female Adult	0.88	2.97			
Female Juvenile	-	3.04			
Male Adult	1.08	1.24			
Male Juvenile	-	1.34			
P. maniculatus (1.72)					
Female Adult		1.03	1.51	0.93	8.36
Female Juvenile		2.97	-	1.59	5.67
Male Adult		1.04	2.28	2.26	1.49
Male Juvenile		1.31	-	-	1.12
Reference					
P. leucopus			(0.71)		
Female Adult	3.00	1.69		0.59	0.47
Female Juvenile	3.19	-		1.21	-
Male Adult	3.86	2.20		0.69	0.09
Male Juvenile	14.2	-		1.06	5.86
P. maniculatus (1.22)		-	-	-	-

breadths relative to *P. leucopus* male juveniles (Table 15).

At the recovery site, *P. leucopus* niche breadths were relatively low compared to those of *P. leucopus* at the high mortality and in process sites (Table 15). *P. maniculatus* female niche breadths increased dramatically (fall 1993) after the disappearance of *P. leucopus* in spring 1993 (Table 15). In comparison to the in process site, *P. maniculatus* male juveniles had relatively low niche breadths (Table 15).

At the reference site, *P. leucopus* niche breadths were relatively low (especially female adults) compared to those of *P. leucopus* at other sites except during summer 1992 (Table 15). All sex and age class niche breadths tended to get smaller from summer 1992 to fall 1993, but male juveniles had much higher niche breadths than male juveniles at other sites (Table 15). Male juveniles tended to have less intraspecific microhabitat segregation at the reference site than male juveniles at the high mortality and recovery sites (Table 14).

Interspecific Seasonal Microhabitat Shifts - A natural experiment occurred due to the disappearance of *P. leucopus* from the recovery site in the spring of 1993. This situation allowed for the comparison of *P. maniculatus* microhabitat use in the presence and absence of *P. leucopus*. *P.*

maniculatus populations from both 1992 and 1993 and the *P. leucopus* population from 1992 were analyzed with CDA (Figs. 27A and B). The same analysis was carried out for both *Peromyscus* species populations at the in process site (Figs. 27C and D). Only variables that were stable over the two year study period were used in the analyses. Refer to Table 3 (Ch. 1) for sample sizes of each population used in the analyses.

At the recovery site, the summer 1992 and 1993 *P. maniculatus* population's microhabitat use significantly differed from that of the summer 1992 *P. leucopus* population. The summer 1993 *P. maniculatus* population (df=6, 126, F=4.87, p=0.0002) had a greater difference in microhabitat use from the summer 1992 *P. leucopus* population than did the summer 1992 *P. maniculatus* population (df=6, 126, F=2.24, p=0.043). The summer 1993 *P. maniculatus* population did not shift into microhabitat previously used by *P. leucopus*.

The fall 1993 *P. maniculatus* population did shift towards microhabitat previously used by *P. leucopus* in fall 1992. The fall 1993 *P. maniculatus* population's microhabitat use did not significantly differ from the fall 1992 *P. leucopus* population's microhabitat use (df=9, 181, F=1.81, p=0.068), however the fall 1992 *P. maniculatus* population

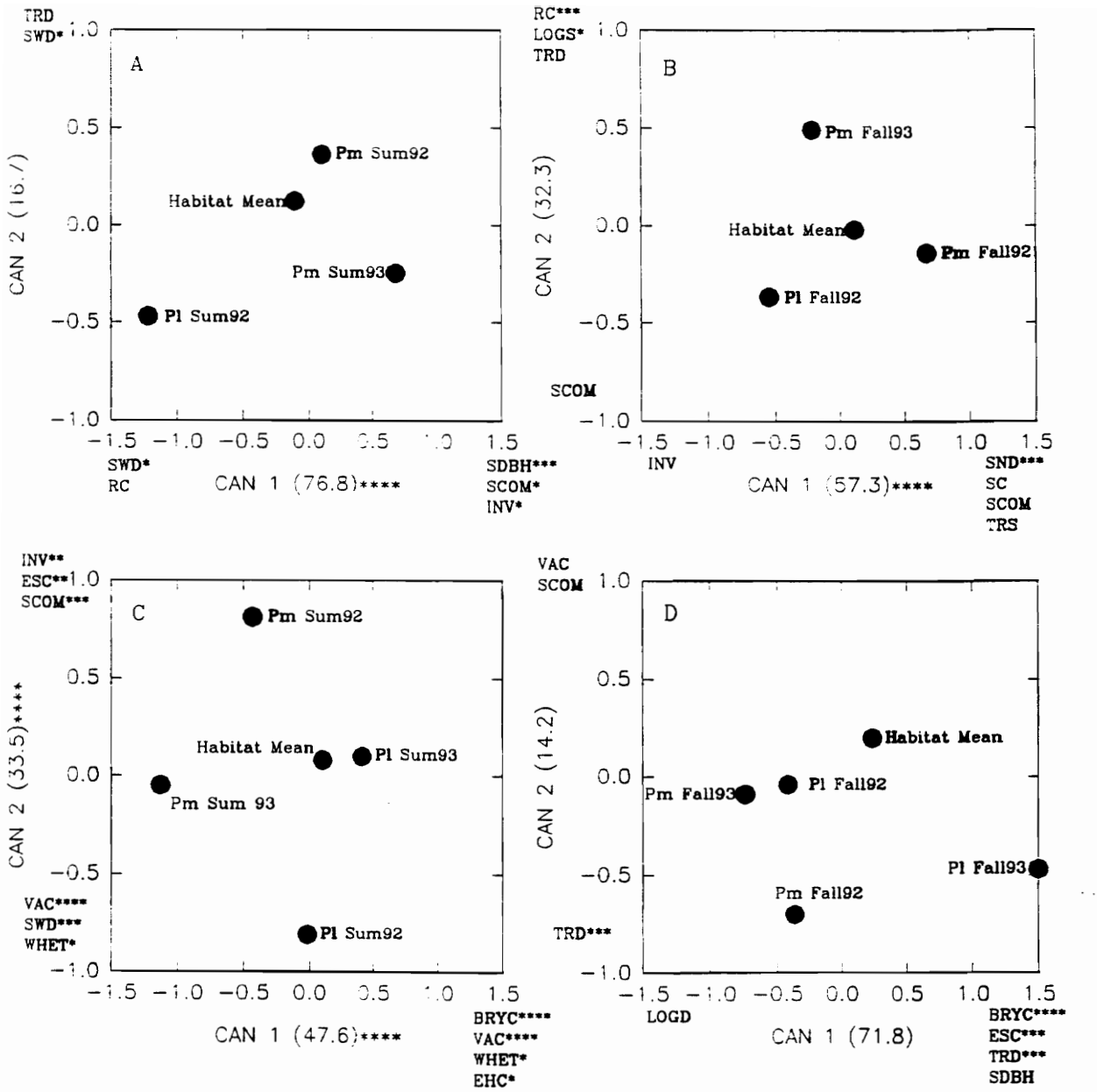


Fig. 27 - A comparison of *P. leucopus and P. maniculatus* habitat use between years for summer and fall with CDA; A) recovery (summer), B) recovery (fall), C) in process (summer), D) in process (fall). Refer to Figure 19 for the interpretation of the figure. Overall habitat segregation as determined by Wilks' Lambda multivariate F approximations: (A) df=18, 357, F=2.20 p=0.0034, (B) df=27, 529, F=1.75, p=0.012, (C) df=32, 735, F=2.70, p<0.0001, (D) df=32, 569, F=2.05, p=0.0007.

significantly differed from the fall 1992 *P. leucopus* population (df=9, 181, F=2.85, p=0.0036). Microhabitat use significantly differed between the fall 1992 and fall 1993 *P. maniculatus* populations (df=9, 181, F=2.32, p=0.017). The fall 1993 *P. maniculatus* population shifted into microhabitat with more snags and rock cover, less shrub cover, and larger logs relative to the fall 1992 *P. maniculatus* population (Fig. 27B). The results of these analyses coincide with the increase of niche breadth (fall 1993) by *P. maniculatus* after the disappearance of *P. leucopus* (Tables 7 and 15).

At the in process site, all summer populations of *P. leucopus* and *P. maniculatus* used significantly different microhabitat (df=8, 199, $p<0.05$). The summer 1993 populations separated along the first canonical axis with *P. leucopus* using microhabitat with more moss and evergreen herbaceous cover, higher blueberry densities, and greater vertical woody heterogeneity relative to *P. maniculatus* (Fig. 27C). The summer 1992 populations separated along the second canonical axis with *P. maniculatus* using microhabitat with higher invertebrate abundance, more compact soil and evergreen shrub cover, less blueberries, and less complex ground cover (SWD, WHET) relative to *P. leucopus* (Fig. 27C). Moss cover and evergreen herbaceous cover were more

important in 1993 than 1992.

The fall 1993 *P. leucopus* population's microhabitat use significantly differed from all other populations ($df=8, 154, p<0.01$), but all other populations used similar microhabitat ($df=8, 154, p>0.50$). The fall 1993 *P. leucopus* population used microhabitat with more moss and evergreen shrub cover, more logs, and less trees relative to other populations (Fig. 27D). Moss cover is important to the 1993 *P. leucopus* population, but not to the 1992 *P. leucopus* population.

Chapter 2

Discussion

Demographic structure of *Peromyscus* populations varied with habitat structure indicating that gypsy moth disturbance had a marked effect on *Peromyscus* populations. Relative to other *P. leucopus* populations, the high mortality site populations were the most stable and exhibited microhabitat segregation among sex and age classes at high abundances. Contrary to this pattern, the reference site populations were the least stable and very little microhabitat segregation among sex and age classes at high abundances. The results of this study suggest that gypsy moth disturbance of areas dominated by chestnut oaks at least temporarily improves habitat quality for *P. leucopus* populations.

The high mortality site populations had higher proportions of adult females and reproductively active males and smaller fluctuations in their abundances than reference site populations. The in process site population had lower fluctuations in adult female proportions and abundances and higher proportions of reproductively active males and females than the reference site populations. Females have

higher reproductive costs (i.e. gestation, lactation, raising young) than males (Bowers and Smith, 1979, Morris, 1984a), making it reasonable to infer that habitats that can maintain high proportions of adult females have the requirements to sustain their presence and a population with high reproductive potential (Johnson, 1994). The high reproductive levels at the in process site can be explained by increases in food resources due to increases in early successional plants, which allocate large amounts of energy to flower and seed production (Newell and Tramer, 1978, Halama and Dueser, 1994), and increases of invertebrates associated with fallen and dead trees (Lovejoy, 1975). Halama and Dueser (1994) suggested that greater cover from visually oriented predators, and the large food base provided by early successional habitats with high herbaceous cover may temporarily increase the fitness of *P. leucopus* populations relative to undisturbed habitats. Although their was not an overabundance of early successional herbaceous species present at the high mortality site, increased shrub cover and log densities could increase the fitness of these populations. Logs provide quiet runways that *Peromyscus* species use to decrease detection by auditory predators such as owls (Planz and Kirkland, 1992 and Barnum et al., 1992), and shrub cover provides protection

from visually oriented predators such as hawks (Kotler, 1984). Microhabitat with greater protection from predators allows for longer safe foraging bouts and more access to available resources, which should increase the fitness of individuals using those microhabitats (Thompson, 1982, Brown et al., 1988).

P. maniculatus populations at the recovery and in process sites were similar in demographic attributes except the in process site population was half as abundant as the recovery site population. The main difference between these populations, besides residing in different habitat, was the recovery site population was not in the presence of *P. leucopus* after winter 1993. Both *P. maniculatus* populations seem to be demographically stable, but the in process site population may be limited numerically because it shares microhabitat space with a *P. leucopus* population (Ch. 1).

Reference site populations had very high abundances in summer 1992 and crashed by spring 1993. This emphasizes that high abundances do not necessarily indicate a high quality habitat (Van Horne, 1983). Most unstable high abundance populations that have been reported in the literature were located in recently disturbed habitat (Sullivan, 1979, Van Horne, 1981, Martell, 1983, Linzey, 1989). Populations in recently disturbed habitat are usually

characterized by periods of very high juvenile recruitment and high demographic instability (Van Horne, 1981). In general, populations residing in low quality habitat have low survivorship, high proportions of juveniles, and temporal instability of demographic performance (Van Horne, 1981, Adler and Wilson, 1987, Adler, 1987). Adler and Wilson (1987) noted that *P. leucopus* populations in low quality habitat can at times perform similar to populations in high quality habitat when favorable resources are readily available. Reference site populations may have performed in this manner as indicated by their very high abundances in summer 1992 and their very low abundances throughout the rest of the study. The short duration of this two year study might have aided in masking an even greater quality difference between the disturbed and undisturbed habitats.

