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Title: The Role of Small Mammals as Dispersers of Mycorrhizal Fungal Spores Within Variously Managed Forests and Clearcuts

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Small-mammal community composition, microhabitat selection, and dispersal of mycorrhizal fungal spores were studied in southwestern Oregon. Sampled habitats exhibited structural variation resulting from silvicultural practices.

In 1981, the effect of clearcut treatment on these phenomena was evaluated. In 1982, the effect of forest structure was studied. Discriminant function analysis (DFA) and principal component analysis (PCA) were used to distinguish and characterize clearcut, edge, and forest habitats of study sites. Microhabitat preferences of small-mammal species were examined using DFA. For each habitat in every site, species diversities and related community parameters were calculated. Relationships among habitat structure, microhabitat preferences, and community composition parameters were examined using partial correlation analysis. Distances moved by small mammals between the clearcuts and forests were determined for common species. Spore abundances in fecal pellets were calculated for small-mammal species that moved among the three habitats.

In 1981, 1273 individuals of 11 species were captured. Deer mice (Peromyscus maniculatus) and chipmunks (Tamias spp.) comprised 81.6 percent of all trapped animals. As degree of forest structure increased, the relative abundances of deer mice decreased and those of chipmunks and red-backed voles increased. Thus, small-mammal community composition changed with increasing habitat complexity.

Only deer mice and chipmunks moved among all habitats, and no consistent effect of clearcut treatment was observed on movements of either species. Chipmunks excreted more kinds and greater quantities of fungal spores than deer mice.

In 1982, 1287 individuals of seven small-mammal species were captured; golden-mantled ground squirrels (Spermophilus lateralis), deer mice, and yellow pine chipmunks (Tamias amoenus) were the most numerous. Relative abundances of small-mammal species varied with overall habitat complexity. As degree of forest structure increased, the relative proportions of forest specialists influenced small-mammal community composition.

Ground squirrels, deer mice, and chipmunks moved among the three habitats. Differences in movements between habitats among these species reflected habitat affinities. Abundance of spores in feces was highest for Siskiyou chipmunks (Tamias siskiyou) followed by ground squirrels, deer mice, and yellow pine chipmunks. For all small-mammal species combined, the greatest spore abundance was recorded for samples from the least disturbed forest.

Small-mammal and fungal communities respond to habitat alteration. Principal small-mammal mycophagists and fungi occur in greater numbers in minimally disturbed forests and untreated clearcuts. To maximize inocula availability in disturbed sites, adjacent forests and the understory in clearcuts should be left undisturbed.

THE ROLE OF SMALL MAMMALS AS DISPERSERS OF MYCORRHIZAL FUNGAL SPORES WITHIN VARIOUSLY MANAGED FORESTS AND CLEARCUTS

by

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THE ROLE OF SMALL MAMMALS AS DISPERSERS OF MYCORRHIZAL FUNGAL SPORES WITHIN VARIOUSLY MANAGED FORESTS AND CLEARCUTS

INTRODUCTION

This disertation attempts to answer several questions concerning the ecological interrelationships between small mammals (Delany 1974), mycorrhizal fungi, and coniferous forests of the Pacific Northwest. Recently, Maser et al. (1978a) applied a holistic philosophy to investigations of management situations. My research was undertaken within this philosophical framework.

Mycorrhizal fungi and most vascular plants form an obligatory symbiosis whereby each participant receives important benefits from the other (Marks and Kozlowski 1973). This association is required by conifer seedlings in all sites, but it is critical to regeneration of harsh sites (Mikola 1970, Molina and Trappe 1982, Wright 1957). In forest soil, mycorrhizal associations are established by direct contact between the host rootlet and existing mycorrhizae or fungal spores. Clearcutting a forest can eliminate active mycorrhizae (Harvey et al. 1980), and, in turn, their fruiting bodies (sporocarps). Thus, the mycorrhizal inoculum potential for newly planted seedlings in clearcuts is drastically reduced.

Most, if not all, forest-dwelling small mammals consume various kinds and quantities of fungal sporocarps and egest viable spores (Fogel and Trappe 1978, Maser et al. 1978a, McIntire 1984, Trappe and Maser 1976). Hypogeous (subterranean) sporocarps, as opposed to epigeous fungi (mushrooms), consistently comprise the greatest portion of the fungal diet. These types depend on mycophagous species for spore dispersal. Sullivan et al. (1984) reported the probable dissimenation of the conifer seed fungus Caloscypha fulgens by Douglas squirrels. Tevis (1952) suggested that mycophagous small mammals could be a source of fungal inocula for disturbed sites. Mycophagous small mammals, therefore, are thought to be a major source of hypogeous, naturally occurring inocula for devastated soil.

Spatial variation in resources accounts for many observed patterns in small-mammal species abundances (Brown 1973, 1975; M'Closkey 1975; Price 1978; Rosenzweig and Winakur 1969). Specifically, horizontal and vertical variation in habitat structure creates more potential niche components (MacArthur et al. 1962).

Resource partitioning via microhabitat selection in structurally variable habitats may account for the coexistance of sympatric species (Brown 1973, MacArthur 1972, McNaughton and Wolf 1970) and has been observed for small mammals (Holbrook 1978, 1979; Meredith 1972; M'Closkey and Fieldwick 1975; Price 1978; Rosenzweig and Winakur 1969; Stamp and Ohmart 1978). Species richness and relative abundance within observed small-mammal communities are thought to vary directly with the number of distinct, available microhabitats (Price 1978). Thus, the numbers and abundances of sympatric species are directly related to total structural variability (Klopfer and MacArthur 1960).

Uneven-aged coniferous forests of the Pacific Northwest are complex habitats. Deaths of large trees create openings in the forest canopy, resulting in increased undergrowth, woody debris, and patchiness (Franklin et al. 1981). Logging directly affects this habitat structure. Severe habitat alteration can eliminate many microhabitats and thus modify small-mammal community structure (Martell and Radvanji 1977). Resident small-mammal species respond differentially to the change in successional stage resulting from disturbance (Gashwiler 1970, Hooven and Black 1976, McIntire 1984). Small-mammal community composition and concomitant microhabitat selection in a variety of residual forest habitats (left after various logging/stand maintenance practices) have not been studied in detail, however.

The goal of this study, therefore, was to evaluate the influence of residual habitat structure on small-mammal community composition, movements within and among different habitats, and species' mycophagies and concomitant dispersal of fungal spores from adjacent fungal reservoirs into disturbed sites.

Methodologies, results, and conclusions of my study are presented as two manuscripts. The first concerns interrelationships of structural differences among study site habitats, and small-mammal community composition and microhabitat selection. A major analytical tool used to examine structural differences among habitats and small-mammal microhabitat selection was multivariate analysis. This statistical technique simultaneously incorporates several variables into mathematical manipulations that summarize input data.

The use of multivariate analysis to study microhabitat selection by sympatric species is illustrated by M'Closkey and Fieldwick (1975). They used discriminate function analysis (DFA) to examine habitat separation by Peromyscus leucopus and Microtus pennsylvanicus based on foliage height diversity, tree basal area, and depth of dead perennial grass. Dueser and Shugart (1978, 1979) described the microhabitat configurations of four sympatric small-mammal species in a second-growth deciduous-evergreen forest in eastern Tennessee. They applied DFA to eight habitat variables measured at live-trap stations and then interpreted species' relative niche positions and niche breadths in terms of the resulting two or three discriminant functions.

Kitchings and Levy (1981) repeated Dueser and Shugart's (1978) basic methodology in a different vegetation community but within the same county. They concluded that structural habitat components quite similar to those reported by Dueser and Shugart (1978) contributed to these same niche structures. Van Horne (1982) used principal component analysis (PCA) to describe Microtus longicaudus habitat relative to its densities. By averaging factor scores for each capture station and comparing these means with the overall grid mean, differential microhabitat selection for various densities over time was observed.

The second manuscript concerns the effects of differential habitat structure on small-mammal movements among habitats, species' relative consumption of fungi, and observed quantities of fungal

spores in small-mammal feces at distances into clearcuts and forests.

By examining components of these ecological interrelationships, and focusing on small mammals as a link to forest regeneration, this study offers a new perspective for resource managers as well as additional verification of basic ecological theory concerning small-mammal community structure. By considering these relationships in forest planning, managers may better serve the multiple-use mandate set by law (Dana and Fairfax 1980) and provide for greater regeneration potential.

CHAPTER I

SMALL-MAMMAL COMMUNITY STRUCTURE WITHIN RESIDUAL CONFIEROUS FOREST HABITATS

by

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ABSTRACT

Small-mammal community composition and concomitant microhabitat selection were studied in nine forest-to-clearcut study sites in southwestern Oregon from 1980 to 1982. Sampled habitats, resulting from various silvicultural practices, varied greatly in overall structural components. A preliminary phase in 1980 sampled small-mammal populations via live trapping in a 16 year-old clearcut and adjacent forest.

In 1981, 1273 individuals of 11 species were captured over four sites. Deer mice (Peromyscus maniculatus) and chipmunks (Tamias spp.) comprised 81.6 percent of all trapped animals. Principal component analysis (PCA) characterized the clearcut, edge, and forest habitats of each site in terms of 24 habitat variables. Discriminant function analysis (DFA) successfully distinguished clearcut and forest areas among and within habitat types. DFA also quantified microhabitat preferences of four species. Correlation analyses determined significant associations among species' relative abundances, community composition parameters, and habitat characterizations. Relative abundances of deer mice and chipmunks retained a highly significant negative correlation over all habitats. Relative abundances of deer mice were negatively correlated with species diversities and increasing size of logs (PC2) per habitat. Relative abundances of red-backed voles (Clethrionomys californicus) were positively correlated with increasing log size. Species diversity was negatively correlated with weighted mean niche breadth. As vertical forest complexity increased throughout these habitats, relative abundances of deer mice decreased, and those of chipmunks and red-backed voles increased. Small-mammal community composition thus changed with increasing habitat complexity.

In 1982, 1287 individuals of seven species were captured in four additional sites. Golden-mantled ground squirrels (Spermophilus lateralis), deer mice, and yellow pine chipmunks (Tamias amoenus)

were the most numerous over all sites. Habitats were characterized by their degree of vertical complexity. Small-mammal relative abundances varied with habitat complexity and heterogeneity. Proportions of Siskiyou chipmunks (Tamias siskiyou) were highly correlated with increasing forest structure and weighted mean niche breadth throughout all sites. Species richness and unweighted mean niche breadth had a significant and negative association.

For both years, the occurrence of highly complex forest habitat was hypothesized to limit the abundance of deer mice. Forest specialists, e.g. Siskiyou chipmunks and red-backed voles, were more numerous in highly complex habitat.

INTRODUCTION

Species assemblages vary in composition and abundances of resident taxa over space and time. Community ecologists have sought explanations for these observed patterns of variation (Cody and Diamond 1975). For small-mammal communities, resouce availability has been hypothesized as a primary determinant of community structure (Price 1978, Price and Waser 1984).

Spatial variation in resources accounts for many observed patterns in small-mammal species abundances (Brown 1973, 1975; M'Closkey 1976; Price 1978; Rosenzweig and Winakur 1969). Specifically, horizontal and vertical variation in habitat structure creates more potential niche components.

Resource partitioning via microhabitat selection in structurally variable habitats may account for the coexistance of sympatric species (Brown 1973, MacArthur 1972, McNaughton and Wolf 1970) and has been observed for small-mammals (Holbrook 1978, 1979; M'Closkey and Fieldwick 1975; Meredith 1972; Price 1978; Rosenzweig and Winakur 1969; Stamp and Ohmart 1978). Species richness and relative abundance within small-mammal communities may vary directly with the number of distinct, available microhabitats (Price 1978). Thus, the

numbers and abundances of sympatric species are directly related to total structural variability (Klopfer and MacArthur 1960).

Horizontal and vertical variability in habitat physiognomy have been termed "heterogeneity" or "patchiness," and "complexity," respectively. As explained by August (1983), complex habitats have well-developed vertical strata while patchy habitats have horizontally dissimilar components. He reported a positive correlation between the total number of mammal species and habitat complexity, but not between the number of species and habitat heterogeneity.

Uneven-aged coniferous forests of the Pacific Northwest are complex habitats. Death of large trees creates openings in the canopy that result in increased undergrowth, woody debris, and patchiness (Franklin et al. 1981). Logging practices, however, directly affect this habitat structure. Severe habitat alteration can eliminate many microhabitats and thus modify small-mammal community structure (Martell and Radvanji 1977). Resident small-mammal species respond differentially to the change in successional stage resulting from disturbance (Gashwiler 1970, Hooven and Black 1976, McIntire 1984).

Small-mammal community composition and concomitant microhabitat selection in a variety of residual forest habitats (left after various logging/stand maintenance practices) have not been studied in detail, however. The goal of this study, therefore, was to evaluate the influence of residual habitat structures on small-mammal community composition. Our objectives were to: quantify species specific microhabitat selection within the sites; quantify major habitat components to characterize structural variability; quantify small-mammal community structure (species abundance, richness, and diversity; evenness, and niche breadth) within these sites; and examine the relationship between small-mammal community structure and the availability of preferred microhabitat.

Study sites with homogeneous habitat structure were selected to represent a wide range of habitat complexity and heterogeneity. We also wanted to examine the above relationships within differently treated clearcuts adjacent to similar forests and within distinct forest habitat adjacent to similar clearcuts. The clearcut/forest interface (edge), recognized as a distinct habitat (Thomas et al. 1979), was available for study as well. By selecting adjacent habitats, we could better control for environmental variation and subsequent bias in the sample data.

Three different study areas were used, one for each field season (1980-1982). In the preliminary phase during the first summer, general patterns of species occurrence and microhabitat selection were determined within a single study site. These results enabled us to select target species and define pertinent habitat variables for subsequent summers. During the second summer, microhabitat preferences and small-mammal community compositions were studied within two severely treated and two untreated clearcuts and adjacent forests (four study sites). The treated clearcuts represented simple, early successional habitats, whereas the untreated clearcuts were more heterogeneous. The third summer's efforts concerned community structure and microhabitat associations in three structurally different forest types adjacent to a common clearcut.

Study Areas

The 1980 study area was an old-growth mixed conifer forest and an adjacent 44.6 ha clearcut in northeast Jackson Co., Oregon, at approximately 1400 m elevation in the white fir (Abies concolor [Gord. and Glenn.] Lindl. ex Hildebr.) zone of the High Cascades Province (Franklin and Dyrness 1973). The clearcut was characterized by variously-sized logs and woody debris, log piles, and interspersed shrubs, herbs, and patches of bare ground. The site was clearcut in 1964 and broadcast burned in 1965.

In 1981, three large (260 ha) clearcuts, owned and managed by the Weyerhaeuser Corporation, and adjacent to U.S. Department of the Interior, Bureau of Land Management forests, were selected in the Little Chinquapin Mountain area of northeast Jackson Co., Oregon, approximately 19.3 km south of the 1980 study site. Two trapping sites were established on portions of the clearcut, edge, and forest along the west (Little Chinquapin 3 West, LC3W) and south (Little Chinquapin 3 South, LC3S) boundaries of one clearcut which had been intensively prepared for seedling planting. The cutover portions of these two sites served as duplicates of thorough slash and ground treatment and were characterized by heavily disturbed mineral soil with scattered large, burned logs, log piles, and an extensive cover of large herbaceous plants dominated by Cirsium vulgare (Savi) Tenore and Verbascum thapsus L. Two separate but similar clearcuts (Little Chinquapin 5, LC5; Soda Creek, SoCr) with no site treatment were selected as controls. These untreated clearcuts contained numerous small patches of forest habitat comprised of understory and/or small overstory conifers with accompanying forest-type vegetation, woody debris, and the duff and/or small woody litter component of the forest floor. Thus, two sites were sampled for each of the management schemes.

The 1981 sites were selected after treatment had occurred. Because the clearcut treatment was not applied randomly, the study design resulted not in a true experiment but rather in a replicated descriptive study which should give increased precision (Hayne 1978).

In 1982, four trapping sites were established around the south, west, and north sides of a 260 ha Weyerhaeuser clearcut near Buck Peak, Klamath County, Oregon, approximately 16.1 km southeast of the preliminary study site and 20.9 km northeast of Little Chinquapin Mountain. These sites were in the transition plant community between the white fir and red fir (Abies magnifica Murr. var. shastensis Lemm.) zones of the High Cascades Province (Franklin and Dyrness 1973, Hopkins 1979). Two trapping sites (Southeast, SE; Southwest, SW) were selected on the south edge of

the clearcut. The forested areas within these sites were former old-growth white fir forests and had been subjected to a shelterwood preparatory cut in 1973-74 and a final overstory removal cut in 1980. The residual habitat was diverse patchy areas of woody logging debris, dense clumps of smaller overstory and/or understory trees, and open areas of low, woody or herbaceous vegetation. The West forest was also an old-growth white fir forest that had been subjected to a shelterwood preparatory cut in 1978 followed by piling and burning of slash. The resulting stand was characterized by a low density of large, even-aged overstory trees with little understory, shrub layer, or woody debris. The forest within the North site was an uneven-aged white fir-Shasta red fir stand with a well developed understory. In 1978, the west one-third of this site was partially cut to open small areas around landing decks and skid trails. Thus, three forest types varying in horizontal patchiness and vertical complexity were sampled.

Various areas within the Buck Peak clearcut were subjected to different site preparation treatments. The entire section was cutover in 1976. Basic site preparation occurred in 1977 and included slash windrowing and burning, soil scarification, and partial herbicide spraying. Ponderosa pine (Pinus ponderosa Dougl.) was planted in 1978. In 1980, the clearcut was poison-baited for pocket gophers, with initial herbicide spraying in the SW site and a repeat spraying in the SE site. In 1977, a portion of the SE site was included in an unsuccessful broadcast burn that resulted in various configurations of large partially burned logs.

Characteristic details of the 1981 and 1982 study sites are given in Appendix 1.

METHODS

Sampling Design

Systematically determined sampling points served as both live trapping stations and plot centers for habitat measurement. In 1980, one 4.39 ha sampling grid, 14 rows by 16 columns, with an interpoint interval of 15 m, was set out half in the forest and half in the clearcut.

In 1981, the design was changed to accommodate additional objectives reported elsewhere. Three sets of two parallel transects, each consisting of ten sample points, were centered on the hypothetical edge line (defined by the section boundary) with 15 m between the sampling points and transects, and 30 m between sets of parallel transects. Each transect of a set was offset 7.5 m from the other. Corresponding pairs of transects were placed at 15 m intervals into the forest and clearcut, with only one transect per distance, to a distance of 97.5 m from the edge line. Thus, a total of 60 sampling points were placed in each of the three habitat types (Fig. I.1). This design was repeated in 1982.

Small-mammal Community Structure

Resident populations of small mammals were sampled by live trapping. In 1980, live-trap data were gathered for a total of 16 days between 11 August to 7 September. One 7.7 x 7.6 x 25.4 cm Sherman live trap was placed within a one m radius of each sample point and covered with a cardboard shield. Traps were checked twice daily and baited when necessary with a mixture of rolled oats and bird seed. Captured animals were examined for species and reproductive state and toe-clipped for identification.

In 1981, small-mammal populations were sampled for two periods on each site. Two sites were sampled simultaneously. Edge traps (lines A and B, Fig. I.1) were checked twice daily for four days and

in the morning only on the fifth day. Forest and clearcut traps (lines E, F and C, D, respectively, Fig. I.1) were set and checked twice daily for the next five days as above. The dates of each period for each study site were: LC3W, 30 June to 12 July, 29 July to 8 August; LC5, 30 June to 13 July, 29 July to 8 August; LC3S and SoCr, 15 July to 25 July, 12 August to 22 August. Traps were closed for one night at LC3W and LC5 due to excessive cold. The total number of trap-nights per site was 3120, 3120, 3240, and 3240, respectively, for a yearly total of 12,720. All traps were set within 1 m of the sample point or trap station, baited with a rolled oats-bird seed mixture, and moved roughly 180° within the 1 m trapping radius on the third day of each five day period. Every trap was protected by an aluminum cover (Feldhamer 1977). Capture procedures were identical to those of 1980.

The 1981 trapping design was repeated in 1982 in each of the four Buck Peak sites. The trapping periods were: SE and North, 28 June to 10 July, 3 August to 13 August; SW, 12 July to 23 July, 18 August to 29 August; and West, 12 July to 23 July, 18 August to 28 August. During the first period, traps were checked twice on all trapping days. The number of trap nights for each site was 3420, or 13,680 for the summer. Capture procedures were identical to those of the previous summer.

Small-mammal community parameters were calculated for the 1981 and 1982 live trap data only. Species diversity for each of the three habitats (clearcut, edge, and forest) of every site was calculated by the Shannon-Weaver Information measure (Shannon and Weaver 1949):

$$H'' = -\sum_{i=1}^{S} (n_i/N) \log_e (n_i/N),$$

where n_i is the number of individuals in the ith species, N is the total number of individuals captured in an area, and S is the total number of species in the sample. Individuals could be included in more than one sample because movement between areas did occur. Evenness, a measure of relative species dominance, was calculated using Pielou's (1975) equation:

$$J_H = H''/H''_{Max}$$

where H'' is the calculated diversity, and H''_{Max} is the maximum diversity given N and S. Niche breadth per species (McIntire and Overton 1971, after Levins 1968) was calculated by:

$$B_i = e^{\sum_{i=1}^{k} (P_{ij}/R_i) \log_e (P_{ij}/R_i)}$$

where P_{ij} is the proportion of the ith species in the jth area, and R_i is the sum of a species' proportions over the K areas. The average weighted and unweighted niche breadths per area (McIntire and Overton 1971) were also calculated:

$$\bar{B}_j = \frac{1}{S} \sum_{i=1}^{S} B_i$$

$$W\bar{B}_j = 1/N \sum_{i=1}^{S} n_i B_i$$

where $\bar{B}_j$ and $W\bar{B}_j$ are the unweighted and weighted mean niche breadths, respectively, n_i is the number of individuals of the ith species, S is the number of species, B_i is the niche breadth of the ith species, and N the total number of individuals in the jth area. Average niche breadth catagorizes a site as to the equality of occurrence over all sites (B_i) of its resident species (McIntire and Overton 1971). If the average niche breadth is high, then that habitat accomodates mostly ubiquitious species; if it is low, then some less common species occur as well. Unweighted mean niche breadth ($\bar{B}_j$) represents the average niche breadth for species per area. Weighted mean niche breadths ($W\bar{B}_j$), however, represent the average niche breadth per area that incorporates the proportional abundance of each species in that habitat. Thus, this measure has two components: the equality with which each species occurs over the range of habitats and the particular abundance at a specific site. General ecological characteristics can be

interpreted from the first component. Site specific relationships between a species and the immediate habitat may be inferred from the second.

Habitat Sampling

1980

Our habitat sampling, conducted on every other trap section in the clearcut ($n = 56$), was based on that of Dueser and Shugart (1978). Two perpendicular 15 m measuring tapes, used to determine percentage of cover and centered on the trap station, determined a 177 m^2 circular plot with four subplots. Cover of herbaceous and woody vegetation, rocks, stumps, bare ground, logs, woody litter, and wood piles was recorded as the number of cm intersected by each object along each of the tapes. The distance to, diameter, length, and decomposition class (Maser et al. 1979) of, the nearest log to the trap station in each of the four subplots was recorded. The distance to the nearest woodpile and the number of woodpiles in each subplot was recorded as well.

1981

The 1980 habitat sampling was changed to accomodate the new sampling design. Sample points for habitat analysis were systematically chosen for all four sites. Nine points in each of the four lines, C, D, E, and F, each separated by at least two non-sampled points, were selected; seven were selected along the edge (A and B) trap lines, for a total of 50 per study site. Additional points were substituted subjectively during the summer to balance the number representing presence and absence of small-mammal species. Accidental intrusion of adjacent site preparation into the LC5 clearcut after trapping but before completion of habitat sampling resulted in the loss of nine plots. Therefore, the total number sampled for LC3W, LC3S, LC5, and SoCr were 50,50,43,and 51, respectively, for a total of 194. Sampling occurred from 29 July to 2 September.

The sampling techniques were essentially those used in 1980. The following changes and additions were made, however, to increase sampling efficiency and to record additional habitat components. Cover measurements were recorded as the first object struck below the 15 m tapes by a 2 m pole dropped vertically at every meter. Foliage height density (after Nudds 1977, Morris 1979) was recorded as the percentage of a 5 x 10 cm rectangle covered by vegetation read, at three systematically selected points, a distance of 1 m from the trap station. Readings were taken at 10 cm intervals from ground level to one meter, then at 1.2 m, 1.4 m, and 1.6 m. Mat (organic litter and partially decayed organic matter) and humus depths were measured at the three foliage density sampling points around the trap station. Cover of individual herbaceous and woody species was estimated and recorded by cover class (Daubenmire 1959, 1968) within a 16 m^2 plot centered on the trap station (Mueller-Dombois and Ellenberg 1974).

Foliage height diversity (FHD) was calculated for each sampled station using the McIntosh (1967) index

$$FHD = N - \left(\sum_{i=1}^{S} n_i^2 \right)$$

where N is the total percentage of vegetation summed over all layers, n_i is the percentage in the ith layer, and S equals the number of layers in which vegetation was recorded.

1982

The 1981 sampling scheme was essentially repeated in 1982. Minor changes improved efficiency so that more stations could be sampled, increasing precision. Habitat component cover readings along the 15 m tapes were taken every 0.5 m. Woody litter was recorded as two types: twigs and limbs, and chips (broken, irregularly shaped pieces of wood). The distance to the nearest snag and the number of snags were recorded for each of the four subplots. Foliage density was read at 10 cm, 20 cm, 30 cm, 40 cm, 60 cm, 80 cm, 100 cm, and 140 cm above ground level. The initial

number of stations sampled per site was increased to 72. Stations at which rare small-mammal species were captured but not initially selected for analysis were also included. The total number of stations sampled were: SE, 82; SW, 78; West, 78; and North, 81; for a yearly total of 319. Sampling occurred between sites from 12 July to 10 September.

Habitat measurements and definitions for 1980-82 are given in Appendix 2.

STATISTICAL ANALYSIS

Habitat Comparison

For 1981 and 1982, the A and B line edge stations were included in the clearcut and forest data sets, respectively, unless specific edge analyses were conducted.

