Habitat preferences of *Peromyscus leucopus*, *Blarina brevicauda* and *Glaucomys volans* in Northern Lower Michigan

by

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ABSTRACT

I assessed the influence of microhabitat variables on the abundance and spatial structure of small mammals across three types of forest, deciduous (Colonial Point), hardwood-pine (the Burn Plots) and cedar swamp (Reese's Swamp), at the University of Michigan Biological Station (UMBS), in Cheboygan County, northern lower Michigan. Traps have been placed in these forests twice a year for 18 years since 1989 by Professor Philip Myers, and I based my study on his trapping records. I created a four by four meter square plot centered on each trap station and measured habitat variables on each plot in late September and early October 2006.

Over 2,000 captures of sixteen small mammal species were recorded in 6,480 trapnights over eighteen years. Four species were commonly captured: eastern chipmunk (*Tamias striatus)*, white footed mouse (*Peromyscus leucopu*s); short-tailed shrew (*Blarina brevicauda*); and southern flying squirrel *(Glaucomys volans*). I eliminated *Tamias* because its trapping records were clearly strongly influenced by daily weather, and I focused on the remaining three. For *P. leucopus* and *B. brevicauda*, I included trapping records for only the most recent four years, as those species are short-lived, and ecological variables such as woody debris and ground cover change from year after year. For *G. volans*, which is longer-lived, I used all 18 years of trapping records. Also, *G. volans* is much less common than *P. leucopus* or *B. brevicauda*, and sample sizes were too small to analyze unless all years were included.

The preferences of each species across three transects located in the different forests were evaluated by statistical methods including Poisson regression models, principal component analysis, analysis of variance and analysis of covariance. The spatial structures of the populations of each species were examined by spatial autocorrelation analysis using Moran's I.

In deciduous and pine-hardwood forests, white footed mice were found to be habitat generalists. In the cedar swamp, on the other hand, they were likely to be habitat specialists limited by food availability and predation risks. A relatively high spatial autocorrelation of the number of captures/station was found only for *P. leucopus* in the hardwood forest in the fall. Spatial distribution of food in patches over the series of adjacent trap stations may explain for this pattern, but none of my measurements test this hypothesis. Short-tailed shrews preferred deciduous forest that is characterized by many trees, much leaf litter and large variety of ground cover species. In the cedar swamp, they preferred sites with large trees, moss/lichen cover on the ground, much woody debris and many snags. Limiting factors for them were likely to be soil moisture and food availability. Most southern flying squirrels were found in the deciduous forest, where they were not habitat selective. In the pine-hardwood forest, *G. volans* preferred sites with greater diversity of trees and larger trees. No preference for snags was found. In the cedar swamp, no *G. volans* was found over the eighteen year study.

INTRODUCTION

Populations of plants and animals do not inhabit an ecosystem independently of each other. Populations of different species share limited resources, interact within an ecosystem and form a community. Interaction with other species may force a species to restrict use of space, foods or other resources. As a result, related animal species that coexist in the same community show partitioning of available resources such as feeding on different foods, being active during different times or foraging in different areas.

As with other organisms, the availability of suitable habitat for small mammals is a significant determinant of their distribution in the forest. The importance of microhabitat features in determining the variety and abundance of small mammals at a site has been examined by a number of investigators, who have reported that the number and diversity of small mammal captures depend on ecological factors such as food availability, temperature, predation risk, interspecific competition, nesting and roosting sites (M'closkey, 1976; Price, 1978; Wywialowski, 1987; Loeb, 1999).

Interestingly, the relative importance of each ecological feature may vary from site to site (Kaufman et al, 1983). Differences in usage of ecological features are probably associated with the interaction of microhabitat variables such as food sources, nests or shelters, climate conditions and competition with other species. For example, high densities of *Peromyscus leucopus* were found in drier areas (Getz, 1961a), but moisture alone does not seem to be the major cause of this species' avoidance of wet areas. Rather, year-round food supplies tend to be more reliable in drier habitats (Getz, 1961a). In spruce-birch-larch swamp in Michigan, *Blarina brevicauda* was absent where a large amount of debris covered the ground, even though this species is sometimes associated with downed logs and moist soil. Apparently, *B. brevicauda*

was absent because available food was insufficient (Getz, 1961b). In a hardwood-pine forest in Arkansas, *Glaucomys volans* avoided harvested areas and even-aged pine monocultures (Taulman, 1999). However, in another study Healy and Brooks (1988) found that southern flying squirrel did not differ in their use of mature hardwoods and immature stands (12-14yr). The extent to which species vary from site to site in their ecological characteristics, and the factors that determine how a species behaves in a particular community, are poorly understood. Locally focused studies that explore niches and interspecific interactions in well-defined communities, such as this one, are much needed in the effort to build more general models of community composition and structure.

Several studies have shown that small mammal populations are characterized by spatial structure (autocorrelation) at fine scales (several hundred meters; Bowman et al, 2000; Bowman et al, 2001; Krohne and Burgin, 1990), and such spatial structure is also affected by microhabitat features. For example, variation in ecological factors such as resources, competition and predator abundance influence fine-scale spatial patterns of variation in small mammal populations (Bowman et al, 2000).

In northern Michigan, small mammal distributions, habitat preferences and spatial variability of populations in different types of forest are not well understood. In this study, my objectives are to answer the following research questions.

1. In northern Michigan, do the small mammal species found in an area and their capture rates vary among three transects traversing different types of forest, and why do those differences occur?
2. Is the number of captures of a species at trap sites within each transect related to microhabitat variables such as vegetation type, the abundance of woody debris

(WD), canopy density and ground cover type?

3. Is there detectable spatial structure in small mammal populations within each transect, and if so, why do those patterns exist?

Analyses of the relationship between trapping success and microhabitat features are useful for predicting habitat preferences and for illustrating how resources are separated among coexisting species in a community (Yahner, 1982). In order to examine habitat preference of these species, I combined a large dataset of trapping records constructed by Prof. Philip Myers, who trapped in three types of forests in University of Michigan Biological Station (UMBS) over an 18-year period (1989-2006), with measurements of microhabitat features made in 2006 at each of his trap sites. I analysed the relationships between small mammal capture rates and ecological variables at a microhabitat scale (within each forest) and at macrohabitat scale (across the three types of forests). I focused on three common species in northern Lower Michigan: white footed mice (*Peromyscus leucopus*), short-tailed shrews (*Blarina brevicauda*), and southern flying squirrels (*Glaucomys volans*). A fourth species, eastern chipmunk (*Tamias striatus*), is also common, but its activity is strongly influenced by daily weather (Snyder, 1982) and I felt that its numbers were not reliably estimated. I excluded it from further analysis.

The habitat preferences of these species differ. *Peromyscus leucopus* uses woody debris as travel routes for predator avoidance, presumably because mice traveling on woody debris make less noise (Barnum et al, 1992; Fitzgerald, V.J. and Wolff, V. J., 1988; Planz and Kirkland, 1992). Large trees provide nest, refuge, and foraging sites for members of this species (Barry and Francq, 1980, Kaufman, et al, 1985). *Peromyscus leucopus* feeds on acorn and other nuts, seed, fruits, and insects that inhabit woody debris (Baker, 1983; Caldwell, 1993). Ground cover type also affects the habitat preference of this species. For example, *P. leucopus* avoids grassy

sites in the forest (Getz 1961a) and walking on dry leaf litter (Fitzgerald and Wolff, 1988). This species' habitat is also characterized by an abundance of woody plant species, larger stumps, wider tree dispersion and lower percent of evergreens in the overstory and shrub strata (Dueser and Shugart, 1978). In addition, *P. leucopus* prefers areas with complex vertical structure created by trees and avoid open areas (Kaufman, et al, 1982).

In typical woodlots in southern Michigan, *B. brevicauda* is most common on moist and spongy soils covered with leaf litter, although these shrews have been reported to occur in a large variety of habitat types (Baker, 1983; Yahner, 1982). High humidity or a relatively high availability of free water is required by this species, apparently because it has a high evaporation rate and is unable to regulate evaporation in low humidity (Getz, 1961b). *Blarina brevicauda* also needs an abundant food supply because this species has a very high metabolic rate (Pearson, 1947). In addition to moisture and good food availability, *B. brevicauda* prefers areas of high log density (Kitchings and Levy, 1981), high stump density, few shrubs and a dense overstory (Kitchings and Levy, 1981). The center of activity of *B. brevicauda* is the nest, which is usually found in grass cover, under logs, in dead stumps, or under debris (Baker, 1981).

Glaucomys volans is a forest-dependent species that prefers deciduous forests or mixed forests of hardwoods and conifers (Dolan and Carter, 1977; Weigl, 1978). Cavities in trees and snags are critical components of the habitat of *G. volans*, since these squirrels nest in cavities but do not excavate their own (Bendel and Gate, 1987; Muul, 1974; Weigl, 1978). Optimum habitat components for *G.volans* include large trees (allowing long glides; Bendel and Gates, 1987), tree cavities, snags and mature woods for nesting (Bendel and Gates, 1987; Gilmore and Gate, 1985; Muul, 1974; Weigl, 1978; Taulman, 1999), and hard mast such as acorns and beechnuts (Baker, 1981; Harlow and Doyle, 1990).

METHODS

Study area— The study was carried out in three types of forest at the University of Michigan Biological Station (UMBS), located in Cheboygan Co., northern lower Michigan (Fig. 1). The first, Colonial Point (CP; 45°28'N, 84°40'W) is an example of northern hardwood-hemlock forest in which northern red oak (*Quercus rubra*) and white pine (*Pinus strobus*) are dominant in the overstory and sugar maple (*Acer saccarum*) and beech (*Fagus grandifolia*) are subdominant. Approximately 50 to 90% of the ground at Colonial Point is covered by leaf litter and 5 to 20% by fallen branches and logs. Reese's Swamp (RS; 45°32'N, 84°40'W) is a wet coniferous forest located between Douglas Lake and Burt Lake. It is dominated by northern white cedar *(Thuja occidentalis*) and balsam fir (*Abies balsamea*). Log distribution at this site and the amount of grass and moss on the ground is the highest among three forests. The Burn Plots (BP; 45°33'N, 84°42'W) lie in forest where the last major fire occurred in 1911 and are dominated by white pine, red pine (*Pinus resinosa*) and red maple (*Acer rubrum*). Coverage by leaf litter is slightly lower than at Colonial Point, and bracken fern (*Pteridium aquilinum*) covers 5 to 30% of the ground. Climate in UMBS is humid continental, featuring hot and humid summers and extremely cold and stormy winters (Donald and Chagnon, 1976).

Trapping procedures—In an ongoing study, Professor Philip Myers has placed traps in these forests twice a year for 18 years since 1989. Small mammals are routinely captured once in May before the first spring litters are weaned, and once in September after the last litters have dispersed. In each forest, traps are set along permanent transects. Each transect consists of 20 trap stations. Trap stations are spaced 10m apart at the Reese's swamp site, 20m apart at the Burn Plots and 25m apart at Colonial Point. At Reese's swamp, the traps are arranged in an "L,"

which runs north-south and east-west (Fig. 2). At Colonial Point, trap sites are in a straight line running north-south. At the Burn Plots, the traps are arranged in the form of a "T." One branch of the T runs east-west, and the other branch runs north-south. Three Sherman folding live traps (H.B. Sherman Traps, Inc., Tallahassee, FL), two small and one large, are baited with oats and placed at each trap station on three consecutive nights and checked the following mornings. Traps are put within 2m of the stake marking each station. For all captured rodents, season, forest type, station number, species, sex, weight (except *Blarina brevicauda*), reproductive condition and age (*Peromyscus leucopus* only) are recorded. *Peromyscus* age is determined by pelage color, and captured individuals are classified as juvenile, subadult, or adult. Reproductive condition is determined by the position of the testes in males and the status of nipples in females. Males are categorized as being either scrotal or abdominal and females are categorized as having tiny nipples without evidence of lactation or enlarged nipples with or without evidence of lactation (but very few obviously lactating females are found). Prof. Myers records pregnant females when he finds them, but not many individuals have been categorized this way, because pregnancy is only detectable by external exam a few days before the animal gives birth. The presence of botflies, general condition and torpor are also noted. Captured animals are marked temporarily by fur-clipping to allow recognition of animals recaptured during the same trapping period.

Habitat sampling— Based on a suggestion by Harrington (2006), I created a 4 X 4 meter square plot centered on each trap station. Habitat variables were measured on each plot in late September and early October 2006. I selected habitat variables that are possibly associated with the numbers of small mammal capture based on the literature review. Habitat variables included

percent canopy cover, size and species of woody plants, ground cover percentage, fine and coarse woody debris (FWD and CWD), presence of snags and presence of stumps. I recorded the following measurements (Table 1):

1. Average canopy density –Percent of the canopy obscured by leaves. I measured this variable with a spherical densiometer and averaged readings taken while facing north, south, east and west.
2. Woody plants—Plants with diameter at breast height (DBH) > 1.5cm. I recorded number, species, DBH and the distance and bearing of the closest tree to the stake marking each trap site.
3. Ground cover— percentage of ground cover falling into each of the categories below (Bonham, 1989). I averaged the measurements of two 2m squares randomly selected from four squares created by dividing the 4 X 4 meter square plot. I also recorded dominant ground cover species within a plot.
    a. saplings
    b. living wood
    c. dirt
    d. grass
    e. ferns
    f. leaves
    g. moss
    h. lichen
    i. slash

4. FWD (fine woody debris) and CWD (coarse woody debris) --measured by the line intercept method (Harmon and Sexton, 1996). At each trap site, I established lines going north-south and east-west through the stake. I recorded FWD (> 2cm diameter and < 10cm diameter) and CWD (> 10cm diameter) along each line. Measurements included the following:
    a. decay class (Harmon et al. 1995)
    b. length of the woody debris (WD) part located within the plot
    c. total length (including the part outside of a plot) and diameter
    d. volumes of FWD and CWD (Harmon and Sexton, 1996).
5. Snags and stumps—for snags, decay class and DBH were recorded. For stumps, the base diameter and decay class were recorded.

Statistical analysis— Twenty-nine ecological variables reflecting habitat structure and species richness were utilized to predict the relationship between small mammal capture rate and ecological variables (Table 1-3). I focused on three species, *Peromyscus leucopus*, *Blarina brevicauda*, and *Glaucomys volans*. For *P. leucopus* and *B. brevicauda*, I included trapping records for only the most recent four years as those species are short-lived and have high reproductive potential, so they are expected to react to ecological variables such as woody debris and ground cover that may change from year to year. For *G. volans*, a longer-lived species with slower reproduction, I used all 18 years of trapping records, because I expected this species to respond to the species and size composition of trees at the trapping sites, which change more slowly than woody debris or ground cover. Also, *G. volans* is much less common than *P.*

leucopus or *B. brevicauda*, and sample sizes were too small to analyze unless all years were included.

I examined the effects of ecological variables on habitat use by small mammals at two levels: (1) among trap stations within each transect (microhabitat level), and (2) among the three transects located in three forest types (macrohabitat level). SAS 9.1 and SPSS 14.0 statistical packages were used for statistical analysis.