Contrary to other studies of disturbances (i.e. clearcutting, prescribed burns), the most disturbed habitats had the most stable populations. Gypsy moth disturbance is very different from clearcutting and prescribed burning in that the understory remains intact. It has also been noted that gypsy moths generally have their greatest impacts on habitat of low quality to small mammals (Yahner and Smith, 1991). The reference site is largely comprised of chestnut

oaks with a few interdispersed red oaks. There was no hard mast crop in fall 1992 and very little hard mast crop in fall 1993. The monotypic tree composition of this habitat and the cyclic nature of oak masting (3 years for the white-oak group, Sork et al., 1993) could have produced the demographic instability observed at the reference site. In general, others have reported *P. leucopus* population increase in abundances (Batzli, 1977, Mcshea and Franq, 1984) and shift into oak microhabitat in the presence of acorns (Mcshea and Gilles, 1992). Acorns from the white-oak group (subgenus *lepidobalanus*, chestnut oak belongs to this group) have tannin and lipid levels generally four times lower than acorns from the red-oak group (subgenus *erythrobalanus*) (Short and Epps, 1976). It has been demonstrated that *P. leucopus* that are not used to feeding on red oak acorns can incur tannin poisoning (Briggs and Smith, 1989), which suggests that animals that readily eat red oak acorns may have to make physiological adjustments to maintain consumption of high tannin levels. When present, chestnut oak acorns could be a relatively easy to digest, nutritious food source that could be very important in overwinter survival. Given the above circumstances, it is believed that the high abundances reported for summer 1992 could have been a lag response of the reference site

populations to a very good mast crop in fall 1991.

At the high mortality site, sex and age discrimination of microhabitat further suggests the improvement of habitat quality due to gypsy moth disturbance. During fall, at high abundances, adult females segregated from the rest of the sex and age classes into the most optimal habitat. Female adults resided in microhabitats with more large logs and higher rock cover relative to male adults and female juveniles. Male adults consistently used microhabitat with greater breast height stem densities than female adult microhabitat, but at this site, where shrub cover is homogeneous, this variable should not be the determining variable for optimal microhabitat. Male juveniles were usually excluded from male adult microhabitat. The only time male juveniles overlapped into male adult microhabitats was when they were at very low abundances (fall 1992) and probably had very little influence on the population. Male juvenile niche breadths were also very low, which suggests that they were very limited in the resources that they could exploit.

Although home ranges were not measured in this study, microhabitat segregation between sex and age classes implies that there was some degree of territoriallity among sex and age

classes. Territoriallity of female *P. leucopus* has been well documented (Metzgar, 1971, Bowers and Smith, 1979) and seems to be density dependent (Metzgar, 1971, Wolff, 1985b). Territoriality of adult males is thought to be a mechanism by which subordinate juveniles are excluded from optimal habitat during breeding seasons (Fairbain, 1977) and at high population densities (Nadeau et al., 1981, Adler and Tamarin, 1984). High mortality site populations seem to follow the "ideal-despotic" model proposed by Fretwell (1972). This model suggests that intraspecific aggression is greater at high abundances in favorable habitat where socially dominant (i.e. female and male adults) individuals occupy the highest quality habitat and through territoriallity prevent density-dependent food resource depletion (Fretwell, 1972, Halama and Dueser, 1994).

The *P. maniculatus* population at the recovery site also had significant microhabitat segregation among sex and age classes at high abundances, however, the *P. leucopus* population did not exhibit this same pattern. Based on the disappearance of the *P. leucopus* population after winter 1993, it is thought that *P. maniculatus* was the dominant species at this site throughout the study. *P. maniculatus* and *P. leucopus* used significantly different microhabitats when coocurring in the fall of 1992 (Ch 1). If *P.*

maniculatus was the dominant competitor and excluded *P. leucopus* from the most favorable microhabitat types, this would permit *P. maniculatus* to discriminate in microhabitat use by sex and age class. *P. leucopus* may have occupied the least optimal microhabitat, which could have resulted in intraspecific scramble competition for resources and the resulting lack of microhabitat discrimination by sex and age class. Seagle (1985) demonstrated that in the presence of a dominant competitor (*Ochrotomys nuttali*), *P. leucopus* was unable to sexually discriminate microhabitat, but in the absence of a dominant competitor, *P. leucopus* did sexually discriminate microhabitat.

At the in process site, there was very little sex and age class discrimination at high or low abundances within *P. leucopus* and *P. maniculatus* populations. *P. leucopus* and *P. maniculatus* microhabitat use was significantly different except for fall 1992 when *P. leucopus* was at high abundances. It is possible that these species were selecting preferred microhabitat at low abundances (Rosenzweig, 1981, Rosenzweig and Abramsky, 1986) and at high abundances moved into and colonized the other species microhabitat space with perhaps little or no aggression from the other species. This might have occurred if resources were over abundant, but in the fall, this would have been unlikely at these sites

because of the absence of hard mast (Gotschalk, 1989). An alternative explanation would be that competition did exist and the discrete segregation of microhabitat between these species was a result of constant competitive exclusion (Dueser and Hallet, 1980).

It may be reasonable to infer that competition was limiting these populations at the in process site based on the low degree of social segregation observed for both species. The absence of microhabitat discrimination among sex and age classes could result in reproductive females sharing optimal microhabitat with conspecifics, thus reducing available resources for fulfillment of reproductive costs. *P. leucopus* and *P. maniculatus* populations at the in process site on average had the highest proportions of reproductively active females, which would predict that these populations would have higher abundances relative to the other sites, but only *P. leucopus* had comparable abundances to populations where their congener was absent within this study and other studies conducted in similar habitat types (i.e. Morris, 1987, Halama and Dueser, 1994). It could be possible that *P. leucopus* was the dominant species at this site, but that would only be based on abundance. In the last sample of this study (fall 1993), *P. maniculatus* abundances exceeded those of *P. leucopus,* which

would suggest that there could be fluctuations in the dominant species. This study was too short to observe annual fluctuations in dominance, but it is conceivable that these species have close to equal effects on each other, which would be associated with temporal fluctuations of numerical dominance depending upon temporal fluctuations of preferred resources. Further, if competition was prevalent between these species at the in process site, the removal of one species should coincide with an increase in the other species abundance and social organization.

The reference site populations exhibited very little microhabitat segregation of sex and age classes at high abundances in summer 1992 and some segregation at low abundances. Female adults did use significantly different microhabitat from male adults and female juveniles at high abundances. They occurred in microhabitat with less rock cover, more herbaceous ground cover, and higher evergreen shrub cover relative to male adults and female juveniles. This habitat was missing some key attributes that are important to *P. leucopus* populations (i.e. high log densities, homogeneous cover, high invertebrate abundances), but adult females did segregate into the most optimal habitat. The missing important habitat characteristics would indicate that the microhabitat occupied by adult females at

the reference site was less optimal than adult female microhabitat at the disturbed sites. Besides adult females, microhabitat segregation between sex and age classes did not exist at the reference site at high abundances. As stated earlier, the temporary exceptional abundances of these populations was probably due to the intermittent presence of a chestnut oak mast.

Unlike other populations, the reference site populations reached their peak abundances in summer 1992 and had no juvenile recruitment in fall 1992. It is possible that reference site populations do follow the "ideal despotic" model (Fretwell, 1972), but temporal heterogeneity of an abundant food resource allowed populations to quickly exceed the carrying capacity of that habitat in a normal year, and thus over exploitation occurred after the temporary resource was gone and no substantial territories could be established by adult females to regulate the population. High density populations have the potential to manifest social factors that inhibit reproduction and cause high juvenile mortality (Van Horne, 1981), and this may have occurred at the reference site between summer and fall 1992.

In summary, extensive gypsy moth disturbance at least temporarily improved habitat quality for *P. leucopus* populations at the high mortality and for both *Peromyscus*

species at the in process site. Due to tree species composition (mixed hickory and red oak), the recovery habitat was probably of high quality regardless of gypsy moth disturbance and only was impacted in years of heaviest gypsy moth infestation when it becomes a dispersal sink for moths from heavily impacted oak habitats (Campbell and Sloan, 1977a).

Gypsy moth disturbance creates a mosaic of habitats varying in quality which is dependent upon the initial conditions of habitat structure. This study was limited in scope by its duration and the number of habitats sampled. Animal population responses to variation in changes of habitat structure and habitat quality resulting from gypsy moth disturbance needs to be explored at the population (habitat types) and metapopulation (landscape scale) scales. *P. leucopus* populations in a fragmented landscape can segregate into genetically distinct demographic units within a relatively small area (16 Ha) (Krohne and Baccus, 1985), which suggests that gypsy moth disturbance could have microevolutionary implications for animals that reside in impacted habitats.

Difficulties in controlling gypsy moth disturbance insures permanent alteration of the eastern deciduous forest ecosystem. Because many animals are going to have to adapt

to these changes, future work on this problem should try to understand dispersal patterns of animals between disturbed and undisturbed segments of the habitat and what this means to the longterm fitness of populations. Longterm patterns of population and community dynamics after disturbance have to be developed to gain any understanding of these dispersal patterns. Successional changes in habitat structure after disturbance will affect mechanisms that limit animal populations and dispersal patterns of individuals within these populations. Changes in interspecific and intraspecific competition, predation vulnerability, resources (i.e. microhabitat, food, nesting sites), and physiological constraints (i.e. reproductive strategies, acclimation to new environments) need to be experimentally investigated to gain information on how gypsy moth disturbance and the resulting habitat fragmentation can alter dispersal patterns of animals and contribute to microevolutionary changes in animal populations.

Literature Cited

Adler, G.H. 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. Canadian Journal of Zoology 65:903-912.

Adler, G.H. and R.H. Tamarin. 1984. Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. Canadian Journal of Zoology 62:58-64.

Adler, G.H. and M.L. Wilson. 1987. Demography of a habitat generalist, the white-footed mouse, in a heterogeneous environment. Ecology 68:1785-1796.

Ahlgren, C.E. 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry 64:614-617.

Barnum, S.A., C.J. Manville, J.R. Tester, and W.J. Carmen. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. Journal of Mammalogy 73:797-801.

Barry, R.E., Jr., M.A. Botje, and L.B. Grantham. 1984. Vertical stratification of *Peromyscus leucopus* and *Peromyscus maniculatus* in southwestern Virginia. Journal of Mammalogy 65:145-148.

Barry, R.E., Jr., A.A. Heft, and T.E. Baumer. 1989. Spatial relationships of syntopic white-footed mouse, *Peromyscus leucopus*, deer mice, *P. maniculatus*, and red-backed voles, *Clethrionomys gapperi*. Canadian Field-Naturalist 104:387-393.

Batzli, G.O. 1977. Population dynamics of the white-footed mouse in floodplain and upland forests. The American Midland Naturalist 97:19-32.

Boag, P.T. and P.R. Grant. 1981. Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galapagos. Science 214:82-85.

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

Briggs, J.M. and K.G. Smith. 1989. Influence of habitat on acorn selection by *Peromyscus leucopus*. Journal of Mammalogy 70:35-43.

Brown, J.H., Jr., D.B. Halliwell, and W.P. Gould. 1979. Gypsy moth defoliation: impacts in Rhode Island forests. Journal of Forestry 77:30-32.

Brown, J.S. 1989. Coexistence on a seasonal resource. The American Naturalist 133:168-182.

Brown, J.S., B.P. Kotler, R.J. Smith, and W.O. Wertz, II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408-415.

Buckner, C.A. and D.J. Shure. 1985. The response of *Peromyscus* to forest opening size in the Southern Appalachian Mountains. Journal of Mammalogy 66:299-307.

Campbell, R.W. and R.J. Sloan. 1976. Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. Environmental Entomology 5:1211-1217.

Campbell, R.W. and R.J. Sloan. 1977a. Forest stand responses to defoliation by gypsy moths. Forest Science Monograph 19:1-34.

Campbell, R.W. and R.J. Sloan. 1977b. Natural regulation of innocuous gypsy moth populations. Environmental Entomology 6:315-322.

Carnes, B.A. and N.A. Slade. 1982. Some comments on niche analysis in cannonical space. Ecology 63:888-893.

Chesson, P. and M.L. Rosenzweig. 1991. Behavior, heterogeneity, and the dynamics of interacting species. Ecology 72:1187-1195.

Collins, S. 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. Ecology 42:836-838.

Cottam, G. and J.T. Curtis. 1956. The use of distance measures in phytological sampling. Ecology 37:451-460.

Cranford, J.A. and M.S. Maly. 1986. Habitat associations among small mammals in an oldfield community on Butt Mountain, Virginia. Virginia Journal of Science 37:14-18.

Cranford, J.A. and M.S. Maly. 1990. Small mammal population densities and habitat associations on Chincoteague National Wildlife Refuge, Assateague Island, Virginia. Virginia Journal of Science 41:321-329.

Dooley, J.L., Jr. and R.D. Dueser. 1990. An experimental examination of nest-site segregation by two *Peromyscus* species. Ecology 71:788-796.

Dueser, R.D. and J.G. Hallet. 1980. Competition and habitat selection in forest floor small mammal fauna. Oikos 27:251-258.