For the Little Chinquapin Mountain sites, 43 habitat variables were generated from the 32 habitat measurements per site. We calculated Pearson correlation coefficients (SPSS PEARSON CORR, Nie et al. 1975) for all variables within seven categories: all sites combined, all clearcuts, all forests, LC3W plus LC3S clearcuts, LC3W plus LC3S forests, LC5 plus SoCr clearcuts, and LC5 plus SoCr forests. We then used the following procedure to define new sets of uncorrelated habitat variables that represented major structural components per habitat for four of the categories that were most appropriate for subsequent analyses. These four categories were: the treated clearcuts; the untreated clearcuts; all clearcuts combined; and all forests combined. For pairs of variables each with $r > \pm 0.70$ with other variables in the set, the variable that had the greater number of high correlations ($r > \pm 0.70$) with other variables was excluded. If neither exhibited high correlations with other variables, then that variable needed to complete the overall habitat physiognomy categories (overstory, understory/shrub, herb,

ground level) was retained. All variables concerning the percent and proportion of vertical vegetation density were excluded due to high intercorrelations. Variables common to the four categories comprised a new category: all sites combined. Of these five new sets of variables, three were used in subsequent analysis: all clearcuts, 13 variables; all forests, 21 variables; and all sites combined, 12 variables.

Frequency distributions of habitat variables within data categories were tested for departure from normality. The arcsine square root and log(x + 1) transformations were applied to nonnormal frequency and meristic/continuous data, respectively (Sokal and Rohlf 1981).

Discriminant function analysis (DFA) maximizes group differences among multivariate data sets (Klecka 1980). We applied direct discriminant analysis (SPSS DISCRIMINANT, Nie et al. 1975) to appropriate data categories to investigate differences between sites. Analysis categories were all clearcuts (number of groups, g, = 4; number of variables, p, = 13; sample size, n, = 91), all forests (g = 4, p = 21, n = 103), all edges (g = 4, p = 12, n = 55), clearcuts grouped by treatment (g = 2, p = 21, n = 103), both treatments and all forests combined (g = 3, p = 12, n = 194), and all forests and clearcuts (g = 8, p = 12, n = 194). Homogeneity of within-group variance-covariance matrices was assessed using Box's M test, the multivariate analog of Bartlett's test (Pimental 1979).

The statistical assumptions of DFA include homogeneity of group variance-covariance matrices, a condition seldom achieved in ecological research (Green 1971, 1974). Rejection of homoscedasticity, however, invalidates the test of equality of group centroids in a statistical sense. Inequality of group dispersions affects the true magnitude of Type I and Type II errors (Pimentel 1979) and tends to distort the discriminant functions, especially affecting the classification equations (Klecka 1980). The degree of sensitivity exhibited by these tests of centroid equality to moderate departures from homoscedasiticity as well as multivariate

normality is not totally understood. Generally, large and equal sample sizes render such tests rather insensitive to moderate violations of these assumptions (Ito and Schull 1964, Pimental 1979). Ironically, large sample sizes produce increasing degrees of freedom and correspondingly lower Type II error rates (see Morrison 1984). Green (1974) suggested calculating the discriminant functions in any event and judging their "ecologial significance" based on interpretability and the degree of significance in centroid differences. Highly segregated groups in a statistical sense are probably ecologically separated as well. We followed Green's reasoning in this paper.

We applied principal component analysis (PCA) (SPSS FACTOR, Nie et al. 1975) to the correlation matrix of the data set for all sites combined to more easily characterize the various sites relative to each other. Derived components were rotated using the VARIMARX procedure to simplify interpretation. Mean component scores were calculated for each clearcut, edge, and forest area to quantify the habitat in terms of the type and proportion of information contained in the component.

Analyses of habitat variables for 1982 were basically identical to those for 1981. Only the original 72 systematically selected stations per site were used in these analyses. DFA categories were all clearcut areas ($g = 4$, $p = 22$, $n = 144$), all forests ($g = 4$, $p = 20$, $n = 144$), all edges ($g = 4$, $p = 21$, $n = 96$), all forests and clearcuts ($g = 8$, $p = 21$, $n = 288$), and every two way comparison ($n = 12$) of forest sites ($g = 2$, $p = 20$, $n = 72$). PCA was performed on all sites combined.

The final habitat variable sets are given in Table I.1. These variables will be referenced henceforth by the corresponding mnemonic.

Small-mammal Microhabitat Selection

Chi-square tests of independence (Sokal and Rohlf 1981) were used to examine general habitat affinities of single and grouped small-mammal species. Single classification with equal expectations (a priori) analysis was applied to individual species abundances over the four sites. Multiple classification (a posteriori R X C contingency tables) was applied to >1 species per site and habitat type. For 1981, the abundances of the five most common species were tested for equal occurrence among sites. Species' independence of habitat was tested for 2-4 species over all sites, all clearcuts, and all forests, as well as treated clearcuts, untreated clearcuts, and adjacent forests. For 1982, the abundances of six small-mammal species were tested among sites. A posteriori analysis followed that for 1981.

A basic assumption of this study was that the habitat components around sample points produced a three dimensional configuration, or niche gestalt (James 1971), that was selected for use by the trapped individual. For 1980, associations between captured small-mammal species and the surrounding habitat structure were examined initially using Pearson correlation coefficients. Data pairs consisted of live-trap data categories (the total number of small-mammal captures, species, individuals, and first captures; and the number of individuals captured per species), and the various habitat variables. Stepwise multiple regression was used on these variables to select the best models of small-mammal/microhabitat associations according to full and partial F tests (Neter and Wasserman 1974). Additional stepwise models were constructed using variables representing various woody and ground cover components of the clearcut habitat. Results of these models were used to refine the selection of the next year's habitat variables.

For 1981, microhabitat selection by trapped small-mammal species was investigated by the forementioned Pearson correlation coefficients and two group DFA. Correlation coefficients were

calculated for all habitat variables and the number of individuals at each sampled trap station for chipmunk, deer mice, red-backed voles, long-tailed voles, and golden-mantled ground squirrels. Each of the two groups for DFA was defined by habitat sampling stations where a species either was or was not captured. Due to sample size criteria, analysis was warranted for the four most abundant species only. Cases were not weighted for multiple captures or individuals. Analysis categories were all sites combined ($g = 2$, $p = 12$, $n = 194$); LC3W and LC3S clearcuts, and adjacent forests ($g = 2$, $p = 12$, $n = 100$); LC5 and SoCr clearcuts, and adjacent forests ($g = 2$, $p = 12$, $n = 94$); and all forests combined ($g = 2$, $p = 21$, $n = 103$). Discriminant function scores from DF1 for all sites combined were grouped by clearcut and forest of each site and subjected to a one-way analysis of variance (SPSS ONEWAY, Nie et al. 1975) to examine availability of preferred microhabitat for each small-mammal species. The Scheffé test of all possible contrasts (Sokal and Rohlf 1981) was used to determine which habitat group means were significantly different. The nonparametric Kruskal-Wallis one-way analysis of variance (Hull and Nie 1981) was used to examine DFA scores by habitat for those one-way analyses of variance that exhibited heteroscedasticity.

Interspecific differences in microhabitat associations were investigated using a four group DFA. The groups were trapping stations at which each of the four small-mammal species occurred over all sites. This discrimination was expected to be incomplete because stations could be included in more than one group.

Analysis procedures for the 1982 data were the same as those for 1981. The 31 additional sample points were added to the data set to incorporate microsites where less common species occurred. DFA categories for the six examined species were all sites combined ($g = 2$, $p = 21$, $n = 318$), and all forests combined ($g = 2$, $p = 19$, $n = 167$). Each forest and adjacent clearcut ($g = 2$, $p = 21$, $n = 78$-82), and all clearcuts combined ($g = 2$, $p = 22$, $n = 151$) were examined with DFA for the four species that occurred in every site. Multigroup DFA included five species.

To examine interrelationships of habitat structure, microhabitat selection, and compositions of small-mammal communities for 1981 and 1982, we first calculated Pearson and Spearman correlation coefficients (Sokal and Rohlf 1981) for all data pairs within and among these data categories: community composition parameters (H'', S_j, J_H, $\bar{B}_j$, and $W\bar{B}_j$), relative proportions of species, and absolute species abundances. Correlation coefficients also were calculated for each of the three preceeding data categories and the mean scores per habitat and site for the first, second, and third principal components, values that characterize overall habitat structure. We then calculated Spearman correlation coefficients for species' relative proportions, species' mean DF1 scores (all sites combined), and mean PC1, PC2, and PC3 scores per site and habitat to specifically examine the assumption that preferred habitat structures and species' abundances are positively associated.

Partial correlation coefficients measure the association between two variables while a third and common variable is held constant or is not involved in the calculation (Snedecor and Cochran 1980). Partial correlation analysis thus eliminates confounding associations that hinder the interpretation of results. We used first and second order (holding one and two variables constant, respectively) partial correlation analysis to examine significant intercorrelations between small-mammal community parameters, species proportions, and mean PC1, PC2, PC3, and DF1 scores per habitat and site to determine the primary correlations within the data sets. Thus, a more accurate examination of small-mammal community compositon within the various habitat structures was possible.

RESULTS AND DISCUSSION

Preliminary Study Site, 1980

Small-Mammal Community Composition

A total of 254 individuals of 11 species was captured during 7168 trap nights, or 3.54 individuals per 100 trap nights (Table I.2). We initially assumed that the only endemic chipmunk species was the Siskiyou chipmunk, Tamias siskiyou. Preserved specimens were not identified until 1982 when a few yellow pine chipmunks, Tamias amoenus, were discovered. Since the exact numbers of T. siskiyou and T. amoenus are not known for 1980 and 1981, chipmunks will be considered as Tamias spp.

Tamias spp. were ubiquitious throughout the grid. Spermophilus lateralis (the golden-mantled ground squirrel) was concentrated along the edge, and Clethrionomys californicus (red-backed vole) was more abundant in the forest. Peromyscus maniculatus (deer mice) used both the edge and clearcut while Sorex trowbridgei (Trowbridge shrews) was more abundant in the clearcut than in other habitats as were Microtus longicaudus (long-tailed voles), Microtus oregoni, Phenacomys intermedius, and Thomomys mazama. One short-tailed weasel (Mustela ermina) was captured in the forest. Five species were captured in the forest, four at the edge, and nine in the clearcut. Clearly, different small-mammal assemblages occurred within the three types of habitat (Table I.2).

Microhabitat Associations

The largest correlation between any capture category and habitat variable was that for total Tamias captures per clearcut station and total number of wood piles ($r = .465$, $P \leq .01$). Other variables correlated with Tamias captures were nearest wood pile ($r = -.409$, $P \leq .01$), wood pile cover ($r = .382$, $P \leq .01$), and mean log volume ($r = .366$, $P \leq .01$). Total Spermophilus captures were negatively

correlated with woody litter cover ($r = -.347$, $P \leq .02$), and those for Peromyscus were associated with the standard deviation of the mean log distance from the trapping station ($r = .400$, $P \leq .01$). Clethrionomys and Sorex captures were correlated with wood pile cover ($r = .342$, $P \leq .02$, and $r = .327$, $P \leq .02$, respectively). Microtus captures exhibited significant associations with the mean log distance ($r = -.323$, $P \leq .02$) and woody plant cover ($r = .289$, $P \leq .05$). The greatest correlation for any dependent variable was that for the total number of species captured and wood pile cover ($r = .467$, $P \leq .01$).

Results of multiple regression analysis indicate that differential microhabitat selection occurred in the clearcut habitat (Table I.3). Chipmunk and red-backed vole captures were associated with logs and woodpiles whereas ground squirrels occurred at stations varying in log distance and lacking woody litter and herbaceous cover. Deer mouse captures increased at stations lacking ground cover and varying in log distance. Long-tailed vole captures were associated with woody species cover, perhaps shrubs, away from logs.

Little Chinquapin Mountain, 1981

Habitat Comparisons

Clearcut Differences via DFA. Discriminant function analysis detected site centroid differences (Table I.4). The first two discriminant functions for all clearcuts ($g = 4$) accounted for 84.6 percent of the variation or discriminating power within the clearcut data set. DF1 segregates the average scores of clearcut treatments (Fig. I.2). Both treated clearcuts exhibited similar, negative mean values (LC3W, $\bar{x} = -1.165$; LC3S, $\bar{x} = -0.955$) and both untreated clearcuts had larger positive means (LC5, $\bar{x} = 1.980$; SoCr, $\bar{x} = 0.979$). Herb species richness, duff and mat provided the greatest discrimination between treated and untreated clearcuts. LC5 and SoCr had, in fact, larger mean values of these three

variables than either LC3W or LC3S. Clearcut sites within treatment groups differed along DF2, however. Differences between the untreated clearcuts in TLOG, DUFF, OVRDNS, and HBSPP (Table I.1) become apparent. DF3 also separates LC3W and LC3S clearcuts.

The untreated clearcuts had significantly greater herbaceous species richness and mat and duff depths than the treated clearcuts. Because duff depth in the untreated clearcuts was correlated with canopy cover, total logs, and understory tree density (all structural components of forest islands), these results reflect the relatively undisturbed nature of the post-harvest habitat. Herb species richness in the four clearcuts reflected almost exactly the respective number of species in the adjacent forest stands; no differences due to clearcut treatment were detected. The LC3W clearcut was an open, herb dominated habitat with some irregular bare ground, woody litter and larger, mostly burned or piled logs, and little remaining forest floor or island habitat. The LC3S clearcut was quite similar overall to LC3W clearcut but had fewer herb species and more duff, mat, and woody litter. The untreated clearcuts exhibited greater within replicate structural differences than the treated sites. LC5 was characterized by the greatest mean number of herb species, but not herb cover, of any clearcut and was the more homogeneous of the two untreated sites. SoCr had more residual forest patches as well as open areas of log and herb cover.

Forest Differences via DFA. DFA successfully separated the adjacent forest areas by degree of vertical complexity (Table I.4). The first discriminant function incorporated 69.4 percent of the discriminating variation and exhibited a high correlation with the discriminating variables (canonical correlation coefficient, $R_c = .862$). Average scores per forest followed a three dimensional configuration similar to that of the clearcut means; along DF1, means are separated by adjacent clearcut treatment (LC3W, $\bar{x} = -0.888$; LC3S, $\bar{x} = -2.318$; LC5, $\bar{x} = 2.013$; SoCr, $\bar{x} = 0.881$),

while overlap occurrs along DF2 and DF3. The two group DFA on forest sites pooled by treatments reiterates this separation.

Forest differences may be a function of past logging activity (Appendix 1) that resulted in canopy openings and associated herbaceous growth and stump and woody cover. LC5 had the least canopy cover, woody thickness, and understory tree density of the four sites; it had the greatest herb species richness and herb cover. LC3S, however, was a more closed forest with areas of dense uneven-aged structure; this forest had the most canopy cover, greatest woody thickness and understory density, but the least herb species richness and cover. LC3W and SoCr were somewhat intermediate with LC3W having more understory and shrub growth.

Clearcut and Forest Differences via DFA. The first three functions of DFA for all forests and clearcuts as groups (g = 8) incorporated 86.7 percent of the total discriminating information (Table I.4). DF1 represents the gradient from denser vertical and horizontal forest structure to areas of more open canopy with increasing herbaceous cover, to total absence of upper vegetation levels and much greater herb cover and logging artifact. Clearcuts and adjacent forests separate by clearcut treatment along DF1, but LC5 and SoCr forests overlap the clearcuts, leaving LC3W and LC3S forests well segregated from the other six areas (Fig. I.3). DF2 separates the eight habitats into three groupings by degree of forest floor disturbance, herb species richness, and the number of stumps present, a variable that represents decreasing forest structure. DF3 separates areas with more logs, duff, and herb cover from areas with greater shrub cover and herb species richness.

Habitat Characterization via PCA. Habitat characterization and additional separation were refined by principal component analysis. The first principal component (PC1) represents a general gradient from decreasing overstory density and associated vertical complexity to open areas of high herb species richness and greater herb cover

with more stumps and woody dead and down cover (Table I.5). This axis might characterize, most basically, logged and unlogged sites. PC2 specifically represents a size gradient for the woody ground cover, and PC3 correlates highly with duff ($r = .832$) and mat ($r = .761$) depths, thus characterizing the organic component of the upper soil layers (Table I.5).

Mean PC1 scores may indicate structural complexity (August 1983). For the Little Chinquapin Mountain sites, all clearcut habitats had positive PC1 mean scores (Table I.6). Both LC3W and LC3S edges had negative score means, and LC5 and SoCr edges had positive means. Average scores for forests were variable. OVRDNS correlated most highly with CANCO ($r = .569$, $P \leq .001$), UNDNS ($r = .510$), and WL ($r = .472$) over the entire data set. Some other significant correlations were with THIK ($r = .301$), AVUNDI ($r = .369$), AVLOGLN ($r = .322$), HRB ($r = -.363$), and HBSPP ($r = .341$). Habitats with greater negative mean scores along PC1 (LC3S and LC3W forests) would be characterized, therefore, by more complex vertical forest structure with fewer and/or smaller openings in the forest canopy. Larger, positive mean scores (LC5 forest, all clearcuts) indicate a lack of overstory with resulting herbaceous vegetation and some woody cover. Along PC2 more positive means would indicate areas of larger logs as opposed to points with more numerous, usually smaller, dead and down woody material. NLOGDI and NLOGLEN are highly correlated with various log variables; NLOGLEN exhibited some association with CANCO ($r = .303$), AVOVRDI ($r = .309$), and THIK ($r = .228$). TLOG was negatively correlated with CANCO ($r = -.369$). Large means along PC3 indicate areas of less disturbed forest soil presumably within complex forest structure. Over all areas, DUFF had a negative correlation with BRGD ($r = -.402$), as did MAT ($r = -.492$). In the four forests, DUFF was associated with AVUNDI ($r = .267$), and in the untreated clearcuts, DUFF was correlated with CANCO ($r = .426$, $P \leq .01$), TLOG ($r = .387$), and UNDNS ($r = .450$).

Small Mammal Community Composition

Species Abundances. At the Little Chinquapin Mountain sites, 1273 individuals of 11 species were captured during 12,720 trap-nights (I_{100} = 10.0) (Table I.7). Peromyscus maniculatus was the most numerous species, accounting for over half of all animals. Peromyscus and Tamias comprised 81.6 percent of all individuals captured at all sites, and, with Clethrionomys californicus, occurred in each of the three habitat types. Abundances of these three rodents differed with study site (X^2 = 115.8, P $\leq$.01), as did Peromyscus and Tamias (X^2 = 53.6, P $\leq$.01). Primary contributors to the former, large X^2 statistic were low Tamias numbers in LC3S and low Clethrionomys numbers in LC3S and SoCr. A priori X^2 analysis of abundance among sites for each of Peromyscus, Tamias, Clethrionomys, Microtus longicaudus, and Spermophilus lateralis resulted in high X^2 values (P <.01) for each except Spermophilus (.025> P >.01).

Deer mice were most abundant in clearcuts (49.2 percent to 81.0 percent of total small-mammal clearcut populations, Table I.7) and were more abundant in the clearcuts than other habitats (56.9 percent to 68.0 percent of all mice per site occurred in the clearcuts). These interhabitat proportions decreased at the edges and were minimal in the forests. Chipmunks exhibited the opposite trend; a highly significant and negative association (r = -.901) existed between these two species' relative proportions over all habitats.

Peromyscus, Tamias and Microtus abundances varied among the four clearcuts (X^2 = 79.0, P <.01); Peromyscus, Tamias, and Clethrionomys numbers varied with forests (X^2 = 62.0, P <.01). In the treated clearcuts, Peromyscus, Tamias, Microtus, and Spermophilus abundances were independent of site (X^2 = 5.0, P >0.10), but in the adjacent forest, Peromyscus, Tamias, and Clethrionomys numbers differed with site (X^2 = 22.0, P <.01). In the untreated clearcuts, Peromyscus, Tamias, and Microtus were independent of site (X^2 = 1.4, P >.25), but in the two forests,

these species plus Clethrionomys differed by site (X^2 = 21.2, $P < .01$).

Species' abundances were quite variable among the four study sites, and between the clearcuts and forests within sites. Sample populations within the clearcuts were similar in sites within treatment categories, but those for the forests were not. Previous results of habitat comparisons indicated that the clearcut areas differed in structure more between than within treatment categories. Species' abundances likewise were more dissimilar between than within clearcut types.

Community Composition Parameters. Community composition parameters varied considerably between habitats. The largest H'' value was calculated for LC5 edge and forest (Table I.8). The treated clearcuts exhibited the least species diversity. The least even communities, as measured by J_H, were those in the treated clearcuts and the LC3S edge. Relative proportions of occurrence per habitat for Peromyscus (Table I.7) were correlated with both H'' ($r = -.706$, $P < .02$) and J_H ($r = -.689$, $P < .02$) over the twelve habitats.

Total species' absolute abundances were positively correlated with species' niche breadths ($r = .812$, $P < .01$) (B_i, Table I.7). The more abundant species (Peromyscus and Tamias spp.), therefore, occurred more equally over the 12 habitat areas. $\bar{B}_j$ values were negatively correlated with species richness (S_j) over the 12 habitats ($r = -.927$, $P < .01$). Thus, small-mammal communities with few species were comprised of abundant, commonly occurring species.

$W\bar{B}_j$ values were uncorrelated with S_j ($r = -.315$, $P > .05$), indicating that the number of species in a habitat was unrelated to whether or not the most abundant species in the area also were abundant throughout the sites. $W\bar{B}_j$ values were correlated with H'' ($r = -.798$), however, and $\bar{B}_j$ values were not ($r = -.461$). This result is presumably a mathematical artifact.

Species diversity was a partial function of species richness and was affected by the presence of dominant and widely distributed species ($W\bar{B}_j$). Species richness, in turn, was highly associated with the relative spatial abundance ($\bar{B}_j$) of small-mammal species. Primary correlations resulting from partial correlation analysis were H'' and $W\bar{B}_j$ ($r = -.839$), H'' and S_j ($r = .801$), S_j and $\bar{B}_j$ ($r = -.947$), and proportions of Peromyscus and Tamias ($r = -.942$).

Microhabitat Associations

Peromyscus maniculatus. Deer mice were ubiquitous but were absent from microsites of complex forest habitat and those with high herb species richness (Table I.9). Although statistically significant, the discriminating power of the data set for Peromyscus presence and absence over all habitats seems marginal ($R_c = .341$, $\lambda = .884$, $P = .028$). The mean value of each discriminating variable in Table I.9 was significantly greater for the absence group.

The number of Peromyscus individuals captured per station were correlated with BRGD ($r = .384$, $P < .01$), AVUNDI ($r = -.360$), and CANCO ($r = -.305$). Also, the mean of the absence group along DF1 (0.509, $n = 65$) was larger than that of the presence group (-.256, $n = 129$). If discrimination of the two groups was defined by the most abundant one (Carnes and Slade 1982), then variables exhibiting large, positive correlations with DF1 describe microsites of deer mouse absence (Table I.9).

No clear distinction in the availability of preferred Peromyscus microhabitat was evident although one-way ANOVA on combined clearcut and forest mean DF1 scores for Peromyscus indicated greater differences among than within areas ($F = 19.27$, $P < .001$). The Scheffé test indicated that the LC3W and LC3S clearcuts were distinct from the LC5 and SoCr forests. Significant differences in mean DF1 scores among clearcuts resulted from ANOVA analysis ($F = 18.95$, $P < .001$). Between treatment differences in Peromyscus habitat preference were indicated by the Scheffé test. Similar

results were noted for forest mean comparisions. Preferred Peromyscus microhabitat occurred in less complex habitats.

Tamias spp. Chipmunks were captured at stations with greater overstory density, intact forest floor, and longer logs. Numbers of captured Tamias individuals were associated with CANCO ($r = .446$), OVRDNS ($r = .394$), AVUNDI ($r = .333$) and BRGD ($r = -.372$) over all areas. Tamias exhibited significant microhabitat preference in three of five discriminant categories (Table I.9). All positively correlated variables (Table I.9) in the presence group have greater means than those in the absence group, indicating preferential use by Tamias of forest structure components. All negatively correlated variables exhibited the opposite relationship. For all areas, the discriminant function exhibited intermediate success in discerning microhabitat preference ($R_c = .488$ $\lambda = .762$, $P \leq .001$) although group variance-covariance matrices were unequal ($M = 184.6$, $P \leq .001$).

Mean DF1 site scores for Tamias differed significantly between all eight habitats ($F = 20.23$, $P \leq .001$) but no distinct pattern of microsite occurrence was evident. Between clearcut differences of DF1 score means for Tamias were also significant ($F = 13.59$, $P \leq .001$), with clearcuts grouping by treatment. Forest differences were marginally significant ($F = 2.99$, $P = .035$) Thus, the greatest difference in availability of preferred habitat of chipmunks existed between clearcuts grouped by treatment.

DFA distinguished Tamias microhabitat differences within the treated clearcuts and adjacent forests ($R_c = .525$, $\lambda = .725$, $P = .003$; $M = 188.7$, $P \leq .001$) but not within the unteated clearcuts and adjacent forests ($R_c = .419$, $\lambda = .825$, $P = .165$; $M = 126.8$, $P = .153$). Also, differential microhabitat use was observed for Tamias within all clearcuts ($R_c = .538$, $\lambda = .710$, $P = .008$; $M = 161.6$, $P \simeq .002$). Tamias capture numbers correlated with THIK ($r = .533$, $P < .01$), OVRDNS ($r = .463$), AVUNDI ($r = .461$), and DUFF ($r = .447$) throughout the four clearcuts. Successful capture

stations were characterized by greater log numbers, duff depth, and overstory density (Table I.9).

Most discriminating variables for Tamias (Table I.9) also correlated with the habitat discriminant functions (Table I.4, Fig. I.3), especially DF2 of the eight group analysis which separated the treated clearcuts from the other six areas. These two clearcuts, therefore, had less preferred microhabitat than other areas. Greater discrimination within the combined treated clearcuts plus forests data set than that for the untreated clearcuts plus forests would be expected because greater differences existed in overall habitat structure between the treated clearcuts and adjacent forests. Differences between untreated clearcuts and adjacent forests were less, and microhabitat preferences could not be defined statistically with this analysis.