At the microhabitat level, I analyzed the relationship between ecological variables and the number of small mammals caught at each trap station within a transect as follows:

1. I compared the species counts within a transect as a function of each ecological variable, using a simple Poisson regression model to test the importance of each variable in determining the number of small mammal captures. The Poisson regression model is appropriate when the dependent variable is a count of rare events, as in this case, because we cannot assume that the dependent variable has a normal distribution (Allison, 2000).
2. I used principal component analysis (PCA) to characterize the structure of the relationships among potentially intercorrelated ecological variables. In order to reduce the number of variables included in PCA to less than the sample number, 20, I excluded ecological variables that had a value near 1.0 in the correlation matrix among variables and selected nineteen variables which were significantly associated with the number of small mammals captured in simple Poisson regressions. Because the ecological variables were measured on widely different scales (e.g., DBH vs. number of ground cover species), the ecological variables were standardized prior to running the PCA. To do this, I computed mean and standard deviation for each variable and recorded each measurement as its distance from the mean in standard deviation units. A standardized

score of 1.0 indicates that the value is 1 standard deviation above the mean of the variable, while a standardized score of 0 indicates that the value of the variable is at its mean, and a standardized score of -1.0 indicates that the value is 1 standard deviation below the mean for that variable. This allows each variable to be weighted similarly in the PCA, without allowing the units of measurement to influence the analysis. Components with eigenvalues greater than 1.0 were retained. I rotated the axes defined by PCA by the varimax rotation method of orthogonal rotation to maximize the variance within each factor. Each trap station was treated as a "sample" of the forest ecosystem; thus the analysis of each forest was based on n = 20.

3. I ran multiple Poisson regressions using principal component scores derived from PCA as predictor and each species' captures at each season along each transect as dependent variable, in order to identify the important integrated ecological predictors for each species' captures.
4. Because a large number of ecological predictors were measured, I wished to compare models with different ecological predictors to see which had the strongest relationship to the species count (using regression appropriate for dependent variables with Poisson distribution). Because I found no software available to carry out a stepwise Poisson regression, I used the following protocol to select the ecological variables that were most predictive of the species count during each season and within each transect. I started with simple Poisson regression models (based on single ecological variables) that were significantly associated with small mammal captures. Then, I added each variable one at a time. Combinations of variables that were significant were kept for the next model procedure. In each subsequent procedure, each ecological variable was added to the

models in the presence of the combinations of variables which were already considered as significant. I stopped this procedure when the combinations of variables became insignificant. Because all combinations of significant variables were examined, the order of entering additional variables was unimportant.

5. Then the Bayesian Information Criterion (BIC) was used to compare models. This criterion, which compares the log likelihood of competing models, while adjusting for the number of predictors in the model, is somewhat akin to the adjusted R-square criterion that is used in simple linear regression problems. While the log likelihood can only increase (or stay the same) by adding additional variables, the BIC can actually decrease, if the addition to the log likelihood is not enough to overcome the penalty for including another predictor. For a given model, BIC is calculated as follows:

$$BIC = \log (L) - 0.5*\log (n)*(k)$$

where L is the value of maximized likelihood of the model, n is the sample size, and k is the number of parameters in the model (Nagin, 1999).

6. Finally, I created prediction maps of the captures of each small mammal species and residual maps which shows the difference between the number of actual and predicted number of captures. The best models with largest BIC value were used to create prediction maps.

At the macrohabitat level, I again used Poisson regression models to compare counts of individuals captured along three transects located in different forest types. The overall significance of each model was assessed using a likelihood ratio (LR) chi-square test, which compares the log likelihood of the model with the predictors to that of the model with the intercept only. The LR chi-square test has been shown to have good statistical properties in

situations where the sample size is small, as in this case (Jennings, 1986). The comparison of species counts across individual transects was carried out using Wald chi-square post-hoc tests in the Poisson regression model. The Wald tests are formed by taking the difference in the parameter estimates for any two selected transects, divided by the standard error of the difference, and then squaring the resulting test statistic. This test, although asymptotic (that is, valid for large sample sizes), is useful in this context, because we cannot carry out LR chi-square tests for these pairwise comparisons.

Following this, I compared the mean of the ecological variables across transects using ANOVA models, assuming that the distribution of the residuals for these models was normal. This assumption was checked by examining the residuals from each model. The Tukey method for multiple comparisons was used when making post-hoc comparisons of the means of the ecological variables across transects. The values of ecological variables with right skewed distributions were log transformed.

Then, in order to determine if the slope for an ecological variable was different across transects, for each ecological variable I carried out Poisson regression models including all transects, with each transect as a categorical predictor, the ecological variable as a continuous predictor, and an interaction term between each transect and the continuous ecological predictor. I then compared the slopes of number of captures on the ecological variable across the three transects. The purpose of this test is to examine whether the linear regressions of the number of small mammals captured on each ecological variable are the same in Colonial Point, the Burn Plots and Reese's Swamp. Again, the significance of each predictor variable in these models was assessed using a LR chi-square test. Here I have referred to this type of analysis as an ANCOVA (analysis of covariance-type) model, even though the dependent variable is not

normally distributed, because of its essential similarity to an ANCOVA model (in that the slopes of a continuous predictor are being compared across levels of a categorical predictor).

Geostatistical analysis- I calculated Moran's I values for each small mammal species along each transect to determine whether the numbers of small mammals captured within nearby areas are more similar to one another than would be expected under spatial randomness. Departures from randomness indicate spatial patterns. Moran's I is the most popular spatial autocorrelation index (Assuncao and Reis, 1999).

GeoDa 0.9.5-i was used for Moran's I calculations. Moran's I values were visualized by Moran scatter plot, which provides a Moran's I value to determine the extent of linear association between the values in a given location (x-axis) with values of the same variable in neighboring locations (y-axis) (Anselin et al, 2006).

Dispersal distance of small mammals is related to home range size, and home range size is good predictor of dispersal distance (Bowman et al., 2002). Therefore, I used the home range of each species to define "nearby area," which I then used to create a weight matrix. This weight matrix defines neighbors by a binary function, with neighbors defined as 1 and non-neighbors as 0. The following studies were used to form estimates of home range size. For *P. leucopus,* the average home range is 0.1ha (Lackey et al, 1985), although home range size varies seasonally, with the smallest size in the winter and the largest during summer.. For *B. brevicauda*, Blair (1940) reported that in Michigan, the largest female home range (0.35 ha) and largest male home range (1.77 ha) were found in September. Blair (1941) and Buckner (1966) also found the average home ranges of *B. brevicauda* were about 0.4 ha or larger. Based on these results, I set 1.2 ha as the home range of *B. brevicauda*. For *G. volans*, the mean estimated home range for

adult was 2.45ha for males and 1.95ha for females, and juveniles had a mean home range of 0.61ha (Bendel and Gates, 1987). Home ranges of 0.53ha for adult males and 0.41ha for adult females (Madden, 1974), and 3.8 and 7.8ha (Stone et al .1997) have also been reported (Hayne, 1949). I used 2.0 ha as the home range of *G. volans* based on these results.

To check if counts of small mammals that are spatially autocorrelated are clumped spatially or are random over a transect, I determined wether the distribution of the counts within each plot followed a negative binomial distribution or a Poisson distribution. The Poisson distribution has the characteristic that the mean of the distribution is equal to the variance. The variance of the negative binomial distribution, in contrast, is greater than the mean. The formulas below show the relationship between the mean and variance for the Poisson and negative binomial distributions.

Poisson distribution: $E(Y) = \lambda$, $Var(Y) = \lambda$

Negative Binomial distribution: $E(Y) = \lambda$, $Var(Y) = \lambda + \alpha \lambda 2$

The parameter α in the equation for the variance of the negative binomial distribution above represents the magnitude of overdispersion, which can result from unobserved heterogeneity in the counts, which may be due to spatial autocorrelation.

To decide if captures per trap station fit a Poisson distribution, which assumes independent observations throughout the sample space, vs. a negative binomial distribution, which is consistent with "clustering" of counts spatially, I ran a negative binomial regression, and tested whether the parameter α = zero. This is equivalent to testing whether the distribution of small mammal counts is Poisson, and therefore independent spatially.

MICROHABITAT ANALYSIS RESULTS

Trap success- Over 500 captures of nine small mammal species were recorded in 1,440 trapnights over four years (Table 2), and over 2,000 captures of sixteen small mammal species were recorded in 6,480 trapnights over eighteen years (Table 3; in Tables 2 and 3, recaptures on the second or third night of trapping were excluded). Over both four year and eighteen year periods, more than ninety percent of captures were of four species, *P. leucopus* (64.1% over four years and 60.4% over eighteen years), *B. brevicauda* (15.2% and 12.9%), *Glaucomys volans* (1.6% and 1.4%) and *Tamias striatus* (11.9% and 17.6%). *Glaucomys volans* was not found in Reese's Swamp. As explained above, *Tamias* was excluded from further analysis because its trappability is highly sensitive to daily weather conditions (Snyder, 1982; Myers, personal communication).

Microhabitat preference- Table 4a-c shows the association between microhabitat variables and the number of small mammals captured at each trap station. At Colonial Point during the spring, the number of captures of *P. leucopus* was positively significantly associated only with percentage of ground cover made up by living wood. At the Burn Plots, in contrast, the number of spring captures of *P. leucopus* was positively associated with only the mean diameter of woody debris. At Reese's swamp, spring captures were positively associated with the percentage of ground cover made up of leaves, and negatively associated with the number of plant species present in the ground cover.

During the fall, no associations between the numbers of *P. leucopus* captured and ecological variables were discovered at Colonial Point (Table 4a). At the Burn Plots, the number of mice was negatively associated with average decay class of woody debris. At Reese's

Swamp, positive associations for *P. leucopus* were found with average canopy density, percentage of ground cover made up of leaves, percentage made up of slash, and average diameter of woody debris. Number of mice was negatively associated with percentage of ground cover made up of living wood and moss/lichen.

Too few *B. brevicauda* were captured in the spring to allow statistical analysis. In the fall, captures of *B. brevicauda* in Colonial Point were positively associated with the number of trees, number of tree species and number of ground cover species. The number of *Blarina* captured was negatively associated with decay class of woody debris and weakly negatively associated with maximum length of woody debris (Table 4b). In the Burn Plots, the only significant association for the number of *B.brevicauda* captured was with the grass component of ground cover. In Reese's Swamp, I found a positive association between *B. brevicauda* captures and average canopy density, number of trees, DBHs, total basal area, percentage of ground cover made up by moss/lichen, number of WD, and number of snags. Negative associations included percentage of the ground covered by slash, WD length and average diameter of stumps.

During the spring, too few *G. volans* were found for statistical analysis. During the fall, at Colonial Point no significant association of number of *G. volans* captured was found with any ecological variable (Table 4c). At the Burn Plots, *G. volans* captures were positively associated with the number of tree species, total basal area and the number of trees with DBH larger than 9.0cm.

Principal Component Analysis (PCA of habitat structure) - I interpreted the forest structure sampled by each transect based on the factor loadings obtained from principal component analysis (PCA). For Colonial Point, PCA of the data matrix of ecological variables produced six

components with eigenvalues greater than 1.0 (Table 5a). Those six components explained 86.88% of the total variance in ecological variables. The variables loading most highly on PC1 represented a gradient in tree diameter, with high scores on this axis indicating large trees. PC2 was positively associated with number of trees and shrubs. PC3 described a gradient from the closed canopy with dense leaf cover on the ground (low factor loadings) to open canopy with more slash and larger WD on the ground (high factor loadings). PC4 indicated a gradient with extremes of dense leaf cover on the ground (high scores) to dense grass cover (low scores). PC5 was positively related to average length of WD and amount of woody cover on the ground, and negatively related to the number of ground cover species. PC6 was positively associated with the number of items of WD and average decay class of WD.

For the Burn Plots, PCA yielded seven PCs with eigenvalues greater than 1.0; these components explained 85.79% of total variance in ecological variables (Table 5b). PC1 represented increasing number and diameter of trees. PC2 was positively associated with number, length, diameter and decay class of WD, and negatively associated with the number of ground cover species. PC3 indicated a gradient from dense moss/lichens to ground cover consisting of dense leaves. PC4 was positively related to the amount of woody cover and negatively related to the amount of slash cover on the ground. PC5 was positively associated with the average diameter of stump and the number of ground cover species. PC6 was positively correlated with the numbers of snags and trees, and negatively correlated with average DBH of trees. PC7 was positively associated with percent ground cover made up of grass.

At Reese's Swamp, seven PCs with eigenvalues greater than 1.0 resulted from a PCA of ecological measurements (Table 5c). These seven PC's explained 86.79% of total variance of microhabitat variables. PC1 represented the number and diameter of trees. PC2 was positively

associated with average and maximum DBH of trees and the number of snags, and negatively associated with average length and diameter of WD. PC3 represented diversity of plant species on the ground. PC4 was positively associated with percentage of ground cover made up of slash, number of items of WD and average decay class of WD. PC5 represented the gradient from grass to moss in the ground cover. PC6 was positively associated with the percent of ground cover made up by living wood, and negatively associated with average canopy density and average diameter of WD. PC7 was positively correlated with average diameter of stumps.

Microhabitat use by each small mammal species along each transect was determined by regressing number of captures on each principal component derived from PCA (spring, Table 6a; fall, Table 6b). In the spring, the captures of *P. leucopus* were positively associated with grassier sites (PC7) at the Burn Plots and negatively associated with the diversity of ground cover species (PC3) at Reese's Swamp. In the fall, I found a negative association between number of *P. leucopus* captures and shrubbiness of sites (PC6) at Reese's Swamp. No significant associations of number of *P. leucopus* with number or size of trees, WD or percent of ground covered by leaves were found.

In the fall, numbers of *B. brevicauda* were positively associated with number of trees (PC2) at Colonial Point and amount of grass in the ground cover (PC7) at the Burn Plots. The relationships of this species and habitat are more complex at Reese's Swamp, with high numbers of shrews recorded at sites with large trees (PC1), especially with minimal WD (PC2), and in mossy (vs. grassy) habitats (PC5). Numbers of *B. brevicauda* captured were negatively related to area covered by small trees, amount of living wood on the ground (PC6) and number of stumps (PC7). Surprisingly, no association of *B. brevicauda* with WD was found.

During the fall, number of captures of *G.volans* at the Burn Plots was positively related only to number, size, and diversity of trees. No significant associations were found at Colonial Point.

Multivariate Poisson Regressions- Multivariate Poisson regression models were calculated in which the number of captures of each species was regressed on all microhabitat variables. Separate models were calculated for each species in spring and in fall. Significant relationships with multiple micorohabitat variables were found only for *P. leucopus* (fall) at Reese's Swamp and *B. brevicauda* (fall) at Colonial Point and Reese's Swamp (Table 7). Number of captures of *P. leucopus* at Reese's Swamp in the fall was negatively associated with percentage of ground made up of living wood and moss/lichen. For fall captures of *B. brevicauda* at Colonial Point, number of tree species and number of ground cover species were significant predictors. At Reese's Swamp during the fall, I found a significant association of number of captures of *B. brevicauda* with average canopy density, average tree density, number of ground cover species and number of snags.

The model of *B. brevicauda* in Reese's Swamp shows the highest model fitness (Fig. 3). The models of *P. leucopus* in the Burn Plots and Reese's Swamp indicate relatively higher model fitness than the other models.

Finally, I noted that the distribution of captures of white footed mice was unevenly distributed along the Reese's Swamp transect. Mice tended to concentrate along the north side of the transect (Station c1-k1, Fig. 4, Table 8).

MACROHABITAT ANALYSIS RESULTS

Comparison of small mammal captures- In the spring, many more *P. leucopus* were captured at Colonial Point than at the Burn Plots or Reese's Swamp (Table 9). In the fall, more white footed mice were captured at all sites, but the total at Colonial Point remained the highest. The mean number of *B. brevicauda* captured in fall was significantly greater at Colonial Point than at the Burn Plots and Reese's Swamp, and greater at Reese's Swamp than at the Burn Plots. *Glaucomys volans* capture rates did not differ significantly among transects, but the number of flying squirrels captured was very small.