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

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

Dueser, R.D., J.H. Porter, J.L. Dooley, Jr. 1989. Direct tests for competition in North American rodent communities: synthesis and prognosis. Pp. 105-125, in Patterns in the structure of mammalian communities. D.W. Morris et al., ed. Texas Tech University Press, Lubbock, Texas.

Fairbain, D.J. The spring decline in deer mice: death or dispersal? Canadian Journal of Zoology 55:84-92.

Feldhamer, G.A., R.S. Klann, A.S. Gerard, and A.C. Driskell. 1993. Habitat partitioning, body size, and timing of parturition in pygmy shrews and associated soricids. Journal of Mammalogy 74:403-411.

Fox, B.J. 1990. Changes in the structure of mammal communities over successional time scales. Oikos 59:321-329.

Fox, B.J. and G.L. Kirkland, Jr. 1992. An assembly rule for functional groups applied to North American soricid communities. Journal of Mammalogy 73:491-503.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, USA.

Geier, A.R. and L.B. Best. 1980. Habitat selection by small mammals of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44:16-24.

Getz, L.L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology 49:276-286.

Gottschalk, K.W. 1989. Gypsy moth effects on mast production. Pp. 42-50, in Proceedings of the Workshop on Southern Appalachian Mast Management. C.E. McGee ed. Cherokee National Forest, U.S.D.A., Forest Service and the Department of Forestry, Wildlife, and Fisheries, University of Tennessee.

Grace, J.R. 1986. The influence of gypsy moth on the composition and nutrient content of litter fall in a Pennsylvania oak forest. Forest Science 32:855-870.

Halama, K.J. and R.D. Dueser. 1994. Of mice and habitats: tests for density-dependent habitat selection. Oikos 69:107-114.

Hansen, L. and G.O. Batzli. 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Canadian Journal of Zoology 56:2530-2541.

Harlowe, R.F. and A.T. Doyle. 1990. Food habits of southern flying squirrels (*Glaucomys volans*) collected from red-cockaded woodpecker (*Picoides borealis*) colonies in South Carolina. The American Midland Naturalist 124:187-191.

Harney, B.A. and R.D. Dueser. 1987. Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. Ecology 68:1084-1091.

Hix, D.M., D.E. Fosbroke, R.R. Hicks, Jr., and K.W. Gottschalk. 1991. Development of regeneration following gypsy moth defoliation of Appalachian plateau and ridge and valley hardwood stands. Pp. 347-359 in, 8th Central Hardwood Forest Conference. West Virginia Agricultural and Forestry Experiment Station, Scientific Article No. 2252.

Houston, D.R. 1981. Forest stand relationships. Pp. 267-281, in C.C. Doane and M.L. McManus (eds.), The gypsy moth: Research toward integrated pest management. US Department of Agriculture, Washington, D.C. Tech. Bull. 1584.

James, F.C. and H.H. Shugart. 1970. A quanatative method of habitat description. Audobon Field Notes 24:727-737.

Johnson, S.D. 1994. Sex ratio and population stability. Oikos 69:172-176.

Kirkland, G.L., Jr. 1976. Small mammals of a mine waste situation in the central Adirondacks, New York: case of opportunism by *Peromyscus maniculatus*. American Midland Naturalist 95:103-110.

Kirkland, G.L., Jr. 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos 59:313-320.

Kirkland, G.L., Jr., T.R. Johnston, and P. Steblein. 1985. Small mammal exploitation of a forest-clearcut interface. Acta Theriologica 30:211-218.

Kitchings, J.T. and D.J. Levy. 1981. Habitat patterns in a small mammal community. Journal of Mammalogy 62:814-820.

Kleinbaum, D.G., L.L. Kupper, K.E. Muller. 1988. Applied regression analysis and other multivariable methods. PWS-Kent Publishing Company, Boston, Massachusetts.

Kotler, B.P. 1984. Predation risk and the structure of desert rodent communities. Ecology 65:689-701.

Krefting, L.W. and C.E. Ahlgren. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. Ecology 55:1391-1398.

Krohne, D.T. and R. Baccus. 1985. Genetic and ecological structure of a population of *Peromyscus leucopus*. Journal of Mammalogy 66:529-537.

Krohne, D.T., J.F. Merritt, S.H. Vessey, and J.O. Wolff. 1988. Comparative demography of forest *Peromyscus*. Canadian Journal of Zoology 66:2170-2176.

Levins, R. 1968. Evolution in changing environments: some theoretical explanations. Princeton University Press, Princeton, New Jersey, USA.

Linzey, A.V. 1989. Response of the white-footed mouse (*Peromyscus leucopus*) to the transition between disturbed and undisturbed habitats. Canadian Journal of Zoology 67:505-512.

Linzey, A.V. and M.H. Kesner. 1991. Population regulation in white-footed mice (*Peromyscus leucopus*) in a suboptimal habitat. Canadian Journal of Zoology 69:76-81.

Linzey, A.V. and D.W. Linzey. 1971. Mammals of Great Smokey Mountains National Park. University of Tennessee Press, Knoxville, Tennessee, USA.

Lovejoy, D.A. 1975. The effect of logging on small mammal populations in New England northern hardwoods. University of Connecticut, Occasional Papers Biological Series 2:269-291.

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical ecology: A primer on methods and computing. John Wiley and Sons, New York, New York, USA.

Martell, A.M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Canadian Field Naturalist 95:325-328.

Martell, A.M. 1983. Demography of southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) after logging in north-central Ontario. Canadian Journal of Zoology 61:958-969.

McConnell, S.P. 1988. Effects of gypsy moth defoliation on acorn production and viability, litterfall, and litter layer depth and biomass in north-central Virginia and western Maryland. Unpublished M.S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 124 pp.

M'Closkey, R.T. 1975. Habitat succession and rodent distribution. Journal of Mammalogy 56:950-955.

McShea, W.J. and E.N. Francq. 1984. Microhabitat selection by *Peromyscus leucopus*. Journal of Mammalogy 65:675-678.

McShea, W.J. and A.B. Gilles. 1992. A comparison of traps and florescent powder to describe foraging for mast by *Peromyscus leucopus*. Journal of Mammalogy 73:218-222.

Metzgar, L.H. 1971. Behavioral population regulation in the woodmouse, *Peromyscus leucopus*. American Midland Naturalist 86:434-448.

Morris, D.W. 1984a. Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraint? Oecologia 65:51-57.

Morris, D.W. 1984b. Patterns and scale of habitat use in two temperate zone small mammal faunas. Canadian Journal of Zoology 62:1540-1547.

Morris, D.W. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs 57:269-281.

Nadeau, J.H., R.T. Lombardi, and R.H. Tamarin. 1981. Population structure and dispersal of *Peromyscus maniculatus*. Canadian Journal of Zoology 59:793-799.

Newell, S.J. and E.J. Tramer. 1978. Reproductive strategies in herbaceous plant communities during succession. Ecology 59:228-234.

Parren, S.G. and D.E. Capen. 1985. Local distribution and coexistence of two species of *Peromyscus* in Vermont. Journal of Mammalogy 66:36-44.

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

Pianka, E.R. 1970. On r and K selection. American Naturalist 102:592-597.

Pielou, E.C. 1984. The interpretation of ecological data. Wiley and Sons, New York, New York, USA.

Planz, J.V. and G.L. Kirkland, Jr. 1992. Use of woody ground litter as a substrate for travel by the white-footed mouse, *Peromyscus leucopus*. Canadian Field-Naturalist 106:118-121.

Powell, R.A. and W.S. Brooks. 1981. Small mammal changes following tornado blowdown in northern mixed forest. Journal of Mammalogy 62:397-400.

Rosenzweig, M.L. 1981. A theory of habitat selection. Ecology 62:327-335.

Rosenzweig, M.L. and Z. Abramsky. 1986. Centrifugal community organization. Oikos 46:339-348.

SAS Institute. 1990. SAS/STAT user's guide, release 6.04 edition. SAS Institute, Inc., Cary, North Carolina, USA.

Schloyer, C.R. 1977. Food habitats of *Clethrionomys gapperi* on clearcuts in West Virginia. Journal of Mammalogy 58:677-679.

Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:702-726.

Schoener, T.W. 1982. The controversy over interspecific competition. American Scientist 70:586-595.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist 122:240-285.

Seagle, S.W. 1985. Patterns of small mammal microhabitat utilization in cedar glade and deciduous forest habitats. Journal of Mammalogy 66:22-35.

Seagle, S.W., H.H. Shugart, and D.C. West. 1984. Habitat availability and animal community characteristics. Oak Ridge National Laboratory Technical Manual 8864, Publication 2217 of the Environmental Sciences Division, Oak Ridge, Tennessee, USA.

Short, H.L. and E.A. Epps, Jr. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. Journal of Wildlife Management 40:283-289.

Shugart, H.H. and B.C. Patten. 1972. Niche quantification and the concept of niche pattern. Pp. 284-327, in B.C. Patten ed. Systems analysis and simulation in ecology. Vol.2. Academic Press, New York, New York, USA.

Sly, G.R. 1976. Small mammal succession on strip-mined land in Vigo County, Indiana. American Midland Naturalist 95:257-267.

Smith, H.R. 1985. Wildlife and the gypsy moth. Wildlife Society Bulletin 13:166-174.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research, Second edition, W.H. Freeman and Company, San Fransisco, California, USA.

Sork, V.L., J. Bramble, O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528-541.

Stapp, P. 1992. Energetic influences on the life history of *Glaucomys volans*. Journal of Mammalogy 73:914-920.

Stewart, C.A. 1991. A note on the microdistribution of the red-backed vole, *Clethrionomys gapperi*, in the E.N. Huyck Preserve, New York. Canadian Field-Naturalist 105:274-275.

Sullivan, T.P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Canadian Journal of Zoology 57:1636-1648.

Swihart, R.K. and N.A. Slade. 1990. Long-term dynamics of an early successional small mammal community. American Midland Naturalist 123:372-382.

Thompson, S.D. 1982. Structure and species composition of desert Heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecology 63:1313-1321.

Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology 59:1045-1061.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63:992-1003.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vickery, W.L. 1981. Habitat use by northeastern forest rodents. American Midland Naturalist 106:111-118.

Whitaker, J.O. 1963. Food of 120 *Peromyscus leucopus* from Ithica, New York. Journal of Mammalogy 44:418-419.

Wolff, J.O. 1985a. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. Canadian Journal of Zoology 63:2657-2662.

Wolff, J.O. 1985b. Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. Canadian Journal of Zoology 63:1548-1555.

Wolff, J.O. and R.D. Dueser. 1986. Noncompetitive coexistence between *Peromyscus* species and *Clethrionomys gapperi*. Canadian Field-Naturalist 100:186-191.

Wolff, J.O., R.D. Dueser, and K.S. Berry. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 66:795-798.

Wolff, J.O., M.H. Freeberg, and R.D. Dueser. 1983. Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). Behavioral Ecology and Sociobiology 12:237-242.

Wrazen, J.A. and G.E. Svendsen. 1978. Feeding ecology of a population of eastern chipmunks (*Tamias striatus*) in southeast Ohio. American Midland Naturalist 100:190-201.

Wrigley, R.E., J.E. Dubois, and H.W.R. Copland. 1979. Habitat abundance, and the distribution of six species of shrews in Manitoba. Journal of Mammalogy 60:505-520.

Yahner, R.H. 1985. Microhabitat use by small mammals in even-aged forest stands. American Midland Naturalist 115:174-180.

Yahner, R.H. and H.R. Smith. 1991. Small mammal and habitat relationships on deciduous forested sites with different susceptibility to gypsy moth defoliation. Environmental Management 15:113-120.

Zegers, D.A. and J.C. Ha. 1981. Niche separation of *Peromyscus leucopus* and *Blarina brevicauda*. Journal of Mammalogy 62:199-201.

Appendix 1

Table 1A - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe small mammal distributions at each site in the summer of 1992.

Variable	High Mortality	In Process	Recovery	Reference
TRD	0.007	0.02		
WHET	0.04			0.07
EHC	0.02	0.08	0.0006	
STUD	0.06			
SNS	0.05			
SWD	0.06	0.02		0.006
WD	0.11			0.005
SDBH		0.13	0.004	
INV		0.15	0.009	
SCOM			0.002	0.12
HS			0.03	
BRYC			0.02	0.06
CC			0.06	0.12
LOGD			0.13	
LOGS				0.06
SOC				0.14

Table 1B - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe small mammal distributions at each site in the fall of 1992.

Variable	High Mortality	In Process	Recovery	Reference
TRD		0.04		
TRS				0.004
LD	0.0001			
EHC			0.03	
RC	0.001		0.002	
SEED92	0.04	0.08		0.009
SAPD	0.06			0.05
SND	0.09		0.01	
WS	0.10			
ESC	0.03			0.05
SC				0.002
STUS		0.03		
STUD			0.11	0.14
SNS		0.10		
SWD	0.06	0.13		
WD				0.003
SDBH		0.06		
HD		0.07	0.03	
SCOM				0.08
LOGS		0.005	0.0001	

Table 1C - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe small mammal distributions at each site in the winter of 1993.