The results for Tamias incorporate microhabitat associations of two species, T. siskiyou and T. amoenus, and are probably less distinct than would be desired. T. siskiyou is the former subspecies Eutamias townsendii siskiyou A. H. Howell (Sutton and Nadler 1974). Townsend chipmunks occur in more mesic, closed forest habitats (Gashwiler 1976, Larrison 1947, Maser et al. 1981, McIntire 1984, States 1976, Tevis 1955) while yellow pine chipmunks are associated with more open forests and brushfields (Larrison 1947, States 1976, Tevis 1955). Townsend chipmunks do use older clearcuts, however (Gashwiler 1970).

Clethrionomys californicus. Clethrionomys microhabitat separation was detected only for the treated clearcuts and forests (R_c = .474, λ = .775, P = .024). Low presence-group size prevented the calculation of Box's M, and this analysis will be considered descriptive. No Clethrionomys were captured in the treated clearcuts and only two occurred in LC3S forest; the presence-group, then, represents successful trapping stations within the LC3W forest. Red-backed voles in this habitat were associated with increasing shrub cover, foliage height diversity, and log length. The discriminant function for all sites was not significant.

Microtus longicaudus. Microtus were captured at microsites of increasing vertical vegetation in open habitats. Although somewhat rare (Table I.7), Microtus exhibited microhabitat preference over all sites (R_c = .419, λ = .825, P $\leq$.001; M = 161.0, P = .044), untreated clearcuts and adjacent forests (R_c = .623, λ = .612, P <.001), and all forests (R_c = .565, λ = .681, P = .03). Box's M for the last two analyses could not be computed due to low presence-group numbers. When analyzed with ANOVA, mean scores for clearcuts exhibited no differences (F = 0.29, P = .834), but those for the forest areas did (F = 6.52, P $\leq$ .001). This result is especially interesting because both untreated clearcuts exhibited the greatest numbers of Microtus individuals; the treated clearcuts were almost depauperate in this species. The distribution of voles was presumably serverly restricted to specialized microhabitat. Also, inadequate sample size may have precluded the accurate discimination of microsites so that these results are suspect.

Multispecies DFA. Multispecies DFA over all sites successfully defined relative microhabitat associations for Peromyscus, Tamias, Clethrionomys, and Microtus along the first discriminant function (R_c = .323, λ = .819, P $\simeq$ .007; M = 265.8, F $\simeq$ 0.91, P = .819). The remaining two functions were statistically insignificant. Open areas of herbaceous and shrub cover vs. forested microsites generally segregated the four species along DF1 (Table I.10). Tamias and Clethrionomys, with positive mean DF1 scores (.244 and .362, respectively) exhibited niche structures characterized by forest variables. Peromyscus occupied an intermediate position along the structural niche axis ($\bar{x}$ = -.230). Microhabitat of Microtus ($\bar{x}$ = -1.091) is characterized by reduced canopy with increased stumps, herbaceous cover, and vertical density of vegetation. These results of the four species DFA essentially generalize those of the individual species analysis.

Habitat Structure and Small-mammal Communities

Community Composition Parameters and PCA. Relative abundances of deer mice decreased in habitat characterized by larger logs and more intact forest floor. Chipmunk proportions increased with increasing forest floor depth. Relative proportions of deer mice were correlated with mean PC2 (log size) and PC3 scores (forest floor) per habitat ($r = -.778$ and $-.709$, respectively). Those for chipmunks were associated with only PC3 mean scores ($r = .736$). Species diversity and mean PC2 scores were correlated also ($r = .666$, $P < .05$).

Chipmunk and deer mouse proportions per habitat remained highly and negatively correlated with each other after two first order analyses with mean PC2 and PC3 scores ($r = -.908$ and $-.794$, respectively). Chipmunk and deer mouse proportions retained their association after a second order analysis with H'' and mean PC2 scores held constant ($r = -.942$). Other significant second order partial correlations resulting from analysis with these four variables include mean PC2 scores and deer mice proportions ($r = -.688$, $P \leq .05$). Deer mouse proportions were also correlated with H'' ($r = -.675$, $P \leq .05$), as were those for chipmunks ($r = -.607$, $P \leq .05$). Species diversity and mean PC2 scores were uncorrelated ($r = -.162$).

Relative abundances of deer mice and chipmunks, species diversity, and log size were all interrelated. The foregoing analysis determined that the reciprocal abundances of deer mice and chipmunks remained the dominant relationship in the Little Chinquapin small-mammal communities and affected species diversity values.

Throughout the Little Chinquapin Mountain sites, red-backed vole numbers were related to specific forest habitat components, namely vertical vegetation (Table I.9) and logs, and were not uniquely associated with the presence or abundance of other species. The relative abundance of red-backed voles over all habitats was correlated with mean PC2 scores ($r = .878$, $P \leq .001$) and deer mouse

proportions ($r = -.748$, $P \leq .005$). Second order analysis, controlling for deer mouse proportions and H'' per habitat area, resulted in a highly significant correlation between red-backed vole proportions and mean PC2 scores ($r = .848$, $P \leq .005$).

Species diversity was positively associated with species richness and negatively correlated with weighted mean niche breadth over all areas. As dominance, or relative abundance, of commonly occurring species increased over all habitats, diversity and the number of species declined. Species richness and $\overline{WB}_j$ values were not associated, however; dominance of the Little Chinquapin Mountain small-mammal communities by widely occurring and common species did not determine the occurrence of rare types, e.g. Clethrionomys. As proportions of Peromyscus decreased and those of Clethrionomys increased along the habitat gradient defined by increasing log size (PC2), $\overline{WB}_j$ values decreased (Fig. I.4). Thus, the association between species' relative abundances and community composition, as defined by $\overline{WB}_j$, was related to changing habitat structure.

Community Composition Parameters and DFA. Peromyscus and Tamias relative abundances were significantly correlated with mean DF1 scores for all clearcuts and forests for their respective two group discriminant function ($r_s = -.762$, $P = .015$; $r_s = .995$, $P = .002$; respectively). Each species' proportions were correlated significantly with the other's mean DF1 scores, as well. Of these four variables, Peromyscus proportions and mean DF1 scores retained the greatest association ($r_s = -.991$, $P \leq .02$). No other combinations resulted in a significant correlation.

Relative abundances of deer mice covaried negatively with those for chipmunks as well as with increasing log size (PC2) and H'' values. Deer mouse proportions were highly and negatively correlated with mean DF1 scores per habitat, values representing microhabitat configurations at which deer mice were absent. As forest complexity increased over all areas, deer mice numbers decreased. Deer mice were the most ubiquitous species, however

(Table I.7). Microhabitat that distinguished low numbers of deer mice also characterized the increasing occurrence of chipmunks (Table I.9). Thus, deer mice may distinguish less distinct preferred microhabitat that does not include complex forest structure. Their proportional abundance may be limited, therefore, by intact forest microsites.

Specific limiting microhabitat for deer mice was increasing log size and forest floor. These components characterized habitats with decreased deer mouse proportions. Mean DF1 scores for Peromyscus over all clearcuts and forests combined were significantly correlated with mean PC3 scores (r_s = .976, P $\leq$.001). First order analysis with these two variables holding Peromyscus proportions constant reiterated their association (r_s = .958, P $\leq$.001). Proportions of deer mice and mean PC3 scores were not correlated (r_s = .317, P >.05) while controlling for mean DFI scores. Negative mean PC3 scores were calculated for the treated clearcuts and LC3S forest (Table I.6), areas of greater deer mouse abundance. Large, positive means characterized SoCr clearcut and forest.

Interrelationships by Habitat. The treated clearcuts (LC3W, LC3S) were characterized by the lowest H'', J_H, and with the LC3W forest, S_j values (Table I.8) and the highest proportions of deer mice. These clearcuts were distinguished from the other six clearcut and forest areas along the habitat DF2 axis (Fig. I.3) by the same variables that characterized the absence of deer mice (Table I.9). The open, disturbed nature of these habitats along with the lack of limiting microhabitat in these two areas perhaps contributed to high Peromyscus numbers and their dominance of these communities.

The untreated clearcuts (LC5, SoCr), in contrast, were characterized by the largest H'' values of any clearcut or forest area (Table I.8). As vertical complexity and horizontal patchiness increased in the untreated clearcuts (Table I.6), additional structural variation was available for use by the newly occurring

or less common small-mammal species. These clearcuts were distinguished from the treated clearcuts by their forest islands and greater herbaceous species richness (Figs. I.2 and I.3, Tables I.5 and I.6). As a result, perhaps, deer mouse numbers were lower in these clearcuts. Additionally, chipmunk and long-tailed vole abundances increased significantly above those in the treated clearcuts. The Scheffé procedure significantly distinguished greater chipmunk mean DF1 scores for the untreated clearcuts. No distinction resulted for Microtus clearcut means. Red-backed voles occured in the untreated clearcuts but were rare (Table I.7); no microhabitat preferences in the untreated sites could be calculated (Table I.9). The composition of these small-mammal communities corresponds to the previously stated conclusion that species richness and the dominant occurrence of common species (Peromyscus) were generally unrelated.

Forested habitats within the Little Chinquapin Mountain sites were quite variable in overall structure (Fig. I.3). Associated small-mammal communities were generally dominated by Tamias spp. and all but SoCr had H'' values greater than that of the adjacent clearcut (Table I.8). Relative proportions of chipmunks were minimal in the LC3S forest, the most closed canopied of the four, and maximal in the SoCr forest. Proportions of chipmunks increased over all sites with increasing forest structure but were greatest in heterogeneous (more open yet mature) forests. The greatest absolute number of chipmunks, as well as total number of individuals of all species combined, occurred in the LC3W forest. This area had an intermediate canopy with shrub cover and larger logs (Table I.6) contributing to greater productivity.

Edge habitats in 1981 exhibited the widest range of H'' and S values (Table I.8). These habitats also exhibited wide variation in mean PC scores. Every captured species occurred in at least one edge area (Table I.8). The influence of edge structure on small-mammal communities is reported elsewhere (S. P. Cross, pers. comm.).

Buck Peak, 1982

Habitat Comparisons

Clearcut Differences via DFA. Although the clearcuts appeared to be very similar in overall structure, they were separated by DFA. The SE clearcut had greater woody cover, and the SW clearcut had greater herb species richness plus concentrations of woody cover and bareground. The West clearcut had more herb cover and the North more shrub, and less woody, cover. DFA derived two significant functions for all clearcuts (g = 4), indicating that most remaining discriminating information had been extracted by the second function (Table I.12). DF1 represents a gradient from smaller woody debris to vegetative cover. DF2 is a similar gradient but represents greater herb cover in contrast to more woody litter and herb species. Mean site scores along DF1 indicate three groupings. The SE ($\bar{x}$ = -1.221) and North ($\bar{x}$ = 1.267) clearcuts are most different due to greater quantities of woody litter and logs, and more shrub and herb cover, respectively. The West ($\bar{x}$ = 0.007) and SW ($\bar{x}$ = -0.053) clearcuts are intermediate and do not separate along DF1. For DF2, however, the opposite pattern of separation is evident, with the West ($\bar{x}$ = -0.890) and SW ($\bar{x}$ = 0.927) clearcuts exhibiting the greatest difference and SW ($\bar{x}$ = -0.041) and North ($\bar{x}$ = 0.004) being very close and intermediate.

Forest Differences via DFA. DFA on the four forests produced three significant discriminating functions (Table I.11). DF1 represents a gradient of the lower structural levels from open herbaceous areas to those with larger logs and more woody thickness and litter. DF2 separated sites based on log quantities and shrub cover vs. canopy cover, duff, and woody thickness. DF3 indicates separation based on shrub cover vs. number of stumps and log size. Separation of forests' mean scores along DF1 illustrates the West forest's depauparate understory vegetation and low overstory and understory tree densities (Fig. I.5). The SE and SW forests remain close on DF1 as well as DF2, along which their greater log

quantities and densities segregate them from the West and North forests. DF3 separates SE and SW forests primarily based on the latter's greater shrub and bare ground components.

Forest Comparisons by Pairs. All discriminant analyses on forest comparisons by pairs resulted in statistically significant separation. The SW and SE forests were most similar (R_c = .664, λ = .560, P = .021). These forests differed by SHRB (r = .559) and TSTUMP (r = -.338). The SE and West forests differed (R_c = .825, λ = .320, P <.001) in terms of TWL (r = .413) and BRGD (r= -.383). The SE and North forests, however, differed (R_c = .768, λ = .419, P <.001) due to CANCO (r = .391) and HBSPP (r = -.431). DFA segregated the SW and West forests (R_c = .818, λ = .331, P <.001) based on THICK (r = .479) and HBSPP (r = -.274). The SW and North forests differed (R_c = .706, λ = .502, P >.005) due to SHRB (r = .316), CANCO (r = -.509), and MAT (r = -.353). DFA on the West and North forests produced the greatest separation (R_c = .840, λ = .295, P <.001); contributing variables were TWL (r = .500), THIK (r = .401), HBSPP (r = -.453) and BRGD (r = -.314). Thus, these forests differed from one another by habitat components that were directly affected by habitat alteration through logging.

Clearcut and Forest Differences via DFA. DFA on clearcuts and forests (eight groups) clearly illustrates these habitats' similarities and differences (Table I.11, Fig. I.6). DF1 is positively correlated with TWL, THIK, CANCO, OVDRNS, and negatively associated with SHRB, BRGD, and HBSPP. This axis separates the eight habitats based on increasing forest complexity and woody litter. Interestingly, the four clearcuts and the west forest are grouped in the negative region of DF1 and are characterized by open, less complex structure. The SW and SE forests are somewhat intermediate as a result of their heterogeneous habitats; the North forest has maximum forest structure. DF2, having positive correlations with TLOG, LOGDNS, and TWL separates the SW and SE

forests from the West and North forests, and more distinctively, the West forest from the other seven areas. DF3 clearly separates the four clearcuts, and the SE and SW forests, relative to shrub and smaller understory vs. herb species richness.

Habitat Characterization via PCA. PC1 represents a gradient from open, bare or herbaceous patches through increasing vertical complexity to maximum forest structure (Table I.12). PC2 describes woody dead and down size information, and PC3 represents log cover and quantity. SE and SW forests, as well as all clearcuts, have similar score means along all three axes (Table I.6). In particular, SE and SW forests are intermediate to the West and North forests along PC1 and PC2 and have the largest mean scores on PC3.

The foregoing results of the habitat analysis directly correspond to past management activities within the various sites (Appendix 1). Overstory removal and lack of site preparation in the SE and SW forests resulted in heterogeneous habitats of very little canopy with horizontal variation in clumps of poles and saplings, leftover logging slash of various sizes in different concentrations, open grassy and herbaceous areas, and well-developed shrub cover, especially in the SW site. A shelterwood cut and subsequent piling and burning of slash in the West forest resulted in a very even-aged stand with virtually no understory and a well developed herbaceous vegetation; woody cover was obviously lacking. No consistent management activity in the North forest meant less disturbance to the uneven-aged forest structure. This forest, with a prominent understory interspersed with some open areas, was the more structurally complex of any; its significantly greater canopy cover and thickness of woody vegetation were dominant characteristics of this stand.

Small-mammal Community Composition

Species Abundances. Over all Buck Peak sites, 1288 individuals of seven species were captured during 13,680 trap-nights

(I_{100} = 9.4). Spermophilus lateralis was the most abundant species, followed by Peromyscus maniculatus and Tamias amoenus. No species accounted for >28 percent of the total number of individuals (Table I.13). These three species, considered together, were associated with study site (X^2 = 27.0, P $\leq$.001). Peromyscus with T. amoenus abundances only, however, occurred independently of site (X^2 = 3.02, P >.25). Considering abundances among clearcuts, Peromyscus with T. amoenus and Spermophilus did not vary with site (X^2 = 12.09, P >.05). Within the forests, however, these species were associated with site (X^2 = 33.64, P <.001). A priori chi-square analysis on each species' (except Sorex) abundance over all sites indicated that only Peromyscus and Microtus numbers were not related to site.

Of the four species that were present in every habitat of each site, only T. siskiyou increased in average proportion from the clearcut through the edge and into the forest. Peromyscus exhibited the greatest range in mean proportions per habitat; those for Spermophilus remained fairly constant (Fig. I.7). These variations in relative proportions per habitat were reflected in species niche breadth measures of which Spermophilus exhibited the largest value and T. siskiyou the smallest for the four common species (Table I.13). Relative proportions of T. amoenus and Peromyscus were negatively correlated with those of T. siskiyou (r = -.737 and r = -.800, respectively, P $\leq$.01) over all 12 areas. Within sites, Peromyscus consistently occurred in greater proportions in the clearcuts than the two other habitats. T. amoenus had a variable pattern of occurrence for which the greatest difference occurred between the North clearcut and forest. Proportions for T. siskiyou were greater in three of the four forests than in any edge or clearcut (Table I.13).

Community Composition Parameters. H'' values in the West and North forests were less than three of the four edge values and approached the largest clearcut value. This phenomenon probably

reflects fewer, more evenly proportioned species in the West forest and dominance by T. siskiyou in the North forest. Species diversity generally increased along the clearcut to forest habitat gradient (Table I.8). H'' was maximal in the SW forest and minimal in the SW clearcut. H'' values were not correlated with J_H values but were with proportions of Spermophilus ($r = -.752$, $P \leq .01$). Numbers of individuals per species over all sites combined and species' niche breadths were positively correlated ($r = .895$, $P < .01$).

Like the 1981 data, community composition parameters (S_j, H'', $\bar{B}_j$, $W\bar{B}_j$) were initially intercorrelated. The primary correlation resulting from partial correlation analysis was S_j and $\bar{B}_j$ ($r = -.944$). As the number of species increased per habitat, less abundant types occurred. Little biological information can be gained from this relationship alone, however, due to the mathmatical association between S_j and $\bar{B}_j$.

Microhabitat Associations

Four of the six species entered into two group DFA exhibited some degree of differential microsite occurrence (Table I.14). Spermophilus and Microtus were the only species for which microhabitat preference could not be calculated. The other four species exhibited significant microsite segregation for all sites combined and for all forests combined; within each site, however, differences among species became apparent.

For every significant discriminant function, heterogeneity of group variance-covariance matrices was indicated. In a few analyses, the number of cases within the presence group was less than p and Box's M could not be calculated. These functions will be presented and discussed, however.

Peromyscus maniculatus. Peromyscus were limited over all sites by complex forest structure that occurred primarily in the North forest. DFA on Peromyscus occurrence over all sites ($R_c = .403$, $\lambda = .837$, $P < .001$) was characterized by variables (Table I.14) with

significantly larger mean values within the absence group. These variables also were negatively correlated (except BRGD) with the number of captured individuals. This function, therefore, represents microsites of deer mouse absence. ANOVA on mean DF1 scores per area indicated significant differences between them ($F = 24.14$, $P < .001$) although heterogeneity of group variances was evident (Bartlett-Box $F = 10.11$, $P < .001$). The Kruskal-Wallis one-way nonparametric procedure indicated significant differences between area means ($X^2 = 90.4$, $P < .001$). The Scheffé procedure produced three groups. The first included six of the eight means; those for the SE and North forests comprised the second and third group, respectively. Analysis of clearcut means ($n = 4$), however, resulted in no evident differences ($F = 0.74$, $P = .526$). That for forest means revealed differences ($F = 15.71$, $P < .001$). The North forest's mean comprised one of the two resulting subgroups.

Peromyscus exhibited significant segregation of microsites within all forests ($R_c = .437$, $\lambda = .809$, $P = .025$) and at the North site ($R_c = .688$, $\lambda = .526$, $P = .003$) (Table I.14). In both cases, discriminating variables had negative correlations with deer mouse abundance. Deer mice, therefore, were present in more open areas with less vertical structure as opposed to those with typical forest components within defined layers.

Tamias amoenus. T. amoenus, like Peromyscus, was limited by forested areas and occurred in open, less complex habitat. DFA on Tamias amoenus occurrence resulted in significant discrimination functions for all sites ($R_c = .495$, $\lambda = .755$, $P < .001$), all forests ($R_c = .549$, $\lambda = .699$, $P < .001$), SW forest plus clearcut ($R_c = .668$, $\lambda = .554$, $P = .011$), and North forest plus clearcut ($R_c = .750$, $\lambda = .438$, $P < .001$) (Table I.14). For all analyses, univariate F values and relative among group magnitudes of the means of discriminating variables indicated T. amoenus presence in non-forested microsites. Although DF1 score means differed ($F = 26.16$, $P < .001$), homoscedasticity was rejected ($F = 6.91$,

P <.001). The Kuskal-Wallis test also denoted differences (X^2 = 98.2, P <.001). Forest means also were separate but heteroscedasticity was indicated. For the all-forests discriminant category, additional variables with significant univariate F values were BRGD, HBSPP, LOGDENS, LOGCO, AVLOGDI, NLOGLEN, and AVLOGLN. Of these, all log related variables, except LOGDENS, had greater mean values in the absence group; BRGD and HBSPP had larger presence group means. Within forests, T. amoenus were present in open areas lacking large logs.

Tamias siskiyou. T. siskiyou exhibited a pattern of occurrence opposite that of T. amoenus or Peromyscus; increasing values of TWL, THIK, OVRDNS, and MAT characterized the presence of Siskiyou chipmunks. More open areas of bare ground or herbaceous cover characterized their absence. Significant microsite segregation by T. siskiyou occurred in all but one (SE site) category (Table I.14). Discriminating ability within data sets varied; the best group separation occurred for the North site (R_c = .720, λ = .483, P <.001), the least for all-forests (R_c = .564, λ = .682, P >.001). Over all sites, T. siskiyou numbers of captured individuals were correlated with TWL (r = .638, P $\leq$.001), THIK (r = .612), CANCO (r = .592), OVRDNS (r = .485), UNDNS (r = .482), HRB (r = -.492) and BRGD (r = -.339). In all forests, quite similar associations resulted.

Differences among the eight DF1 score means were highly significant (F = 41.54, 310; P <.001) although heterogeneity of group variances was indicated (F = 5.60, P <.001). Three subgroups resulted from the Scheffé test: all clearcuts plus the West forest; SE and SW forests; the North forest. Again, mean rankings were significant (X^2 = 150.5, P <.001). In the West forest, T. siskiyou was associated with larger logs and woody litter presumably due to the lack of understory cover. In this open forest, these chipmunks evidently adjusted their activities to include the available ground cover. The clearcut means differed

($F = 3.90$, $P = .01$) as did the group variances ($F = 3.86$, $P = .009$). Differences among forest means were more distinct ($F = 22.08$, $P < .001$) due to differences among habitats.

Clethrionomys californicus. Clethrionomys, like T. siskiyou, occupied microsites of definite forest structure. In addition to the given discriminating variables (Table I.14), AVLOGLN, NLOGLEN, and NLOGDI had significantly larger mean values for the presence group; LOGCO, LOGDENS, and TLOG did not. As in the Little Chinquapin Mountain sites, log size, not quantity, apparently was important to this species. Clethrionomys exhibited significantly different microsite occurence over all sites ($R_c = .553$, $\lambda = .694$, $P < .001$), within all forests ($R_c = .570$, $\lambda = .675$, $P < .001$), and within the North site ($R_c = .736$, $\lambda = .458$, $P < .001$). Low vole numbers precluded analyses for the other sites. Over all sites, Clethrionomys occurred at only 23 of the sampled 318 trap stations (7.2 percent) and maximally correlated with CANCO ($r = .407$, $P \leq .001$). Significant differences between score means resulted for all groups and for all forests but sample variances were not equal. The SE and SW, West, and North forests comprised the three Scheffé subgroups, respectively; these groups correspond to Clethrionomys relative abundances within the forests. Significant separation of the eight area means was indicated by the Kruskal-Wallis test ($X^2 = 122.6$, $P < .001$).

Spermophilus lateralis and Microtus longicaudus. The lack of discernable microsite segregation by Spermophilus corresponds to the relative absence of significant correlations between numbers of individuals and habitat variables. Within all forests, the maximal association is with BRGD ($r = .411$, $P \leq .001$); within all clearcuts, it is with AVUNDI ($r = .416$). Group means and univariate F ratios for DF1 variables in all discriminant categories suggests that this species may prefer more open areas but distinct evidence is lacking. Within all forests, CANCO ($F = 4.68$, $P = .032$)

and FHD ($F = 4.79$, $P = .03$) differed between Microtus DFA groups; occupied sites were characterized by less canopy cover and more foliage density.

Multispecies DFA. Peromyscus, Tamias spp., Spermophilus and Clethrionomys exhibited microhabitat partitioning based on canopy cover, thickness of understory, woody litter, and density of overstory trees (Table I.15). DFA on groups defined by the presence of these species resulted in one significant discriminant function that incorporated 86.3 percent of the variance ($R_c = .498$, $\lambda = .714$ $P < .001$). This function correctly classified only 34.5 percent of the original cases, however. The DF1 score mean (2.211) for Clethrionomys indicated capture sites characterized by relatively greater forest structure. The much larger mean value for Clethrionomys may have been influenced by its small sample size (Dueser and Shugart 1982, Van Horne and Ford 1982), and reflects this species' exclusive occurrence in forest habitat. T. siskiyou exhibited the largest mean score (0.628) of the remaining four species. Spermophilus occupied an intermediate position ($\bar{x} = -0.105$) between Peromyscus ($\bar{x} = -0.388$) and T. amoenus ($\bar{x} = -0.404$) and the above forest-dwelling species.

Habitat Structure and Small-mammal Communities

Community Composition Parameters and PCA. Correlations between H'' and both PC1 and PC2 score means initially were not significant over all areas ($r = .550$, $.504$, $P > .05$, respectively). When the North forest data pairs are removed from analysis, however, then both correlations become statistically significant ($r_1 = .858$, $P < .01$; $r_2 = .631$, $P \leq .05$).

The primary correlations resulting from partial correlation analysis were T. siskiyou proportions and mean PC1 scores ($r = .858$), and T. siskiyou proportions and $\overline{WB}_j$ ($r = -.806$). Relative abundances of the Siskiyou chipmunk were associated with weighted mean niche breadths and vertical forest complexity (PC1).

Siskiyou chipmunks were more numerous in forested habitats in which deer mice and yellow-pine chimpunks, overall ubiquitous types, decreased in abundance. As forest complexity increased decreasing $\overline{WB}_j$ values reflected the greater dominance of these communities by less ubiquitious species.