Comparison of ecological variables- Significant differences in ecological variables were found among the three sites based on Tukey tests. At Colonial Point, average canopy density and the number of deciduous trees were higher than at the Burn Plots or Reese's Swamp (Table 10). The number of trees, number of tree species, av. DBH, max. DBH and total basal area did not vary significantly among the three transects. With respect to ground cover, percentage of moss/lichen and percentage of grass were higher at Reese's swamp than at Colonial Point and the Burn Plots. A higher percentage of leaf cover was found at Colonial Point than at the Burn Plots and at the Burn Plots than at Reese's Swamp. On the other hand, the number of ground cover species was higher at Reese's Swamp than at the Burn plots and at the Burn Plots than at Colonial Point. Percentage of slash was higher at Reese's Swamp and Colonial Point than at the Burn Plots, but no significant difference was found between Reese's Swamp and Colonial Point. Percentage of the ground covered by living wood did not differ significantly among the transects. The length and diameter of woody debris were largest at Reese's Swamp and both differed significantly between Reese's Swamp and the Burn Plots. The number of woody debris items longer than

10cm, WD average length and WD maximum length within a plot were greater at Reese's Swamp than at Colonial Point. The number of WD items was significantly greater at Colonial Point than at the Burn Plots, although all mean values of woody debris were larger at Colonial Point than at the Burn Plots. Average decay class of woody debris did not differ among forests. The number and average diameter of snag and stump were the largest at Reese's Swamp and significantly larger at Reese's Swamp than at Colonial Point.

In summary, these three sites are differentiated by tree species, ground cover types, and the amount of woody debris and fallen logs. Soil moisture was not measured directly in my field sampling, but the classification of forest types by Pearsal (1995) suggests it also differs among my sites. The forest at Colonial Point is characterized by abundance of large deciduous trees, dense canopy, sparse undergrowth, and ground cover consisting primarily of leaf litter and somewhat excessively drained to moderately well drained soil. The Burn Plots provide a mixture of large pines and hardwoods, ground cover consisting primarily of leaf litter and fern, a small amount of woody debris and excessively drained soil. Reese's Swamp is characterized by an abundance of large coniferous trees, well drained to groundwater-fed soil, ground cover consisting primarily of grass and moss, abundance of woody debris and fallen logs.

Differences in habitat associations- Differences among the three transects in the preference of small mammals for each of the ecological variables were determined by the comparison of slopes of Poisson regressions of the number of captures on each ecological variable across the three transects (as calculated in simple Poisson regressions in the microhabitat analysis). This test shows the difference among transects in the relationship between each ecological variable and the captures of each species at each trap station (Table 4).

In the comparisons of coefficients, spring *P. leucopus* captures differed significantly among transects in their association with the average DBH of snags, and in the fall in their association with average canopy density, percentage of ground cover made up of living wood, and percent made up of leaves (Table 4a). For *B. brevicauda*, different associations of the numbers of capture for each transect were found with a number of ecological variables such as DBH, total basal area, the number of trees , percentage of ground cover made up by moss/lichen, percentage made up of slash, the number of ground cover species, number of WD items, the number of snags, and stump average diameter (Table 4b). For *G. volans*, the relationship of number captured with the number of tree species was the only ecological relationship that differed significantly among transects (Table 4c).

GEOSTATISTICAL ANALYSIS RESULTS

A large spatial autocorrelation was found for the number of *P. leucopus* captured at each trap station at Colonial Point in the fall (Table 11, Fig. 5). Other species captured did not show any significant spatial autocorrelation. The numbers of small mammal captures at each trap stations in three types of forests were shown in figure 4.

The test for negative binomial distribution showed that in the fall, *P. leucopus* at Colonial Point produced an estimated value of α that is actually negative (Table 12) , which is not consistent with spatial clustering of the counts spatially. The 95% Confidence Interval for α includes zero, so I cannot reject the null hypothesis that the parameter α is equal to zero. I conclude that there is no evidence of spatial clustering of *P. leucopus* at Colonial Point in the fall.

DISCUSSION

Microhabitat

Peromyscus leucopus---Small mammal habitat preferences were inferred from regression analyses of microhabitat variables and numbers of small mammal captures at each trap site. At Colonial Point, the number of *P. leucopus* captured was positively associated with the percentage of the ground covered by living wood. Percentage of living wood is different from the number of trees and total basal area (which were not related to the number of mice captured), because it includes shrubs with DBH smaller than 1.5cm. This suggests that *P. leucopus* prefers shrubby habitat, a finding that is consistent with other studies (Getz, 1961a; Kaufman et al., 1983) and which may be related to predator avoidance. In the Burn Plots, more white footed mice were captured at sites with woody debris of large diameter, more grass cover (in the spring) and less decayed woody debris (in the fall). The selection of larger-diameter logs by *P. leucopus* could be explained by the fact that larger logs provide a wide travel surface (Barnum et al, 1992). *Peromyscus leucopus* in hardwood forests of Minnesota and Maryland preferred logs in late stages of decay because they are easy to climb, permitting easy travel to foraging sites (Barnum et al., 1992). In another study, on the other hand, *P. leucopus* preferred unsalvaged pine plots with logs in early stages of decomposition, large diameter and length, to salvaged plots (Loeb, 1999). Thus, it is not clear how the decomposition status of woody debris influences habitats used by *P. leucopus*. Furthermore, other factors may influence habitat use. Although grass-like vegetation under the forest canopy may be avoided by *P. leucopus* (Getz, 1961a), at the Burn Plots, where grass percentage was low (from zero to 20%) and low sweet blueberry (*Vaccinium angustifolium*) was abundant in grassier areas, *P. leucopus* may have selected grassy sites to obtain food.

At Colonial Point and the Burn Plots, no strong habitat preferences for other ecological variables were found. This suggests that *P. leucopus* is a habitat generalist in deciduous forests (Dueser and Shugart, 1978; Rossell and Rossell, 1999; Seagle, 1985).

In Reese's Swamp, several variables were associated with sites where many white footed mice were captured. These included a positive association with the average canopy density in the fall and amount of leaf cover on the ground in both seasons. Other studies have reported *P. leucopus* to select closed canopy instead of open canopy, possibly to avoid predators (Kaufman et al, 1983, Rossell and Rossell, 1999). In addition, several studies reported that *P. leucopus* avoided leaves on the ground, perhaps because of the noisiness of travel across leaf-covered surfaces (Barnum et al, 1992; Fitzgerald and Wolff, 1988). Indeed, when the ground was wet, more than 90% of travel was along ground routes (Fitzgerald and Wolff, 1988). My research showed that the areas with relatively high wet leaf cover coincided with areas of high canopy density, and *P. leucopus* was likely to select areas with high leaf cover as well as areas with high canopy density. Percentage of the ground covered by moss/lichen, percentage of the ground covered by living wood, and the number of ground cover species, on the other hand, were all negatively associated with the capture of *P. leucopus*.

At Reese's Swamp, I found a higher rate of capture of *P. leucopus* on the north leg of the transect (Fig. 2). Pearsal (1995) classified the north side of the Reese's Swamp transect, where percent moss is lower, as a different ecosystem from the east side of the transect, where percent moss is higher. The north side area is well drained to moderately well drained and covered with white pine (*Pinus strobus*) in addition to northern white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). Although oak-hickory forest is the most favorable to *P. leucopus* in terms of year-round food supply (Getz, 1961b), seeds of *P.*

strobus may become important food sources in the autumn and winter (Abbott and Quink, 1970). The areas located on the east side with large numbers of trees were, on the other hand, mainly occupied by northern white cedar (*Thuja occidentalis*) and balsam fir (*Abies balsamea*), which are not likely to be good food sources. Therefore, the north side of the transect, characterized by less moss, may be preferable because food availability is likely to be higher than on the east side of the transect, where the amount of moss is higher. The areas with more ground cover species were also located on the east side where conifer trees were abundant. Most herbaceous species increase in frequency with increasing moisture (Hutchinson et al, 1999). Therefore, fewer captures of *P. leucopus* in the areas with high moisture may be partly due to a response to a less available food supply (Getz, 1961b). Many studies have reported that *P. leucopus* prefers wooded areas (Getz, 1961b; Kaufman et al, 1985), but I found woody ground cover was negatively correlated with the number of captures at Reese's Swamp. Getz (1961b) reported that *P. leucopus* was abundant in the areas covered by many shrubs. Seagle (1985), on the other hand, reported that, in cedar glades, *P. leucopus* was a habitat specialist and inhabited denser woods with fewer shrubs. The pattern that I observed in the current study seems to be consistent with Seagle's result.

Blarina brevicauda---At Colonial Point, positive associations were found between *B. brevicauda* and the number of trees, the number of tree species, the number of deciduous trees and the number of trees with DBH larger than 9.0cm. *Blarina brevicauda* has been reported to be abundant in habitats covered with leaf litter (Pruitt, 1959). At Colonial Point, percent of ground covered by leaves was high, ranging from about 70 to 95%. Leaf litter was not, however, associated with the capture of *B. brevicauda*. Because the coverage by leaf litter was so high, the

prevalence of shrews might have been positively associated with the depth of leaf litter, not with its coverage on the surface. The positive association of number of captures with the number of trees might indicate the preference of *B. brevicauda* for humid areas. The positive association of *B. brevicauda* with the number of ground cover species is also likely to be due to a preference for humid areas.

Getz (1961b) found that *B. brevicauda* did not prefer any particular type of ground cover. In the Burn Plots, however, their numbers were positively associated with the percentage of ground covered by grass. Getz (1961b) also found that in a burned area, most *B. brevicauda* individuals were captured near the edge of a birch-poplar stand that had a greater supply of food. During the fall, the preference of *B. brevicauda* for areas with grass cover, which also had a high density of *V. angustifolium*, could reflect the shrews' use of blueberries (or the insects that feed on them) as food. The positive association of *B. brevicauda* with grass cover might also indicate the use of insects inhabiting in the grasses.

In Reese's Swamp, the number of *B. brevicauda* captured was positively associated with the number of trees, tree DBH, and total basal area. Since at this site, trees are mainly coniferous evergreen trees such as northern white cedar (*Thuja occidentalis)* and balsam fir (*Abies balsamea*), the reasons for this preference could include food availability (in the form of insects attracted to leaves and seeds) and moisture. The number of captures of *B. brevicauda* was also positively associated with percentage of ground covered by moss/lichen and the number of ground cover species. These variables may also be related to moisture. In addition, *B. brevicauda* was positively associated with the amount of woody debris. Woody debris is important habitat for snails and slugs (Caldwell, 1993) which are fed upon by shrews. The observation of fewer captures of *B. brevicauda* at sites with large numbers of shrubs on the

ground was consistent with the study by Kitchings and Levy (1981), but the negative association found here between the number of *B. brevicauda* captured and the number of stumps was inconsistent with their study. In Reese's Swamp, some trap stations with many stumps were partially surrounded by standing water, which this could be one reason for the avoidance of those sites (Getz, 1961b).

Glaucomys volans--- In the present study, *G. volans* was most abundant in Colonial Point. Nevertheless, I found no association of number of flying squirrels captured at a site with any ecological variable. Hard mast such as acorns and beechnuts are primary foods (Harlow and Doyle, 1990), and tree cavities in oak, aspen and red maple are frequently used as nest sites by this species (Muul, 1968; Muul, 1974; Weigl, 1978). At Colonial Point, deciduous trees were most abundant, including overstory red oaks (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*Acer saccarum*) and American beech (*Fagus grandifolia*), which is a cavity prone species that may provide critical nesting sites. The relatively large number of flying squirrels captured at Colonial Point was consistent with research showing a higher capture rates in deciduous forests, such as sugar maple forest, in Maryland (Gilmore and Gates, 1985; Weigl, 1978). Southern flying squirrels might not be habitat selective at Colonial Point because food and roost sites are abundant for them. In the Burn Plots, more southern flying squirrels were captured at trap stations with a higher number of tree species, larger basal area and more trees with DBH larger than 9.0cm. *Glaucomys volans* feeds on nuts and acorns (Baker, 1983; Harlow and Doyle, 1990; Muul, 1968) and stockpiles foods in the fall (Baker, 1983). They also use large trees for long glides (Bendel and Gates, 1987). The preference reported here for larger trees seems to agree with those observations. A greater diversity of tree species possibly indicates

better foraging conditions (Baker, 1983). Strangely, no preference for sites with snags was found in the Burn Plots, although many studies have suggested the importance of snags to this species (Bendel and Gates, 1987; Gilmore and Gates, 1985; Taulman, 1999).

Macrohabitat

Peromyscus leucopus--- In both seasons, more white footed mice were captured along the transect in Colonial Point than in the Burn Plots or in Reese's Swamp (Table 8), although the difference between Colonial Point and the Burn Plots was significant only in the spring. This suggests that in the spring, Colonial Point provides the most suitable habitat for this species. At Colonial Point, the number of deciduous trees was more abundant than at the other two sites. In other studies, *P. leucopus* was captured most often in virgin and second growth hardwood forests (Baker, 1983). That the capture differences between Colonial Point and Burn Plots or Reese's swamp (Table 8) were more pronounced in the spring suggests that the Colonial Point forest may contain more year-round foods, which have a larger impact on the winter survival rate (McCracken et al, 1999). The larger amount of woody debris at Colonial Point compared to the Burn Plots might be also the reason that more white footed mice were captured at Colonial Point.

Blarina brevicauda---In my study, *B. brevicauda* was most abundant at Colonial Point. This result is consistent with other studies which suggested that this species may prefer hardwoods (Degraaf et al, 1991; Getz, 1961b; Kirkland and Griffin, 1974). Baker (1983) noted that *B. brevicauda* is most abundant in habitats covered with leaf litter. Less leaf litter at the Burn Plots and Reese's Swamp may partially account for the lower number of captures of *B. brevicauda* at

these two sites. Preference for areas with enough leaf litter probably results from the indirect relationship of increased humidity under such a cover (Pruitt, 1959). At Reese's Swamp, where the humidity is highest among the three transects, however, the number of captures of *B. brevicauda* was smaller than at Colonial Point. *Blarina brevicauda* has a high metabolic rate, and therefore high food consumption (Pearson, 1947), suggesting that there may be more food available at Colonial Point than the other two forests. Insect abundance was not measured in this study. Positive association with indicators of tree numbers in Reese's Swamp could be due to a positive relation between the number of trees and abundance of insects related to trees and eaten by *B. brevicauda*. However, the smallest number of *B. brevicauda* was captured at the Burn Plots, where more deciduous trees and a higher percentage of ground covered by leaves existed than at Reese's Swamp..

I suspect that *Blarina* may favor Reese's Swamp because there woody debris (which snails and slugs tend to inhabit) was most abundant, and the humidity and organic matter provided by woody debris were highest. Further, *Thuja occidentalis* was abundant, reflecting the existence of basic soil. Under such an environment, earthworms tend to be common (Edwards and Bohlen, 1996). Thus, the positive association with tree DBH, percentage of ground covered by moss/lichen, amount of woody debris and the number of snags at Reese's Swamp found in this study might be due to the dependence of *B. brevicauda* on snails, slugs and other insects as food sources, and those food sources might be more available in Reese's Swamp than at the Burn Plots. In addition, in the Burn Plots, red pine (*Pinus resinosa*) and bigtooth aspen (*Populus grandidentata*), which are tolerant to very dry soil condition, were abundant. According to Pearsal (1995), the soil of the Burn Plots is classified as excessively drained medium sand. Soil moisture may be an important limiting factor at the Burn Plots.