Variable	High Mortality	In Process	Recovery	Reference
TRD	0.03			
EHC				0.0001
RC	0.02			0.004
SEED92			0.10	
SAPD			0.04	
ESC	0.0003			
SC				0.03
STUS	0.003			
SWD			0.06	
HD	0.10			
INV				0.07
SCOM	0.10			
LOGS	0.003	0.0002		
LOGD	0.001	0.04		
SOC	0.03	0.01		
HP	0.03	0.02		
ECC	0.004			
BRYC		0.006	0.0003	0.04
WP			0.002	

Table 1D - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe small mammal distributions at each site in the summer of 1993.

Variable	High Mortality	In Process	Recovery	Reference
EHC				0.09
RC	0.09			
SEED93	0.10			
SAPD	0.11	0.02		
ESC				0.03
SC	0.06		0.11	
LOGD			0.12	0.0007
HP	0.12			0.03
BRYC		0.0001	0.01	
VAC93		0.13		
WP			0.03	
SDBH			0.009	
WHET		0.07		0.02
TRS	0.03			0.06
SNS	0.05			
STUD	0.14		0.11	
WS		0.15		
LD			0.08	

Table 1E - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe small mammal distributions at each site in the fall of 1993.

Variable	High Mortality	In Process	Recovery	Reference
TRD	0.12			
SEED93				0.006
HD				0.0001
INV	0.06			
LOGD	0.08			
HP				0.06
BRYC		0.009		
VAC93	0.10			
SDBH		0.06		
TRS			0.07	
SND	0.14			

Table 1F - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe sex and age class distributions at each site in the summer of 1992.

Variable	High Mortality	In Process	Recovery	Reference
TRD			0.07	
RC			0.10	0.01
EHC				0.04
SEED92	0.08	0.10		
HD	0.14			
INV		0.08		
VAC92		0.03		
SDBH			0.11	
TRS		0.03		
SND	0.07	0.05		
WP	0.02	0.01		
LD	0.02			
WD	0.13	0.05		
BRYC	0.14	0.08		
ECC	0.07			
SWD		0.002		
SOC		0.02		
STUS		0.02		
LOGS		0.01		

Table 1G - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe sex and age class distributions at each site in the fall of 1992. Variables with a p-value greater than 0.15 were analyzed at the in process site because no variable fell in the p < 0.15 range.

Variable	High Mortality	In Process	Recovery	Reference
TRD	0.03		0.07	
RC	0.03			0.05
SEED92		0.16		
SDBH	0.007			
TRS			0.01	
SND	0.14		0.02	
LD			0.05	0.06
SOC			0.05	
LOGD	0.06			
SC	0.04			
SCOM	0.09	0.22		
SNS		0.24		
ESC		0.18		0.07

Table 1H - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe sex and age class distributions at each site in the summer of 1993.

Variable	High Mortality	In Process	Recovery	Reference
TRD			0.009	
RC			0.005	
TRS				0.01
LD		0.12		
SOC		0.12		
LOGD			0.11	0.06
SCOM				0.06
ESC	0.12			
CC	0.009			0.08
INV	0.07	0.08	0.07	0.03
EHC	0.04		0.006	
SAPD	0.05	0.15		
BRYC		0.0009		0.08
HS		0.02		
VAC93		0.06		
SWD		0.09		0.03
WHET				0.04
STUS				0.04
WD				0.11
LOGS				0.13

Table 1I - Variables and their p-values accepted by stepwise discriminant function analysis at a p-value of 0.15 that describe sex and age class distributions at each site in the fall of 1993.

Variable	High Mortality	In Process	Recovery	Reference
TRD		0.04	0.04	
TRS				0.0001
LD				0.01
LOGD			0.12	0.03
ESC	0.002			
INV	0.02			0.10
SAPD	0.11		0.05	0.02
BRYC		0.003		
VAC93	0.002			
SWD	0.05			0.03
WHET			0.12	
STUS				0.09
WD	0.004			0.0001
LOGS		0.10		
SND	0.003			
HD	0.07		0.08	
SDBH	0.06			0.001
WP				0.007
HP				0.02
SEED93				0.003
SC				0.0007

Appendix 2

Table 2A - Overall habitat means and standard deviations for all variables measured at the high mortality site. Refer to Table 1 for variable interpretations.

Variable	N	Mean	Std Dev	Minimum	Maximum
LD	162	2.7249383	1.6496852	0	9.0300000
CC	162	36.6512346	23.5085612	0	80.0000000
SC	162	96.9429012	7.6688182	9.7500000	100.0000000
SOC	162	11.3734568	7.3723741	0	45.0000000
WP	162	10.1179012	4.4960441	0.7800000	24.2200000
HP	162	1.7623457	5.3800927	0	33.7800000
SPD	162	3.6851852	2.0535448	0	13.0000000
WS	162	2.7901235	1.3805755	0	8.0000000
HS	162	0.8888889	1.4098148	0	9.0000000
WD	162	8.4320988	6.2701863	0	28.0000000
SWD	162	6.1851852	5.0944157	0	21.0000000
HD	162	8.1913580	37.1865423	0	379.0000000
SHD	162	7.2592593	35.8432674	0	370.0000000
TMV	162	60.5006173	19.9960990	18.5000000	115.7500000
SCOM	162	7.6393210	2.3057525	3.0800000	25.0000000
BRYC	162	13.4259259	6.3226454	2.5000000	32.5000000
TRD	162	2.7925926	1.6069552	0.1000000	8.0000000
TRS	162	18.8351852	9.2105696	7.6000000	64.4000000
SAPD	162	0.9098765	0.5099275	0.1000000	3.2000000
LOGD	162	1.6753086	1.8913028	0	14.0000000
LOGS	162	10.2925926	3.9969329	0	28.2000000
STUD	162	9.8240741	4.7244022	0	14.0000000
STUS	162	13.6586420	17.5970482	0	66.0000000
SND	162	3.0987654	2.0571339	0.2000000	14.0000000
SNS	162	19.7179012	8.6871784	0	62.5000000
EHC	162	3.9814815	8.1644375	0	42.5000000
ESC	162	80.5555556	21.3899756	0	100.0000000
ECC	162	1.3888889	5.0617307	0	32.5000000
RC	162	5.4783951	6.2463278	0	35.0000000
CCA	162	35.0617284	23.2992126	0	85.0000000
SOCT	162	6.7901235	4.3118817	0	20.0000000
INV	162	4.5864198	5.5433302	0	36.0000000
LD2	162	1.8183333	1.2398544	0	6.4800000
WS2	162	2.9012346	1.2570787	0	6.0000000
HS2	162	0.7407407	1.4078553	0	7.0000000
WD2	162	7.6234568	5.0684941	0	27.0000000
SWD2	162	5.5987654	4.5320938	0	21.0000000
HD2	162	4.1172840	13.5735337	0	136.0000000
SHD2	162	3.2037037	11.9461207	0	135.0000000
HP2	162	0.9319753	2.7360022	0	22.6700000
SD93	162	2.5493827	2.3723366	0	10.0000000
VAC93	162	1.1666667	2.1847865	0	10.0000000
SD92	162	1.5308642	1.9818206	0	9.0000000
VAC92	162	1.1790123	2.4719653	0	12.0000000
WHET	162	6.3239506	2.9949994	0	16.2000000
HDF1	162	4.8950617	35.7638229	0	379.0000000
LDF1	162	2.3520988	1.3080337	0	8.1500000
SOCF	162	8.6419753	5.2728265	0	25.0000000
HPF1	162	0.0459259	0.2463612	0	2.1100000
LDF2	162	3.2141358	1.5593543	0	7.6000000
HDF2	162	1.1975309	6.4870530	0	78.0000000
HPF2	162	0.0588889	0.2772962	0	2.4400000

Table 2B - Overall habitat means and standard deviations for all variables measured at the in process site. Refer to Table 1 for variable interpretations.

Variable	N	Mean	Std Dev	Minimum	Maximum
LD	81	1.5196296	1.5541617	0	8.0000000
CC	81	67.0061728	11.7820026	32.5000000	95.0000000
SC	81	79.1358025	13.9146982	40.0000000	100.0000000
SOC	81	18.4814815	9.5277373	0	40.0000000
WP	81	4.3323457	3.5809682	0	15.0000000
HP	81	8.1671605	14.7369025	0	116.8900000
SPD	81	8.1975309	3.3182064	1.0000000	15.0000000
WS	81	2.0864198	1.3057328	0	6.0000000
HS	81	6.1111111	3.5672118	0	13.0000000
WD	81	7.7654321	7.4820980	0	39.0000000
SWD	81	6.3209877	6.7394866	0	35.0000000
HD	81	37.3456790	54.7035558	0	376.0000000
SHD	81	35.2592593	53.9079720	0	371.0000000
TMV	81	12.4783951	5.0423515	4.2500000	27.5000000
SCOM	81	8.0622222	1.5699626	3.0300000	12.5300000
BRYC	81	21.4814815	11.3659152	0	47.5000000
TRD	81	1.9456790	1.0411591	0.1000000	5.4000000
TRS	81	19.0061728	7.8654203	7.5000000	42.5000000
SAPD	81	1.5469136	0.7655205	0.2000000	3.8000000
LOGD	81	3.2172840	2.7960593	0.1000000	14.0000000
LOGS	81	11.4716049	7.0237496	0	40.0000000
STUD	81	6.6209877	4.1972823	0.9000000	14.0000000
STUS	81	18.3432099	13.3645701	0	52.0000000
SND	81	3.2197531	1.7178053	0.4000000	7.9000000
SNS	81	15.2851852	5.6160286	7.7000000	27.4000000
EHC	81	21.4506173	15.1959297	0	65.0000000
ESC	81	5.0308642	7.3791707	0	32.5000000
ECC	81	0	0	0	0
RC	81	17.8395062	10.0914033	0	45.0000000
CCA	81	53.2098765	19.0239757	2.5000000	92.5000000
SOCT	81	10.4938272	7.7198987	0	35.0000000
INV	81	10.7037037	6.7443392	0	29.0000000
LD2	81	0.8933333	0.7312165	0	3.6000000
WS2	81	2.2222222	1.5968719	0	7.0000000
HS2	81	5.9135802	3.2411323	0	13.0000000
WD2	81	6.2098765	5.9952399	0	26.0000000
SWD2	81	4.8765432	5.1511715	0	21.0000000
HD2	81	35.2345679	35.9472779	0	260.0000000
SHD2	81	28.9876543	33.1720868	0	250.0000000
HP2	81	8.7717284	6.9142879	0	28.0000000
SD93	81	2.4814815	2.5303711	0	11.0000000
VAC93	81	2.1728395	3.5063875	0	13.0000000
SD92	81	2.4320988	2.4286739	0	10.0000000
VAC92	81	3.5061728	6.4403483	0	39.0000000
WHET	81	4.6851852	4.4363586	0	22.0000000
HDF1	81	16.9876543	44.8504442	0	376.0000000
LDF1	81	1.4749383	1.2958261	0	7.8800000
SOCF	81	19.1975309	9.3443429	2.5000000	47.5000000
HPF1	81	0.2017284	0.5094134	0	2.7800000
LDF2	81	3.2456790	1.6231350	0	7.8800000
HDF2	81	13.4938272	17.3097685	0	83.0000000
HPF2	81	1.5032099	2.9815851	0	15.2200000

Table 2C - Overall habitat means and standard deviations for all variables measured at the recovery site. Refer to Table 1 for variable interpretations.