Red-backed voles preferred more specialized microhibitat structure within forest habitats (Tables I.14 and I.15) and occurred in three of the four forests (Table I.13). Red-backed vole abundances were highly correlated with $\overline{WB}_j$ ($r = -.931$, $P \leq .001$), mean PC1 scores ($r = .915$, $P \leq .001$), and proportions of Siskiyou chipmunks ($r = .955$, $P \leq .001$) over all habitat areas (Fig. I.8). Further analyses indicated that the primary correlation existed between the two species' relative abundances ($r = .742$, $P \leq .02$).

Spermophilus, the most widely-occurring small-mammal (Table I.13), evidently had little effect on the relative composition of the Buck Peak communities. No pertinent microhabitat configurations were distinguished for this species. Thus, different habitat structure evidently was not an important factor in the rather constant occurrence of Spermophilus throughout these communities.

Community Composition Parameters and DFA. Relative abundances and mean DFI scores per species exhibited significant correlations for T. siskiyou ($r_s = .881$, $P \leq .002$), and Peromyscus ($r_s = -.762$ $P \leq .02$), but not for Spermophilus ($r_s = .670$, $P > .05$), nor T. amoenus ($r_s = .539$, $P > .05$).

Peromyscus mean DF1 scores per area and T. siskiyou proportions retained a significant correlation ($r_s = -.932$, $P \leq .02$) when Peromyscus proportions were held constant. T. siskiyou mean scores and proportions were not correlated ($r_s = .675$, $P > .10$). First order analyses on Tamias spp. proportions and T. amoenus mean scores, and on Tamias spp. mean scores and T. siskiyou proportions, resulted in a significant association between T. siskiyou abundance and T. amoenus scores ($r_s = -.892$, $P \leq .05$). T siskiyou

scores and proportions were uncorrelated (r_s = .708, P >.05). These results indicate that microsites were differentially used by these species and that preferred microhabitat of one species may be limiting for another.

Mean PC1 scores per clearcut and forest exhibited significant correlations with mean DF1 scores for deer mice (r_s = .881, P $\leq$.05), yellow pine chipmunks (r_s = -.994, P $\leq$.02), and Siskiyou chimpunks (r_s = .881, P $\leq$.05). Further analyses indicated that yellow pine chipmunk mean DF1 scores and mean PC1 scores retained a significant correlation as did those for deer mice. The positive correlation for deer mouse DF1 means, values representing microsites of decreasing deer mouse occurrence, may represent a similar phenomenon to that observed for the Little Chinquapin Mountain sites; increasing forest structure was limiting for this ubiquitous species.

Interrelationships by Habitat. The Buck Peak clearcuts, areas of little or no vertical structure, exhibited low species diversities and richness and large average niche breadths (Table I.8). These communities were dominated by ubiquitous species (Table I.13, Fig. I.7). As habitat complexity and heterogeneity increased throughout the Buck Peak sites, less common species were added to the communities. Species diversity and richness was maximal in habitats of intermediate complexity and maximum heterogeneity (SE and SW forests, Fig. I.5). Species diversity and richness declined in the North forest, a habitat of maximal forest structure and dominated by the Siskiyou chimpunk. Variables that distinguished the forest habitats (Table I.11, Figs. 5 and 6) also discriminated between sites of individual species' presence and absence (Table I.14) as well as among-species microhabitat differentiation (Table I.15). Differences among the Buck Peak small-mammal communities were definitely associated with structural differences among the habitats in which these assemblages occurred.

GENERAL DISCUSSION

Differential logging of the Little Chinquapin Mountain and Buck Peak sites produced varied habitat structures. Generally, logging removes biomass, reduces vegetative cover, disturbs soil and litter, and increases exposure. Logging influences almost all ecosystem components (Barger 1980). Site preparation for slash removal and/or replanting usually reduces vegetation and woody debris while it increases areas of scarified mineral soil. Over time, herbaceous and shrubby growth increase in logged forests (Young et al. 1967). Clearcutting, the most drastic harvest method, reduces stand dimensions from three to two by removing the overstory and some or all understory layers. Subsequent site preparation further destroys or alters ground level components and significantly affects microclimate (Hungerford 1980). Modification of habitat by various silvicultural treatments differentially affects various small-mammal species (Ream and Gruell 1980). We would expect, therefore, that small-mammal communities would respond differently to different logging methods.

At the Little Chinquapin Mountain sites, clearcut habitat varied more between than within treatments. Adjacent forests unexpectedly exhibited structural variation among sites. Small-mammal community composition followed this pattern. Differences in small-mammal types and numbers, therefore, were closely associated with relative differences in habitat.

Reciprocal abundances of Peromyscus and Tamias over Little Chinquapin Mountain influenced differences between communities. Peromyscus-dominated communities had similar composition within clearcut types and contained fewer species. Peromyscus is ubiquitous (Baker 1968). Because no congeners occurred in our study areas, this species was likely less ecologically restricted (Holbrook 1978). Greater densities of Peromyscus have been reported to occur in variously treated clearcuts than in adjacent timbered sites in Oregon (Gashwiler 1959, 1970; Hooven and Black 1976) and

Montana (Ramirez and Hornocker 1981). Petticrew and Sadleir (1974) and Sullivan (1979a), however, reported similar numbers of deer mice in forested and logged habitats in British Columbia. Gashwiler (1970) implied that clearcuts may be suitable habitat for deer mice two to three years after logging. Sullivan (1979a) stated the opposite and suggested that increased deer mouse numbers in the clearcut was a function of juvenile or subordinate dispersal from saturated forest populations.

In our study, presumably greater densities of deer mice in the LC3W and LC3S forests than in the LC5 and SoCr forests before clearcutting could account for observed differences in relative abundances between the four forests (Table I.7). After clearcutting, the dispersal effect (Sullivan 1979a) may have rapidly increased deer mouse numbers in the treated clearcuts. Alternatively, presumably greater reproductive rates in the treated vs. untreated clearcut populations, a phenomenon similar to that reported by Sullivan (1979a), may have resulted in increased dispersal from the treated clearcuts into adjacent forests during the three year interval between cutting and sampling. Temporal fluctuations in population densities may account for these differences as well.

At Buck Peak, less single species dominance of the small-mammal communities was observed. Intersite and interforest differences in species' abundances occurred as well. The association between increasing T. siskiyou proportions and increasing forest structure influenced relative community compostion. T. siskiyou proportions also were associated inversely with weighted mean niche breadth. No substantial effect by dominant species on community composition parameters was determined.

At Little Chinquapin Mountain and Buck Peak, changes in community compositions were correlated with increasing abundances of less common species in specialized microhabitat. Species diversity values were low in sites of simple habitat structure that were dominated by widely occurring species, e.g. Peromyscus. As habitat

complexity and heterogeneity increased, species occurrence was not influenced by the presence of dominant species but rather by the availability of preferred microhabitat. Anthony et. al. (1981) reported a similar phenomenon for forested habitats in Pennsylvania and hypothesized that species diversity was influenced by vegetative structure and/or seed production. In grassland communities, however, high densities of Microtus pennsylvanicus resulted in low species diversity. In our study, interspecific interactions were not studied, but we assume that the low species diversities of the treated clearcuts resulted from habitat alteration and not from active exclusion of other species by deer mice.

Rosenzweig and Winakur (1969) reported that species diversities of heteromyid-dominated communities were correlated with habitat complexity, namely the presence and/or absence of certain vegetative structures. Rodent species diversity was not great in sites of high plant species diversity, suggesting that structure, not richness of vegetation was important to small-mammal diversity. M'Closkey (1976) also reported an association between the vertical diversity of shrub structure and rodent species diversity in coastal sage scrub. These findings correspond with ours. Red-backed voles and long-tailed voles occurred at microsites of increasing shrub cover and vertical vegetative diversity.

Productivity of habitats as indicated by annual rainfall is a critical determinant of rodent species diversity in desert communities (Brown 1975). We did not measure productivity in our study sites. Significantly greater herb species richness in the untreated clearcuts at Little Chinquapin Mountain, however, may have increased the number of available food types. Densities of less common species, e.g. Microtus, may have increased in response to increasing food types. Herb species richness, as a habitat variable, did not contribute to the discrimination of preferred microhabitats of any species in these habitats, however.

McNaughton and Wolf (1970), examined the relationship between dominance and specialization of a species in plant communities and

presented two alternatives for the greater niche breadths of dominant species. These species are either generalists capable of exploiting many resource dimensions, or they are specialists on one abundant yet limiting dimension. If the first explanation is correct, subordinate species coexist within niche space seldom used by the dominants. Dominants thus are generalists, and subordinates are specialists excluded from potentially occupied space. In the second alternative, all species are specialists which occur in direct proportion to the relative abundances of the particular specialties. The former explanation may require at least on-going exploitation competition (Park 1954) whereas the latter does not. On Little Chinquapin Mountain, Peromyscus and Tamias exhibited similar niche breadths (11.0 and 10.8, respectively), but opposite microhabitat preferences. Tamias exhibited significant microhabitat selection in three of five analysis categories whereas Peromyscus did so in only one. According to McNaughton and Wolf's second alternative, Tamias would be considered a forest specialist with little affinity for open and/or heavily disturbed sites. Although usually considered an ecological generalist, Peromyscus would be a specialist on more open and variable habitat that incorporates newly disturbed areas into its range of activities. Just as Tamias did not fully utilize open or disturbed areas, Peromyscus did not increase with increasing forest habitat and tended to dominate less complex sites with fewer species. Dueser and Shugart (1978) also reasoned that McNaughton and Wolf's (1970) second alternative explained observed niche patterns within their study areas.

Rosenzweig (1974) considered habitat selection within the evolutionary paradigm and concluded that optimal phenotypes in fine-grained environments are extreme specialists. He also stated that, within a particular habitat, a specific specialist occurs within each of equally abundant patch types. When patch abundance is variable, two successful phenotypes result: one which is the extreme specialist in the common patch type, and one which uses the mixture of patch types. Thus, spatial abundances of structurally

diverse microhabitats are directly associated with relative species abundances and, therefore, community structure.

Over the Little Chinquapin Mountain sites, Tamias and Peromyscus are specialists on a particular habitat configuration, but Tamias is an extreme specialist confined to forested habitats. Peromyscus uses both habitat patches, one more than the other, however, and is limited by optimal chipmunk microsites.

At Buck Peak, Spermophilus lateralis, the most abundant and widely distributed species (B_i = 11.5), exhibited no discernable habitat preference. This species may have perceived the overall habitat as extremely fine grained (MacArthur and Pianka 1966, Wiens 1976) with little distinction between habitat components. Spermophilus occurred more equally among habitats and appeared to have little effect on differences among small-mammal communities. Peromyscus, Clethrionomys and Tamias spp. exhibited differential microsite occurrence along with variations in relative abundances. Preferred microhabitats of Peromyscus and T. siskiyou, as measured by mean DF1 scores per clearcut and forest habitat, were negatively correlated with the other's relative proportions over all sites. Peromyscus was distributionally more abundant (B_i = 11.2) than T. siskiyou (B_i = 8.5) and used a somewhat broader range of habitat structures. Relative abundances and occupied microsites of T. siskiyou and T. amoenus exhibited similar relationships. Clethrionomys were associated within specialized habitat within forests. Thus, T. siskiyou and Clethrionomys appear to be extreme specialists at Buck Peak with T. amoenus and Peromyscus as secondary specialists on open, variable habitat.

Relative abundances of common species have been shown to be associated with relative occurrence of non-limiting microhabitat. A pertinent question now concerns the addition of rare species to the community. McNaughton and Wolf (1970) considered three alternatives. Assuming that total species niche breadths sum to the environmental carrying capacity (K) per community ($K = \Sigma B_i$), and when K increases, species may be added in direct proportion to, more

rapidly than, or less rapidly than the expanding K. In the first alternative, mean niche breadth and species richness are unrelated. In the second, they are negatively associated, and for the third, positively associated. We assume carrying capacity to be functionally related to increasing forest complexity and heterogeneity. These authors concluded that, for plant species, a decrease in mean niche breadth occurs with increasing species. For birds, they found no relationship between mean niche breadth and species richness.

Anthony et al. (1981) found that unweighted average niche breadth decreased with increasing richness in forest and old-field habitats. Our findings concur, but when considering weighted mean niche breadths ($W\bar{B}_j$), this relationship was not evident for either year ($r = .502$, 1981; $r = .131$, 1982; second order analysis holding $\bar{B}_j$ and H'' constant). The primary association remained unweighted mean niche breadth and species richness for both years. McIntire and Overton (1971) reported similar results for diatom communities on the Oregon coast. Dominance of a site by a common species over our habitat range, indicated by a large $W\bar{B}_j$ value, is evidently unrelated to the number of species within those sites. These results imply that less common species, e.g. T. siskiyou in 1982 and Clethrionomys, were added to the observed communities in direct proportion to the expansion of K. That is, as structural complexity and heterogeneity increased from the more simple clearcut habitats to forest habitats, the required niche components of less common species became available within the study sites.

In conclusion, the composition of small-mammal communities throughout the 1981-82 study sites were associated with the degree of occurrence of habitat specialists. Ubiquitous species generally were more abundant in communities characterized by low H'' values in simple habitat structure. As the overall complexity of habitats increased, species with lower niche breadths were captured in less common microhabitat. In heterogeneous habitats, many species occurred more evenly than in homogeneous simple or complex

habitats. As overall complexity increased, less common species became more abundant than in simple or heterogeneous habitats, and ubiquitous species declined. These relationships are evident from the intercorrelations of $\overline{WB}_j$ values, PC1 and PC2 mean scores, and relative proportions of forest specialists for both years. Thus, severe structural alteration that changes habitat from complex to simple, e.g. clearcutting, directly affects the relative abundances of resident species.

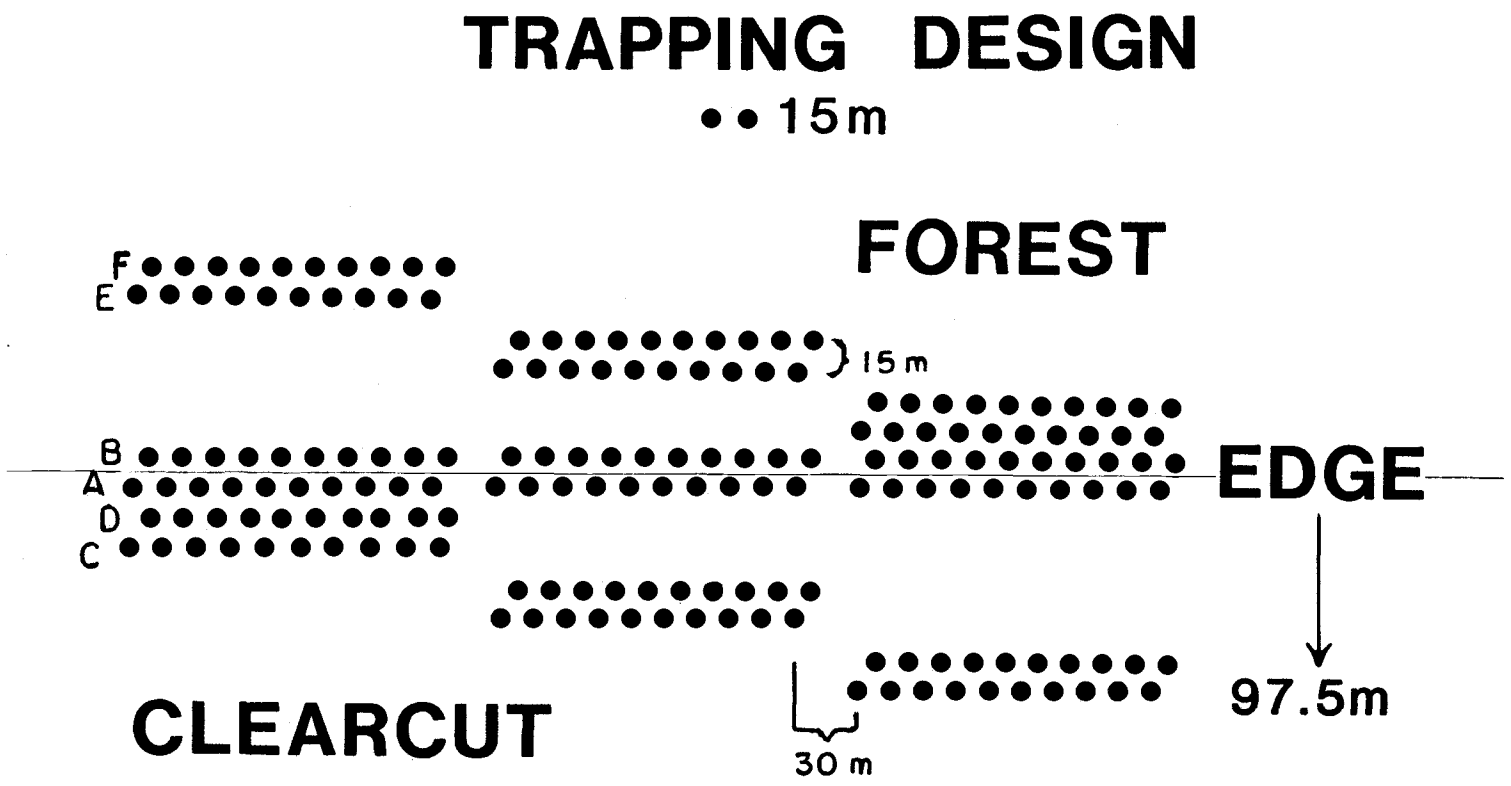

Fig. I.1 Sampling design for habitat analysis and small-mammal live trapping, 1981-1982.

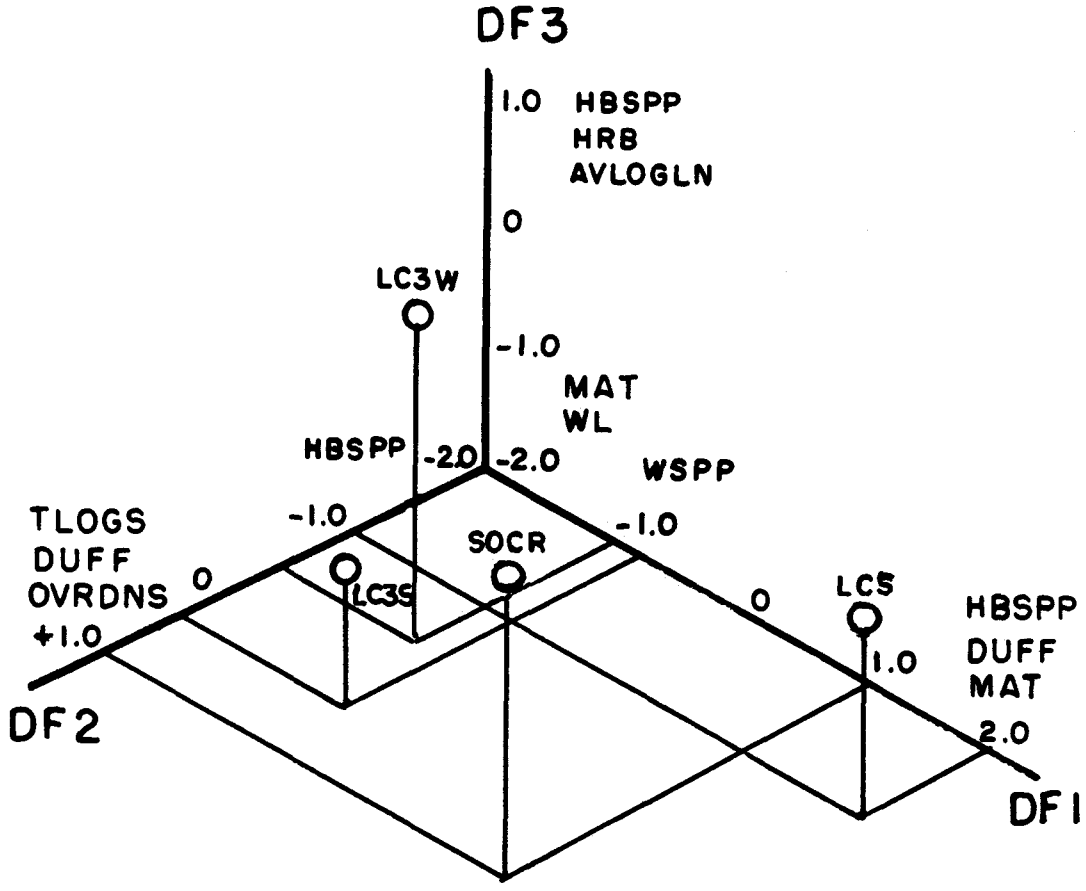

Fig. I.2 Positions of the Little Chinquapin Mountain clearcuts in discriminant space. Clearcuts are represented as mean discriminant scores for each of the three discriminant functions. Habitat variables associated with each axis are given (see Table I.1 for definitions).

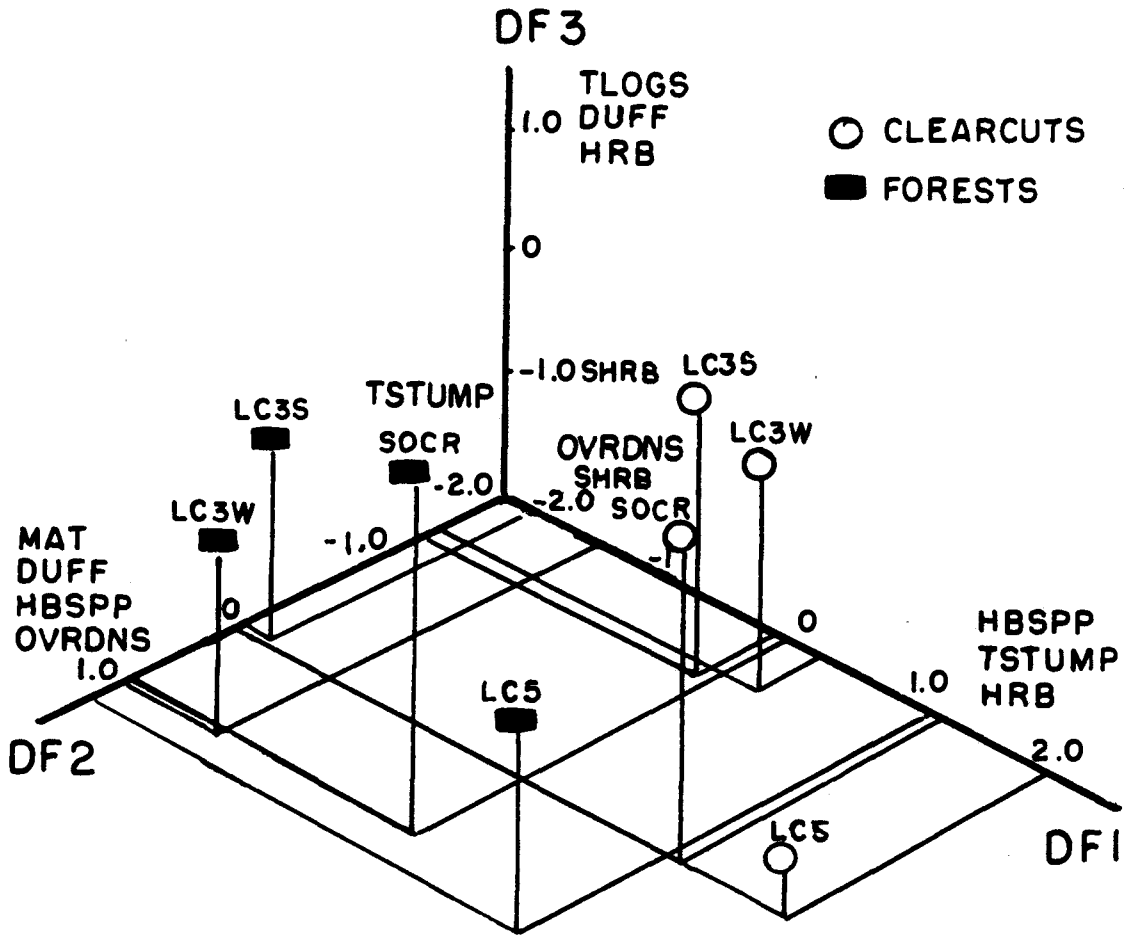

Fig. I.3 Positions of the Little Chinquapin Mountain clearcuts and forests in discriminant space. Clearcuts are represented as mean discriminant scores for each of the first three discriminant functions generated from eight group DFA. Habitat variables associated with each axis are given (see Table I.1 for definitions).

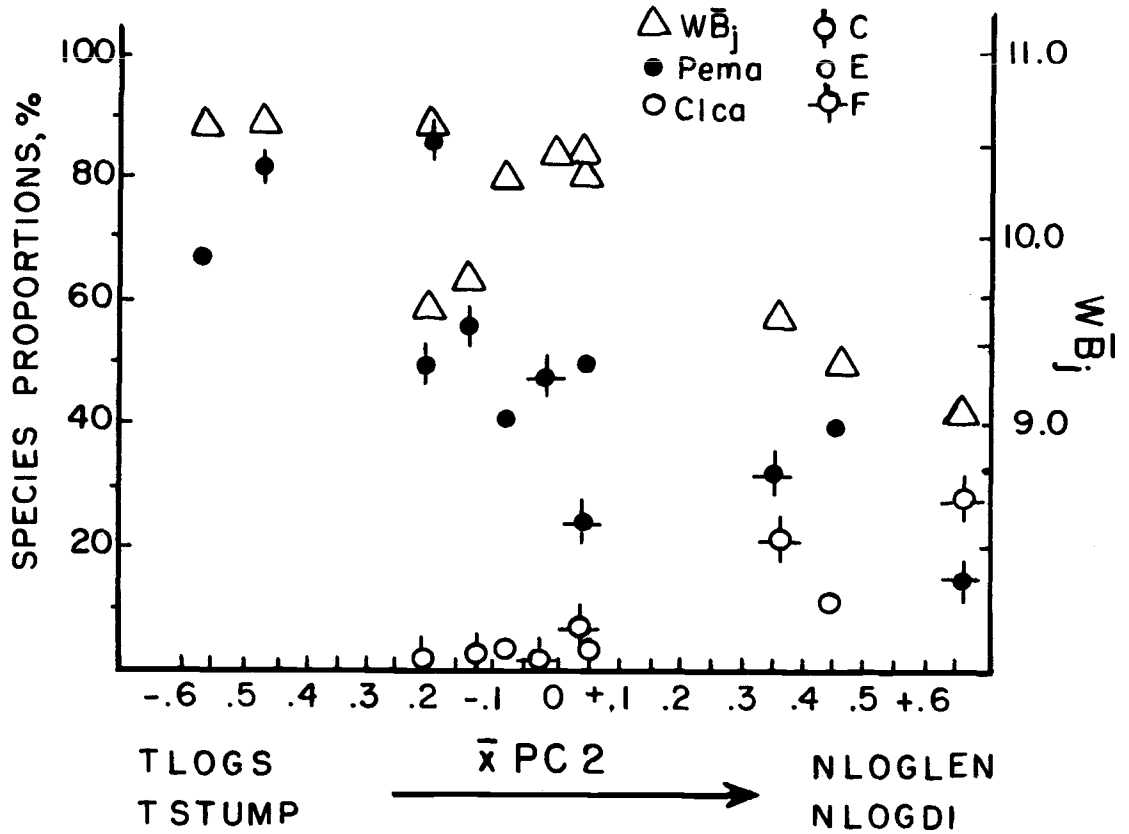

Fig. I.4. Relationships of Clethrionomys (Clca) proportions, Peromyscus (Pema) proportions, and weighted mean niche breadth ($W\bar{B}_j$) with average PC2 scores per habitat (C, clearcut; E, edge; F, forest) and site, 1981. PC2 represents a habitat gradient from smaller, more numerous woody material in open areas to areas of larger and fewer logs. Habitat mnemonics are defined in Table I.1.