Glaucomys volans---More southern flying squirrels were captured at Colonial Point than at the Burn Plots, and none was found in Reese's Swamp. The preferred nesting sites and foods of *G. volans* are generally found in deciduous forest (Weigl, 1978), so abundance of deciduous trees at Colonial Point is the likely reason. The positive association of the number of *G. volans* captured at the Burn Plots with the number of tree species might reflect the variety and amount of food sources at particular stations at the Burn Plots. Reese's Swamp is mostly covered with coniferous trees; deciduous trees that produce seed crops are few. In addition, *G. volans* may compete for dens with red squirrels (*Tamiasciurus hudsonicus*) if entrances to nest cavities are large enough (Baker, 1983; Muul, 1968). *Tamiasciurus* prefers coniferous forests, and is a common resident of Reese's Swamp (but not Colonial Point or the Burn Plots).

Spatial distribution

Moran's I values for the number of captures of *P. leucopus* at Colonial Point in the fall show a relatively high positive spatial autocorrelation, although no spatial clumping of *P. leucopus* at Colonial Point in the fall was found. Since positive autocorrelation over short distances means that the variable takes similar values (Legendre and Fortin, 1989), my result at Colonial Point shows that the number of captures of *P. leucopus* is similar within groups of neighboring trap stations. On the other hand, spatial autocorrelations were not found for *P. leucopus* captured at the other two transects, nor for *B. brevicauda* and *G. volans*.

At Colonial Point in both seasons, numbers of juveniles appeared to be especially clumped; all juvenile *P. leucopus* except one were captured at trap stations which had larger numbers of *P. leucopus* captures than average. Female *P. leucopus* retains their home ranges after weaning litters (Goundie and Vessey, 1986), and in the fall *P. leucopus* was found to be

arranged in family groups consisting of one adult female, several adult males and a number of juveniles (Myton, 1974). Therefore, the trap stations with larger numbers of *P. leucopus* captures at Colonial Point may be a result of the proximity of family members of *P. leucopus* before the juveniles disperse. In addition, juvenile *P. leucopus* captures at the trap stations with larger number of captures than average may also indicate abundance of food at these stations, since reproductive success depends heavily on optimal habitat selection. However, overall, *P. leucopus* in the fall seems to be dispersed more evenly than random, since Moran's I value suggested there is spatial autocorrelation, but the test for clustering showed there is no clustering.

For *B. brevicauda*, no spatial autocorrealation was found. At Colonial Point, *B. brevicauda* was positively associated with the number of trees, which differs even at neighboring trap stations. Positive association with trees may account for the apparent sensitivity of *B. brevicauda* to moisture, which is produced by trees at Colonial Point. At the Burn Plots, the small number of *B. brevicauda* captured is a possible reason that no spatial autocorrelation was found. At Reese's Swamp, only seven stations captured *B. brevicauda*, and they were dispersed. Also, the number of captures was associated with microhabitat variables such as the number of trees, total basal area and the ground covered by moss which fluctuates even at nearby trap stations. Therefore, the lack of spatial autocorrelation of *B. brevicauda* may be due to the presence of food sources and moisture at several scattered locations around trap stations.

Although *G. volans* also may be a habitat generalist at Colonial Point in the fall, the small number of captures of this species might have prevented the finding of positive spatial autocorrelation.

Some improvements will be possible in future studies. Habitat sampling in both the spring and fall will be necessary to make the habitat preferences of these animals clearer, because forest resources change seasonally. Habitat sampling in both seasons will be also useful to examine the possibility of seasonal changes in habitat preference of small mammals. The most significant problem of my research was the small sample size. Only twenty trap stations were observed along each transect. Therefore, I recommend that ecological variables be examined over several years in both seasons to increase sample size. Other factors influencing the number of small mammal capture could include competition with other small or larger mammals, annual fluctuations in seed production, and differences in habitat use by animals of different sex, age or weight difference. All of these should be examined in future studies of the habitat preference of each small mammal species. In the macrohabitat analysis, I compared transects located in different forest types. However, data were available from only a single transect in each type of forest. In order to compare habitat preference of small mammals among three forest types, sampling multiple transects in each forest type will be necessary.

CONCLUSION

Peromyscus leucopus---At Colonial Point, *P. leucopus* preferred shrubby habitat. At the Burn Plots, *P. leucopus* preferred less decayed logs with larger diameters and more grass cover on the ground. Those factors provide them with benefits such as predator avoidance, easier travel surfaces and food. However, *P. leucopus* was not limited in its local distribution by any other microhabitat variables that I measured. In predominantly deciduous forests such as seen at Colonial Point and the Burn Plots, *P. leucopus* is apparently a habitat generalist. In the high population density areas at Colonial Point, most juvenile white footed mice were found with sub

adult and adult mice, perhaps reflecting the aggregation of family members in the high population density areas. In Reese's Swamp, on the other hand, these mice are likely to be habitat specialists because there are unable to make good use of many of the microhabitats present. Factors limiting *P. leucopus* in cedar swamps may be food availability and predation risks, because at Reese's Swamp these mice avoided wet areas dominated by northern white cedar and balsam fir and selected the sites with high canopy density, although they avoided shrubby areas. At Colonial Point, more white footed mice were captured than at the Burn Plots and Reese's Swamp. The large number of deciduous trees, which tend to provide year-round foods, may be one reason that *P. leucopus* was most abundant at Colonial Point. Clearer differences among forests in the number of captures in the spring suggest the importance of year-round foods on the winter survival rate.

Blarina brevicauda--- At Colonial Point, *B. brevicauda* preferred wooded areas that produce leaf litter and sites with a large variety of groundcover species, indicating high soil moisture. At the Burn Plots, however, *B. brevicauda* was less common and positively associated only with percentage of the ground covered by grass. Since the soil at the Burn Plots is excessively drained medium sand, soil moisture may be an important limiting factor for *B. brevicauda* at the Burn Plots. At Reese's Swamp, where *B. brevicauda* was more numerous than at the Burn Plots, invertebrates such as snails, slugs and earth worms are likely to be abundant. There, short-tailed shrews preferred areas covered with moss/lichen, woody debris and snags. These are the same areas preferred by these invertebrates and may indicate the shrews' reliance on them as food sources.

Glaucomys volans--- At Colonial Point, no association with ecological variables was found. Southern flying squirrels might not be habitat selective in Colonial Point, because food and roost sites are abundant for them. At the Burn Plots, *G. volans* preferred sites with greater diversity of trees and larger trees. Those preferences may be due to their selection of areas with high food availability and use of large trees for nest sites or long glides. More southern flying squirrels were captured at Colonial Point than in the Burn Plots, perhaps because of the abundance of deciduous trees at Colonial Point. Strangely, no preference for snags was found in the Burn Plots, although snags are considered to be important roost sites. At Reese's Swamp, no *G. volans* was found over eighteen years. There are few deciduous trees that produce seed crops at Reese's Swamp. In addition, *G. volans* may compete for dens with red squirrels. Limited food sources and competitor avoidance are the likely reason that *G. volans* has never been found at Reese's Swamp.

Macrohabitat analysis--- In an attempt to understand the differences in capture numbers among forest types, I analyzed the differences among the three transects in the number of small mammals captured by comparing across transects the relationship between number of captures and each ecological variable. Substantial differences were found in the slopes of capture numbers on habitat variable. I expect other aspects of macrohabitat to be important, including habitat patch size, predators and microclimate, and they may account for the differences in slopes. The significance of these factors of these could not, however, be addressed in this study. Further research clarifying both macrohabitat and microhabitat effects is much needed

Implications for forest management--- The association of the number of captures of each species with microhabitat variables differed among the three transects, as described above. It is difficult to generalize about the relationships of these species with microhabitat features without considering such more general (macrohabitat) conditions. In designing and implementing forest management plans, forest managers must take both macrohabitat and microhabitat variables into consideration.

Some of my results differed from findings reported by other studies, and it is apparent that the microhabitat characteristics of a species may vary from place to place. This underscores the importance of site-specific studies when the goal is to identify key components of a species' habitat.

Besides emphasizing the importance of basing management strategy on local information at both micro- and macrohabitat scales, the results of my research have some further implications for forest management. Forest management practices such as thinning and prescribed burning are expected to influence the habitats of small mammals. For example, natural regeneration, thinning trees or encouraging ground cover and understory species diversity may enhance habitat suitability of these mammals. On the other hand, burning plant materials such as branches and leaves that are not harvested may have negative impacts on these mammals. Instead, preserving woody debris and a layer of leaf litter may provide small mammals with critical habitat components such as foods, runways and shelters. In addition, in managed forests such as second-growth and plantations, it may be advisable to change silvicultural or harvesting techniques from clear-cutting to selection cutting. Clear cutting results in environmental changes such as loss of food sources and roost sites, soil temperature increase, water loss and creation of large openings. These changes will cause small mammals to avoid

affected portions of the forest. If management is to encourage or at least not diminish the diversity of small mammals at a site, it is essential to minimize habitat destruction and leave resources such as foods and nest sites in the forest.

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APPENDIX: TABLES AND FIGURES

Table 1. Ecological variables recorded and utilized for analysis

Trees	average canopy density
	number of trees
	number of tree species
	average DBH
	maximum DBH
	total basal area
	number of Deciduous trees
	number of trees > DBH 9.0
Ground Cover	percentage of saplings
	percentage of living wood
	percentage of dirt
	percentage of grass
	percentage of ferns
	percentage of leaves
	percentage of mosses or lichens
	percentage of slash
	number of GC species
Woody Debris (WD)	number of WD
	number of CWD (> DBH10cm)
	WD: average length
	WD: maximum length (in plot)
	WD :maximum length (total)
	average decay class
	total volume
	WD: average DBH
Snag/Stump	number of snags
	snag: average DBH
	number of stumps
	stump: average diameter

Table 2. Number of individuals of each species captured in the 3 transects over the most recent four years (2003-2006)

	Spring									
	PL	BB	GV	TS	SC	NI	MP	MF	MUS	total
Colonial Point	40	4	0	8	0	0	0	0	0	52
Burn Plots	20	0	1	3	0	0	0	0	0	24
Reese's Swamp	14	0	0	0	3	3	2	1	0	23
Total	74	4	1	11	3	3	2	1	0	99

	Fall									
	PL	BB	GV	TS	SC	NI	MP	MF	MUS	total
Colonial Point	99	42	4	31	0	0	0	0	0	176
Burn Plots	88	10	3	17	2	0	0	1	0	121
Reese's Swamp	67	22	0	2	10	0	13	1	1	116
Total	254	74	7	50	12	0	13	2	1	413

pl=*Peromyscus leucopus*, bb=*Blarina brevicauda*, gv=*Glaucomys volans*, ts=*Tamias striatus*, sc=*Sorex cinereus*, ni=*Napaeozapus insignis*, mp=*Microtus pennsylvanicus*, mf=*Mustela frenata*, mus=*Mus musculus*

Table 3. Number of individuals of each species captured in the 3 three transects over eighteen years (1989-2006)

	Spring																
	PL	BB	GV	TS	SC	NI	MP	MPIT	PMG	GS	MF	TH	ZH	DV	CG	MUS	total
Colonial Point	117	20	2	88	0	0	0	1	0	0	0	0	0	0	0	0	228
Burn Plots	81	5	3	16	0	0	0	0	1	0	0	0	0	0	0	0	106
Reese's Swamp	44	18	0	0	7	23	9	0	0	1	2	1	1	0	0	0	106
Total	242	43	5	104	7	23	9	1	1	1	2	1	1	0	0	0	440

	Fall																
	PL	BB	GV	TS	SC	NI	MP	MPIT	PMG	GS	MF	TH	ZH	DV	CG	MUS	total
Colonial Point	389	80	14	179	0	0	0	0	2	0	1	0	0	1	0	0	666
Burn Plots	382	42	9	75	3	0	0	0	4	0	3	0	0	0	0	0	518
Reese's Swamp	222	98	0	3	44	4	46	0	0	1	1	1	0	0	1	1	422
Total	993	220	23	257	47	4	46	0	6	1	5	1	0	1	1	1	1606

pl=Peromyscus leucopus, bb=Blarina brevicauda, gv=glaucomys volans, ts=tamias striatus, sc=Sorex cinereus, ni=Napaeozapus insignis, mp=Microtus pennsylvanicus, mpit=Microtus pinetorum, pmg=Peromyscus maniculatus gracilis, gs=glaucomys sabrinus, mf=mustela frenata, th=tamiasciurus hudsonicus, zh=zapus hudsonius, dv=didelphis virginiana, cg=Clethrionomys gapperi, mus=Mus musculus

Table 4. The coefficients of simple Poisson regressions of number of captures of small mammals and ecological variables. Separate analyses were performed for each transect; and the result of ANCOVA comparing coefficients among each forest

a. *P. leucopus* (4years)

	Spring				Fall			
	Colonial	Burn	Reese's	ANCOVA p-value	Colonial	Burn	Reese's	ANCOVA p-value
av. Canopy density	0.4595	0.2443	4.8839	0.2964	-0.6956	0.1937	**2.5654***	**0.0273***
# of trees	0.0540	-0.1577	-0.2259	0.1491	0.0102	-0.0465	-0.0743	0.5749
# of tree species	0.1778	-0.1339	-0.4277	0.1296	0.0915	-0.0282	-0.1528	0.2689
avg. DBH	0.0043	-0.0240	-0.0354	0.3799	-0.0095	-0.0005	-0.0080	0.8573
max. DBH	0.0037	-0.0205	-0.0168	0.4067	-0.0037	0.0059	-0.0091	0.5345
Total basal area	0.2820	-2.4088	-5.4555	0.4466	-0.8940	1.3051	-0.8856	0.6286
# of Deciduous	0.0540	0.0562	0.1351	0.9089	0.0102	0.0090	-0.0099	0.9802
# of trees > DBH 9.0	0.2796	-0.0932	-0.2272	0.0856	0.0268	-0.0212	-0.0531	0.8048
pct. sapling	-5.9570	-6.9709	-0.2484	0.7182	-1.0674	5.2746	0.5260	0.6104
pct. living wood	**9.1778***	-1.8537	-0.9687	0.0922	4.642	3.2034	**-5.7695*****	**0.0027*****
pct. dirt	-2.2459	-1.1392	-6.5795	0.9016	1.3936	-0.1993	2.2665	0.8445
pct. grass	-0.2042	6.3755	0.0382	0.2290	0.0549	0.3903	0.5985	0.9014
pct. fern	-	1.3273	-	-	-	0.4750	-	-
pct. leaf	0.4695	0.6245	**4.1098***	0.1739	-1.1627	0.6542	**1.8514****	**0.0089****
pct. moss/lichen	-	-6.1618	-2.2647	0.4357	-	-1.4822	**-1.4714***	0.9937
pct. slash	-1.0563	-5.4432	0.6204	0.6085	2.1923	-2.8520	**2.2107****	0.2242
# of GC species	-0.1631	-0.0355	**-0.8032***	0.0822	-0.1881	0.0032	-0.1934	0.3436
# of WD	0.0131	0.1707	0.0167	0.7242	0.0544	0.0228	-0.0155	0.7087
# of CWD (>DBH10cm)	-0.0304	0.4155	0.1436	0.4954	0.0053	0.0387	0.1327	0.6612
WD: av. length	0.0019	-0.0017	0.0047	0.5183	0.0015	0.0002	0.0012	0.9756
WD: max. length (in plot)	0.0005	-0.0014	0.0045	0.4295	0.0018	0.0001	0.0011	0.3869
WD: max. length (total)	-0.0002	0.0001	0.0011	0.1182	0.0002	0.0003	0.0002	0.3691
WD: av. decay class	0.0533	-0.0008	-0.4720	0.7612	-0.1462	**-0.4378********	-0.1579	0.3311
WD: total volume	0.0000	0.0000	0.0000	0.5555	0.0000	0.0000	0.0000	0.6364
WD: mean diameter	-0.0328	**0.0604***	-0.0088	0.1220	0.0117	0.0236	**0.081***	0.2282
# of Snag	-	0.2006	-0.0305	0.4196	-	-0.0902	-0.1024	0.9387
Snag: av. DBH	-	-0.1924	-0.0033	**0.0229***	-	0.0018	0.0077	0.6971
# of Stump	-	0.1503	-0.3165	0.2924	-	-0.2663	-0.0519	0.3392
Stump: av. Diameter	-	-0.0005	-0.0150	0.7452	-	-0.0145	0.0147	0.1542