Variable	N	Mean	Std Dev	Minimum	Maximum
LD	81	2.5202469	1.7146282	0	9.0300000
CC	81	79.5061728	9.0261751	52.5000000	97.5000000
SC	81	83.8580247	11.6796390	47.5000000	100.0000000
SOC	81	6.6358025	5.5221216	0	27.5000000
WP	81	3.0239506	2.4962055	0	14.0000000
HP	81	4.2700000	3.0571858	0	14.0000000
SPD	81	5.7901235	2.5382871	0	11.0000000
WS	81	1.1234568	1.0533603	0	4.0000000
HS	81	4.6666667	2.3505319	0	10.0000000
WD	81	2.2592593	2.9907264	0	20.0000000
SWD	81	1.7901235	2.6679395	0	17.0000000
HD	81	20.2962963	13.8928439	0	63.0000000
SHD	81	17.7530864	12.3759150	0	61.0000000
TMV	81	13.1769136	4.2304753	4.5000000	24.0000000
SCOM	81	7.7459259	2.6224553	4.1500000	25.0000000
BRYC	81	9.2283951	7.4229582	0	42.5000000
TRD	81	2.1197531	1.0630639	0.2000000	6.0000000
TRS	81	29.7864198	18.6566594	7.5000000	84.5000000
SAPD	81	1.4209877	0.7597230	0.2000000	4.1000000
LOGD	81	1.5481481	1.3355814	0	6.5000000
LOGS	81	13.2469136	10.2820971	2.0000000	51.0000000
STUD	81	4.7259259	3.3549880	0.3000000	14.0000000
STUS	81	34.2925926	18.6173023	0	85.0000000
SND	81	5.3012346	3.2582777	0.7000000	14.0000000
SNS	81	16.0296296	9.2612559	0	43.6000000
EHC	81	8.7654321	8.7242788	0	30.0000000
ESC	81	0	0	0	0
ECC	81	0	0	0	0
RC	81	17.1913580	17.1363225	0	72.5000000
CCA	81	85.3395062	9.9353621	50.0000000	100.0000000
SOCT	81	5.4444444	3.2834814	0	15.0000000
INV	81	7.6913580	7.0845642	0	40.0000000
LD2	81	1.7714815	1.2217448	0	5.5300000
WS2	81	1.1358025	1.0338410	0	4.0000000
HS2	81	4.6666667	2.2416512	0	9.0000000
WD2	81	2.1234568	2.4309603	0	11.0000000
SWD2	81	1.3703704	1.9393584	0	10.0000000
HD2	81	19.5308642	11.5964288	0	50.0000000
SHD2	81	16.9259259	10.6345872	0	46.0000000
HP2	81	4.8471605	3.3387158	0	14.0000000
SD93	81	1.2962963	1.8127634	0	8.0000000
VAC93	81	0	0	0	0
SD92	81	1.8888889	2.9958304	0	20.0000000
VAC92	81	0	0	0	0
WHET	81	2.3345679	1.6801161	0	7.7000000
HDF1	81	1.1111111	2.2527761	0	9.0000000
LDF1	81	2.3487654	1.2498484	0.5000000	9.7000000
SOCF	81	7.4691358	4.5327597	0	20.0000000
HPF1	81	0.0464198	0.1836730	0	1.2200000
LDF2	81	5.0898765	1.7316780	0.3800000	10.0000000
HDF2	81	0.8024691	1.5445044	0	7.0000000
HPF2	81	0.1091358	0.2393178	0	1.3300000

Table 2D - Overall habitat means and standard deviations for all variables measured at the reference site. Refer to Table 1 for variable interpretations.

Variable	N	Mean	Std Dev	Minimum	Maximum
LD	162	2.4088889	1.9395962	0	10.9500000
CC	162	84.3518519	7.5570067	57.5000000	97.5000000
SC	162	75.8179012	18.5432813	22.5000000	100.0000000
SOC	162	16.9290123	12.3932544	0	65.0000000
WP	162	8.0859259	5.1792526	0	26.2200000
HP	162	2.4095679	4.5809442	0	25.6700000
SPD	162	5.0246914	3.7415754	0	17.0000000
WS	162	2.2839506	0.9618121	0	5.0000000
HS	162	2.7407407	3.7887633	0	15.0000000
WD	162	12.4444444	10.3869244	0	48.0000000
SWD	162	10.4506173	9.2501821	0	38.0000000
HD	162	11.7469136	22.3888037	0	146.0000000
SHD	162	11.3765432	21.4267539	0	141.0000000
TMV	162	33.8996914	27.4630392	3.7500000	132.5000000
SCOM	162	6.5392593	1.9762341	2.6800000	20.2500000
BRYC	162	17.1637654	11.5844767	0	60.0000000
TRD	162	2.3759259	1.1454911	0.1000000	6.3000000
TRS	162	24.5074074	10.7712497	7.6000000	71.0000000
SAPD	162	1.4462963	0.9640197	0.1000000	5.9000000
LOGD	162	4.2166667	3.6749826	0	14.0000000
LOGS	162	10.3703704	9.6078506	0	102.0000000
STUD	162	9.7530864	4.4199319	0.8000000	14.0000000
STUS	162	14.1728395	16.8878803	0	70.0000000
SND	162	6.6648148	3.7655099	0.6000000	14.0000000
SNS	162	13.0839506	9.9315040	0	64.0000000
EHC	162	11.8827160	13.3719535	0	60.0000000
ESC	162	56.8055556	32.0583343	0	100.0000000
ECC	162	4.5679012	10.6598315	0	62.5000000
RC	162	9.7993827	10.5146245	0	42.5000000
CCA	162	84.3827160	7.5596065	57.5000000	97.5000000
SOCT	162	17.0524691	8.8855050	0	42.5000000
INV	162	3.2098765	5.4549904	0	45.0000000
LD2	162	1.6812963	1.5321710	0	8.6800000
WS2	162	2.5123457	1.0876932	0	5.0000000
HS2	162	2.7037037	3.6677017	0	13.0000000
WD2	162	9.0679012	6.3677434	0	29.0000000
SWD2	162	7.6296296	5.7805509	0	26.0000000
HD2	162	11.4320988	20.5202147	0	99.0000000
SHD2	162	11.3950617	20.0905893	0	98.0000000
HP2	162	2.6956790	6.1657649	0	56.0000000
SD93	162	2.1913580	2.1133528	0	10.0000000
VAC93	162	6.4506173	6.2156409	0	25.0000000
SD92	162	1.9753086	2.3981116	0	13.0000000
VAC92	162	9.2407407	10.2465298	0	46.0000000
WHET	162	7.1506173	5.0292344	0	22.4000000
HDF1	162	3.8765432	8.0083539	0	37.0000000
LDF1	162	4.0678395	2.9603707	0	15.6300000
SOCF	162	14.5679012	10.3193580	0	67.5000000
HPF1	162	0	0	0	0
LDF2	162	5.4071605	1.7449959	1.7500000	11.5000000
HDF2	162	3.6111111	10.0898141	0	68.0000000
HPF2	162	0.3470370	1.8675932	0	22.5600000

Appendix 3

Table 3A - Overall habitat use means and standard deviations for all species caught at the high mortality site. Refer to Table 1 for variable interpretations. This table refers to figure 12.

SPE=PLEUCOPUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	286	97.0891608	3.5764711	85.0000000	100.0000000
WP	286	10.6479371	4.5307895	0.7800000	24.2200000
TMV	286	60.8847902	18.9427653	18.5000000	111.5000000
SCOM	286	7.7867483	2.4510199	3.2300000	25.0000000
BRYC	286	12.9895105	6.4090037	2.5000000	32.5000000
TRD	286	2.6076923	1.6924218	0.1000000	8.0000000
TRS	286	19.0258741	8.7755659	7.6000000	43.5000000
SAPD	286	0.8160839	0.4750107	0.1000000	3.2000000
LOGD	286	1.7090909	2.0162814	0	14.0000000
LOGS	286	10.1332168	4.0286929	0	23.2000000
STUD	286	9.7482517	4.8643761	0	24.0000000
STUS	286	12.7734266	16.7406783	0	66.0000000
SND	286	3.1961538	2.1772232	0.2000000	14.0000000
SNS	286	19.6695804	9.0873433	0	62.5000000
EHC	286	3.1381119	6.8575211	0	37.5000000
ESC	286	82.9982517	16.8856057	5.0000000	100.0000000
ECC	286	1.5909091	5.4212501	0	32.5000000
RC	286	5.1048951	6.1585351	0	35.0000000
INV	286	4.2937063	5.2680196	0	36.0000000
HD2	286	4.6223776	17.1160350	0	136.0000000
SD93	286	2.4055944	2.4501708	0	10.0000000
VAC93	286	1.1818182	2.0997456	0	10.0000000
WHET	286	6.3930070	3.0529123	0	16.2000000
WD	286	8.6888112	6.7955879	0	28.0000000
SWD	286	6.0909091	5.2527808	0	21.0000000
CCA	286	36.0314685	23.3279981	0	85.0000000

SPE=BBREVICAUDA

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	50	97.6500000	2.6921086	90.0000000	100.0000000
WP	50	10.2708000	4.0073198	0.7800000	19.8900000
TMV	50	58.7210000	19.8158283	24.2500000	96.5000000
SCOM	50	7.8698000	1.9394303	3.7800000	11.6500000
BRYC	50	11.5000000	5.7587555	2.5000000	25.0000000
TRD	50	3.1080000	1.5207195	0.8000000	7.5000000
TRS	50	19.9160000	10.0349666	7.6000000	43.5000000
SAPD	50	0.9540000	0.5544661	0.1000000	3.2000000
LOGD	50	1.3580000	1.3542209	0.1000000	6.7000000
LOGS	50	10.0320000	4.3100945	6.0000000	26.0000000
STUD	50	10.0140000	4.6706644	0.9000000	14.0000000
STUS	50	14.4000000	18.3783146	0	60.0000000
SND	50	3.7160000	3.0429148	0.7000000	14.0000000
SNS	50	23.2340000	10.4664987	9.5000000	62.5000000
EHC	50	6.1000000	10.5844514	0	42.5000000
ESC	50	80.0000000	24.3434188	5.0000000	100.0000000
ECC	50	2.4500000	4.9613301	0	12.5000000
RC	50	3.9500000	5.2267464	0	35.0000000
INV	50	3.0000000	3.7087871	0	13.0000000
HD2	50	5.5400000	9.2432215	0	33.0000000
SD93	50	1.9600000	1.9373873	0	7.0000000
VAC93	50	1.2000000	1.9059520	0	8.0000000
WHET	50	5.8588000	3.1629111	1.1000000	16.2000000
WD	50	8.3400000	6.4511034	0	22.0000000
SWD	50	5.4400000	4.5137432	0	17.0000000
CCA	50	28.2500000	21.3943179	0	82.5000000

(Table 3A Continued)

---------- SPE=CGAPPERI ----------

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	33	98.3333333	2.9755952	87.5000000	100.0000000
WP	33	11.4472727	4.8885007	2.2200000	19.8900000
TMV	33	68.9727273	21.6827484	22.0000000	111.5000000
SCOM	33	7.5178788	3.5758091	3.7800000	25.0000000
BRYC	33	13.0303030	6.4577224	2.5000000	30.0000000
TRD	33	3.5939394	1.6033051	1.5000000	6.9000000
TRS	33	14.9787879	8.0330084	7.7000000	40.0000000
SAPD	33	1.0575758	0.5836471	0.1000000	2.5000000
LOGD	33	1.5757576	1.5445530	0	4.9000000
LOGS	33	9.3787879	2.3495688	6.0000000	16.0000000
STUD	33	8.6060606	4.4266197	1.4000000	14.0000000
STUS	33	21.0151515	18.4723124	0	60.0000000
SND	33	2.5000000	0.9051933	1.0000000	4.4000000
SNS	33	19.8909091	7.2062197	8.0000000	35.5000000
EHC	33	3.6363636	7.0181380	0	35.0000000
ESC	33	83.4090909	24.4535448	0	100.0000000
ECC	33	1.5151515	4.8789805	0	22.5000000
RC	33	7.1969697	8.6773226	0	35.0000000
INV	33	3.6969697	4.3119373	0	13.0000000
HD2	33	5.4848485	16.6059500	0	67.0000000
SD93	33	2.2121212	2.3285937	0	8.0000000
VAC93	33	0.3333333	0.8164966	0	3.0000000
WHET	33	6.9151515	2.3516113	2.6000000	12.3000000
WD	33	6.9393939	6.2246455	0	27.0000000
SWD	33	4.2727273	4.6319052	0	16.0000000
CCA	33	20.4545455	17.3143562	0	57.5000000

---------- SPE=SOREX ----------

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	29	97.7586207	3.1583808	87.5000000	100.0000000
WP	29	11.3372414	2.9218608	6.5600000	17.4400000
TMV	29	64.0965517	22.5354044	22.7500000	97.0000000
SCOM	29	8.3720690	3.7675829	4.7000000	25.0000000
BRYC	29	13.4482759	6.7946208	5.0000000	32.5000000
TRD	29	3.0965517	1.5112631	0.8000000	6.1000000
TRS	29	19.9413793	8.7854798	7.7000000	40.0000000
SAPD	29	1.0000000	0.5756983	0.2000000	2.5000000
LOGD	29	1.8931034	1.7641127	0	6.7000000
LOGS	29	10.9517241	4.6237447	6.8000000	26.0000000
STUD	29	9.9241379	4.9221551	3.9000000	14.0000000
STUS	29	13.2241379	16.8499609	0	55.0000000
SND	29	3.5034483	3.3225939	0.2000000	14.0000000
SNS	29	21.1586207	8.3573969	7.7000000	44.5000000
EHC	29	1.8103448	2.5788071	0	10.0000000
ESC	29	86.8965517	18.6922345	15.0000000	100.0000000
ECC	29	3.3620690	7.5378764	0	32.5000000
RC	29	6.8103448	9.0113161	0	35.0000000
INV	29	4.4137931	6.3836691	0	29.0000000
HD2	29	4.9655172	10.9331826	0	33.0000000
SD93	29	2.4137931	1.8423053	0	7.0000000
VAC93	29	0.9310345	1.9444249	0	9.0000000
WHET	29	6.8034483	2.2808962	2.7000000	12.3000000
WD	29	5.7241379	3.8162861	1.0000000	14.0000000
SWD	29	3.6551724	3.2213114	0	12.0000000
CCA	29	33.2758621	24.4319705	0	82.5000000

(Table 3A Continued)