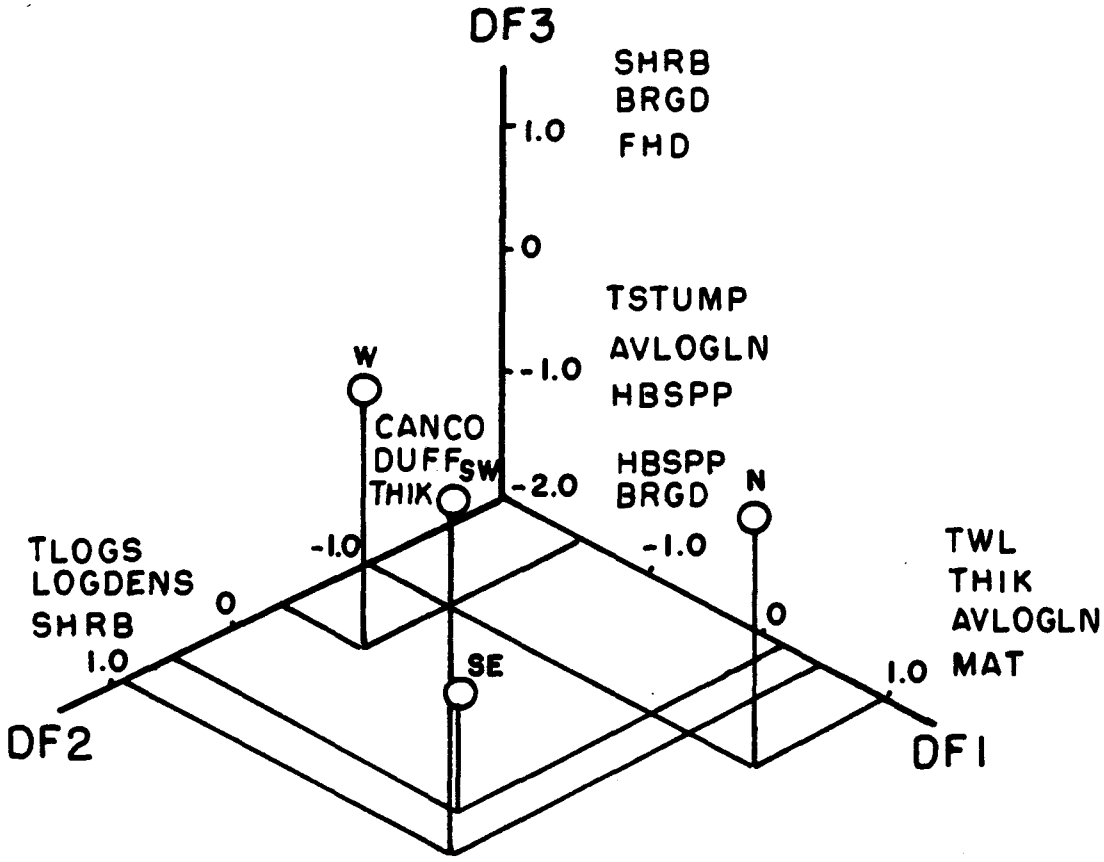

Fig. I.5 Positions of the Buck Peak forests in discriminant space. Forests are represented as mean discriminant scores for each of the three discriminant functions. Habitat variables associated with each axis are given (see Table I.1 for definitions).

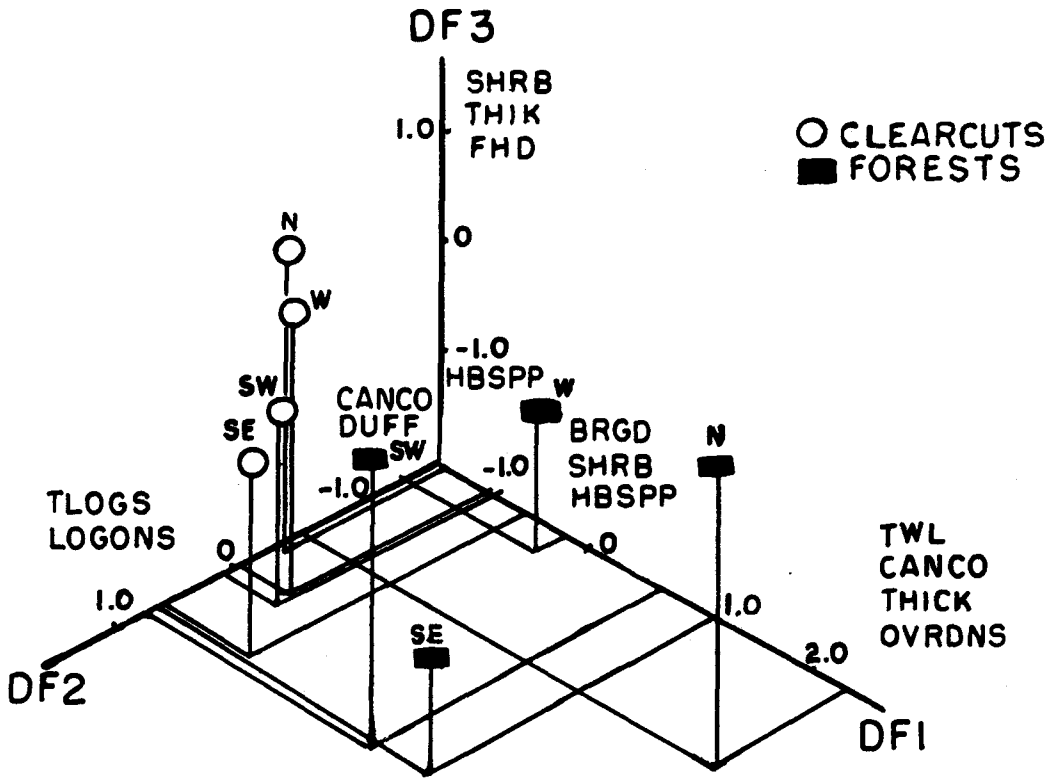

Fig. I.6 Positions of the Buck Peak clearcuts and forests in discriminant space. Habitats are represented as mean discriminant scores for each of the first three discriminant functions generated from eight group DFA. Habitat variables associated with each axis are given (see Table I.1 for definitions).

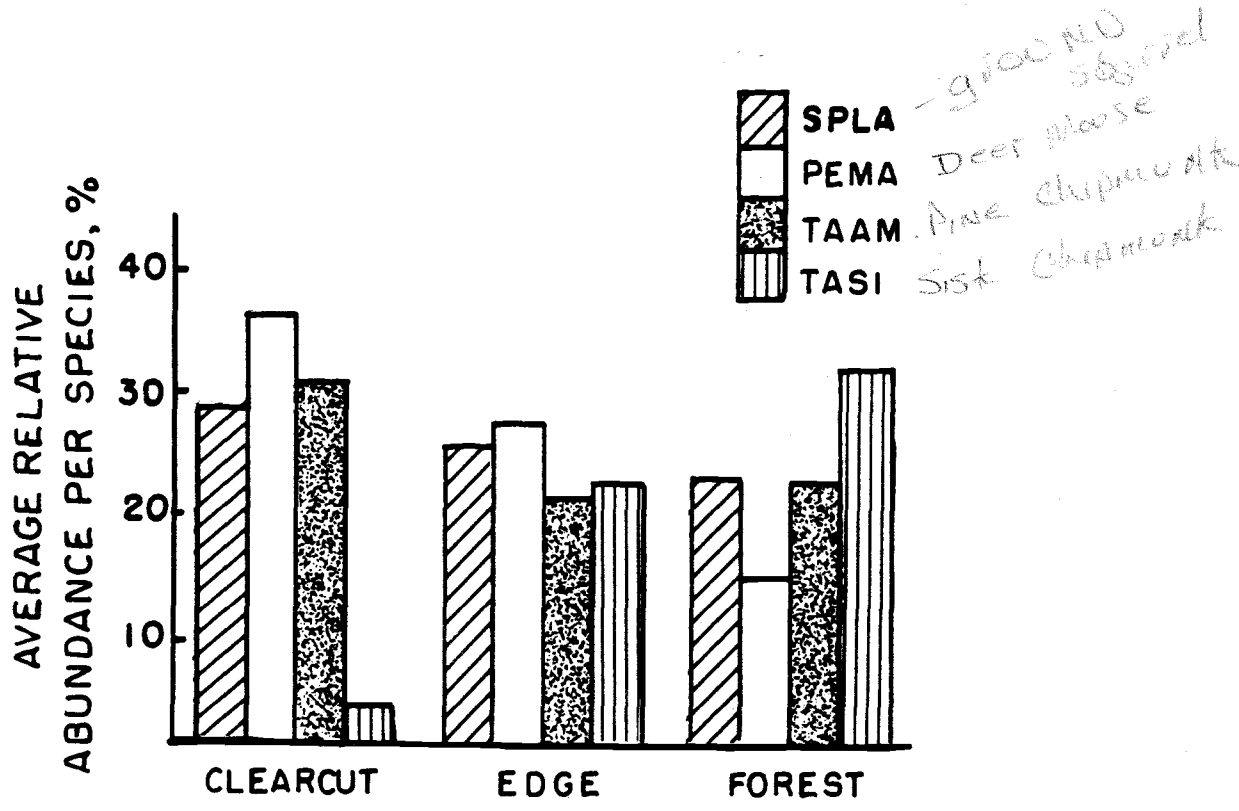

Fig. I.7 Species proportions of total individuals captured per habitat type averaged over the four Buck Peak sites. Given values are for the four most common small-mammal species: Spermophilus lateralis, SPLA; Peromyscus maniculatus, PEMA; Tamias amoenus, TAAM; and Tamias siskiyou, TASI.

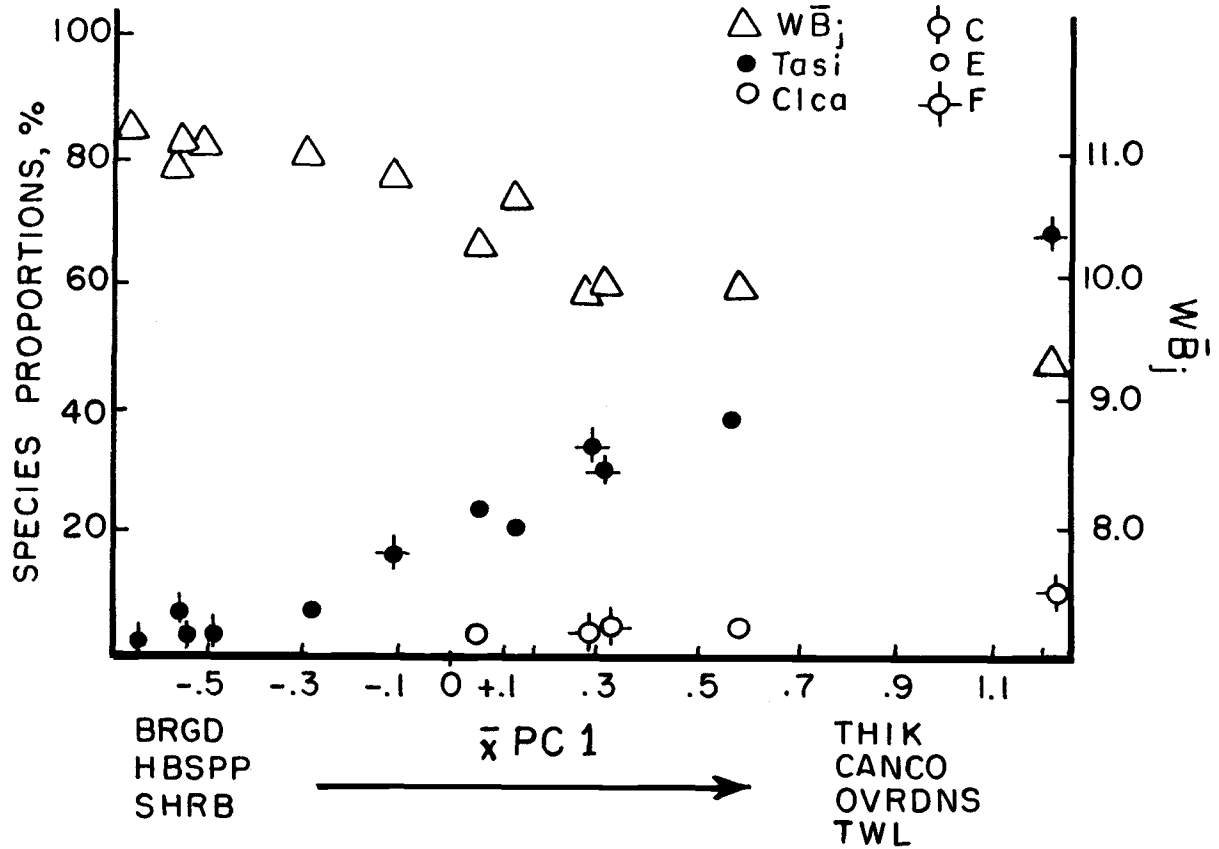

Fig. I.8 Relationships of Tamias siskiyou (Tasi) proportions, Clethrionomys (Clca) proportions, and weighted mean niche breadth ($\bar{WB}_j$) with average PC1 scores per habitat (C, clearcut; E, edge; F, forest) and site, 1982. PC1 represents a habitat gradient of increasing forest complexity. Habitat mnemonics are defined in Table I.1.

Table I.1. Habitat variables, with corresponding mnemonic, of data subsets for 1981 and 1982.

Habitat variable	Mnemonic	1981			1982		
		Clearcuts	Forests	All sites	Clearcuts	Forests	All sites
Percent log cover	LOGCO	**+	**	--	**	**	**
Percent woody litter	WL	*	**	*	--	--	--
Total number logs	TLOG	*	**	*	*	**	**
Average diameter of nearest log	AVLOGDI	**	--	--	**	**	**
Length of nearest log	NLOGLEN	**	**	**	**	**	**
Average length of nearest log	AVLOGLN	**	--	--	**	**	*
Duff depth	DUFF	**	**	*	**	**	*
Number of herb spp.	HBSPP	*	*	*	*	*	*
Number of woody spp.	WSPP	*	*	*	**	*	*
Overstory tree density	OVRDNS	**	**	**	**	**	**
Percent herb cover	HRB	*	**	*	*	--	--
Mat depth	MAT	**	**	*	**	**	**
Diameter of nearest log	NLOGDI	**	**	**	**	**	**
Percent canopy cover	CANCO	--	**	--	--	**	**
Percent shrub cover	SHRB	--	**	**	**	**	**
Percent bare ground	BRGD	--	**	--	*	**	*
Log density	LOGDENS	--	**	--	**	**	**
Average diameter nearest understory tree	AVUNOI	--	**	--	--	--	--
Foliage height diversity	FHD	--	**	**	**	**	**
Thickness of woody vegetation	THIK	--	**	--	--	**	**
Average diameter of nearest overstory tree	AVOVRDI	*	--	--	--	--	--
Total woodpiles	TWP	**	--	**	**	**	
Total stumps	TSTUMP	**	**	*	**		
Understory tree density	UNDNS	**	--	--	--	--	--
Percent total woody litter	TWL	--	--	--	**	*	*
Area of nearest log	NLOGARA	--	--	--	**	--	--
Total number snags	TSNAG	--	--	--	**	--	**
Snag density	SNGOENS	--	--	--	**	--	**

+ * untransformed, ** transformed, -- not included (see text).

Table I.2. The absolute and adjusted number of individuals per species per habitat, 1980.

Species	Clearcut		Edge	Forest		Total no. all habitats combined
	*n_c	n_{cl}	n_e	n_f	n_{fl}	
Tamias spp	68	22.7	19	67	22.3	131
Spermophilus lateralis	29	9.7	24	25	8.3	54
Clethrionomys californicus	2	0.7	0	22	7.3	24
Sorex trowbridgei	14	4.7	0	4	1.3	18
Peromyscus maniculatus	15	5.0	6	0	--	17
Microtus longicaudus	5	1.7	1	0	--	6
Microtus oregoni	1	0.3	0	0	--	1
Phenacomys intermedius	1	0.3	0	0	--	1
Thomomys mazama	1	0.3	0	0	--	1
Mustela ermina	0	---	0	1	0.3	1

*The number of individuals captured in the clearcut, edge, and forest are given by n_c, n_e, and n_f, respectively. The number of individuals captured per pair of grid lines per clearcut and forest (3) are given by n_{cl}, n_{fl}. Only 1 pair of grid lines occurred at the edge. One individual can be counted in >1 habitat category.

Table I.3. Regression equations for selected dependent variables with associated coefficients of determination, degrees of freedom, and partial F values, 1980. All F values are significant at $P \leq 0.01$.

Analysis category	Regression* equation	r^2	df	F
Number of small-mammal species	Y = 1.02 + 0.07WSC + 0.03WPC -0.2WLC + 0.35SDLD	0.355	4,51	7.03
Total *Tamias* captures	Y = 0.58 + 0.23 RC - 0.23 SC -1.33NLV + 4.87MLV + 0.78TWP	0.500	5,50	10.01
Total *Spermophilus* captures	Y = 1.44 - 0.03HC - 0.03WLC + 0.43 SDLD	0.293	3,52	7.17
Total *Peromyscus* captures	Y = -1.50 + 0.15RC + 0.92SDLD	0.224	2,53	7.40
Total *Clethrionomys* captures	Y = 0.38 + 0.10WPC -0.18LC -0.55MLD - 0.79TWP	0.255	4,51	4.36
Total *Microtus longicaudus* captures	Y = 0.90 + 0.04WSC - 0.16MLD -1.30LII	0.249	3,52	5.73

*Habitat variables are: WSC, woody species cover; WPC, wood pile cover; WLC, woody litter cover; SDLD, stand deviation of mean log distance; RC, rock cover; SC, stump cover; NLV, volume of nearest log; MLV, mean log volume; TWP, total wood piles; HC, herb cover; LC, log cover; MLD, mean log distance; LII, log influence index = (area of nearest log)/(distance to nearest log) summed over four subplots.

Table I.4. Discriminant function parameters with associated factor structures, Little Chinquapin Mountain. Variables with P $\leq$.05 for correlations with any significant function are given. At α=.05: r = .204 for n = 91; r = .193 for n = 103; r = .141 for n = 194.

	All clearcuts g = 4, n = 91			All forests g = 4, n = 103			All clearcuts and adjacent forests; g = 8, n = 194		
	Discriminant function								
	1	2	3	1	2	3	1	2	3
Eigenvalue	1.62	.60	.40	2.90	.76	.51	1.75	1.12	.41
Percent variance	61.7	22.9	15.3	69.4	18.3	12.3	46.3	29.5	10.9
Σ percent	61.7	84.6	100.0	69.4	87.7	100.0	46.3	75.8	86.7
Canonical correlation, R_c	.786	.613	.536	.862	.658	.582	.798	.726	.541
Wilk's λ	.170	.445	.713	.096	.375	.661	.077	.211	.446
X^2, df	144.4,39	66.0,24	27.6,11	209.6,63	87.8,40	37.1,19	470.0,84	284.8,66	147.8,50
Habitat variable:									
HBSPP	.673	-.328	.440	.624	-.171	-.044	.713	.336	-.208
DUFF	.354	.460	-.033	.053	.283	.408	-.004	.356	.436
MAT	.342	.335	-.473	-	-	-	.014	.420	.178
WSPP	-.249	-.149	.275	-.118	.141	.236	-.175	-.094	.099
WL	.183	.072	-.281	-	-	-	-	-	-
OVRDNS	.144	.400	.170	-	-	-	-.331	.356	-.005
TLOGS	.106	.500	-.153	.189	.224	.091	.229	-.136	.452
AVLOGLN	-.070	.099	.296	-	-	-	-	-	-
NLOGDI	.044	-.097	-.232	-	-	-	-.002	.206	-.124
HRB	.032	.272	.381	.445	.042	.068	.415	.006	.431
UNDNS	-	-	-	-.267	-.024	-.061	-	-	-
THIK	-	-	-	-.244	.161	-.038	-	-	-
CANCO	-	-	-	-.214	.100	-.009	-	-	-
SHRB	-	-	-	-.163	-.482	.390	.244	.245	-.376
TWP	-		-	.065	.237	.073	-	-	-
AVUNDI	-	-	-	-.144	.059	.359	-	-	-
TSTUMP	-	-	-	.210	.126	-.354	.424	-.427	-.072
LOGDENS	-	-	-	.114	.165	.286	-	-	-
FHD	-	-	-	-.096	-.112	.225	-	-	-
NLOGLEN	-	-	-	-	-	-	-.061	.323	.087

Table I.5. Factor structure for the first three principal components, Little Chinquapin Mountain. Values for habitat variables are correlation coefficients for variable values with the principal component after VARIMAX rotation. At α =.05, r ≃ .141 for n = 194.

Principal component	1	2	3
Eigenvalue	2.30	1.76	1.48
Percent variance	19.20	14.70	12.30
Cumulative percent	19.20	33.90	46.30
Habitat variable			
OVRDNS	-.760	.097	.164
HRB	.753	.113	-.039
HBSPP	.745	.049	.166
TSTUMP	.397	-.274	-.134
TLOGS	.310	-.291	.365
WSPP	.162	-.196	.043
NLOGDI	.082	.843	.050
FHD	-.057	.037	.031
MAT	-.050	.119	.761
DUFF	-.045	.058	.823
NLOGLEN	-.035	.848	.111
SHRB	-.000	.160	.035

Table I.6. Mean PCA scores per habitat for the first three components within each study site, Little Chinquapin Mountain and Buck Peak.

	Little Chinquapin Mountain				Buck Peak			
Habitat	Study site	PC1	PC2	PC3	Study site	PC1	PC2	PC3
Clearcut	LC3W	0.454	-0.474	-0.800	SE	-0.472	-0.207	0.067
	LC3S	0.031	-0.194	-0.322	SW	-0.646	-0.197	0.078
	LC5	0.687	-0.148	0.044	W*	-0.530	-0.273	0.127
	SoCr	0.752	-0.203	0.354	N*	-0.548	0.080	-0.190
Edge	LC3W	-0.285	0.045	-0.670	SE	0.055	0.018	0.043
	LC3S	-0.663	-0.564	-0.327	SW	0.135	-0.052	0.011
	LC5	0.645	0.440	-0.106	W	-0.284	-0.091	0.309
	SoCr	0.165	-0.096	0.841	N	0.569	0.405	-0.897
Forest	LC3W	-0.494	0.355	0.039	SE	0.298	0.100	0.698
	LC3S	-1.390	-0.025	-0.161	SW	0.310	0.298	0.320
	LC5	0.377	0.661	0.260	W	-0.104	-0.529	-0.881
	SoCr	-0.043	0.048	0.768	N	1.217	0.450	0.313

* W = West, N = North.

Table I.7. Niche breadth (B_i) and absolute (n) and relative (%) abundances of small-mammal species in each habitat type for Little Chinquapin Mountain.

		Clearcut								Forest								Edge					
		LC3W		LC3S		LC5		SoCr		LC3W		LC3S		LC5		SoCr		LC3W		LC3S		LC5		SoCr	
	B_i	n**	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Pe ma*	10.96	128	81.0	119	85.6	83	55.3	64	49.2	92	59.4	83	66.9	57	39.3	47	40.2	55	32.4	51	48.1	21	15.7	24	24.5
Ta spp.	10.83	22	13.9	13	9.4	37	24.7	39	30.0	50	32.3	36	29.0	49	33.8	59	50.4	78	45.9	46	43.4	69	51.5	65	66.3
So tr	7.83	+		+		2	1.3	2	1.5	3	1.9	+		3	2.2	4	3.4	1	0.6	5	4.7	2	1.5	2	2.0
Sp la	5.82	5	3.2	1	0.7	1	0.7	+		4	2.6	5	4.0	4	2.8	+		+		1	0.9	+		+	
Cl ca	5.60	+		+		3	2.0	2	1.5	4	2.6	+		17	11.7	4	3.4	36	21.2	2	1.9	36	26.9	6	6.1
Mi lo	4.89	3	1.9	+		22	14.7	22	16.9	1	0.6	+		13	9.0	1	0.9	+		+		6	4.5	1	1.0
Sp be	3.03	+		6	4.3	2	1.3	1	0.8	+		+		+		1	0.9	+		+		+		+	
Gl sa	1.97	+		+		+		+		1	0.6	+		+		+		+		1	0.9	+		+	
Th ma	1.00	+		+		+		+		+		+		+		1	0.9	+		+		+		+	
Pe pa	1.00	+		+		+		+		+		+		2	1.4	+		+		+		+		+	
Mu spp.	++	1		1		+		+		+		+		+		+		+		+		+		1	

* Pe ma, Peromyscus maniculatus; Ta spp., Tamias spp.; So tr, Sorex trowbridgeii; Sp la, Spermophilus lateralis; Cl ca, Cletrhionomys californicus; Mi lo, Microtus longicaudus; Sp be, Spermophilus beechyi; Gl sa, Glaucomys sabrinus; Th ma, Thomomys mazama; Pe pa, Perognathus parvus; Mu spp., Mustela frenata and Mustela ermina.