*p<0.05 **p<0.01 ***p<0.005 ****p<0.001 *****p<0.0001

* "- " indicates that there were not enough sample numbers to conduct tests

Table 4 (cont.).

b. *B. brevicauda* (4years)

	Fall			
	Colonial	Burn	Reese's	ANCOVA p-value
av. Canopy density	2.7979	-1.6564	**5.0621***	0.1144
# of trees	**0.2962*****	-0.0164	**0.3086******	0.0701
# of tree species	**0.3716***	0.1329	0.2461	0.6974
avg. DBH	-0.0120	-0.0290	**0.0694***	**0.0190***
max. DBH	0.0014	-0.0270	**0.0554****	**0.0189***
Total basal area	-0.3675	-6.7895	**14.9381******	**<.0001******
# of Deciduous	**0.2962*****	-0.1159	-0.0974	**0.0354***
# of trees > DBH 9.0	**0.4667****	-0.1142	**0.342******	**0.0330***
pct. sapling	6.9406	13.3911	-0.9931	0.3253
pct. living wood	-1.7983	-12.5974	-12.5974	0.7278
pct. dirt	-2.2144	-5.4235	-326.8440	0.1830
pct. grass	-1.8789	**12.2126***	-2.3080	**0.0218***
pct. fern	-	0.9030	-	-
pct. leaf	1.2125	0.0000	-2.4385	0.1286
pct. moss/lichen	-	-20.3264	**2.8356******	**0.0075****
pct. slash	0.3180	-4.4922	**-4.3468***	0.3350
# of GC species	**0.6464*****	0.4201	**0.4772***	0.7743
# of WD	-0.1129	-0.1322	**0.3846***	**0.0113***
# of CWD (>DBH10cm)	-0.1604	-0.1935	-0.2069	0.9854
WD: av. length	-0.0026	-0.0044	**-0.0107******	0.1021
WD: max. length (in plot)	-0.0012	-0.0030	**-0.0111******	**0.0021****
WD: max. length (total)	**-0.0005***	-0.0017	-0.0003	0.5700
WD: av. decay class	**-0.5182***	0.3898	0.9954	**0.0161****
WD: total volume	0.0000	-0.0001	0.0000	0.8336
WD: mean diameter	-0.0635	-0.0376	-0.1218	0.7610
# of Snag	-	0.0368	**0.6236******	**0.0328***
Snag: av. DBH	-	-0.0829	-0.0659	0.868
# of Stump	-	0.2827	0.1321	0.7741
Stump: av. Diameter	-	-0.0091	**-0.1685******	**0.0006******

*p<0.05 **p<0.01 ***p<0.005 ****p<0.001 *****p<0.0001

* "- " indicates that there were not enough sample numbers to conduct tests

Table 4 (cont.).

c. *G. volans* (18years)

	Fall		
	Colonial	Burn	ANCOVA p-value
av. Canopy density	0.1632	-0.7077	0.7853
# of trees	-0.0842	0.2108	0.1618
# of tree species	-0.0273	**0.8913***	**0.0207***
avg. DBH	0.0003	0.0563	0.2153
max. DBH	0.0106	0.0569	0.1746
Total basal area	2.2519	**14.9017***	0.0673
# of Deciduous	-0.0842	0.2812	0.1156
# of trees > DBH 9.0	-0.0363	**0.3748****	0.2133
pct. sapling	-5.7639	1.0480	0.7440
pct. living wood	0.3055	-4.2274	0.7673
pct. dirt	3.9365	-969.1100	-
pct. grass	0.7417	4.0894	0.5713
pct. fern	-	-10.9106	-
pct. leaf	-2.0594	1.2474	0.2930
pct. moss/lichen	-14.7090	1.2007	0.6853
pct. slash	2.7557	6.5606	0.6771
# of GC species	-0.5108	-0.3409	0.7895
# of WD	0.1062	0.3995	0.3407
# of CWD (>DBH10cm)	0.0559	-0.7054	0.3770
WD: av. length	0.0033	-0.0009	0.3898
WD: max. length (in plot)	0.0046	0.0002	0.3370
WD: max. length (total)	0.0001	0.0000	0.5954
WD: av. decay class	0.2365	-0.1433	0.5511
WD: total volume	0.0000	-0.0001	0.3369
WD: mean diameter	0.0060	-0.1724	0.1951
# of Snag	-	0.2054	-
Snag: av. DBH	-	0.0212	-
# of Stump	-	0.3891	-
Stump: av. Diameter	-	-0.0309	-

*p<0.05 **p<0.01 ***p<0.005 ****p<0.001 *****p<0.0001
* "- " indicates that there were not enough sample numbers to conduct tests

Table 5. Summary of principal component analysis of 16 microhabitat variables for 20 trap stations in each forest after Varimax rotation. Components with eigenvalues greater than 1.0 were reported. Variables with factor loadings greater than 0.4 or smaller than -0.4 were represented by bold letters.

a. Colonial Point

	PC1	PC2	PC 3	PC 4	PC 5	PC6
av. Canopy density	-0.037	0.102	**-0.856**	-0.055	-0.173	0.350
Number of trees	-0.087	**0.857**	-0.061	0.072	-0.182	0.149
Number of tree species	0.052	**0.935**	0.039	0.027	-0.045	0.052
Tree: av. DBH	**0.968**	-0.092	-0.032	-0.129	0.007	-0.110
Tree: max. DBH	**0.918**	0.220	-0.068	0.232	-0.068	0.023
Total basal area	**0.942**	0.117	-0.075	0.230	-0.061	0.097
Number of trees > DBH 9.0	0.224	**0.897**	-0.158	-0.066	-0.001	-0.100
pct living wood	0.357	**0.463**	-0.006	0.340	**0.441**	-0.089
pct grass	0.187	-0.056	-0.229	**0.889**	0.029	-0.063
pct leaf	-0.124	-0.188	**-0.578**	**-0.745**	-0.084	-0.165
pct slash	-0.088	0.125	**0.868**	-0.122	-0.066	0.293
Number of GC species	0.029	0.151	0.003	-0.092	**-0.813**	-0.076
Number of WD	-0.119	0.100	0.049	0.172	0.080	**0.888**
WD: av. length	-0.148	-0.036	0.303	-0.076	**0.801**	0.235
WD: average decay class	0.231	-0.067	-0.059	-0.332	0.358	**0.723**
WD: mean diameter	-0.159	-0.283	**0.889**	-0.027	0.165	-0.005
Name	TREE DBH	TREE NUMBER	OPENNESS	LEAF-GRASS	WD-LENGTH	WD-NUMBER
Eigenvalue	4.007	2.936	2.439	1.920	1.463	1.137
Cumulative variance explained (%)	25.04%	43.39%	58.64%	70.64%	79.78%	86.88%

Ave. moss, Number of Snag and ave. Diameter of stump were excluded from PCA in Colonial Point, because of lack of presence

Table 5 (cont.).

b. Burn Plots

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
av. Canopy density	0.079	0.193	**0.808**	0.384	0.079	-0.057	-0.019
Number of trees	**0.646**	-0.135	-0.001	0.276	0.385	**0.435**	-0.268
Number of tree species	**0.904**	-0.084	0.187	-0.084	0.101	0.155	0.036
Tree: avg. DBH	**0.706**	0.041	0.058	0.042	-0.395	**-0.487**	0.115
Tree: max. DBH	**0.866**	-0.015	0.051	0.229	-0.229	-0.312	0.133
Total basal area	**0.917**	0.049	-0.097	0.140	-0.057	-0.160	0.154
Number of trees > DBH 9.0	**0.885**	-0.012	-0.026	-0.172	0.026	0.222	-0.080
pct living wood	0.145	-0.074	0.159	**0.920**	0.119	0.093	-0.059
pct grass	0.138	-0.019	0.036	-0.044	0.143	0.061	**0.956**
pct leaf	0.143	0.009	**0.944**	0.019	-0.111	0.071	-0.132
pct moss	0.163	-0.166	**-0.816**	0.205	-0.020	0.048	-0.283
pct slash	0.362	0.322	0.191	**-0.555**	0.281	-0.343	-0.054
Number of GC species	-0.398	**-0.595**	0.157	0.072	**0.516**	-0.005	0.200
Number of WD	**0.419**	**0.638**	0.194	-0.273	-0.190	0.050	0.251
WD: av. length	-0.095	**0.880**	0.139	0.015	0.150	-0.145	-0.134
WD: average decay class	-0.040	**0.709**	0.097	-0.393	0.041	0.303	0.230
WD: av. DBH	**-0.429**	**0.620**	0.127	0.135	0.160	-0.045	-0.030
Number of Snag	0.014	0.032	0.006	0.123	-0.212	**0.824**	0.086
Stump: mean Diameter	-0.029	0.164	-0.065	0.035	**0.837**	-0.189	0.134
Name	TREE	WD	MOSS-LEAF	SHRUBBY	STUMP	SNAG	GRASS
Eigenvalue	4.978	3.327	2.318	1.619	1.529	1.455	1.075
Cumulative variance explained (%)	26.20%	43.71%	55.91%	64.43%	72.48%	80.13%	85.79%

Table 5 (cont.).

c. Reese's Swamp

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
av. Canopy density	0.171	0.047	**-0.625**	0.015	-0.053	**-0.581**	-0.275
Number of trees	**0.833**	-0.099	0.352	0.116	0.249	-0.042	-0.208
Number of tree species	**0.911**	-0.021	-0.063	0.012	0.003	0.154	0.035
Tree: av. DBH	0.379	**0.751**	0.041	0.146	-0.119	0.003	0.248
Tree: max. DBH	**0.733**	**0.424**	-0.122	0.352	-0.124	0.039	0.227
Total basal area	**0.866**	0.280	0.030	0.105	0.188	-0.105	0.044
Number of trees > DBH 9.0	**0.630**	0.367	0.332	-0.068	**0.488**	-0.195	-0.096
av. living wood	0.023	-0.127	0.334	-0.242	-0.101	**0.858**	-0.036
av. grass	-0.142	0.193	0.125	-0.347	**-0.827**	-0.105	0.081
av. leaf	0.048	-0.098	**-0.863**	0.163	-0.120	-0.174	0.018
av. moss	0.141	0.288	**0.448**	-0.043	**0.778**	-0.131	0.130
av. slash	-0.370	-0.380	0.060	**0.596**	-0.186	-0.207	-0.372
Number of GC species	0.279	0.109	**0.899**	0.167	-0.007	0.082	0.056
Number of WD	0.066	0.346	0.126	**0.751**	0.318	-0.122	-0.165
WD: av. length	-0.391	**-0.765**	-0.133	0.203	-0.078	0.000	0.050
WD: average decay class	0.274	-0.013	-0.105	**0.771**	0.094	-0.031	0.116
WD: av. DBH	-0.258	**-0.559**	0.098	-0.294	-0.301	**-0.506**	0.185
Number of Snag	-0.217	**0.819**	0.109	0.083	0.041	-0.134	0.055
Stump: mean Diameter	-0.003	0.082	0.095	-0.040	-0.016	-0.007	**0.953**
Name	TREE	STRUCTURE	GC DIVERSITY	WD	GRASS-MOSS	SHRUBBY	STUMP
Eigenvalue	5.779	2.960	2.234	1.929	1.353	1.160	1.075
Cumulative variance explained (%)	30.42%	45.99%	57.75%	67.90%	75.03%	81.13%	86.79%

Table 6. Regression coefficient and standard error associated with regression of number of captures per station and microhabitat variables derived from PCA. The number of captures of *B. brevicauda* and *G. volans* were not enough to conduct this analysis

a. Spring

	PCs	*P. leucopus*
Colonial Point	PC 1	0.0757 (0.1517)
	PC 2	0.2435 (0.1544)
	PC 3	-0.0966 (0.1816)
	PC 4	-0.1018 (0.1853)
	PC 5	0.3595 (0.1842)
	PC 6	0.0013 (0.1622)
Burn Plot	PC 1	-0.2834 (0.2287)
	PC 2	0.4487 (0.2560)
	PC 3	0.0835 (0.2459)
	PC 4	0.0931 (0.2249)
	PC 5	-0.1215 (0.2412)
	PC 6	0.2096 (0.2019)
	PC 7	**0.4530* (0.2196)**
Reese's Swamp	PC 1	-0.417 (0.3365)
	PC 2	-0.0381 (0.2746)
	PC 3	**-0.858* (0.3475)**
	PC 4	-0.0345 (0.2714)
	PC 5	0.0106 (0.2755)
	PC 6	0.0529 (0.2679)
	PC 7	-0.1805 (0.2734)

*p<0.05 **p<0.01 ***p<0.005 ****p<0.001

*The number in parenthesis is the value of standard error of coefficient

Table 6 (cont.). Regression coefficient and standard error associated with regression of number of captures per station and microhabitat variables derived from PCA. *G. volans* was not found in Reese's Swamp in the fall

b. Fall

	PCs	*P. leucopus*	*B. brevicauda*	*G. volans* (18yrs)
Colonial Point	PC 1	-0.1203 (0.1150)	-0.1168 (0.1760)	0.1260 (0.2457)
	PC 2	0.1071 (0.1004)	**0.4749*** (0.1495)**	-0.0698 (0.2800)
	PC 3	0.1103 (0.0903)	-0.0681(0.1715)	0.0950 (0.2446)
	PC 4	0.1060 (0.0895)	-0.3034 (0.2289)	0.1792 (0.2162)
	PC 5	0.1082 (0.1071)	-0.2553 (0.1460)	0.0826 (0.2823)
	PC 6	0.0291 (0.1033)	-0.1109 (0.1572)	0.2679 (0.2809)
Burn Plot	PC 1	-0.0480 (0.1091)	-0.2084 (0.3228)	**1.0019*(0.3901)**
	PC 2	0.0375 (0.1104)	-0.2914 (0.3048)	0.0393 (0.3453)
	PC 3	0.0897 (0.1178)	0.1182 (0.3578)	-0.0656 (0.3239)
	PC 4	-0.2034 (0.1381)	-0.3546 (0.3646)	-0.2078 (0.3636)
	PC 5	-0.1399 (0.1159)	0.1988 (0.2997)	-0.0280 (0.3460)
	PC 6	-0.1228 (0.1167)	0.2398 (0.2800)	0.2713 (0.2893)
	PC 7	0.0402 (0.1083)	**0.6951* (0.3216)**	0.0781 (0.3360)
Reese's Swamp	PC 1	-0.0818 (0.1301)	**0.5681*** (0.1865)**	-
	PC 2	-0.1067 (0.1260)	**0.7561*** (0.2386)**	-
	PC 3	-0.1857 (0.1276)	0.4393 (0.2288)	-
	PC 4	0.0479 (0.1272)	-0.0273 (0.2169)	-
	PC 5	-0.197 (0.1145)	**0.6387* (0.2803)**	-
	PC 6	**-0.4726*** (0.1548)**	**-0.8073** (0.3079)**	-
	PC 7	-0.099 (0.1249)	**-0.5031* (0.2262)**	-

*p<0.05 **p<0.01 ***p<0.005 ****p<0.001

*The number in parenthesis is the value of standard error

Table 7. Multivariate Poisson regression models showing the association of number of small mammals captured at a site with microhabitat variables. The table shows the combinations of variables which are significant and have the largest BIC values in multivariate regression models for each species.