SPE=PMANICULATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	19	98.5526316	2.5434815	92.5000000	100.0000000
WP	19	8.1505263	4.2635646	2.2200000	18.6700000
TMV	19	64.8815789	22.0954948	22.0000000	98.2500000
SCOM	19	8.0794737	4.3670566	4.7000000	25.0000000
BRYC	19	11.5789474	6.3579853	2.5000000	30.0000000
TRD	19	2.6210526	1.8653504	0.4000000	6.3000000
TRS	19	17.6842105	8.5938132	7.6000000	40.0000000
SAPD	19	0.9894737	0.6806000	0.1000000	2.5000000
LOGD	19	1.8210526	3.0833926	0.1000000	14.0000000
LOGS	19	9.5315789	4.1698725	0	19.0000000
STUD	19	11.4263158	3.5464916	4.3000000	14.0000000
STUS	19	9.7105263	13.5516663	0	38.0000000
SND	19	2.7052632	1.0705521	1.1000000	5.0000000
SNS	19	21.7210526	7.4044715	8.1000000	36.6000000
EHC	19	5.9210526	11.6729306	0	42.5000000
ESC	19	72.7631579	36.3518181	0	100.0000000
ECC	19	1.8421053	4.3971349	0	12.5000000
RC	19	6.9736842	8.9976443	0	35.0000000
INV	19	6.5263158	10.0739952	0	36.0000000
HD2	19	9.8947368	20.8803329	0	67.0000000
SD93	19	2.3684211	1.7704527	0	5.0000000
VAC93	19	0.4210526	1.0706068	0	4.0000000
WHET	19	5.2263158	2.9722498	1.6000000	12.3000000
WD	19	7.7894737	6.6213371	0	27.0000000
SWD	19	5.4736842	4.0874934	0	14.0000000
CCA	19	28.6842105	21.9748660	0	75.0000000

SPE=TSTRIATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	18	97.6388889	3.3729266	90.0000000	100.0000000
WP	18	11.1461111	3.5371693	6.8900000	18.6700000
TMV	18	66.4305556	16.3445902	37.7500000	92.2500000
SCOM	18	7.0288889	1.7343176	4.7000000	11.1500000
BRYC	18	14.1666667	8.6602540	2.5000000	30.0000000
TRD	18	4.0055556	2.3241627	0.1000000	7.5000000
TRS	18	14.2444444	7.2603858	8.1000000	40.0000000
SAPD	18	0.9111111	0.3878885	0.1000000	1.5000000
LOGD	18	0.7055556	0.7981392	0	3.2000000
LOGS	18	11.9222222	6.4873230	7.0000000	28.2000000
STUD	18	7.2833333	4.9372831	0.4000000	14.0000000
STUS	18	21.9111111	19.6796667	0	60.0000000
SND	18	2.1222222	0.7765350	0.7000000	3.3000000
SNS	18	26.9555556	15.2067409	9.2000000	62.5000000
EHC	18	9.1666667	11.6316000	0	42.5000000
ESC	18	84.5833333	18.6541669	30.0000000	100.0000000
ECC	18	1.6666667	3.7377250	0	12.5000000
RC	18	7.6388889	8.9307887	0	35.0000000
INV	18	2.0555556	2.4125218	0	6.0000000
HD2	18	3.9444444	5.3189143	0	18.0000000
SD93	18	3.6666667	2.9505732	0	9.0000000
VAC93	18	0.2222222	0.5483189	0	2.0000000
WHET	18	7.5277778	2.4638100	2.9000000	11.2000000
WD	18	10.8888889	7.4981479	1.0000000	27.0000000
SWD	18	8.0555556	5.7340287	0	17.0000000
CCA	18	16.1111111	16.4991582	0	55.0000000

SPE=GVOLANS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	9	97.7777778	2.6352314	92.5000000	100.0000000
WP	9	9.5188889	5.0333524	1.8900000	17.5600000
TMV	9	72.0833333	19.5156187	45.5000000	98.2500000
SCOM	9	7.6700000	1.5572733	5.6500000	10.1300000
BRYC	9	12.5000000	4.5069391	5.0000000	20.0000000
TRD	9	3.4111111	2.1917142	0.4000000	8.0000000
TRS	9	13.7444444	3.8389813	7.6000000	22.0000000
SAPD	9	1.1444444	0.4585605	0.6000000	1.8000000
LOGD	9	2.7111111	4.4205329	0	14.0000000
LOGS	9	11.0777778	6.0697565	0	22.0000000
STUD	9	9.6000000	4.5113745	3.0000000	14.0000000
STUS	9	12.3333333	14.8429276	0	45.0000000
SND	9	2.9777778	2.1941842	0.6000000	7.6000000
SNS	9	19.9777778	7.5426749	11.0000000	30.0000000
EHC	9	2.5000000	3.9528471	0	12.5000000
ESC	9	37.7777778	10.9290642	20.0000000	57.5000000
ECC	9	3.8888889	9.0235033	0	27.5000000
RC	9	11.6666667	10.5326872	0	25.0000000
INV	9	2.8888889	3.5512126	0	11.0000000
HD2	9	7.1111111	17.0619785	0	52.0000000
SD93	9	2.5555556	2.1278576	0	5.0000000
VAC93	9	0.5555556	0.8819171	0	2.0000000
WHET	9	6.0111111	2.1658973	2.9000000	8.6000000
WD	9	5.2222222	5.0689688	1.0000000	17.0000000
SWD	9	3.5555556	5.0277010	0	16.0000000
CCA	9	31.3888889	25.4064187	2.5000000	82.5000000

Table 3B - Overall habitat use means and standard deviations for all species caught at the in process site. Refer to Table 1 for variable interpretations. This table refers to figure 12.

---------- SPE=PLEUCOPUS ----------

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	190	80.4473684	14.6316273	40.0000000	100.0000000
WP	190	5.0842105	4.0010271	0	19.3300000
TMV	190	17.5473684	15.8152275	4.5000000	80.7500000
SCOM	190	8.1453684	1.7650824	3.0300000	12.5300000
BRYC	190	20.8421053	9.9510078	0	45.0000000
TRD	190	1.9931579	0.9412957	0.1000000	5.4000000
TRS	190	19.2615789	7.3985161	7.5000000	40.6000000
SAPD	190	1.4357895	0.7760183	0.1000000	3.8000000
LOGD	190	3.3136842	2.8461284	0.1000000	14.0000000
LOGS	190	10.2694737	5.4807228	0	40.0000000
STUD	190	6.7847368	4.5862261	1.5000000	14.0000000
STUS	190	16.7647368	13.5550794	0	51.0000000
SND	190	3.1363158	1.5364004	0.4000000	7.9000000
SNS	190	15.9952632	5.6685271	7.7000000	29.5000000
EHC	190	19.2500000	14.2839450	0	65.0000000
ESC	190	12.6447368	25.1176880	0	100.0000000
ECC	190	0.0263158	0.3627381	0	5.0000000
RC	190	16.7236842	9.9114448	0	45.0000000
INV	190	10.5210526	7.4462504	0	36.0000000
SD93	190	2.8315789	2.7066551	0	11.0000000
VAC93	190	2.4210526	3.3933609	0	13.0000000
WHET	190	4.8563158	4.0908644	0	22.0000000
WD	190	8.4684211	7.1976299	0	39.0000000
SWD	190	7.1736842	6.6846062	0	35.0000000
HD2	190	31.5526316	32.5976736	0	260.0000000
CCA	190	52.5921053	19.9906907	10.0000000	87.5000000

---------- SPE=PMANICULATUS ----------

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	74	78.5135135	14.6179597	50.0000000	100.0000000
WP	74	3.6459459	3.1675490	0	15.0000000
TMV	74	12.8243243	4.7011238	4.2500000	25.0000000
SCOM	74	8.0522973	1.6499469	3.0300000	12.5300000
BRYC	74	14.4932432	9.9051990	0	35.0000000
TRD	74	1.7648649	1.1063246	0.2000000	5.4000000
TRS	74	19.1405405	9.2647797	7.6000000	40.6000000
SAPD	74	1.5378378	0.7857816	0.2000000	3.6000000
LOGD	74	3.6000000	2.9687413	0.1000000	14.0000000
LOGS	74	11.7229730	7.3329720	0	31.0000000
STUD	74	5.5662162	3.4365592	1.2000000	14.0000000
STUS	74	21.0972973	12.0084784	0	52.0000000
SND	74	3.4689189	1.9622412	0.5000000	7.9000000
SNS	74	15.7702703	5.5211605	8.1000000	25.0000000
EHC	74	17.5675676	11.7039170	0	47.5000000
ESC	74	3.7162162	7.1462612	0	30.0000000
ECC	74	0	0	0	0
RC	74	17.2972973	12.5291219	0	45.0000000
INV	74	11.2972973	7.6940285	0	26.0000000
SD93	74	2.8648649	2.7713027	0	9.0000000
VAC93	74	1.4459459	2.9615892	0	13.0000000
WHET	74	3.8108108	4.0343242	0	22.0000000
WD	74	7.9054054	7.2681872	0	39.0000000
SWD	74	6.5270270	6.8511032	0	35.0000000
HD2	74	33.6081081	23.7693354	0	118.0000000
CCA	74	58.1756757	21.4352214	10.0000000	92.5000000

(Table 3B Continued)

SPE=TSTRIATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	15	80.5000000	12.0341775	60.0000000	92.5000000
WP	15	4.2813333	3.3220688	0	12.8900000
TMV	15	10.8333333	2.4850745	5.7500000	14.2500000
SCOM	15	8.5733333	1.1141728	6.8300000	9.9500000
BRYC	15	13.8333333	8.0104099	0	30.0000000
TRD	15	1.9266667	0.8241590	0.4000000	3.5000000
TRS	15	18.4266667	5.8665476	10.9000000	27.8000000
SAPD	15	1.4866667	1.1325487	0.2000000	3.6000000
LOGD	15	4.6866667	3.5186984	0.4000000	14.0000000
LOGS	15	14.3933333	10.9600226	0	31.0000000
STUD	15	6.6533333	3.8256403	1.2000000	14.0000000
STUS	15	27.2200000	17.0361045	0	52.0000000
SND	15	2.8333333	1.4811514	1.4000000	5.8000000
SNS	15	13.4000000	5.6117224	7.9000000	27.2000000
EHC	15	12.0000000	8.7729291	5.0000000	35.0000000
ESC	15	3.0000000	4.4521263	0	12.5000000
ECC	15	0	0	0	0
RC	15	14.0000000	11.5263673	2.5000000	35.0000000
INV	15	9.2666667	5.3647882	2.0000000	18.0000000
SD93	15	1.4000000	1.0555973	0	4.0000000
VAC93	15	1.1333333	3.2703575	0	12.0000000
WHET	15	4.7400000	4.4610697	0.7000000	18.4000000
WD	15	7.1333333	5.0549363	2.0000000	22.0000000
SWD	15	5.1333333	3.9617216	1.0000000	16.0000000
HD2	15	31.8666667	19.5552940	0	59.0000000
CCA	15	61.1666667	12.6373407	45.0000000	92.5000000

SPE=BBREVICAUDA

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	12	77.5000000	17.8057703	50.0000000	100.0000000
WP	12	3.7225000	2.9574686	0	8.5600000
TMV	12	12.7916667	5.1066282	5.7500000	22.2500000
SCOM	12	8.2200000	2.0331212	6.0800000	12.5300000
BRYC	12	12.2916667	11.4543726	0	32.5000000
TRD	12	2.5250000	1.1856145	0.4000000	3.9000000
TRS	12	17.3833333	7.2822116	7.7000000	26.6000000
SAPD	12	1.2666667	0.9413079	0.3000000	3.8000000
LOGD	12	2.7583333	2.0469304	0.1000000	5.6000000
LOGS	12	12.2166667	9.9709426	6.0000000	40.0000000
STUD	12	5.1250000	4.5317316	1.2000000	14.0000000
STUS	12	24.9250000	19.3634672	0	52.0000000
SND	12	3.5416667	2.2952355	0.5000000	7.9000000
SNS	12	13.3833333	4.4271545	8.6000000	24.1000000
EHC	12	19.5833333	12.9172776	2.5000000	42.5000000
ESC	12	1.8750000	3.7119279	0	12.5000000
ECC	12	0	0	0	0
RC	12	13.9583333	9.1984641	0	35.0000000
INV	12	8.8333333	5.9518268	2.0000000	23.0000000
SD93	12	1.8333333	1.9924098	0	6.0000000
VAC93	12	0.7500000	2.0504988	0	7.0000000
WHET	12	2.8916667	2.5314237	0	9.6000000
WD	12	4.6666667	3.9157800	0	12.0000000
SWD	12	3.4166667	2.5390884	0	8.0000000
HD2	12	37.5000000	30.6401400	0	118.0000000
CCA	12	62.7083333	21.6495416	32.5000000	92.5000000

Table 3C - Overall habitat use means and standard deviations for all species caught at the recovery site. Refer to Table 1 for variable interpretations. This table refers to figure 12.