**One individual can be counted in more than 1 habitat per site.

+ Not captured in this habitat and site

++ Mustela spp were not included in small-mammal community analyses.

Table I.8. Small-mammal community composition parameters for Little Chinquapin Mountain and Buck Peak sites.

Community composition parameter	Habitat*	1981 LC3W	1981 LC3S	1981 LC5	1981 SOCR	1982 SE	1982 SW	1982 West	1982 North
Species richness (S_j)	C	4	4	7	6	5	4	5	5
	E	7	3	7	7	7	5	5	6
	F	4	6	5	5	7	7	4	6
Species diversity (H'')	C	0.63	0.53	1.18	1.18	1.23	1.16	1.23	1.32
	E	1.01	0.76	1.44	1.07	1.57	1.43	1.31	1.46
	F	1.08	1.02	1.19	0.91	1.54	1.61	1.35	1.34
Evenness (J_H)	C	0.454	0.379	0.607	0.657	0.761	0.834	0.767	0.819
	E	0.516	0.689	0.740	0.547	0.808	0.888	0.814	0.815
	F	0.780	0.570	0.738	0.568	0.796	0.826	0.973	0.747
Unweighted mean niche breadth ($\overline{B}_j$)	C	8.13	7.67	7.00	7.19	10.13	10.58	10.13	10.13
	E	6.85	9.21	6.71	6.31	8.27	10.13	10.13	9.17
	F	8.81	7.17	8.03	8.03	8.27	8.27	10.58	9.17
Weighted mean niche breadth ($W\overline{B}_j$)	C	10.69	10.60	9.77	9.72	11.13	11.23	11.17	10.98
	E	10.51	10.74	9.41	10.41	10.28	10.67	11.05	9.97
	F	9.76	10.54	9.14	10.43	9.86	9.94	10.84	9.33

*C, clearcut; E, edge; F, forest.

Table I.9. Factor structure for significant small-mammal two group discriminant functions by species and discriminant analysis category, Little Chinquapin Mountain. Only those variables with r >.300 are given. At α = .01, r ≃ .181 for n = 194.

	Discriminant category									
	All sites combined		LC3W, LC3S		LC5, SoCr		all clearcuts		all forests	
	variable	r	variable	r	variable	r	variable	r	variable	r
Peromyscus maniculatus	MAT**	.525								
	DUFF	.447	NS*		NS		NS		NS	
	OVRDNS	.436								
	HBSPP	.403								
Tamias spp.	OVRDNS	.479	OVRDNS	.576			TLOGS	.519		
	DUFF	.466	NLOGLEN	.555	NS		DUFF	.492	NS	
	TSTUMP	-.483	TSTUMP	-.483			OVRDNS	.484		
	NLOGLEN	.421	DUFF	.466			HBSPP	.415		
	MAT	.310	SHRB	.369			LOGCO	.404		
			HRB	-.360						
Microtus longicaudus	FHD	.593			FHD	.646			NLOGDI	.629
	HRB	.587	NS		HRB	.394	NS		HRB	.429
	NLOGDI	.420			SHRB	.366			HBSPP	.341
					NLOGDI	.366			CANCO	-.339
Clethrionomys californicus	NS		TSTUMP	-.576						
			SHRB	.576	NS		NS		NS	
			FHD	.502						
			NLOGLEN	.410						
			DUFF	.333						

* Discriminant analysis resulted in a non-significant discriminant function.
** For Peromyscus, these variables have significantly greater mean values for the absence group.

Table I.10. Factor structure, univariate one-way F values with associated P values, and species group with the greatest mean value among species DF1 discriminating variables, Little Chinquapin Mountain.

Variable	r	F	P	Largest mean
TSTUMP	-.450	2.62	.051	Microtus
DUFF	.445	2.58	.054	Clethrionomys/Tamias*
OVRDNS	.441	2.65	.049	Tamias
HRB	-.413	4.61	.004	Microtus
FHD	-.371	3.48	.016	Microtus
NLOGLEN	.200	2.25	.082	Clethrionomys
MAT	.182	1.79	.148	Microtus/Clethrionomys*

*Groups have similar means.

Table I.11. Discriminant function parameters with associated factor structure, Buck Peak sites. Variables with P ≤.05 for correlations any with significant function are given. At α = .05: r = .164 for n = 144; r = .117 for n = 288.

	All clearcuts g = 4, n = 144		All forests g = 4, n = 144			All clearcuts and adjacent forests; g = 8, n = 288		
	Discriminant function							
	1	2	1	2	3	1	2	3
Eigenvalue	0.797	0.425	0.904	0.618	0.462	1.409	0.450	0.398
Percent variance	54.1	28.9	45.6	31.1	23.3	51.0	16.3	14.4
Σpercent	54.1	83.0	45.6	76.7	100.0	51.0	67.3	81.7
Canonical correlation	.666	.546	.689	.618	.562	.765	.557	.534
Wilk's λ	.312	.561	.222	.423	.684	.127	.307	.445
X^2, df	151.3,66	75.1,42	197.1,60	112.7,38	49.7,18	561.6,147	322.1,120	220.8,95
	P ≤.001	P ≤.005	P ≤.001	P ≤.001	P ≤.001	P ≤.001	P ≤.001	P ≤.001
Habitat variable:								
TWL	-.579	.353	.526	-.106	-.219	.691	.274	-.190
SHRB	.502	-.113	.103	.283	.549	-.310	.090	.616
WSPP	.232	.230	-.203	.019	.080	.028	-.225	-.113
HRB	.365	-.404	---	---	---	---	---	---
BRGD	-.185	.289	-.375	.030	.350	-.381	-.003	-.047
AVLOGLN	.126	.238	.364	-.122	-.320	.282	.094	.008
HBSPP	.241	.373	-.428	.183	-.284	-.233	-.138	-.428
TSTUMP	.200	.125	-.110	.054	-.333	-.142	-.005	-.158
DUFF	.160	-.012	-.103	-.318	-.096	.049	-.254	.027
TLOGS	-.264	-.219	.221	.408	-.156	-.015	.498	-.010
LOGDENS	-.215	.117	.142	.256	-.011	.018	.323	-.044
NLOGLEN	.096	.210	.310	-.152	-.018	.136	.051	.180
OVRDNS	.092	.184	.283	-.146	-.028	.351	.007	.132
THIK	---	---	.488	-.283	.044	.510	-.016	.350
MAT	---	---	.313	-.242	-.117	.287	-.004	.031
LOGCO	---	---	.298	-.037	-.265	.318	.118	-.040
FHD	---	---	.271	.157	.240	.009	.224	.298
AVLOGDI	---	---	.220	-.151	.167	.221	-.072	.241
TWP	---	---	.203	-.072	-.016	.237	-.033	.075
CANCO	---	---	.239	-.492	-.017	.542	.378	.086
SNGDNS	---	---	---	---	---	.226	.049	.081
NLOGDI	---	---	---	---	---	.163	-.032	.097

Table I.12. Factor structure for the first 3 principal components, Buck Peak. Values for habitat variables are correlation coefficients for variable values with the principal component after VARIMAX rotation. At $\alpha = .05$, $r \simeq .116$ for $n = 288$.

Principal component	1	2	3
Eigenvalue	4.58	2.28	1.81
Percent variance	21.8	10.8	8.6
Cumulative percent	21.8	32.7	41.3
Habitat variable			
THIK	.793	.119	-.164
CANCO	.792	.129	.133
OVRDNS	.784	.151	-.010
TWL	.740	.077	.095
MAT	.631	.077	.046
BRGD	-.534	-.194	-.230
HBSPP	-.402	.010	-.036
LOGCO	.253	.570	.496
SHRB	-.246	.088	-.005
AVLOGLN	.220	.724	-.024
FHD	.145	.018	-.022
WSPP	.110	.048	-.242
LOGDENS	-.099	.005	.730
AVLOGDI	.081	.768	.020
NLOGLEN	.080	.739	-.014
TLOGS	-.053	-.062	.841
NLOGDI	.045	.730	-.044
TSTUMP	-.014	.042	-.047

Table I.13. Niche breadth (B_1) and absolute (n) and relative (%) abundances for small-mammal species in each habitat, Buck Peak, 1982.

		Clearcut								Edge								Forest							
		SE		SW		West		North		SE		SW		West		North		SE		SW		West		North	
	B_1	n**	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Sp la*	11.51	38	24.0	49	35.0	46	34.9	32	19.9	24	17.8	46	28.9	48	35.6	34	21.4	22	15.9	21	16.0	51	34.2	30	25.4
Pe ma	11.21	61	38.6	44	31.4	47	35.6	63	39.1	47	34.8	38	23.9	36	26.7	37	23.3	15	10.9	22	16.8	32	21.5	15	12.7
Ta am	11.06	53	33.5	45	32.1	34	25.8	52	32.3	23	17.0	40	25.2	40	29.6	21	13.2	44	31.9	38	29.0	42	28.2	4	10.8
Ta si	8.53	4	2.5	2	1.4	3	2.3	10	6.2	31	23.0	33	20.8	10	7.4	60	37.7	46	33.3	39	29.8	24	16.1	57	48.3
Mi lo	8.32	2	1.3	+		2	1.5	4	2.5	6	4.4	2	1.3	1	0.7	1	0.6	4	2.9	4	3.1	+		1	0.8
Cl ca	4.41	+		+		+		+		3	2.2			+		6	3.8	5	3.6	5	3.8	+		11	9.3
So tr	2.87	+		+		+		+		1	0.7	+		+		+		2	1.5	2	1.5	+		+	

* Sp la, Spermophilus lateralis; Pe ma, Peromyscus maniculatus; Ta am, Tamias amoenus; Ta si, Tamias siskiyou. Mi lo, Microtus longicaudus; Cl ca, Clethrionomys californicus; So tr, Sorex trowbridgeii;

** One individual can be counted in more than 1 habitat per site.

+ Not captured in this habitat and site.

Table I.14. Factor structure for significant small-mammal two group discriminant functions by species and discriminant analysis category, Buck Peak sites. Only the first five variables for each species are listed. All r values are significant at $\alpha = .05$.

	Discriminant category									
	All sites combined		SW		W		N		All forests	
	variable	r	variable	r	variable	r	variable	r	variable	r
Peromyscus maniculatus	CANCO+	.791	NS*		NS		CANCO+	.616	CANCO+	.674
	THIK	.657					TWL	.571	THIK	.550
	TWL	.635					BRGD	-.431	OVRDNS	.524
	OVRDNS	.594					THIK	.401	TWL	.497
	BRGD	-.478					OVRONS	.396	MAT	.419
Tamias amoenus	CANCO	-.687	CANCO+	.597	NS		TWL	-.641	CANCO+	.676
	THIK	-.561	OVRDNS	.436			CANCO	-.551	MAT	.595
	OVRDNS	-.540	TWL	.427			BRGD	.517	TWL	.566
	TWL	-.507	MAT	.421			SHRB	.435	THIK	.549
	MAT	-.459	AVLOGLN	.419			MAT	-.435	OVRDNS	.541
Tamias siskiyou	TWL	.812	TWL	.617	AVLOGLN	.469	TWL	.710	TWL	.689
	CANCO	.585	HBSPP	-.513	TWL	.323	CANCO	.559	HBSPP	-.517
	THIK	.543	CANCO	.443	AVLOGDI	.306	THIK	.425	THIK	.461
	BRGD	-.478	TWP	.428	NLOGDI	.301	HBSPP	-.382	BRGD	-.434
	MAT	.464	BRGD	-.388	TWP	.244	SHRB	-.358	MAT	.409
Clethrionomys californicus	THIK	.726	NS		NS		CANCO	.505	THIK	.633
	CANCO	.697					TWL	.479	CANCO	.590
	OVRDNS	.683					THIK	.465	OVRDNS	.589
	TWL	.615					BRGD	-.432	TWL	.558
	TWP	.473					MAT	.368	TWP	.450

* Discriminant analysis resulted in a non-significant disriminant function.

\+ These variables have significantly greater means for the absence group.

Table I.15. Factor structure, univariate one-way F values, and species group with the greatest mean value among species DF1 discriminating variables, Buck Peak. All F values are significant at P <.001.

Variable	r	F	Group with largest mean
CANCO	.796	36.7	Clethrionomys/T. siskiyou*
THIK	.747	32.2	Clethrionomys
TWL	.746	32.4	T. siskiyou
OVRDNS	.679	26.8	Clethrionomys
BRGD	-.485	13.8	Spermophilus/Peromyscus*
SNGDENS	.459	12.3	Clethrionomys
AVLOGLN	.450	11.8	T. siskiyou/Clethrionomys*
MAT	.431	11.2	Clethrionomys
TWP	.389	9.2	Clethrionomys
HBSPP	-.372	8.3	T. amoenus/Peromyscus*
LOGCO	.363	7.6	Clethrionomys
NLOGLEN	.301	5.5	Clethrionomys

*Groups have similar means.

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CHAPTER II

SMALL-MAMMAL DISPERSAL OF MYCORRHIZAL FUNGAL SPORES INTO SOUTHWESTERN OREGON CLEARCUTS

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ABSTRACT

Small-mammal dispersal of mycorrhizal fungal spores from variously structured forests into adjacent clearcuts was studied in nine study sites in southwestern Oregon from 1980 to 1982. Sampled habitats, resulting from various silvicultural treatments, varied greatly in overall structural components. A preliminary phase in 1980 sampled, via live trapping, spore dispersal from a mixed conifer forest into an adjacent 16 year-old clearcut.

In 1981, 11 species were captured over four study sites at Little Chinquapin Mountain, Jackson Co., Oregon. Two sites included clearcuts treated for slash disposal; the remaining two included untreated clearcuts. Only deer mice (Peromyscus maniculatus) and chipmunks (Tamias spp.) moved among the clearcut, edge and forest habitats of every site. When between-species differences occurred in distances traveled from one habitat into another, chipmunks always traveled farther than deer mice. No consistent effect of clearcut treatment was observed on movements of either species.

Twenty-four fungal genera were identified in fecal samples taken from live-trapped chipmunks and deer mice in one treated and one untreated clearcut and adjacent forests. Rhizopogon, Leucogaster, Gautieria, and Melanogaster were the most commonly occurring genera. Chipmunks consumed more kinds of fungi than did deer mice. Fungal frequencies of occurrence in the total sample were highly correlated with average spore abundance values per species and habitat over the two sites. Chipmunk samples contained significantly more spores in the untreated clearcut and forests. In every habitat chipmunks had more spores per sample than deer mice. For chipmunks, spore numbers in multiple samples from individuals captured in ≥ 2 were less in clearcut than forest samples in the treated site; no differences were observed in multiple samples from untreated site. Dispersal of fungal spores was considered to be a more important activity in the treated site.

In 1982, seven small-mammal species were captured at Buck Peak, Klamath Co., at four sites along the edge of a single clearcut. Golden-mantled ground squirrels (Spermophilus lateralis), deer mice, Siskiyou chipmunks (Tamias siskiyou), and yellow pine chipmunks (T. amoenus) traveled among the three habitats. Some differences in distances traveled among species within habitat were calculated.

Twenty-two fungal genera were observed in fecal pellet samples from the three sites. Small-mammal species differed significantly in spore abundance per sample: T. siskiyou > Spermophilus > Peromyscus > T. amoenus. The total sample (all species combined) varied significantly among the clearcuts as well as among forests with the most forested sites exhibiting the greatest mean spore values for both habitats. For individual species, T. siskiyou and Spermophilus each differed in the forests and in the clearcuts; spore abundance was the greatest in the North site. Multiple samples in different habitats contained similar quantities of spores.

For both years, habitat structure remaining after logging was hypothesized to be of prime importance in availability of inocula for disturbed sites. Both the small-mammal communities and fungal communities respond to habitat alteration. To maximize availability of inocula, forests adjacent to clearcuts should be left undisturbed.

INTRODUCTION

Mycorrhizal fungi and most vascular plants form an obligatory symbiosis whereby each participant receives from the other important materials as well as other benefits (Marks and Kozlowski 1973). This association is important to conifer seedlings in all sites (Mikola 1970, Molina and Trappe 1982, Wright 1957). In forest soil, mycorrhizal associations are established by direct contact between the host rootlet and existing mycorrhizae or fungal spores. Removal of host species by logging adversly affects their mycobiants. Clearcutting a forest can result in the elimination of active

mycorrhizae (Harvey et al. 1980) and their fruiting bodies (sporocarps). Thus, the inoculum potential of mycorrhizal fungi for newly planted seedlings in clearcuts is low or nonexistant.

Most, if not all, forest-dwelling small mammals consume various kinds and quantities of fungal sporocarps and egest viable spores (Fogel and Trappe 1978, Maser et al. 1978b, McIntire 1984, Trappe and Maser 1976). Hypogeous (subterranean) sporocarps, as opposed to epigeous fungi (mushrooms), consistently comprise the greatest portion of the fungal diet. These types depend on mycophagous species for spore dispersal. Sullivan et al. (1984) reported the probable dissemenation of the conifer seed fungus Caloscypha fulgens by Douglas squirrels (Tamiasciurus douglasii). Tevis (1952) suggested that mycophagous small mammals could be a source of fungal inocula for disturbed sites. Mycophagous small mammals, therefore, are thought to be a major source of hypogeous, naturally occurring inocula for devastated soil.

Logging affects small-mammal populations through habitat alterations (Gashwiler 1970, Hooven and Black 1976, Kirkland 1978, Martell and Radvanyi 1977, Tevis 1956). Some mycophagous species decline in number or disappear after clearcutting; others increase. The numbers and distances of movements into adjacent clearcuts by forest mammals, and, hence, the availability of inoculum of these areas, also may be directly related to habitat structure, a function of severity of disturbance.

Our study had three objectives: to identify mycophagous small-mammal species in southwestern Oregon forests and adjacent clearcuts, to identify those species that act as major fungal dispersers into clearcuts, and to examine the effects of various habitat structure on observed and potential spore dispersal. Major fungal dispersers are those that occur in both clearcuts and forests in relatively large numbers and/or move frequently between forest and clearcut and, concomitantly, excrete pellets containing large numbers of spores. Thus, abundant small-mammal species that frequently traveled between habitat types and consistently consumed various fungi would be primary dispersers.

METHODS

Study Design

Our study was carried out during the summers of 1980 through 1982. Three different study areas, located in southwestern Oregon, were used. In 1980, a preliminary phase was conducted in an older mixed conifer forest and adjacent clearcut in Jackson County at 1400 m elevation. A 4.39 ha sampling grid, with an interpoint interval of 15 m, was set out with half in the forest and half in the clearcut.

In 1981, three large (260 ha) clearcuts were selected in the Little Chinquapin Mountain area of northeast Jackson County, approximately 19.3 km South of the 1980 site but in the same forest type. Two trapping sites were set out over portions of the clearcut, edge, and forest along the West (LC3W) and South (LC3S) boundaries of one intensively prepared clearcut. Two separate but similar undisturbed clearcuts (LC5, SoCr), 2.7 km apart, were selected as controls to examine site preparation effects on small-mammal movements (Appendix 1).

The prepared clearcut was characterized by heavily disturbed mineral soil with scattered large, burned logs, log piles, and an extensive cover of large herbaceous plants dominated by Cirsium vulgare (Savi) Tenore and Verbascum thapsus L. In contrast, the unprepared sites contained small patches of forest habitat and a variety of herbaceous species.

In 1982, we examined the effects of varying forest structure on small-mammal movements. Four study sites were established around the South, West, and North sides of a 260 ha clearcut near Buck Peak, Klamath Co., at 1750 m elevation. Two sites (SE, SW) were selected on the southern boundary of the clearcut, the adjacent forest area having been subjected to a shelterwood cut in 1973-74 and a final overstory removal in 1980. The West site's forest, shelterwood cut in 1978, was characterized by a low density of large

even-aged overstory trees with little understory. The North forest was an uncut, uneven-aged stand with a well-developed understory (Appendix 1).

The 1980 sampling design was altered for 1981 and 1982 because movement data from livetrapping grids may be biased. Hayne (1950) reported that the observed distances moved by captured small mammals within a trapping grid depended on the spacing between traps. As traps were removed and trap spacing increased, one individual was captured at increasingly greater distances to more than twice the pre-experiment maximum. Thus, traps closer to the initial point of capture presumably interfere with potential movements to more distant traps. Because we wanted to sample movements to traps at specific and increasing distances from the edge into the clearcut and forest, we used a modified grid design that excluded traps between those at the edge and at each sampled distance. We set out three sets of two parallel transects centered on the edge line with 15 m and 30 m between the points and transect sets, respectively. Each transect consisted of 10 sample points (one segment) and was offset 7.5 m from the other. Corresponding pairs of transects were placed at 15 m intervals into the forest and clearcut, with only one transect per distance, to a distance of 97.5 m from the edge line. Thus, a total of 60 points were placed in each of the three habitat types (Fig. I.1). This design was repeated in 1982.

Livetrapping

In 1980, one Sherman livetrap was placed within 1 m of every grid point. Conventional data were gathered for toe-clipped small mammals for 16 days from 11 August to 7 September. Traps were checked twice daily and baited with rolled oats and sunflower seeds when necessary. Fecal pellets were taken from live animals and placed in marked vials containing 0.5 cc of 10 percent formaldehyde.

In 1981, we alternately trapped two of the four sites for ten days during each of two trapping periods from 29 June through 22

August. Edge traps were first checked for five days. Clearcut and forest traps were set and checked for the second five day period. The total number of trap nights was 12,720 for the four study sites. In 1982, this trapping design was repeated in each of the four Buck Peak sites from 28 June through 29 August. The total sampling effort was 13,680 trap nights.

Distance Calculations

Intersegment movements were defined and counted as the number of transect segments between one trap location and the next, regardless of time elapsed between captures but within one or the other trap period. Each transect unit equaled 15 m. Thus, these measurements do not represent the actual distance between stations, but rather distance perpendicular to the edge. Also, more than one movement could be recorded per individual.

To calculate maximum distances that fungal spores were moved by small-mammals, the intersegment distance between those two locations at which fecal samples were taken giving the greatest distance per individual were recorded for interarea movements only. Elapsed time was not a criterion.

Captured individuals were also counted in seven categories consisting of each habitat type (clearcut, edge, and forest) as well as every combination of habitat types. An animal could be counted in only one category. These counts are an indication of among habitat movements.

Fecal Pellet Analyses

For the 1980 fecal samples, analysis of spore content was performed on selected samples representing abundant small-mammal species captured throughout the grid. The presence of fungal genera was recorded (McIntire 1984) for each sample to identify target species for subsequent study.

For initial spore analyses for the Little Chinquapin Mountain and Buck Peak sites, samples were randomly chosen representing all species in all sites. Thus analyses indicated that the kinds and quantities of consumed fungi were consistent within species among sites. We therefore selected subgroups of samples from one site of each clearcut treatment in 1981 and from three sites representing the three forest types in 1982. The total number of samples examined per site were: 163, LC3W; 195, SoCr; 255, SE; 284, West; and 287, North. Analyses of samples from LC5 (75 samples examined), LC3S (85), and SW (73) were variously completed.

Subgroups were chosen representing only those small-mammal species exhibiting the greatest abundance, movements, and spore abundances throughout the habitat areas over all sites. For inclusion into this analysis, a species must have moved among the three habitats. Samples were grouped by species and individual within a site. Two groups resulted: one comprised of multiple samples taken from the same individual at different locations, the other of single samples from different individuals. Six samples, three from each trap period, were selected for each transect segment, or distance, from the first group so that the number of different habitats per individual was maximal. If these samples were too few in number, then samples from the second group were randomly selected to complete the required number per segment. Six samples per segment and species were not always available, however. Also, if a species was particularly abundant with numerous multiple samples per site, then additional samples were analyzed to maximize information concerning fungal spore movements.

To subsequently identify the major dispersers of fungal spores, we compared, among species, the kinds and quantities of egested fungi in samples from different distances in clearcut habitats. Also, we assumed that the number of spores per fungal type and sample was generally related to the relative quantity consumed for each type. Spore number per sample, however, does indicate the inoculum potential for each small-mammal species (Kotter and Farentinos 1984).

Fecal samples were macerated and vigorously shaken within each vial. A drop of Melzer's reagent (Stevens 1974) was added to 1-2 drops of pellet solution on a glass slide. One drop of this solution was placed on the counting chamber of a hemacytometer and covered with 22 m^2 cover slip.

Spore number was approximated by counting the number of squares (maximum = 320) in which each genus occurred. These squares comprised the chamber's central mm^2. The entire chamber was then scanned to record the presence of some larger and rarer ascomycetes and Endogonaceae.

To compute spore abundance per gram of fecal sample, we used a variation of the index given by Hayes et al. (in press):

$$SNI = S_{ijs}/W_s/P_{is},$$

where SNI is the spore number index per sample, S_{ijs} is the number of squares of the jth genus in the ith sample for mammal species s, W_s is the average fecal pellet weight for species s, and P_{is} is the number of pellets in the sample. All SNI values per sample were also summed for each sample to give a second index, TSNI.

From 19 (Microtus longicaudus) to 73 (Tamias amoenus) pellets per species per year were oven dried for 24 hr at 70°C and then weighed to the nearest 0.0001 g. These weights were averaged for each species and year and entered into the above equation.

Only those species that exhibited movement among the three habitats were considered capable of dispersing spores. Actual spore dispersers were defined as those individuals whose samples, taken in >1 habitat, contained spores in $\geq$2 habitats. Probable spore dispersers were defined as those individuals exhibiting mycophagy in one of $\geq$2 habitats.

STATISTICAL ANALYSIS

Species Occurrence by Habitat

Independent occurrence of individuals within the seven habitat categories for Little Chinquapin Mountain sites was examined for each species using chi-square analyses. Single classification with equal expectations (a priori) was applied to abundance data of deer mice and chipmunks for the three non-movement categories in each of the four sites. This procedure was repeated for the four movement categories (clearcut-edge-forest, edge-forest, edge-clearcut, and clearcut-forest). The edge-clearcut and edge-forest categories were compared between the two sites in each treatment category. Between site differences within treatment categories (LC3W vs. LC3S, LC5 vs. SoCr) for movement and non-movement categories were examined using a posteriori RxC contingency tables (Sokal and Rohlf 1981).