Species	season	location	Variables	Coefficient	SE	X2	P	BIC
P. leucopus	Spring	Colonial Point	Ave. wood	9.18	4.00	5.27	0.0217	-11.36
			intercept	0.36	0.23	2.45	0.1176	
		Burn Plots	WD mean diameter	0.06	0.03	4.45	0.0349	-16.37
			intercept	-0.26	0.33	0.62	0.4304	
		Reese's Swamp	Number of GC species	-0.80	0.32	6.43	0.0112	-16.44
			intercept	2.80	1.16	5.81	0.0159	
	Fall	Burn Plots	WD ave. decay class	-0.44	0.13	10.81	0.001	3.03
			intercept	2.68	0.35	57.35	<.0001	
		Reese's Swamp	Ave. wood	-5.20	1.88	7.63	0.0057	22.80
			Ave. moss	-1.37	0.59	5.41	0.0201	
			intercept	1.78	0.17	114.62	<0.0001	
B. brevicauda	Fall	Colonial Point	Number of tree species	0.35	0.12	8.97	0.0027	-3.81
			Number of GC species	0.60	0.23	7.04	0.0080	
			intercept	-0.92	0.49	3.58	0.0584	
		Burn Plots	ave. grass	12.21	5.02	5.02	0.0149	-15.44
			intercept	-1.68	0.61	7.45	0.0064	
		Reese's Swamp	Ave. Canopy density	36.94	10.23	13.04	0.0003	4.60
			Ave. DBH	0.14	0.07	4.57	0.0326	
			Number of GC species	2.37	0.59	16.28	<.0001	
			Number of Snag	0.83	0.27	9.38	0.0022	
			intercept	-45.09	12.30	13.45	0.0002	
G. volans	Fall	Burn Plots	Number of tree species	0.89	0.36	6.23	0.0125	-14.12
			intercept	-2.88	1.05	7.57	0.0059	

*BIC = Bayesian Information Criterion

*No ecological variables which have significant association with the number of small mammal capture were found for *P. leucopus* and *G. volans* in Colonial point in fall

Table 8. The result of two sample t-test showing the difference in the numbers of *P. leucopus* captured between the north side transect and the east side transect at Reese's Swamp

	mean numbers of capture		P-value
	North	East	
Spring	1.22	0.27	0.017
Fall	4.67	2.27	0.012

Table 9. Mean number of small mammal captures and the result of Wald chi-square post-hoc tests in the Poisson regression model. Wald chi-square post-hoc tests were used to compare the number of capture across individual transects

Spring (4 years data)

species	Mean			P-value		
	Colonial	Burn	Reese's	Colonial vs. Burn	Colonial vs. Reese's	Burn vs. Reese's
P. leucopus	2	1	0.7	**0.0114**	**0.0007**	0.306

**B. brevicauda* was not found in the Burn Plots or Reese's Swamp in the spring

Fall (4 years data)

species	Mean			P-value		
	Colonial	Burn	Reese's	Colonial vs. Burn	Colonial vs. Reese's	Burn vs. Reese's
P. leucopus	4.95	4.4	3.35	0.4214	**0.0136**	0.0927
B. brevicauda	2.1	0.5	1.1	**<.0001**	**0.014**	**0.0387**

Fall (18 years data)

species	Mean		P-value
	Colonial	Burn	Colonial vs. Burn
G. volans	0.7	0.45	0.3011

**G. volans* was not found in Reese's Swamp in the fall

Table 10. Mean numbers of ecological variables and the result of Tukey test contrasting the three transects. The values of ecological variables with right skewed distribution were log transformed.

species	Mean			P-value		
	Colonial	Burn	Reese's	Colonial vs. Burn	Colonial vs. Reese's	Burn vs. Reese's
av. Canopy density	0.87	0.71	0.76	**0.0024**	**0.0477**	0.5229
number of trees	2.80	3.70	3.40	0.4276	0.6829	0.9085
Ln number of tree species	0.97	0.96	0.83	0.9984	0.5290	0.5625
Ln av. DBH	2.35	2.17	2.24	0.8251	0.9375	0.9663
Ln max. DBH	2.77	2.59	2.57	0.8630	0.8336	0.9981
Ln Total basal area	0.07	0.05	0.06	0.6760	0.9269	0.8834
Ln number of Deciduous	1.22	0.61	0.44	**0.0045**	**0.0002**	0.6095
Ln number of trees > DBH 9.0cm	0.64	0.85	0.87	0.5381	0.4871	0.9961
Ln pct sapling	0.01	0.02	0.05	0.9804	0.1197	0.1499
Ln pct living wood	-0.20	-0.26	0.47	0.9431	0.2204	0.1559
Ln pct dirt	0.24	-0.08	-0.16	0.5562	0.4135	0.9689
Ln pct grass	-0.50	-0.30	0.80	0.5915	**0.0006**	**0.0022**
Ln pct fern	-0.57	1.03	-0.46	**<0.0001**	0.6991	**0.0000**
pct leaf	0.76	0.62	0.19	**0.0181**	**0.0000**	**0.0000**
Ln pct moss/lichen	-0.50	-0.24	0.74	0.2362	**0.0016**	**0.0191**
Ln pct slash	-0.03	-0.59	0.63	**0.0103**	0.1560	**0.0018**
number of GC species	1.35	2.70	4.35	**0.0004**	**0.0000**	**0.0002**
number of WD	4.05	2.00	5.10	**0.0025**	0.1800	**<0.0001**
Ln number of CWD > DBH10cm	0.24	0.16	0.88	0.8260	**0.0001**	**<0.0001**
WD:av. length	162.71	130.19	287.68	0.4613	**0.0001**	**<0.0001**
WD:max. length (in plot)	280.60	270.98	398.00	0.2805	**0.0074**	**0.0001**
Ln WD: max. length (total)	6.01	4.62	6.98	0.1188	0.0758	**0.0007**
WD av. decay class	2.58	2.39	2.68	0.9300	0.9552	0.7149
Ln WD total volume	7.78	5.93	9.37	0.0856	**0.0107**	**0.0001**
Ln WD: mean diameter	1.80	1.46	2.27	0.4128	**0.0169**	**0.0013**
Ln number of Snag	0.16	0.42	0.70	0.2007	**0.0022**	0.1755
Ln Snag: av. DBH	0.20	1.03	1.97	**0.0260**	**<0.0001**	0.0665
Ln number of Stump	0.03	0.19	0.76	0.2144	**0.0004**	**0.0068**
Ln Stump: av. Diameter	0.24	0.97	2.16	0.3294	**0.0004**	0.0962

Table 11. Moran's I values for the captures of small mammals in three transects

		Colonial Point Moran's I	Burn Plots Moran's I	Reese's Swamp Moran's I
Spring	*P. leucopus*	-0.1250	-0.1218	0.1235
Fall	*P. leucopus*	0.4827	-0.0341	0.0444
	B. brevicauda	-0.1754	-0.0231	-0.0637
	G. volans	0.081	-0.0282	-

Table 12. The test for a negative binomial distribution vs. Poisson distribution. We tested whether the parameter α = zero, which is equivalent to testing whether the distribution of small mammal counts is Poisson, and therefore independent spatially.

P. leucopus in the fall

	Estimated α	Wald 95% Confidence Limits
Colonial Point	-0.027	-0.1111, 0.0861
Burn Plots	0.0079	-0.1111, 0.1609
Reese's Swamp	0.1658	-0.1429, 0.4954

Figure 1. The locations of study sites in UMBS in northern Michigan

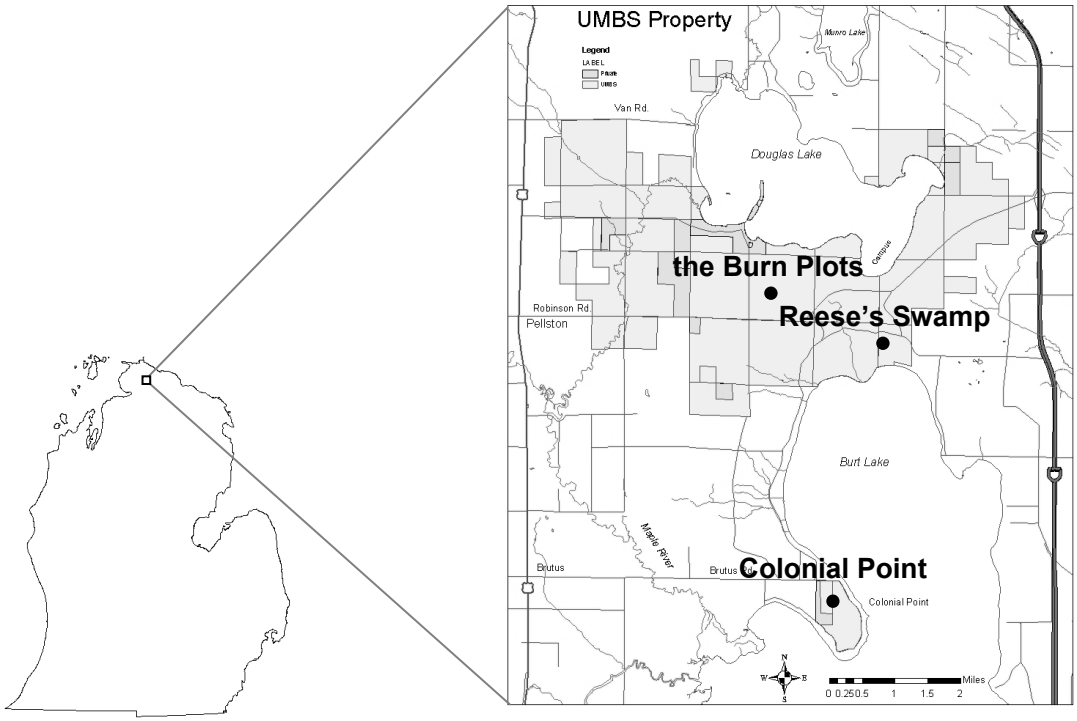


Figure 2. The arrangements of three trapping sites. Each point shows one trap station and each trapping site is composed of twenty trap stations.

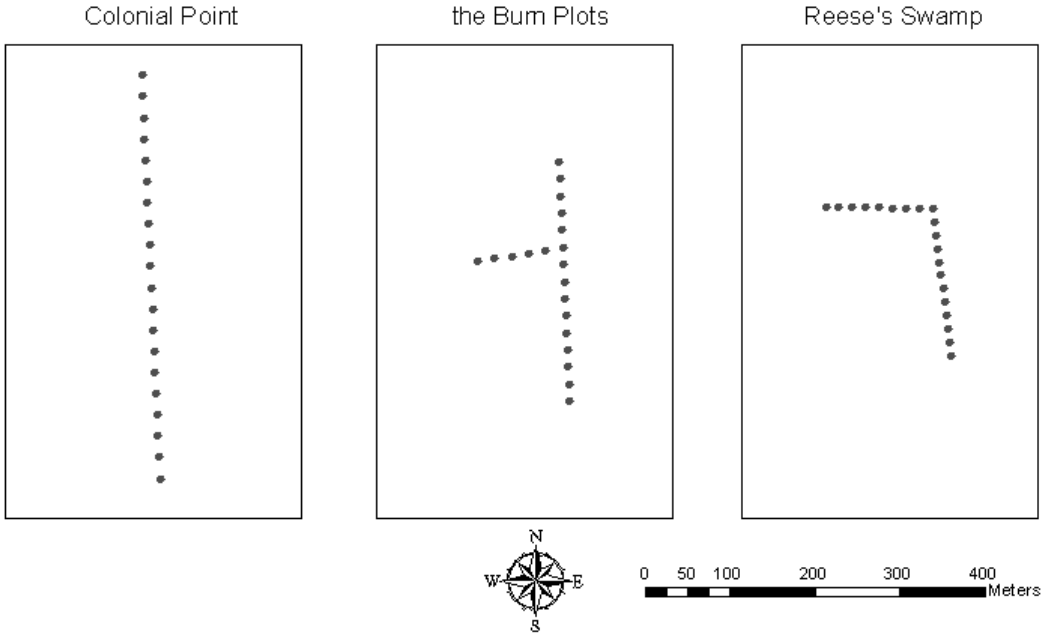
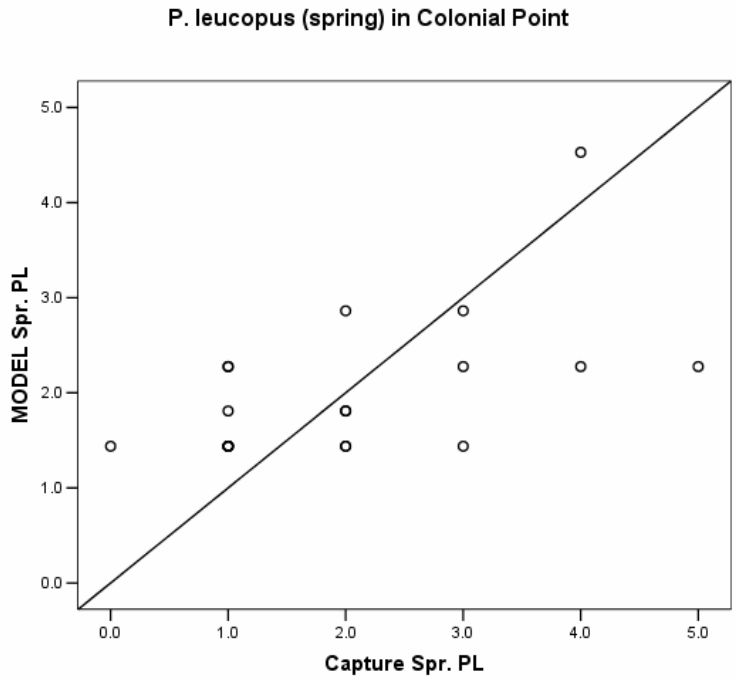


Figure 3. The difference between the actual number of captures and the number of captures estimated by Poisson regression models. Closeness to the regression line indicate model accuracy.