SPE=PMANICULATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	153	84.8529412	11.7233576	47.5000000	100.0000000
WP	153	3.6297386	2.5598887	0	14.0000000
TMV	153	13.9639869	4.3661100	6.0000000	24.0000000
SCOM	153	8.2186928	3.6311349	4.1500000	25.0000000
BRYC	153	9.6078431	8.0250310	0	42.5000000
TRD	153	2.0980392	1.0491520	0.2000000	6.0000000
TRS	153	32.1575163	19.9096270	7.5000000	84.5000000
SAPD	153	1.4156863	0.7566475	0.2000000	3.1000000
LOGD	153	1.3986928	1.1881535	0	6.5000000
LOGS	153	13.2346405	10.1486668	2.0000000	51.0000000
STUD	153	4.8535948	3.6382295	0.3000000	14.0000000
STUS	153	32.3065359	19.7972974	0	85.0000000
SND	153	5.6470588	3.7166775	0.7000000	14.0000000
SNS	153	16.4542484	10.0791538	0	43.6000000
EHC	153	8.0718954	7.9030762	0	30.0000000
ESC	153	0	0	0	0
ECC	153	0	0	0	0
RC	153	19.4771242	19.0192371	0	72.5000000
INV	153	8.9934641	7.2051669	0	40.0000000
HD2	153	18.4575163	11.2185156	0	50.0000000
SD93	153	1.6143791	2.2627539	0	8.0000000
VAC93	153	0	0	0	0
WHET	153	2.5392157	1.7281811	0	7.7000000
WD	153	2.4117647	3.3236185	0	20.0000000
SWD	153	1.8300654	2.9664591	0	17.0000000
CCA	153	86.1111111	9.7833812	50.0000000	100.0000000

SPE=PLEUCOPUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	60	80.8750000	13.0256022	47.5000000	100.0000000
WP	60	3.2403333	2.2321639	0	7.5300000
TMV	60	12.3083333	4.1579938	4.5000000	24.0000000
SCOM	60	7.2196667	1.4419631	4.8800000	13.8800000
BRYC	60	7.8333333	5.3175968	0	22.5000000
TRD	60	1.8666667	0.9338578	0.3000000	4.6000000
TRS	60	27.4166667	15.2780353	7.5000000	80.6000000
SAPD	60	1.4083333	0.8868706	0.2000000	4.1000000
LOGD	60	1.4933333	1.2240343	0	6.5000000
LOGS	60	10.8533333	6.2348247	2.0000000	31.0000000
STUD	60	4.4983333	3.2111824	0.5000000	14.0000000
STUS	60	34.4216667	18.0208833	0	85.0000000
SND	60	4.2416667	2.6134134	1.0000000	14.0000000
SNS	60	16.0233333	8.8223208	0	39.1000000
EHC	60	6.0000000	7.3386601	0	30.0000000
ESC	60	0	0	0	0
ECC	60	0	0	0	0
RC	60	13.1666667	11.9751390	0	60.0000000
INV	60	8.4000000	8.2136719	0	40.0000000
HD2	60	19.8000000	9.2384605	0	39.0000000
SD93	60	1.5666667	1.9077599	0	8.0000000
VAC93	60	0	0	0	0
WHET	60	2.3316667	1.7357157	0	7.7000000
WD	60	2.5833333	3.1745368	0	20.0000000
SWD	60	2.0500000	2.8249794	0	17.0000000
CCA	60	84.5833333	8.3382754	50.0000000	100.0000000

SPE=BBREVICAUDA

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	37	84.3918919	12.6162016	50.0000000	100.0000000
WP	37	2.7394595	1.9410377	0	7.0000000
TMV	37	14.2837838	4.3569716	4.5000000	23.0000000
SCOM	37	8.8464865	4.3686530	4.4000000	25.0000000
BRYC	37	12.9054054	10.8094852	0	42.5000000
TRD	37	2.1783784	1.3864694	0.2000000	6.0000000
TRS	37	30.5783784	22.6511238	8.3000000	80.9000000
SAPD	37	1.5000000	0.7947746	0.6000000	4.1000000
LOGD	37	1.4486486	0.9048086	0	3.2000000
LOGS	37	18.6729730	12.6964923	6.0000000	45.0000000
STUD	37	5.5351351	4.4038630	0.5000000	14.0000000
STUS	37	31.8270270	21.3316881	0	85.0000000
SND	37	5.8378378	3.1494577	1.3000000	14.0000000
SNS	37	15.6891892	8.6838542	0	37.1000000
EHC	37	8.7837838	7.6290204	0	27.5000000
ESC	37	0	0	0	0
ECC	37	0	0	0	0
RC	37	24.7972973	22.8322565	0	72.5000000
INV	37	5.8918919	5.8773756	0	23.0000000
HD2	37	17.1351351	12.4413338	0	39.0000000
SD93	37	1.0000000	1.1547005	0	5.0000000
VAC93	37	0	0	0	0
WHET	37	2.6324324	2.3663209	0	7.7000000
WD	37	1.9729730	3.4033193	0	20.0000000
SWD	37	1.7027027	2.9237045	0	17.0000000
CCA	37	85.8108108	8.5807855	62.5000000	100.0000000

SPE=TSTRIATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	28	90.5357143	8.2315209	70.0000000	100.0000000
WP	28	3.3653571	1.8449460	0.8900000	7.5600000
TMV	28	16.5089286	3.4970107	10.2500000	23.0000000
SCOM	28	9.0228571	4.8545419	4.1500000	25.0000000
BRYC	28	13.5714286	10.7889812	0	42.5000000
TRD	28	2.1821429	1.2739712	0.3000000	6.0000000
TRS	28	33.0000000	25.2865211	8.3000000	80.9000000
SAPD	28	1.4035714	0.7781660	0.3000000	3.1000000
LOGD	28	1.0392857	0.7410400	0.1000000	2.2000000
LOGS	28	16.2178571	12.0828330	6.0000000	45.0000000
STUD	28	6.4571429	4.1516109	0.5000000	14.0000000
STUS	28	28.2892857	22.6948410	0	72.0000000
SND	28	5.0250000	3.3202661	0.7000000	14.0000000
SNS	28	14.6071429	6.9433650	0	32.5000000
EHC	28	12.1428571	7.3192505	0	30.0000000
ESC	28	0	0	0	0
ECC	28	0	0	0	0
RC	28	30.1785714	20.9709739	5.0000000	72.5000000
INV	28	6.1428571	6.8514085	0	23.0000000
HD2	28	15.6785714	14.6617506	0	39.0000000
SD93	28	0.7857143	1.2279807	0	4.0000000
VAC93	28	0	0	0	0
WHET	28	3.1714286	1.9895760	0.3000000	7.5000000
WD	28	2.2500000	2.3979158	0	9.0000000
SWD	28	1.8928571	2.2987804	0	9.0000000
CCA	28	82.5000000	12.9814683	50.0000000	100.0000000

SPE=SOREX

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	19	80.1315789	10.6872745	62.5000000	97.5000000
WP	19	2.8484211	2.4399277	0.3300000	7.5600000
TMV	19	12.6710526	4.9763696	6.5000000	24.0000000
SCOM	19	7.6268421	1.2913948	5.4000000	9.9000000
BRYC	19	10.6578947	6.3923840	0	22.5000000
TRD	19	2.0526316	1.1427882	0.4000000	4.6000000
TRS	19	27.7894737	13.6140407	8.5000000	57.2000000
SAPD	19	1.5526316	0.5834461	0.4000000	2.3000000
LOGD	19	1.3789474	1.1306728	0.2000000	5.0000000
LOGS	19	14.9947368	12.9189987	6.0000000	51.0000000
STUD	19	4.2157895	2.8910327	0.3000000	9.4000000
STUS	19	40.7842105	21.0272380	11.5000000	85.0000000
SND	19	4.5263158	2.4004264	0.7000000	9.5000000
SNS	19	11.8263158	4.3861958	7.5000000	21.8000000
EHC	19	14.3421053	9.4956900	0	30.0000000
ESC	19	0	0	0	0
ECC	19	0	0	0	0
RC	19	14.7368421	11.2080928	2.5000000	42.5000000
INV	19	6.4736842	5.9848737	0	23.0000000
HD2	19	19.2631579	10.1206176	3.0000000	38.0000000
SD93	19	1.0000000	1.3743685	0	5.0000000
VAC93	19	0	0	0	0
WHET	19	2.5578947	2.0664827	0.7000000	7.7000000
WD	19	2.5263158	4.5505607	0	20.0000000
SWD	19	1.8421053	3.8335240	0	17.0000000
CCA	19	87.8947368	10.7452560	62.5000000	97.5000000

SPE=CGAPPERI

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	17	86.0294118	9.9238831	70.0000000	100.0000000
WP	17	2.8823529	2.4189087	0	8.7800000
TMV	17	12.8235294	2.9814068	6.7500000	18.7500000
SCOM	17	9.6735294	4.8764330	4.1500000	25.0000000
BRYC	17	20.1470588	12.9443094	5.0000000	42.5000000
TRD	17	1.8176471	0.9180382	0.9000000	3.6000000
TRS	17	18.6411765	12.5186890	8.3000000	57.2000000
SAPD	17	1.6176471	0.7195791	0.3000000	3.1000000
LOGD	17	1.2058824	1.1216453	0	4.3000000
LOGS	17	17.4470588	13.6417153	6.0000000	40.0000000
STUD	17	5.1529412	3.7674789	1.2000000	14.0000000
STUS	17	26.7941176	16.5376264	0	57.0000000
SND	17	4.1117647	2.4581198	0.7000000	9.0000000
SNS	17	17.0823529	6.6259184	8.3000000	28.0000000
EHC	17	13.9705882	7.5030631	2.5000000	30.0000000
ESC	17	0	0	0	0
ECC	17	0	0	0	0
RC	17	37.5000000	25.4490913	0	72.5000000
INV	17	8.9411765	7.9094136	0	20.0000000
HD2	17	11.5882353	6.5484619	2.0000000	28.0000000
SD93	17	1.4117647	1.6605279	0	5.0000000
VAC93	17	0	0	0	0
WHET	17	2.4882353	2.1295194	0	7.7000000
WD	17	3.7647059	5.0439247	0	20.0000000
SWD	17	3.0588235	4.5616689	0	17.0000000
CCA	17	83.8235294	14.0622958	50.0000000	97.5000000

Table 3D - Overall habitat use means and standard deviations for all species caught at the reference site. Refer to Table 1 for variable interpretations. This table refers to figure 12.

SPE=PLEUCOPUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	252	79.5138889	13.2129066	22.5000000	100.0000000
WP	252	8.4781746	5.1990469	0	26.2200000
TMV	252	40.7490079	21.0431240	4.7500000	132.5000000
SCOM	252	6.3322222	1.7216643	2.6800000	10.9000000
BRYC	252	15.6547619	10.6706329	0	47.5000000
TRD	252	2.3178571	1.1218753	0.1000000	6.3000000
TRS	252	24.1003968	11.0168234	7.6000000	71.0000000
SAPD	252	1.3706349	1.0042593	0.1000000	5.9000000
LOGD	252	4.3170635	3.8688853	0	14.0000000
LOGS	252	10.3142857	10.0338250	0	102.0000000
STUD	252	10.4448413	4.3095943	3.8000000	14.0000000
STUS	252	12.0436508	15.8666505	0	70.0000000
SND	252	6.5444444	3.8790900	0.6000000	14.0000000
SNS	252	13.2182540	10.4493382	0	64.0000000
EHC	252	9.4841270	12.6664907	0	60.0000000
ESC	252	64.1964286	32.9315375	0	100.0000000
ECC	252	5.2281746	11.2058127	0	57.5000000
RC	252	8.3829365	9.2840944	0	37.5000000
INV	252	3.3134921	5.0779714	0	45.0000000
HD2	252	7.0833333	14.9035745	0	89.0000000
SD93	252	2.2182540	2.2414033	0	10.0000000
VAC93	252	6.3571429	5.7711527	0	23.0000000
WHET	252	7.2043651	4.8998273	0	22.4000000
WD	252	12.9126984	10.2894522	0	48.0000000
SWD	252	10.7857143	9.0149121	0	38.0000000
CCA	252	84.0575397	7.3256401	57.5000000	97.5000000