Movements

Each movement consisted of two distance components. First, the net distance traveled by individual small mammals into the clearcut or forest of each site was defined as that portion of a movement occurring in the object habitat as measured from the corresponding edge transect (Line A or B) to the segment of termination. For example, a chipmunk initially captured 45 m into the forest and subsequently captured 30 m from the A line into the clearcut would exhibit a net forest-to-clearcut movement of 30 m. Net distances were compared within sites between directions and between species per direction using the nonparametric Wilcoxon rank test. Net distances for each direction per species were compared using the Kruskal-Wallace procedure (Snedecor and Cochran 1980). Secondly, total distances traveled per individual were calculated as the perpendicular distance between two successive points of capture in different habitats. Total net distances into clearcut or forest, as

proportions (P_c or P_f) of the total distance traveled per species, were used to examine relationships between the presumed habitat affinities of species and their movement into adjacent habitat.

Spore Abundance

For the 1981 fecal samples, detailed analysis was performed on Tamias and Peromyscus data since these were the only species that moved among the three habitats in every site. Due to non-normal distributions of SNI and TSNI values per sample, SNI and TSNI values were transformed by log(x+1). Further analysis used log(TSNI) values only. To examine differences in spore abundance per species and habitat, two-way analyses of variance (ANOVA, Nie et al. 1975) on samples with TSNI >0, using the regression approach due to unequal sample sizes, included species by habitat (clearcut or forest) over LC3W, SoCr, and LC3S, and species by LC3W and SoCr clearcut and either one or the other, or both combined, adjacent forests. One-way ANOVA (ONEWAY, Nie et al. 1975) was used to examine log(TSNI) values for each species over three sites, the three clearcuts, and the three forests, as well as the LC3W and SoCr clearcuts and forests, as above. To identify specific habitat effects on spore abundance, a posteriori contrasts of group means were examined using the Scheffe test for the latter one-way ANOVA. For all one-way analyses characterized by heteroscedasticity and/or small sample sizes, the Kruskal-Wallace nonparametric procedure was used to verify these results.

Log(mean TSNI) values per transect segment per site and species were calculated to examine associations between spore abundance and distance using Spearman rank correlation coefficents (Sokal and Rohlf 1981). Spearman and Pearson r values were also calculated for both species' fungal frequencies and species' mean log(TSNI) values per habitat and site.

Differences between multiple samples in the clearcut and forest

per site and species were examined using a t-test (T-TEST, Nie et al. 1975). Differential spore occurrence per individual in two movement categories, edge-clearcut and edge-forest, was examined using paired t-tests on log(mean TSNI) values per individual in each movement category (Snedecor and Cochran 1980).

The foregoing analyses were repeated for the 1982 data for Tamias amoenus, T. siskiyou, P. maniculatus, and Spermophilus lateralis. One-way ANOVA designs included each species over all sites, all clearcuts, and all forests. Additional one-way analyses were for all species combined over each clearcut and each forest, as well as for each species in each of three forests and in each of the three clearcuts. Two-way designs included the four species by two habitats (clearcut and forest) over each of the three sites, and over all sites combined, as well as four species by the three forests.

RESULTS

Preliminary Phase, 1980

Areas of Occurrence

A total of 254 individuals representing 11 species were captured during 7168 trap nights, or 3.502 individuals per 100 trap nights. Only two species occurred in each of the seven possible habitat categories (Table II.1).

Movements

Tamias traveled farther into the clearcut than did any other species. Of the 31 Tamias individuals moving between the edge and clearcut, 10 (32.3 percent) exhibited maximum movements of 90 m; the average maximum distance between these areas was 57.1 m. In contrast, only one ground squirrel traveled 75 m into the clearcut; the average was 39.4 m. One deer mouse traveled 90 m, with the average being 48.4 m.

Mycophagy

A total of 222 fecal pellet samples were examined, 163 (73.4 percent) of which contained ≥1 fungal spore genera (Table II.2). A total of 17 genera were recorded; at least 15 are hypogeous mycobiants. Rhizopogon spp. were the most common. Other common basidiomycetes were Leucogaster, Gautieria and Hysterangium species. Geopora was the most common ascomycete. Various Endogonaceae were also peresent.

All Spermophilus samples contained ≥1 fungal genera (Table II.2); 31 (56.4 percent) contained ≥4 kinds. Spores were observed in 62.3 percent of the Tamias samples; only 17 (13.9 percent) contained ≥4 types. For Clethrionomys, 95 percent of the samples contained spores. Of these, 7 (35.0 percent) had ≥4 kinds; 14 (70 percent) contained ≥3 genera.

Only Tamias and Spermophilus exhibited dispersal among habitats. Three golden-mantled ground squirrels were actual spore dispersers; a sample from each was taken at 15, 30 and 60 m into the clearcut. Three actual and one potential chipmunk dispersers were captured in the clearcut at distances of 15, 30, 30, and 90 m.

The results of the preliminary phase indicate that forest dwelling sciurids traveled from the forest into the clearcut and undoubtedly carried spores of mycorrhizal fungi between habitats. Also, deer mice and red-backed voles certainly exhibited the potential for doing so. Thus, continued study of the role of small mammals as spore dispersers was warranted.

Little Chinquapin Mountain, 1981

Areas of Occurrence

Eleven species were captured in the four sites (Chapter I). Of these, four species (Spermophilus beechyi, Glaucomys sabrinus, Thomomys mazama, and Perognathus parvus) were present in only one or two habitats over all sites.

Concerning small-mammal species abundances in the non-movement habitat categories (Table II.3), chi-square analysis indicated that Tamias spp. occurred in signficantly greater ($P \leq .005$) numbers within each of the four forests. Peromyscus, conversely, did so ($P \leq .005$) within the clearcuts. Clethrionomys numbers were greater ($P \leq .005$) in the LC5 forest, but no difference was found among habitats in SoCr ($P > .25$).

Tamias spp. numbers within the four movement categories (Table II.3) differed significantly ($P \leq .005$) for each site due to greater edge-forest movement. Peromyscus exhibited greater edge-clearcut numbers ($P \leq .005$) in each site.

Separate a posteriori chi-square comparisons of the three non-movement categories for both Tamias and Peromyscus between LC3W and LC3S, and between LC5 and SoCr, indicated that each species' abundances in the three habitats were similar between sites ($P > .10$). Analyses of the movement categories gave similar results.

The foregoing results indicate moving and non-moving chipmunks occurred in the edge and forest. Peromyscus used the edge and clearcut. Clethrionomys, Microtus, and Spermophilus lateralis exhibited little movement among habitats (Table II.3).

Interhabitat Distances

Tamias spp. traveled a presumably greater average distance from the edge and clearcut into the forest than from the edge and forest into the clearcut in LC3S and LC5 (Table II.4). An opposite trend was indicated for LC3W and SoCr. Peromyscus individuals traveled farther into the clearcuts than forest in every site.

For Tamias, P_f values (Table II.4) are consistently greater than P_c values regardless of the average distance traveled into either habitat. Chipmunks, therefore, traveled a greater distance in the forest when moving from the edge or clearcut than in the clearcut when moving from the edge or forest. P_c and P_f values for SoCr were similar, however. For Peromyscus, relative magnitudes of P_c and P_f values were consistent with that habitat exhibiting

the greater average distance except for LC3W where $P_f > P_c$. Thus, habitat affinities of chipmunks were reflected in P_c and P_f values, but no pattern was evident for deer mice. Also, differences between clearcut habitats may account for these differences in chipmunk P_f and P_c values, but no consistent trend was observed. These differences were not statistically determined, however.

Results of the Wilcoxon rank test comparing forest and clearcut movement distances, by site and species, indicated that movements into clearcuts were greater than movements into forests for Tamias ($P = 0.019$) and Peromyscus ($P = 0.024$) in SoCr. Ranks of individual distances did not differ for the other three sites.

Comparisons of Tamias with Peromyscus distances per direction and site indicated that these species differed in LC3S ($P = .002$) and SoCr ($P = .003$) for clearcut movements, and in LC3W ($P = .045$) and SoCr ($P = .003$) for forest movements. In every case, chipmunks exhibited greater distances than did deer mice. Among-site Kurskal-Wallace comparisons of distances traveled by each species indicated no significant differences for either direction.

Between-species differences for either direction traveled, as well as within-species differences between directions, were inconsistent within clearcut treatment categories. No specific habitat effect was evident for either species. Chipmunks, however, generally traveled a greater proportion of a forest movement in the forest habitat (Table II.4).

Mycophagy

General Characteristics. A total of 24 fungal genera representing three classes was identified in 358 samples taken from chipmunks and deer mice captured in LC3W and SoCr (Table II.5). Rhizopogon was the most commonly occurring genus in each habitat in samples from chipmunks. Other common basidiomycetes were Leucogaster, Gautieria, and Melanogaster. In samples from deer mice, Leucogaster was the most frequently encountered genus in the

LC3W clearcut but occurred equally with Rhizopogon in the SoCr clearcut.

Chipmunk samples contained 14 and 16 genera in the LC3W and SoCr clearcuts, respectively. Less than half the samples taken in the LC3W clearcut contained Melanogaster, the second ranked type in this habitat and fifth ranked type in the SoCr clearcut. Eighteen and 20 genera where identified in samples taken from the two forests.

Fewer deer mice than chipmunks ate far fewer types of fungi; only six and eight genera were recorded for samples from the LC3W and SoCr clearcuts, respectively (Table II.5). In the LC3W forest, however, deer mice consumed a total of 16 types but ate only six in the SoCr forest. The occurrence of less common basidiomycetes and ascomycetes unique to the LC3W forest samples accounted for this difference.

Fungal frequencies of occurrence and mean log(TSNI) values for Peromyscus and Tamias combined were significantly correlated over LC3W and SoCr ($r = .929$, $P < .01$; $r_s = .946$, $P \leq .01$).

Spore Abundance and Distance From the Edge. Log(mean TSNI) values per trapping transect for chipmunks exhibited a significant negative association with distance from the forest into the clearcut at LC3W ($r_s = -.591$, $P \leq .05$, Fig. II.1). No relationship was evident when evaluating values from the forest to the edge ($r_s = -.250$, $P > .05$), however. Thus, decreasing TSNI values from the edge into the clearcut ($r_s = -.771$, $P \leq .01$) account for most of the overall negative association. Rhizopogon, Leucogaster, and Melanogaster comprised the greatest proportion of the total sample per clearcut transect. At SoCr, TSNI values remained fairly constant into the clearcut (Fig. II.1). Rhizopogon was the most abundant genus at each distance throughout the entire site. In the LC3W clearcut, the decline in spore abundance with distance could result from the following: animals entering the clearcut from the forest may defecate closer to the edge, on average, than at greater distances into the clearcut. If little or no fungi was available in

the treated clearcut, then we would expect reduced spore abundances in fecal samples taken farther from the edge compared to those taken closer to the edge. At SoCr clearcut, hypogeous sporocarps occurring in islands of forest habitat would provide a widely occurring fungal resource throughout this clearcut.

Log(mean TSNI) values per transect for deer mice were quite varied over LC3W and SoCr (Fig. II.1). No significant associations between spore abundance and distance were observed for either site.

Multiple Sample Analyses. Multiple samples for chipmunks differed in spore abundance between the forest and clearcut in LC3W ($t = -6.35$, $df = 72$, $P \leq .001$) with fewer spores per sample in the clearcut, but not in SoCr ($t = 0.23$, $df = 79$, $P = .817$). These results presumably reflect increased fungal availability in SoCr clearcut. Those for deer mice exhibited the opposite pattern with greater consumption in the SoCr forest. No apparent reasons for this phenomenon were evident.

Analysis of log(mean TSNI) values per habitat per individual as paired data indicated no differential occurrence of spores in either LC3W or SoCr for either species (Table II.6). For chipmunks, mean differences (D) were less for the SoCr data. Chipmunk dispersers traveled farthest into the forest at LC3W and into the clearcut at SoCr. Statistical significance of these differences was not determined.

Results of ANOVA's. Results of the two-way ANOVA on log(TSNI) values for deer mice vs. chipmunks in the LC3W clearcut and forest indicated that between species differences ($F = 40.56$, $P \leq .001$) accounted for most of the observed variation among analysis categories. Spore content differed by habitat as well ($F = 15.37$, $P \leq .001$), interactions were insignificant. Samples from SoCr exhibited the same pattern of differential spore abundance; between species differences were much greater, however ($F = 326.28$, $P \leq .001$), and two-way interactions were significant ($F = 12.85$, $P \leq .001$).

Chipmunk samples contained significantly more spores than did those for deer mice in each habitat separately and combined over the three sites (one-way ANOVA). Comparisons of chipmunk and deer mouse spore abundances with the additional two-way ANOVAS on samples from LC3W and SoCr clearcuts with either or both adjacent forests (six cells) resulted in significantly greater log(TSNI) values in chipmunk samples. One-way analysis on chipmunk values alone resulted in highly significant differential occurrence of spores for each of the three analyses. The Scheffé procedure produced the same two groups for each run: treated clearcut samples vs. untreated clearcut plus forest samples. Results for samples from deer mice were less distinct, however, and no subgroups resulted from the Scheffé procedure. The Kruskal-Wallace X^2 statistic, however indicated significant differences when both forests ($P = .028$) and SoCr forest ($P = .040$) were used in the analysis; consumption was greater in the SoCr forest.

Summary of 1981 Results

Over all Little Chinquapin Mountain sites, only chipmunks and deer mice exhibited movement between the three habitat areas. Relatively more chipmunks than deer mice traveled between habitats (Table II.3), but the actual distances moved did not consistently differ between these two small mammals. When differences did occur, chipmunks traveled farther than deer mice. Also, no consistent clearcut treatment effect was observed on either species. Mycophagy did differ between chipmunks and deer mice. Chipmunks consumed more kinds and presumably greater quantities of hypogeous mycobiants, especially in the untreated clearcut and the two forests. Both species did transport spores into clearcuts, however. Thus, chipmunks would be considered as the primary dispersers over the Little Chinquapin Mountain sites.

Buck Peak Sites, 1982

Areas of Occurrence

Over all sites, seven small-mammal species were captured (Chapter I) and four were captured in every habitat of every site (Table II.7). Yellow pine chipmunk abundance varied among habitats in the SE ($P \leq .005$) and North ($P \leq .005$) sites, and Siskiyou chipmunk abundances varied in every site ($P \leq .005$). Numbers of golden-mantled ground squirrels did so in the SE site ($P \leq .005$), and deer mouse abundances differed among habitats in the SE ($P \leq .005$), West ($P \leq .05$), and North ($P \leq .005$) sites.

Numbers of yellow pine chipmunks differed among movement categories ($P \leq .005$) in the North site where few individuals were captured in the forest. Siskiyou chipmunk abundances varied among categories in the SE ($P \leq .005$), SW ($P \leq .005$), and North ($P \leq .005$) sites due to low clearcut numbers, and ground squirrel numbers did so in the SW ($P \leq .005$) and West ($P \leq .005$) sites. Numbers of deer mice exhibited significant differences in movement categories in every site ($P \leq .005$). Edge-clearcut vs. edge-forest abundances of each species varied significantly in direct relation to the specific habitat affinities displayed by the individuals that were categorized in the non-movement groups.

Interhabitat Distances

Only *T. siskiyou* exhibited consistently greater average distances for a given direction; these chipmunks traveled farther into the forest from the clearcut and edge than the opposite way in every site (Table II.8). Also, each species' range of average distances was greater for movements into forests over all sites except that for *T. siskiyou*. This species exhibited the greatest range in average distances into the clearcuts. Generally, P_c values are greater than corresponding P_f values for all species but *T. siskiyou*; when moving into the clearcut, the other species moved a greater proportion of a given distance in the clearcut as

opposed to distance traveled in the forest. These values are quite varied, however (Table II.8).

Differential distances traveled per direction were indicated for Siskiyou chipmunks in the SE ($P \leq .005$) and SW site ($P \leq .001$). In each case, distances moved into forests were greater than those into clearcuts (Wilcoxon rank test). Distances moved into clearcuts were greater than into forests for yellow pine chipmunks in the West clearcut ($P \leq .02$) and for deer mice in the North clearcut ($P \leq .02$).

Comparisons among species by direction and site indicated significant differences in the SW site for into-clearcut distances ($P < .01$); lack of movement by Siskiyou chipmunks contributed to this difference. Correspondingly, Siskiyou chipmunks were the only species to display significantly different into-clearcut distances ($P \leq .05$) when sites were compared. Yellow pine chipmunks moved significantly farther distances in the SW forest ($P \leq .005$) than in other forests. Thus, these small-mammal species responded differently to varying habitat structure relative to distances traveled within and between forests and clearcuts.

Mycophagy

General Characteristics. Twenty-two fungal genera were recorded for 827 samples taken from the common small-mammal species exhibiting among habitat movements throughout three Buck Peak sites (Table II.9). Rhizopogon and Glomus were the only genera to occur in samples from every species in every clearcut and forest. Spermophilus consumed an average of 12.3 genera per site. Peromyscus and T. siskiyou ate 11.2 and 10.3 types per site, respectively. T. amoenus consumed only 6.3 genera per site.

Over all forests, fungi was recorded for 95.2 percent of T. siskiyou samples. All forest samples for Spermophilus contained ≥ 1 fungal genera. For these two species, relative occurrences of the common basidiomycetes decreased in samples from the West forest relative to those from the SE forest and increased maximally in the North forests' samples.

More deer mouse samples from the three forests contained the common basidiomycetes than did those from the clearcuts. The maximum number of genera (14) recorded for deer mice was observed in North clearcut samples. Relatively few yellow pine chipmunks consumed ascomycetes or basidiomycetes; more chipmunks ate Glomus than any other kind (Table II.9).

For all small-mammal species combined, increasing numbers of individuals consuming fungi were associated with increasing spore abundances in the fecal samples. Over the SE, West, and North clearcuts, mean log(TSNI) values per species and species' frequencies of fungi were significantly correlated ($r = .720$, $df = 9$, $P \leq .01$; $r_s = .652$, $n = 11$, $P \leq .05$). This association was observed for the forests ($r = .699$, $df = 8$, $P \leq .05$; $r_s = .915$, $n = 10$, $P \leq .01$) and for the three sites combined ($r = .813$, $df = 19$, $P \leq .01$). As more fungi became available for consumption over a broad area, presumably greater concentrations of sporocarps occurred in individual foraging areas. We must assume, however, that TSNI values reflect relative consumption.

Spore Abundance and Distance From the Edge. No relationships between log(mean TSNI) values per transect and distance were evident for any species in three sites (Fig. II.2). Spore quantity per sample did not increase nor diminish for any species relative to distance into or from the forest or clearcut. A great degree of variation in spore abundance at these distances within and among species over the three sites is apparent from these graphs, however. T. siskiyou and Spermophilus exhibit the greatest consistency in larger spore numbers across every site. Chipmunk values in the West forest decrease considerably relative to the other two sites, however. T. amoenus and Peromyscus exhibit wide variations among sites; deer mouse pellets generally contained more spores than those of yellow pine chipmunks, especially in the North site.

Multiple Sample Analyses. Concerning comparisons of multiple samples, only Speromophilus in the SE site ($t = -2.24$, $df = 15$, $P = .04$) and T. siskiyou in the North site ($t = -2.02$, $df = 89$, $P = .046$) exhibited marginally different spore abundances between habitats. No differences were evident, however, in log(mean TSNI) values between habitats in either movement category for every species in the three sites (paired t-test). Thus, fecal pellets from individuals moving between habitats presumably contained similar quantities of spores. This result would explain the lack of association between spore abundance and distance noted above.

Results of ANOVA's. Results of two-way ANOVA analyses on log(TSNI) values per species and habitat over all sites combined indicated that among species differences rather than habitat accounted for most of the observed variation in spore abundance ($F = 101.5$, $P \leq .001$). Habitat effects were significant, however ($F = 6.2$, $P = .013$). No interaction effects were indicated. This phenomenon was reiterated by a separate two-way analysis for each site.

One-way ANOVA on species' spore values over all sites combined denoted highly significant among-species differences ($F = 125.5$; $df = 3,518$; $P \leq .001$). Yellow pine chipmunks exhibited the smallest mean (2.41) and Siskiyou chipmunks the largest (3.99). Heteroscedasticity was indicated, however (Bartlett-Box $F = 7.44$, $P \leq .01$); the Kruskal-Wallace X^2 statistic was significant ($X^2 = 208.1$, $P \leq .001$). Each species comprised an independent group (Scheffé procedure) with mean values ranked in this order: T. siskiyou > Spermophilus > Peromyscus > T. amoenus.

Separation of spore abundance values by small-mammal species over all clearcuts combined was somewhat less distinct, however. Although among-species differences were significant ($F = 43.1$; $df = 3,233$; $P \leq .001$), the Scheffé procedure combined deer mouse and ground squirrel values to form a total of three independent groups.

Over all forests, species differences were again significant ($F = 62.4$; $df = 3,281$; $P \leq .001$). Siskiyou chipmunk and ground squirrel values formed a single grouping with the largest mean (Scheffé procedure).

Two-way ANOVA analysis on four species in the three forest habitats indicated that among-species differences were highly significant ($F = 33.0$, $P \leq .001$) and that some forest effects were present as well ($F = 3.9$, $P \leq .020$); no interaction effects were suggested. Species-specific characteristics of mycophagy determined most of the differences in spore abundance. Differences in forest structure presumably affected the fungal resource and are reflected to some degree in spore abundance values. Further one-way analysis to examine total spore abundances of combined samples in each forest indicated differential consumption by the small-mammal species as a group within each stand ($F = 40.1$, $P \leq .001$). When considering the mycophagous species as a group greater differences between forests are observed. The SE and West forests' samples were grouped and considered distinct from those of the North forest.

Repeating this analysis for all species combined in each clearcut resulted in significant between-area differences ($F = 10.2$, $P \leq .001$). Samples from the North's clearcut exhibited the largest mean and formed one of two groups. Small mammals in this clearcut had more spores in their pellets than those in the other two clearcuts.

One-way analysis on each small-mammal species in the three forests indicated differential spore abundance among forests for *T. siskiyou* ($F = 27.8$, $P \leq .001$) and *Spermophilus* ($F = 4.9$, $P \leq .02$). These results concur with the relative distribution of spore abundances over the trap segments illustrated in Figure II.3; little overlap among the three sites occurred for *T. siskiyou*. The Scheffé procedure grouped the SE and West forests' samples; those of the North forest formed the second group for each species.

One-way analysis for each species in the three clearcuts resulted in significant differences in spore abundance for

Spermophilus samples ($F = 12.4$, $df = 2.59$, $P \leq .001$). Samples from the North clearcut formed one of the two groups. T. siskiyou exhibited an insignificant ANOVA statistic ($F = 2.8$, $P = .071$) but the Kruskal-Wallace X^2 statistic was significant ($x^2 = 7.9$, $P = .019$). Although only three samples from the West clearcut were used in this analysis, their mean rank value (7.0) was well below those of the SE (19.3) and North (26.8) clearcuts.

Summary of 1982 Results

Over the Buck Peak sites, species' abundances, movements, and mycophagy varied among habitats. Both chipmunk species exhibited greater into-forest distances in the SW site; T. siskiyou did so in the SE site as well. T. amoenus, however, traveled farther into the West clearcut, as did Peromyscus into the North clearcut. When comparing species distances within a single site, however, interspecific into-clearcut distances differed within the SW site only; species did not differ in distances moved into forests. Within a particular site, then, the different small-mammal species responded in a similar manner with little difference in distances traveled being observed. Among sites, however, a particular species in one site responded differently than in others. Spermophilus exhibited no differential distances in any site.

Species' differences in consumption of fungi were consistent among sites. For all species (4) combined and over all forests (3), a highly significant association existed between frequencies of occurrence of fungi in the total sample and the average log(TSNI) value per forest and species ($r_s = .969$); greater population-wide occurrence of fungi and greater spore abundances in the fecal samples were related. Species specific differences in spore quantitites explained more variation in the spore data than did among-site differences. No distinct linear relationships were observed between spore abundances and distances from or into different habitats. Accordingly, little difference between multiple samples from individuals in different habitats was observed.

Samples from the North forest and clearcut exhibited significantly greater abundances of spores when species were combined. Also, spore abundance in samples from Siskiyou chipmunks was significantly greater in the North forest compared to those from the other two forests. Thus, the observed consumption of fungi by these small-mammal species, and especially T. siskiyou, was presumably influenced by habitat since relative differences in consumption varied little among sites.

Spermophilus and T. siskiyou would be considered primary spore dispersers over the Buck Peak sites. Both exhibited consistently larger quantities of spores in samples taken over all habitats, and carried spores from adjacent forests into clearcuts. Speromophilus, however, exhibited longer average movements than T. siskiyou which had maximum distances of 30, 0, and 30 m into three clearcuts.

DISCUSSION

Results of habitat analysis (Chapter I) indicated that measured habitat structure differed among the treated and unteated clearcuts and adjacent forest of the Little Chinquapin Mountain sites. The untreated clearcuts were characterized by greater herbaceous species richness and depth of the mat and humus layers. Remnant forest islands were scattered about these habitats. The treated clearcuts were open, disturbed habitats dominated by thistle and mullein.

The four adjacent forest habitats differed in degree of canopy closure and associated herbaceous growth and cover of stumps and woody debris. The LC5 forest was the most open canopy with the least woody thickness, or understory, and understory tree density. The LC3S forest was characterized by the most canopy cover and greatest density of understory trees. The LC3W and SoCr forests were intermediate in overall structure.

Species diversities and richness of small-mammal communities within these habitats varied in relation to various residual forest

structures. Generally, Peromyscus or Tamias dominated these communities. We determined that deer mice preferentially occurred at open microsites lacking canopy cover, thick understory, and intact forest floor. Chipmunks, however, favored these habitat components. Within the four clearcuts, chipmunks occurred at microsites characterized by increasing numbers of logs, intact forest floor, and overstory tree density. Within clearcut treatment categories, preferred microhabitat, consisting of forest components, could be determined for only the treated clearcuts and adjacent forest. In the Little Chinquapin sites, overall forest complexity was hypothesized to be a primary determinant of the observed small-mammal communities (Chapter I).

Relative abundances of species is assumed to be correlated with the overall occurrence of perferred microhabitat (MacArthur and Levins 1964). Individuals, however, are not restricted to homogeneous areas of optimal habitat; movements by small mammals between very different types of habitats have been observed (Gashwiler 1959, Martinsen 1968, Sullivan 1979b). In our study, the number of individuals per species making interhabitat movements in the Little Chinquapin Mountain sites varied directly with species' habitat affinities as well as relative abundances in those habitats. The actual distances traveled, however, showed no consistent relationshp with habitat type.