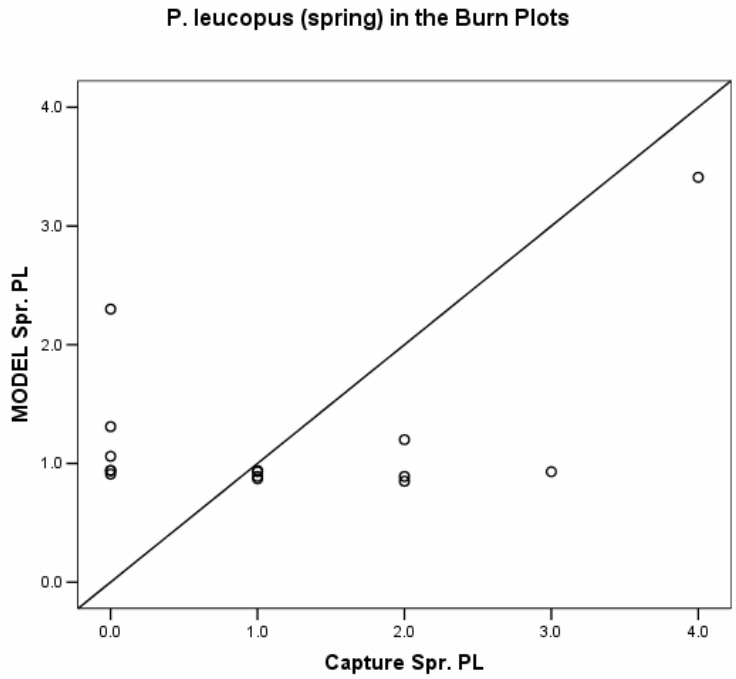
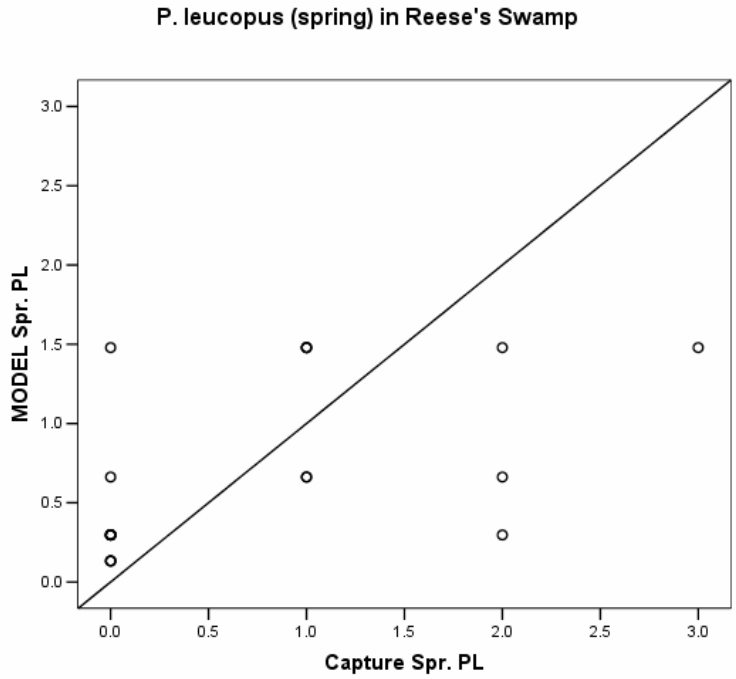
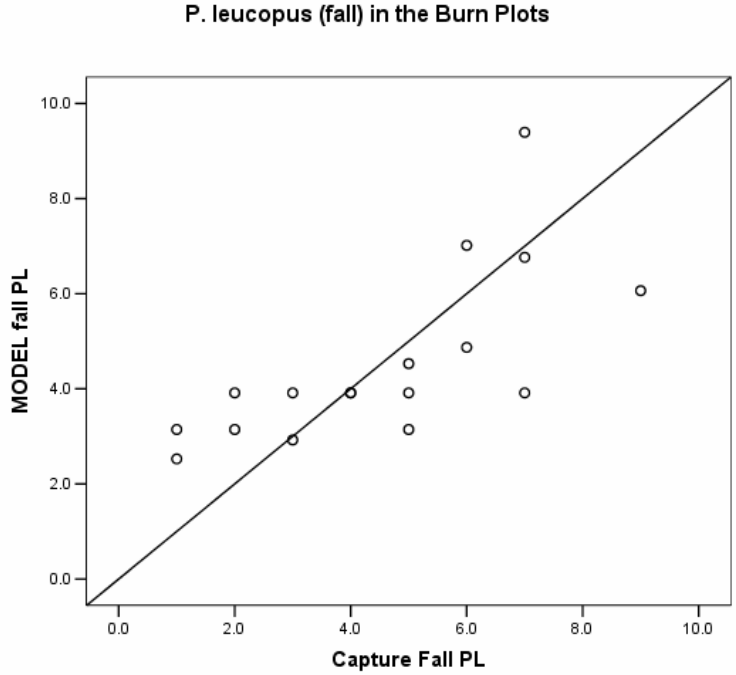


Figure 3 (cont.).





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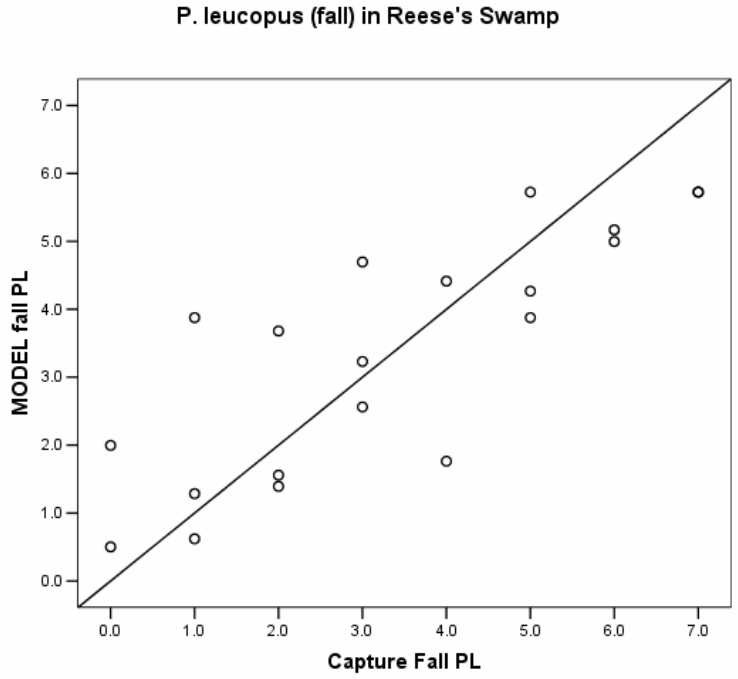

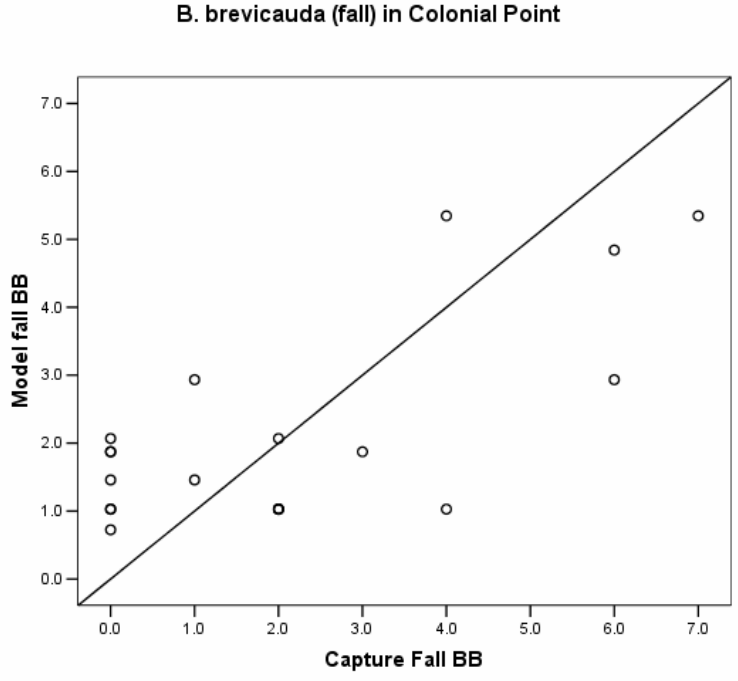

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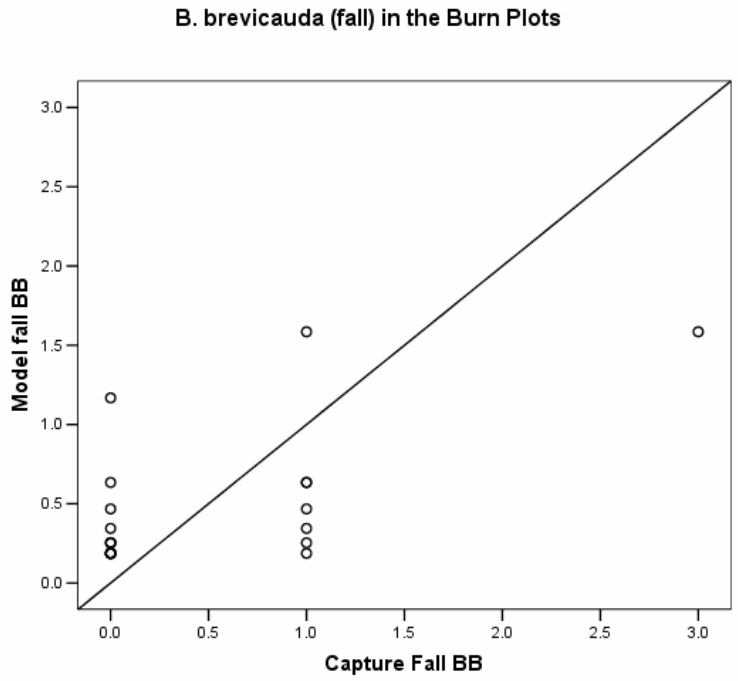

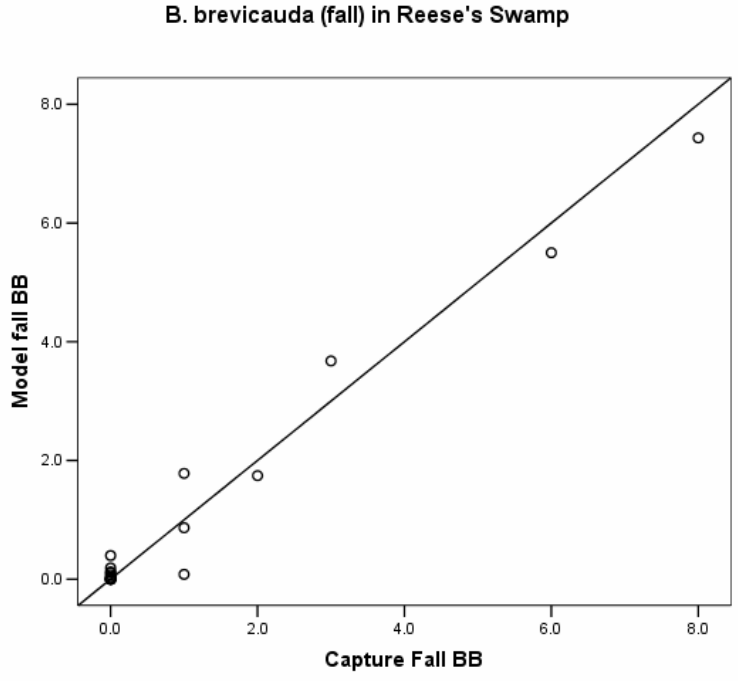

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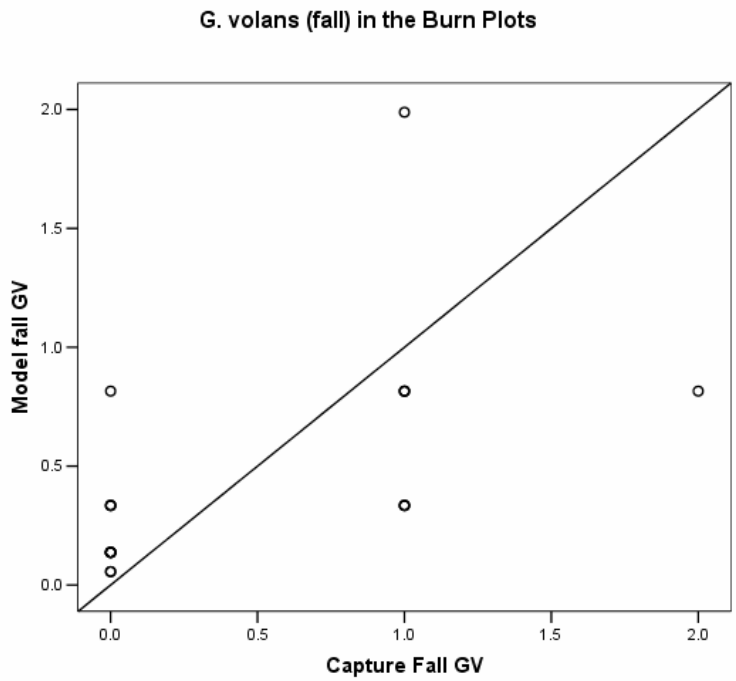


Figure 4. The number of captures of each species at each trap station in three types of forest.

a. Colonial Point

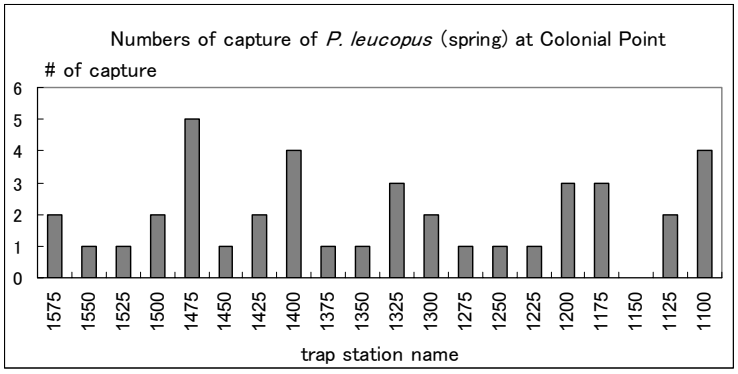
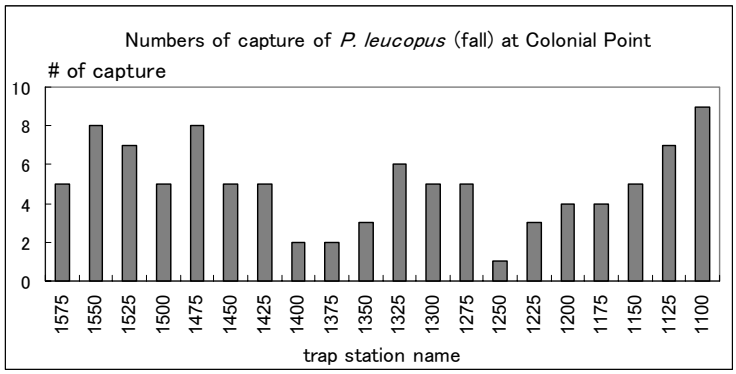
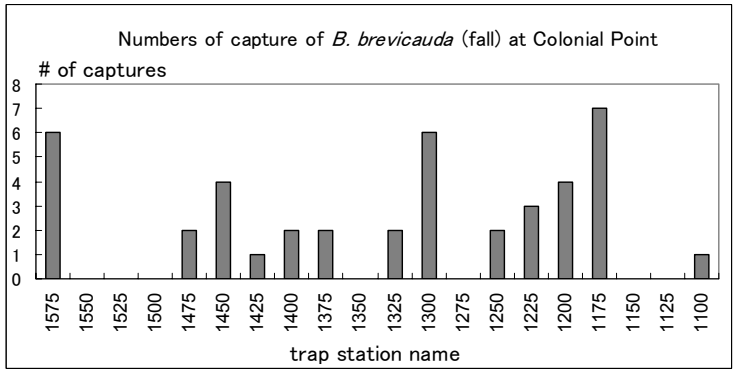
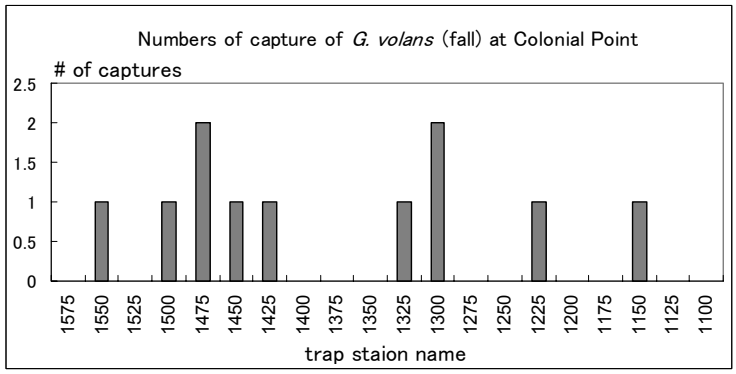


Figure 4 (Cont.).