SPE=BBREVICAUDA

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	17	78.5294118	19.9032587	42.5000000	100.0000000
WP	17	10.3847059	7.7370570	0.8900000	23.4400000
TMV	17	38.4852941	29.0460936	7.5000000	87.7500000
SCOM	17	6.1623529	1.8412582	2.6800000	9.1500000
BRYC	17	13.8235294	8.5292533	2.5000000	37.5000000
TRD	17	2.1176471	1.0272751	0.1000000	4.0000000
TRS	17	32.3470588	12.4269927	10.5000000	50.0000000
SAPD	17	1.2764706	1.4346295	0.1000000	5.9000000
LOGD	17	5.2235294	5.2192587	0.5000000	14.0000000
LOGS	17	8.4176471	10.5081656	0	46.0000000
STUD	17	10.5176471	4.3331910	3.6000000	14.0000000
STUS	17	15.8941176	23.1994739	0	70.0000000
SND	17	6.3941176	4.3868369	1.6000000	14.0000000
SNS	17	12.0294118	7.9339275	0	30.7000000
EHC	17	12.2058824	13.3135960	0	37.5000000
ESC	17	50.4411765	38.3164791	0	100.0000000
ECC	17	4.4117647	8.5936664	0	32.5000000
RC	17	8.3823529	7.9520623	0	25.0000000
INV	17	2.5882353	4.0782782	0	12.0000000
HD2	17	9.5882353	24.0131704	0	97.0000000
SD93	17	2.5294118	2.4524897	0	7.0000000
VAC93	17	6.3529412	6.7540837	0	18.0000000
WHET	17	8.2823529	7.5438083	0.9000000	22.4000000
WD	17	15.8823529	16.5411697	1.0000000	48.0000000
SWD	17	11.6470588	13.1288860	0	38.0000000
CCA	17	84.7058824	5.5819431	70.0000000	92.5000000

SPE=PMANICULATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	16	71.7187500	16.6011734	47.5000000	100.0000000
WP	16	8.2362500	4.1704482	0.8900000	13.3300000
TMV	16	32.1562500	31.5887473	9.0000000	105.0000000
SCOM	16	6.0143750	1.5678519	2.6800000	8.9800000
BRYC	16	14.3750000	12.2644473	2.5000000	55.0000000
TRD	16	3.0000000	1.5418603	0.2000000	6.3000000
TRS	16	22.9000000	11.8345821	10.1000000	49.6000000
SAPD	16	1.3687500	0.8684997	0.3000000	2.8000000
LOGD	16	4.2312500	2.9488345	1.1000000	14.0000000
LOGS	16	10.1375000	4.6218142	0	20.0000000
STUD	16	9.9187500	3.9561292	5.2000000	14.0000000
STUS	16	14.2250000	16.4332387	0	50.0000000
SND	16	6.8187500	3.1604259	3.2000000	14.0000000
SNS	16	13.3500000	7.9328011	0	29.2000000
EHC	16	13.5937500	13.8734984	0	40.0000000
ESC	16	52.9687500	32.2776851	2.5000000	100.0000000
ECC	16	3.9062500	6.8901349	0	20.0000000
RC	16	9.8437500	9.3304497	0	30.0000000
INV	16	3.0625000	3.5112913	0	9.0000000
HD2	16	12.4375000	28.2558991	0	97.0000000
SD93	16	2.3125000	2.1203380	0	8.0000000
VAC93	16	7.0000000	8.0746517	0	22.0000000
WHET	16	8.2875000	6.6192522	1.1000000	20.8000000
WD	16	11.2500000	9.9766394	1.0000000	36.0000000
SWD	16	9.5625000	8.9960640	0	30.0000000
CCA	16	82.1875000	8.1073526	70.0000000	97.5000000

SPE=TSTRIATUS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	14	91.2500000	10.0837836	65.0000000	100.0000000
WP	14	9.4600000	4.6267433	0	17.7800000
TMV	14	58.2500000	22.5923319	18.5000000	104.5000000
SCOM	14	6.0642857	1.7038450	3.5300000	8.9000000
BRYC	14	17.3214286	9.6308941	5.0000000	37.5000000
TRD	14	2.1785714	1.1116022	0.1000000	3.9000000
TRS	14	19.4571429	9.3541200	9.0000000	39.4000000
SAPD	14	1.1071429	0.6533515	0.1000000	2.4000000
LOGD	14	4.4857143	4.2925440	0.4000000	14.0000000
LOGS	14	10.1571429	6.5268339	0	22.0000000
STUD	14	12.4642857	3.9049490	3.0000000	14.0000000
STUS	14	5.3571429	13.6866422	0	41.0000000
SND	14	7.7071429	4.9153550	1.2000000	14.0000000
SNS	14	9.3000000	7.7579736	0	21.0000000
EHC	14	3.7500000	7.3215961	0	25.0000000
ESC	14	89.2857143	22.3053239	15.0000000	100.0000000
ECC	14	2.6785714	4.0978754	0	12.5000000
RC	14	3.0357143	4.5126501	0	17.5000000
INV	14	3.2142857	5.4515851	0	16.0000000
HD2	14	3.3571429	8.5898611	0	26.0000000
SD93	14	1.5000000	2.1031112	0	8.0000000
VAC93	14	7.6428571	5.7325943	0	18.0000000
WHET	14	7.3000000	4.4642167	0	14.3000000
WD	14	12.4285714	7.8418432	1.0000000	24.0000000
SWD	14	11.0000000	7.5038452	1.0000000	24.0000000
CCA	14	85.0000000	5.5470020	72.5000000	92.5000000

(Table 3D Continued)

SPE=GVOLANS

Variable	N	Mean	Std Dev	Minimum	Maximum
SC	13	93.6538462	12.2735906	55.0000000	100.0000000
WP	13	10.1615385	6.0755066	4.0000000	23.4400000
TMV	13	64.1538462	24.9803128	11.2500000	102.0000000
SCOM	13	5.7230769	1.6234243	2.6800000	8.4800000
BRYC	13	9.4230769	6.5474109	2.5000000	22.5000000
TRD	13	1.5307692	0.6536878	0.6000000	2.4000000
TRS	13	22.1538462	11.3078598	9.0000000	49.6000000
SAPD	13	0.8384615	0.7331876	0.1000000	2.6000000
LOGD	13	5.5307692	4.9622550	1.0000000	14.0000000
LOGS	13	8.1846154	5.9379915	0	21.5000000
STUD	13	11.9538462	3.4721788	5.5000000	14.0000000
STUS	13	9.4230769	16.3577787	0	41.0000000
SND	13	8.2692308	4.2289448	2.0000000	14.0000000
SNS	13	10.1384615	6.5037859	0	21.0000000
EHC	13	3.7692308	2.1371260	0	7.5000000
ESC	13	91.1538462	24.0142185	12.5000000	100.0000000
ECC	13	9.0384615	18.7510683	0	62.5000000
RC	13	2.3076923	2.3851840	0	7.5000000
INV	13	2.0769231	3.3030677	0	8.0000000
HD2	13	0	0	0	0
SD93	13	1.6153846	1.8045526	0	6.0000000
VAC93	13	7.6153846	7.6978185	0	23.0000000
WHET	13	8.4076923	5.7667815	3.4000000	22.4000000
WD	13	13.8461538	13.5698572	2.0000000	48.0000000
SWD	13	10.8461538	10.3105622	0	38.0000000
CCA	13	85.0000000	5.7735027	70.0000000	92.5000000

Curriculum Vitae

Name: David Christian Tomblin
Home Address:
204 Marlington Street
Blacksburg, VA 24060
Phone: (703)-951-9305
Major Professor:
Jack A. Cranford

May 15, 1994
University Address:
Virginia Polytechnic
Institute and State
University
Department of Biology
Blacksburg, VA 24061
Phone: (703)-231-8921
Room 2094, Derring Hall

Education

1991 Old Dominion University, Norfolk, VA -Biology Major, Environmental Health Minor - B.S. Degree

1994 Virginia Polytechnic Institute and State University, Blacksburg, VA - M.S. in Zoology

Employment

1986-87 Landstuhl Child Development Center, Landstuhl, Germany - Preschool Teaching Assistant

1989-90 Old Dominion University, Norfolk, VA - Maintenance Assistant

1991 Virginia Polytechnic Institute and State University, Blacksburg, VA, Office of Academic Enrichment - Tutor (Biology)

1992-94 Virginia Polytechnic Institute and State University, Blacksburg, VA, Department of Biology, Teaching Assistantship: Mammalogy Lab, Ornithology Lab, General Biology Lab

1993 Mountain Lake Biological Station, Mountain Lake, VA - Field Biologist for the Twin Springs Longterm Forest Dynamics Project (Fall 1993) - Supervisor: Dr. Jesse Parker, Smithsonian

1994-95 Smithsonian Tropical Research Institute, Barro Colorado Island, Panama - Research Assistantship:

Population limitation in a Neotropical fruit-eating rodent: an experimental study - Supervisor: Dr. Greg H. Adler

Technical Skills

Habitat Analysis (measurement of 36 habitat variables at over 500 traps stations), **Small Mammal Trapping** (Sherman traps, tomahawk traps, pitfalls, recording demographic data), **Plant Identification** (trees and herbaceous plants), **Herbaceous Plant and Tree Sampling Techniques** (point quarter, transects, quadrat method etc.), **Multivariate Statistics, Computer Word Processing and Graphics, Surveying.**

Society Memberships

Virginia Academy of Science
American Society of Mammalogists
Ecological Society of America
Sigma Xi, The Scientific Research Society (National Chapter)

Honors

Beta Beta Beta Biological Honor Society (Kappa Epsilon) 1990-91

Third Place Poster Presentation in the Science Category at the Virginia Polytechnic Institute and State University Graduate Research Symposium

Service

Education Conservation Committee, Wildlife Society (VPI & SU Chapter) - 1991

Biology Graduate Student Assoc. Election Committee - 1993

Publications

Tomblin, D.C. and J.A. Cranford. 1994. Ecological niche differences between *Aloutta palliata* and *Cebus capucinus* comparing branch use, feeding modes, and diet. **Primates** 35(3):265-274.

(In Prep)

Cranford, J.A. and D.C. Tomblin. ?. Habitat preference shifts in white-footed mice (*Peromyscus leucopus*) when infected with bot fly larva. Journal to be submitted to: **Journal of Mammalogy.**

Tomblin, D.C. and J.A. Cranford. ?. Differential niche characteristics, microhabitat use, and interactions between species among small mammal assemblages at different stages of gypsy moth disturbance. Journal to be submitted to: **Ecology.**

Tomblin, D.C. and J.A. Cranford. ?. Suitability of habitat created by gypsy moth disturbance form the perspective of *Peromyscus leucopus* and *Peromyscus maniculatus* populations. Journal to be submitted to: **Journal of Mammalogy.**

Presentations at Scientific Meetings

Oral Presentations (Published Abstracts)

Tomblin, D.C. and J.A. Cranford. 1994. Sex and age class habitat discrimination by *Peromyscus* spp. at different stages of gypsy moth disturbance. **Virginia Academy of Science, Harrisonburg, VA.** Virginia Journal of Science 45:?.

Tomblin, D.C. and J.A. Cranford. 1993. Effects of gypsy moth defoliation on small mammals. **Virginia Academy of Science, Norfolk, VA.** Virginia Journal of Science 44:115.

Cranford, J.A. and D.C. Tomblin. 1993. Habitat preference shifts in white-footed mice (*Peromyscus leucopus)* when infected with bot fly larvae. **Ecological Society of America, Madison, WI.** Bulletin of Ecological Society of America 74:458.

Poster Presentations (Published Abstracts)

Tomblin, D.C. and J.A. Cranford. 1993. Effects of gypsy moth defoliation on small mammals. **Ecological Society of America, Madison, WI.** Bulletin of Ecological Society of America 74:201.

Invited Oral Presentations

Tomblin, D.C. and J.A. Cranford. 1994. Small mammal population dynamics and habitat use in gypsy moth impacted and non-impacted areas. **Association of Virginia Gypsy Moth Managers Fourth Review, Charlottesville, VA.**

Other Poster Presentations

Tomblin, D.C. and J.A. Cranford. 1993. Small mammal responses to three different stages of gypsy moth disturbance within oak communities. **Association of Virginia Gypsy Moth Managers Third Review, Roanoke, VA.**

Tomblin, D.C. and J.A. Cranford. 1993. Small mammal responses to defoliation disturbances in the eastern deciduous forest ecosystem. **Graduate Research Symposium, VPI&SU.**

Grants Received

Sigma Xi Grant, November 1992 (Master's Research)	$375
Department of Biology , VPI&SU (Master's Research)	$375
Virginia Academy of Science, May 1993 (Master's Research)	$964
Department of Biology, VPI&SU (Master's Research)	$500

Undergraduate Research Projects

Ecological niche differences of two sympatric species, *Alloutta palliata* and *Cebus capucinus* comparing feeding modes, branch use, and diet - Curu Wildlife Preserve, Curu, Costa Rica - Summer 1990. Supervisors: Dr. Dusty Becker, University of Alberta and Dr. Michael Costello, University of California at Riverside.

Ecological factors determining the spatial patterns of *Chimaphila maculata* at Blackwater Ecological Preserve - Zuni, VA - 1990-1991. Supervisor: Dr. Gerald F. Levy, Old Dominion University.

The effects of display behaviors on pirating activities of bald eagles (*Haliaeetus leucocephalus*) - Eagle Beach, Alaska - Summer 1991. Supervisor: Dr. Carl Tomoff, Prescott College.

Current Research

Experimental and descriptive work determining ecological factors important to the distribution of two morphologically similar rodent species (*Proechimys semispinosus* and *Hoplomys gymnurus*) within a fragmented landscape in Panama.

Importance of spatial scales to small mammal distributions.