b. Burn Plots

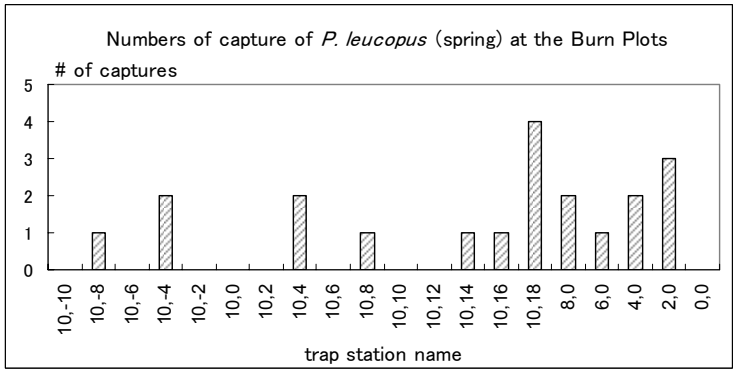
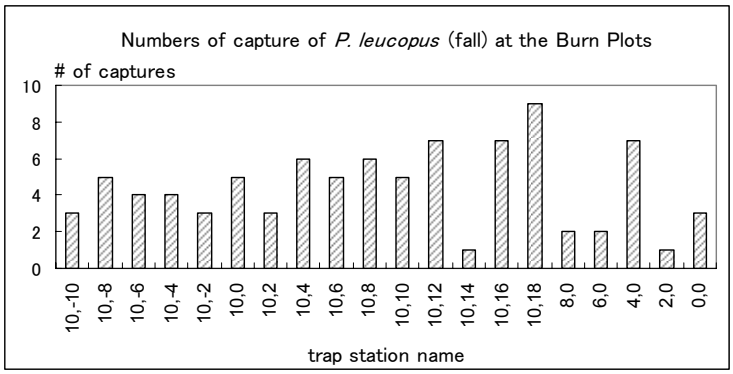
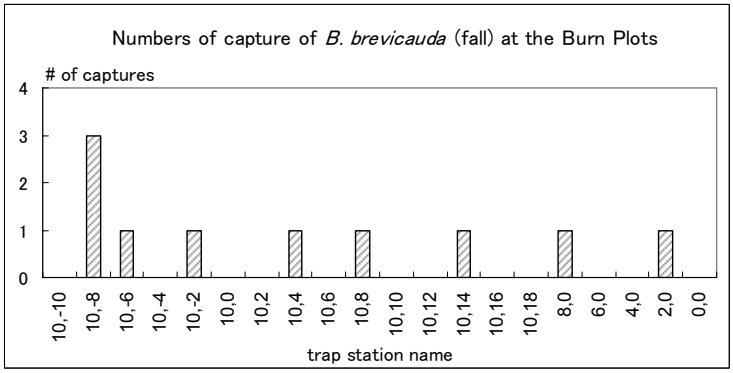
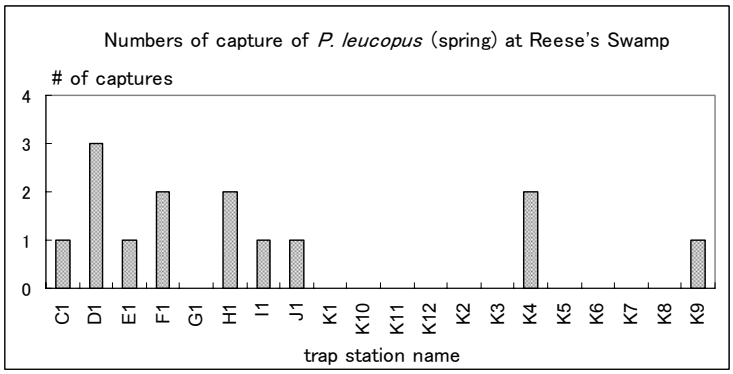


Figure 4 (Cont.).





c. Reese's Swamp



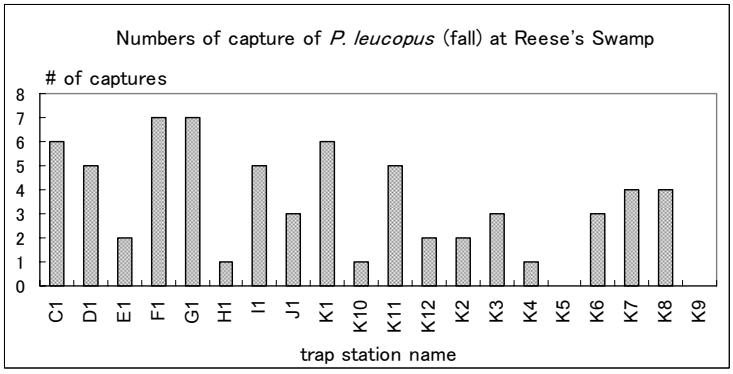


Figure 4 (Cont.).

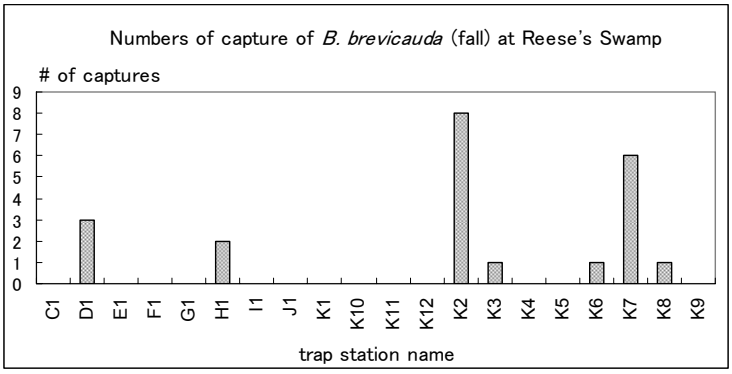
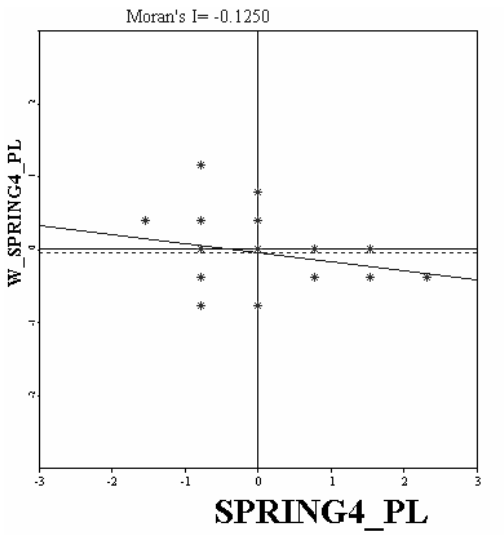


Figure 5. Moran scatter plot showing Moran's I value for number of captures for each species in each season.

P. leucopus at Colonial Point (spring)



P. leucopus at Colonial Point (fall)

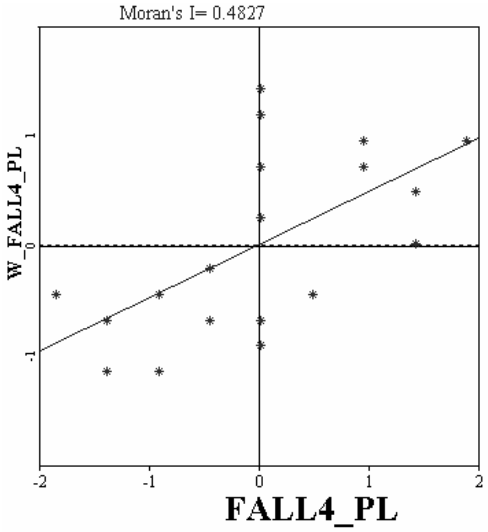
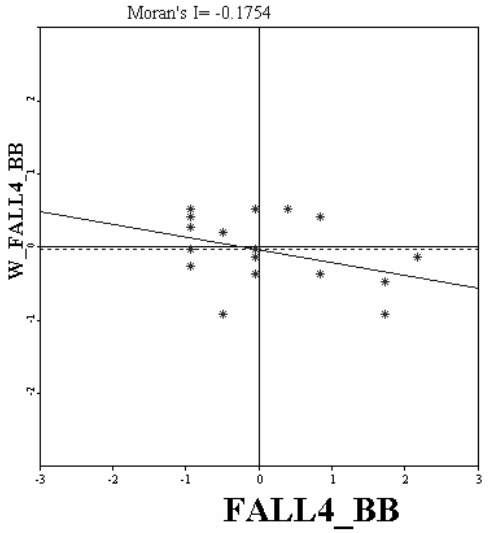
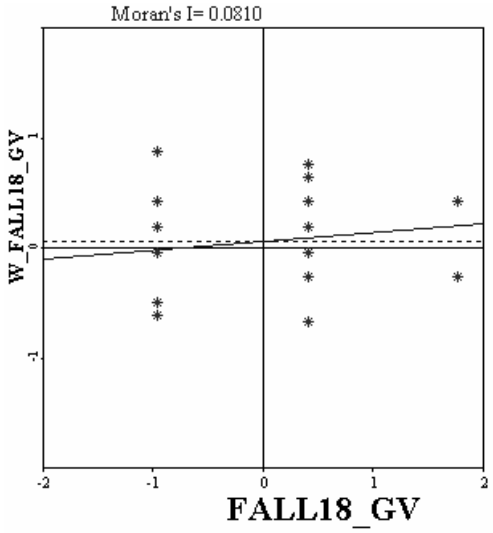


Figure 5 (Cont.).

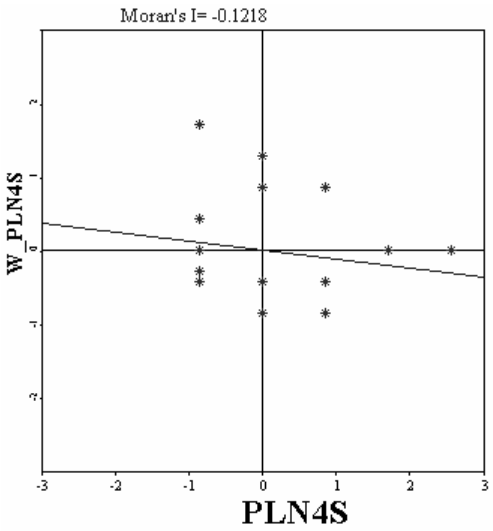
B. brevicauda at Colonial Point (fall)



G. volans at Colonial Point (fall)



P. leucopus at the Burn Plots (spring)



P. leucopus at the Burn Plots (fall)

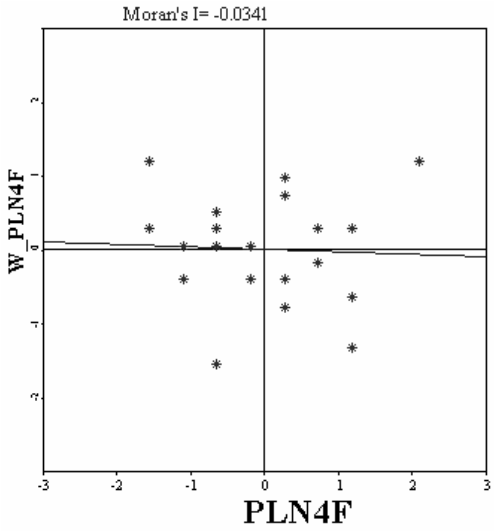
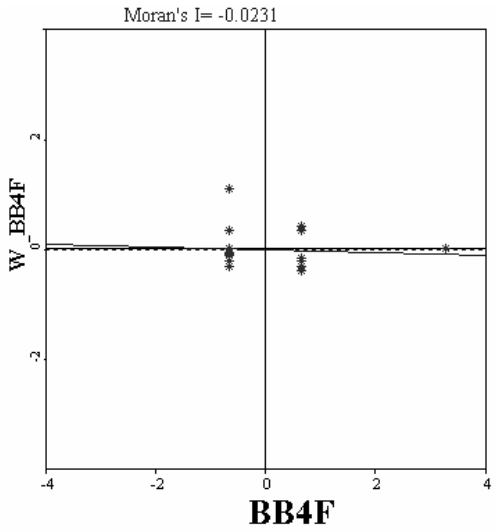
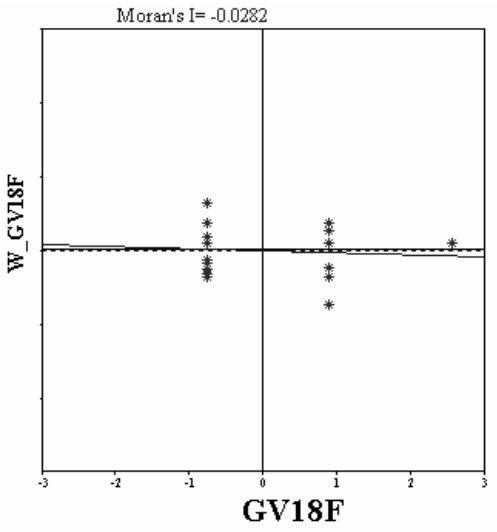


Figure 5 (Cont.).

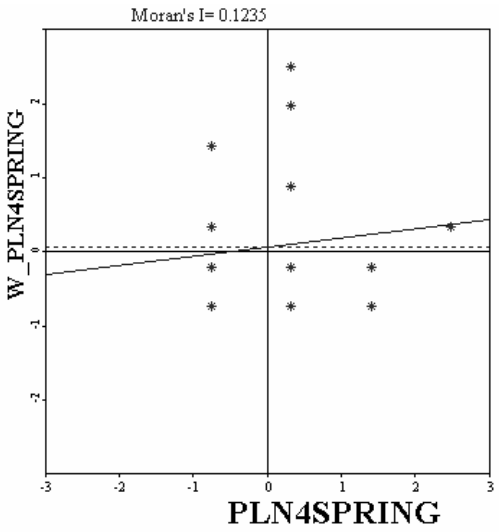
B. brevicauda at the Burn Plots (fall)



G. volans at the Burn Plots (fall)



P. leucopus at Reese's Swamp (spring)



P. leucopus at Reese's Swamp (fall)

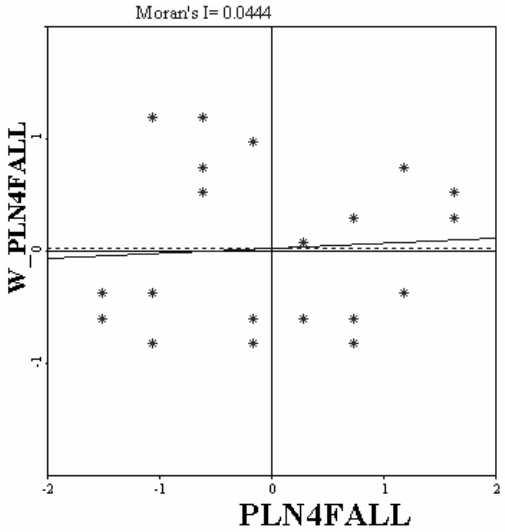
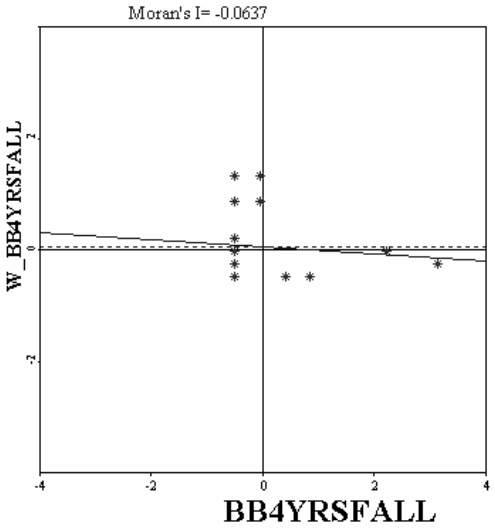


Figure 5 (Cont.).

B. brevicauda at the Burn Plots (fall)