Mycophagy, however, did consistently differ over the 1981 sites. Chipmunk samples from the clearcuts and forests contained more kinds and greater quantities of fungal spores than did those of deer mice. This finding agrees with that of Maser et al. (1978b) who compared fungal contents of stomachs and fecal pellets among a number of small-mammal species. In our study, chipmunks had significantly greater quantities of spores in samples from the untreated clearcut and either forest. Deer mice showed no pattern of differential spore abundance among habitat types.

Many mycorrhizal fungi and their sporocarps occur in association with various configurations of organic matter such as forest floor,

decayed wood, and rotting logs (Kropp 1982, Maser and Trappe 1984, McIntire 1984). Fogel (1976) observed increasing numbers of hypogeous sporocarps up to 2 m from the nearest Douglas-fir tree with an optimum zone less than half the mean distance between trees. Many of the observed fungal genera are known to display various degrees of host specificity with the types of conifer trees (Douglas-fir, white fir, ponderosa pine, and incense cedar) that comprised the forested habitats. Thus, consumed sporocarps presumably occurred nonrandomly throughout these sites (McIntire 1984).

Probable sites of sporocarp occurrence coincided with preferred microsites of Tamias throughout the Little Chinquapin Mountain sites. Hypogeous fungi are primary components of chipmunk diets at various times throughout the year (Maser et al. 1978b, Tevis 1952). Thus, relatively greater consumption of hypogeous sporocarps by chipmunks would be expected. Deer mice, however, occurred in more open areas of less complex forest structure and correspondingly fewer conifer hosts. Deer mice are dietary generalists and usually consume less fungi than chipmunks (Fogel and Trappe 1978; Jameson 1952; Maser et al. 1978b; Martell and Macauly 1981; Schloyer 1976; Tevis 1952, 1953). In our study, fewer samples from clearcuts than from forests contained spores. Thus, observed microhabitat preference and mycophagies of deer mice and chipmunks and the presumed distribution of hypogeous sporocarps were related.

For chipmunks in the treated clearcut (LC3W), spore abundances decreased with distance from the edge and were significantly less in multiple samples from recaptured individuals. Decreased resource availability would explain these results. Samples, from known dispersers, taken in the clearcut and edge, however, contained similar quantities of spores. It is likely that most or all of the fungi in these samples were consumed in the edge or forest.

In the untreated clearcuts, remnant forest habitat served a vital function as residual patches of the fungal resource. We observed small pits dug through the litter into the humus in these

islands; they quite resembled those dug by small-mammals finding hypogeous sporocarps. Thus, consumption and dissemination of spores by small-mammals from these islands into the clearcut was highly probable. Spore abundances in samples from the clearcut and forest were similar; numbers of spores in multiple samples from known dispersers were also similar. Increased resource availability in this clearcut presumably led to increased overall consumption and the significantly greater quantity of spores.

At Buck Peak, the clearcut habitats were structurally similar but varied in shrub and woody litter cover. The forests varied greatly. The SE and SW forests were the least dissimilar; both habitats were heterogeneous and were characterized by very little canopy with horizontal variation in patches of small conifers, variously sized logging slash, and open grassy areas. The SW forest was distinguished by a well developed shrub field dominated by Ceanothus velutinus Dougl.

The West forest was an even-aged stand of larger overstory trees with very little understory and woody litter. This site had the least overstory and minimal mean values for woody litter, thickness of woody vegetation, log length, log cover, total logs, log density, and mat depth. It had the most bare ground and greatest herb species richness of the four forest habitats.

The North forest, having had no consistent mangement activity, was an uneven-aged old growth conifer forest and was the most structurally complex of any. This forest and that of the West site exhibited the greatest structural differences; relative quantities of woody litter, understory thickness, herb species richness, and bare ground contributed to these differences. The North forest had the greatest canopy cover, understory thickness, mat, duff, and log cover of any stand.

Small-mammal community structures in the Buck Peak sites varied among habitats in relation to increasing forest complexity and spatial heterogeniety. Tamias siskiyou was regarded as a forest specialist that occurred at microsites of greater woody litter,

understory thickness, and overstory tree density. T. amoenus and Peromyscus occurrence was characterized by more open, less complex habitat; Peromyscus was the more ubiquitous of the two. Spermophilus exhibited no significant microhabitat preferences.

At Buck Peak, Siskiyou chipmunks traveled greater average distances into each forest of every site than into the clearcuts, and significantly so in the SE and SW sites. These chipmunks also made more movements into the forest, a phenomenon presumably related to greater forest abundance. Tevis (1956) suggested that Townsend chipmunks avoided large areas of bare ground. As succession proceeds within clearcuts, however, more complex vegetation structure provides greater cover; chipmunk numbers increase (Gashwiler 1970). Wegner and Merriam (1979) reported that Tamias striatus (eastern chipmunk) avoided grass fields adjacent to a beech-maple wood. In our study, microhabitat preferences indicate that most Siskiyou chipmunks would likely avoid open areas and that distances traveled, as a function of time and cover, would be less. Greater average distances in the North clearcut may have been related to its relatively greater shrub cover and foliage height diversity.

Yellow pine chipmunks exhibited significantly greater distances traveled in the SW forest vs. clearcut and in the West clearcut vs. forest. States (1976) observed yellow pine chipmunks foraging more frequently at shrubs and over open ground than at slash piles, trees, rocks, and stumps or logs. At Buck Peak, the West clearcut and SW forest had similar shrub cover, the greater of any clearcut or forest, respectively. Longer foraging forays in greater shrub cover may have resulted in longer movements in each habitat.

Deer mice and golden-mantled ground squirrels displayed less distinctive movements. We could distinguish no preferred microhabitat for ground squirrels. Evidently, similar use of available microhabitat was reflected in similar movements within habitats.

Consumption of fungi differed greatly among species. Spermophilus consumed the greatest average number of genera per habitat and site, but T. siskiyou had greater spore abundance per sample. T. amoenus samples exhibited minimal kinds and quantities of spores. Among-species differences characterized patterns of mycophagy at Buck Peak, and the overall degree of mycophagy for all samples was highly associated with species' mean spore abundance per sample and habitat. Very consistent differences existed among species on a population-wide level.

Greater consumption of fungi was detected for samples from the North site's forest and clearcut for all species combined, T. siskiyou, and Spermophilus. For Tamias spp. and Peromyscus, observed microhabitat associations coincided with these species' mycophagies. T. siskiyou was considered a specialist on vertically complex forest habitat (Chapter I). Increasing abundances of T. siskiyou and an increasing hypogeous fungal resource were presumably related. T. amoenus and Peromyscus occurred primarily in habitat with little or no forest components. These species probably ate less fungi relative to other food types (Martell and Macauly 1981, Meserve 1976, Schloyer 1976). Peromyscus, however, did exhibit increased occurrence of fungi in forest samples, indicating that this species may be opportunistic when foraging in areas of greater fungal abundance. This phenomenon was not observed for Spermophilus. Ground squirrels, being less arboreal than chipmunks, may have used the habitat in a more horizontal manner. These animals may have consumed fungi either specifically during peak fruiting periods (Maser et al. 1978b, Tevis 1953) or more randomly as sporocarps were encountered. Actual rates of consumption were not recorded, however.

Habitat structure apparently had a two-fold effect on dispersal at Buck Peak. First, the relative compositions of the small-mammal communities within these habitats varied directly with habitat structure (Chapter I). Because overall movement and mycophagy characteristics varied to different degrees among species, potential

dispersal of spores by small mammals would be directly associated with habitat type. Secondly, hypogeous sporocarp availability is environmentally determined; numbers and kinds of fruiting fungi are temporally related to temperature and moisture (Fogel 1976). Thus, overall dispersal potential of mycophagists in open, dry sites would be minimal if relative sporocarp abundance is low.

At Little Chinquapin Mountain and Buck Peak, different logging schemes variously altered the pre-existing mature forest. Residual habitat ranged from severely disturbed early seres through early-to-mid heterogeneous habitats with patches of forest to vertically complex forests with varying canopy closures. Within these habitats, small-mammal and, presumably, mycorrhizal-fungal communities changed in response to the degree of alteration of the original forest. In less disturbed sites, mycophagous species generally exhibited greater spore abundances. Actual differences between spore numbers in samples from known dispersers from clearcuts and forests were slight, however. Therefore, abundances of sporocarps and primary mycophagists in the less disturbed, adjacent habitat would affect the overall inoculum availability of a more disturbed site.

The forgoing discussion attempts to integrate some basic characteristics of a complicated ecological relationship to discover overall patterns of community level responses by small mammals to habitat alteration. These responses, in turn, affect what we determine as their role in forest regeneration. Many factors are involved, yet most have not been investigated. A major gap in our understanding concerns the actual micro-distribution of the consumed fungal genera in differently altered habitats. These data are necessary for the continued study of the role of fungal productivity, phenology, and microhabitat association in small-mammal resource partitioning and niche relationships. Other questions concerning relative rates of consumption and egestion in relation to species' energetics, deposition of and decomposition of fecal pellets in disturbed habitats, and community dynamics of mycorrhizal fungi in relation to plant succession should be examined.

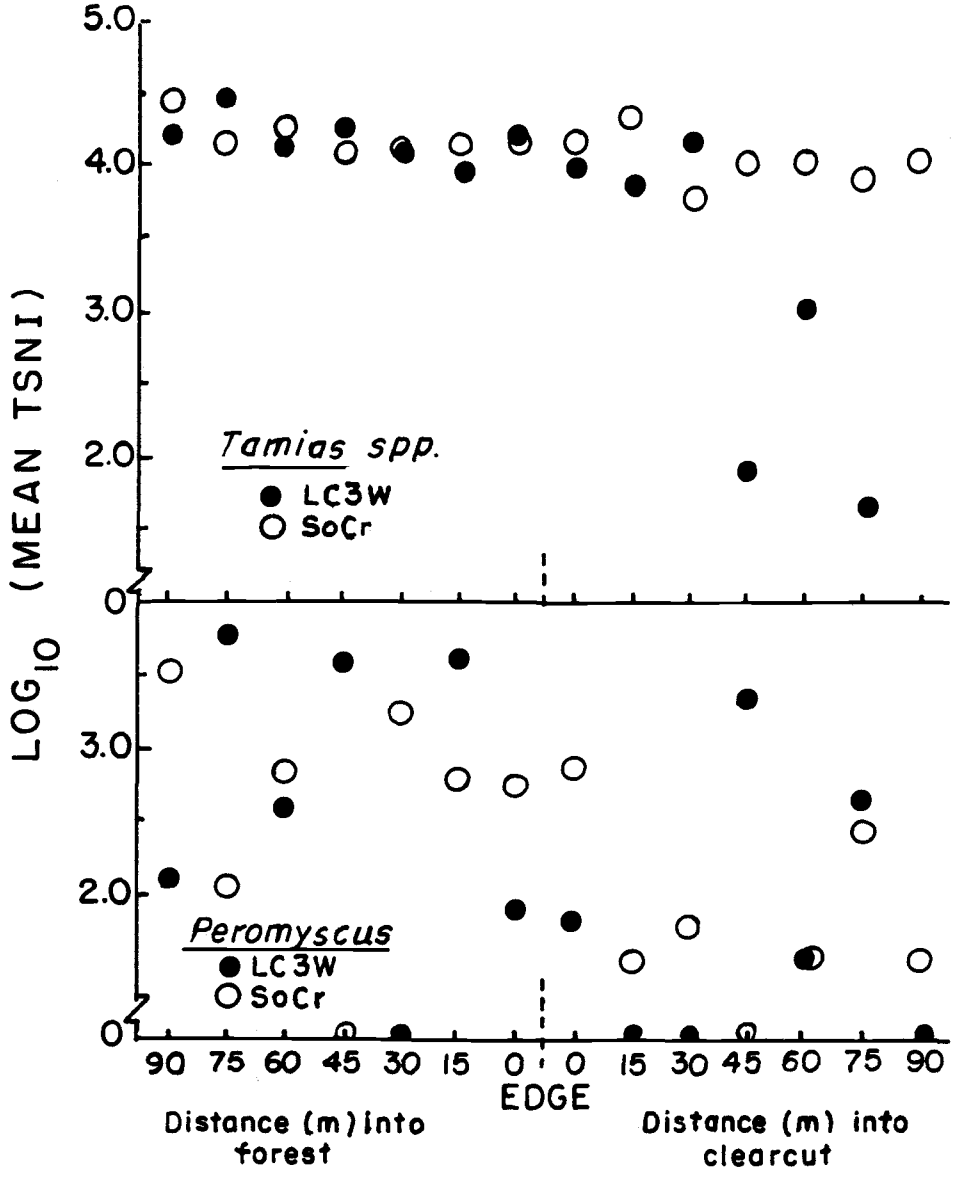

Fig. II.1. Log values of the spore number index (SNI) per genus totaled over all genera per sample (TSNI) and averaged over all samples for each trapping segment at 15 m intervals from the edge lines into the forest and clearcut for Tamias and Peromyscus, 1981. Values for LC3W and SoCr are given.

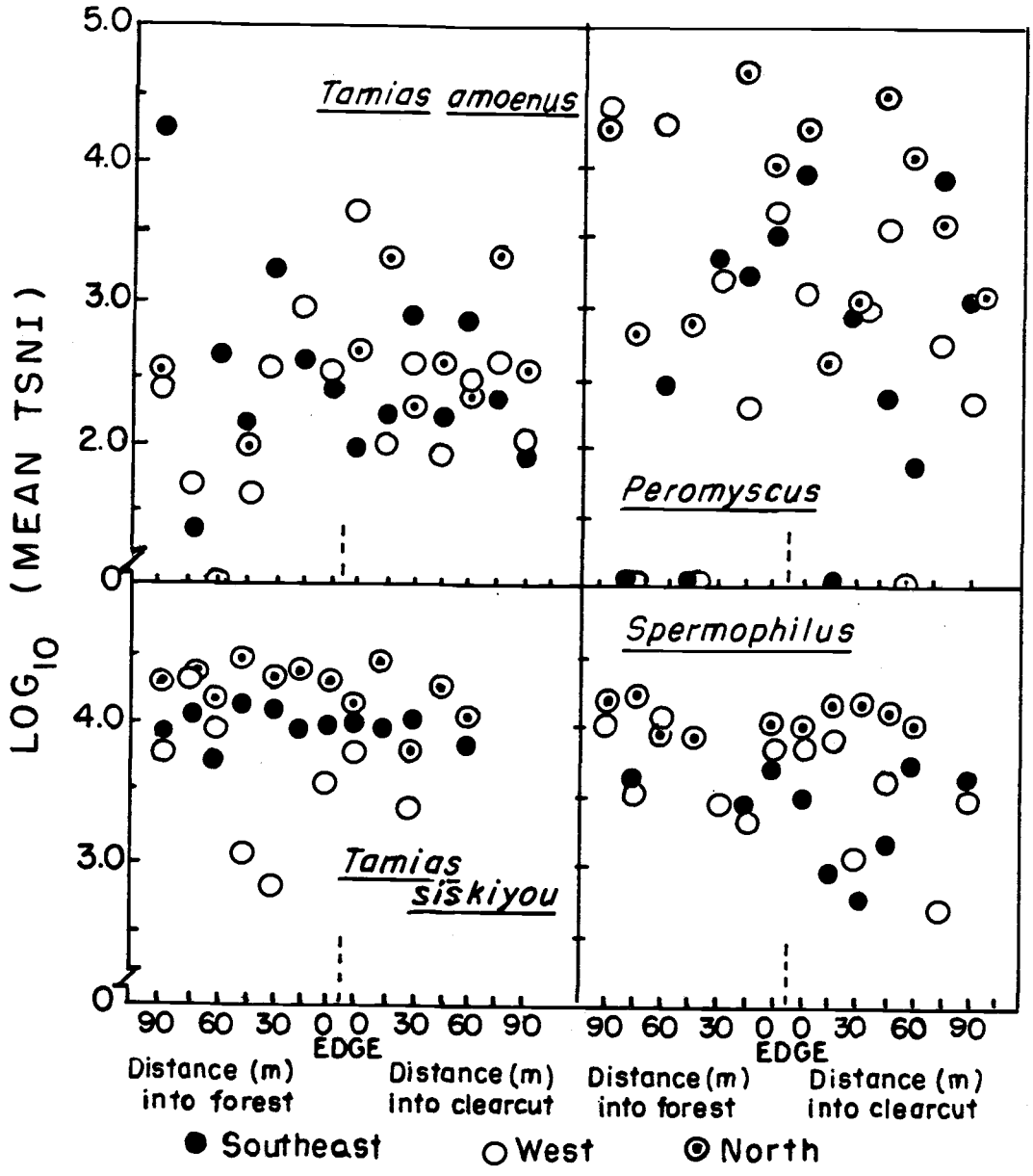

Fig. II.2. Log values of the spore number index (SNI) per genus totaled over all genera per sample (TSNI) and averaged over all samples for each trapping segment at 15 m intervals from the edge lines into the forest and clearcut for Tamias amoenus, T siskiyou, Peromyscus maniculatus, and Spermophilus laterialis, 1982. Values for the SE, West (W), and North (N) sites are given.

Table II.1. Numbers of individuals per small-mammal species captured in 1980. An individual can be counted in only one of the seven possible habitat categories. Percentage of the species total for each category is given in parentheses.

	Habitat categories*							
Species	C	E	F	CEF	EF	EC	CF	Total
Tamias spp.	38 (29.0)	7 (5.3)	47 (35.9)	3 (2.3)	9 (6.9)	19 (14.5)	8 (6.1)	131
Spermophilus lateralis	21 (38.9)	6 (11.1)	8 (14.8)	5 (9.3)	11 (20.4)	2 (3.7)	1 (1.9)	54
Clethrionomys californicus	2 (8.3)	+	22 (91.7)	+	+	+	+	24
Sorex trowbridgei	14 (77.8)	+	4 (22.2)	+	+	+	+	18
Peromyscus maniculatus	11 (64.7)	2 (11.8)	+	+	+	4 (23.5)	+	17
Microtus longicaudus	5 (83.3)	1 (16.7)	+	+	+	+	+	6
Microtus oregoni	1 (100.0)	+	+	+	+	+	+	1
Phenacomys intermedius	1 (100.0)	+	+	+	+	+	+	1
Thomomys mazama	1 (100.0	+	+	+	+	+	+	1
Mustela ermina	+	+	1 (100.0)	+	+	+	+	1
Total	94	16	82	8	20	25	9	254

* C, clearcut only; E, edge only; F, forest only; CEF, clearcut, edge and forest; EF, edge and forest; EC, edge and clearcut; CF, clearcut and forest.
‡ Not recorded for this category.

Table II.2. Numbers of samples with fungal spores (n) and percentage (%) of total number of samples per habitat type for each small-mammal species exhibiting mycophagy 1980. The total number of samples containing spores is given also.

		Clearcut		Edge		Forest		Total	
Species	N*	n	%	n	%	n	%	n	%
Tamias spp.	122	28	42.4	7	70.0	46	100.0	81	66.4
Spermophilus lateralis	55	24	100.0	10	100.0	21	100.0	55	100.0
Peromyscus maniculatus	21	12	100.0	+	+	+	+	12	57.1
Clethrionomys californicus	20	2	10.5	+	+	17	89.5	19	95.0
Microtus longicaudus	2	1	50.0	+	+	+	+	1	50.0

* N = the total number of samples examined for each species.
+ Not recorded for this habitat.

Table II.3. Number of individuals (n) captured per species in one of seven possible habitat categories, Little Chinquapin Mountain sites, 1981. Percentage of the species total for each category (%) is given also.

		Habitat categories*														
		C		E		F		EC		EF		FC		CEF		
Species	Site	n	%	n	%	n	%	n	%	n	%	n	%	n	%	Total
Peromyscus maniculatus	LC3W	100	44.4	46	20.4	30	13.3	24	10.7	21	9.3	3	1.3	1	0.4	225
	LC3S	89	45.2	32	16.2	23	11.7	25	12.7	23	11.7	2	1.0	3	1.5	197
	LC5	51	41.8	22	18.0	13	10.7	28	23.0	4	3.3	1	0.8	3	2.5	122
	SoCr	41	40.2	15	14.7	14	13.7	22	21.6	9	8.8	+	+	1	1.0	102
Tamias spp.	LC3W	6	5.8	7	6.7	47	45.2	13	12.5	28	26.9	1	1.0	2	1.9	104
	LC3S	6	9.4	8	12.5	22	34.4	4	6.3	21	32.8	+	+	3	4.7	64
	LC5	19	17.0	13	11.6	41	36.6	10	8.9	21	18.8	3	2.7	5	4.5	112
	SoCr	17	15.3	14	12.6	32	28.8	15	13.5	26	23.4	3	2.7	4	3.6	111
Clethrionomys californicus	LC3W	+	+	4	10.0	36	90.0	+	+	+	+	+	+	+	+	40
	LC3S	+	+	+	+	2	100.0	+	+	+	+	+	+	+	+	2
	LC5	3	5.4	15	26.8	36	64.3	+	+	2	3.6	+	+	+	+	56
	SoCr	2	16.7	4	33.	6	50.3	+	+	+	+	+	+	+	+	12
Microtus longicaudus	LC3W	3	75.0	1	25.0	+	+	+	+	+	+	+	+	+	+	4
	LC3S	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0
	LC5	20	52.6	11	28.9	4	10.5	1	2.6	1	2.6	1	2.6	+	+	38
	SoCr	22	91.7	1	4.2	1	4.2	+	+	+	+	+	+	+	+	24
Spermophilus lateralis	LC3W	4	50.0	3	37.5	1	12.5	+	+	+	+	+	+	+	+	8
	LC3S	1	14.3	4	57.1	1	14.3	1	14.3	+	+	+	+	+	+	7
	LC5	+	+	3	75.0	+	+	1	25.0	+	+	+	+	+	+	4
	SoCr	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0

* C = captured in clearcut only; E = edge only; F = forest only; EC = edge and clearcut; EF = edge and forest; FC = forest and clearcut; CEF = clearcut, edge, and forest.
+ Not captured in this category.

Table II.4. Number of movements (n), average net distance per movement ($\bar{D}$), proportion of total distance traveled in the object habitat (P), and maximum distance traveled (d_{max}) for Tamias and Peromyscus in each site, Little Chinquapin Mountain.

		Forest and edge into clearcut*				Clearcut and edge into forest**			
Species	Site	n	$\bar{D}_c$	P_c	d_{max}	n	$\bar{D}_f$	P_f	d_{max}
Tamias	LC3W	18	51.7	0.80	90	29	48.1	0.92	90
	LC3S	8	37.5	0.41	90	23	50.9	0.88	75
	LC5	16	40.3	0.61	90	26	51.9	0.83	90
	SoCr	20	52.5	0.74	90	34	40.6	0.75	90
Peromyscus	LC3W	28	35.9	0.62	90	22	23.8	0.66	90
	LC3S	25	36.6	0.85	90	23	30.7	0.80	60
	LC5	33	45.5	0.84	75	4	33.8	0.82	45
	SoCr	22	33.4	0.93	60	12	23.8	0.76	75

* Net distances from the edge and forest trap line segments into the clearcut are measured from the A line to the segment of capture.

** Net distances from the edge and clearcut trap line segments into the forest are measured from the B line to the segment of capture.

Table II.5. Total number of samples taken and percentage with >1 genera of fungi per site and habitat for Tamias and Peromyscus, Little Chinquapin Mountain sites. Frequency of occurrence (percent) per observed fungal genus is given also.

	Tamias				Peromyscus			
	LC3W		SoCr		LC3W		SoCr	
	C*	F*	C	F	C	F	C	F
No. of samples	38	60	49	72	38	27	50	24
Percent with fungi	81.6	98.3	81.6	100.0	23.7	63.0	20.4	40.0
Basidiomycetes								
Rhizopogon**	71.7	88.3	77.6	97.2	7.9	44.4	12.1	41.7
Leucogaster	26.3	81.7	61.2	56.2	15.8	44.4	12.1	29.2
Gautieria	34.2	68.3	42.9	55.6	10.5	37.0	6.0	4.2
Melanogaster	42.1	58.3	20.4	33.3	7.9	48.1	8.0	4.2
Hysterangium	7.9	36.7	6.1	13.9	+	7.4	+	+
Thaxterogaster	13.2	30.0	8.2	12.5	2.6	14.8	+	+
Martellia	7.9	10.0	24.5	41.7	+	+	+	+
Gastroboletus	+	6.7	2.0	13.9	+	3.7	+	+
Nivatogastrium	+	6.7	+	2.8	+	3.7	+	+
Octavianina	2.6	3.3	2.0	26.4	+	3.7	2.0	+
Hymenogaster	+	3.3	+	6.9	+	3.7	+	+
Ascomycetes								
Geopora	10.5	41.7	12.2	12.5	+	7.4	+	+
Hydnotrya	21.1	30.0	6.1	13.9	+	7.4	+	+
Balsamia	7.9	23.3	6.1	5.6	+	3.7	+	+
Genea	+	+	+	1.4	+	11.1	+	+
Genabea	7.2	20.0	4.1	2.8	+	3.7	+	+
Elaphomyces	+	1.7	6.1	9.7	+	+	4.0	+
Tuber	+	3.3	+	+	+	+	+	+
Picoa	+	2.6	+	+	+	+	+	+
Choiromyces	+	+	+	+	+	3.7	+	+
Terfezia	+	+	+	1.4	+	+	+	+
Phycomycetes								
Glomus	26.3	+	8.2	13.9	2.6	14.8	6.0	16.7
Endogone	+	+	16.3	12.5	+	3.7	2.0	4.2
Sclerocystis	2.6	+	+	+	+	+	+	+

* C = clearcut + A line samples; F = forest + B line samples.
** Includes several other closely related genera with similar spores.
+ Not present in this category.

Table II.6. Results of paired t-test on log(mean TSNI) values per individual, Little Chinquapin Mountain. Given values are: sample mean difference, D; t values; degrees of freedom, df; and average distance traveled between habitats, $\bar{d}_i$. All t values are insignificant at $\alpha = .05$.

	Tamias				Peromyscus			
	LC3W		SoCr		LC3W		SoCr	
Values	E-F*	E-C*	E-F	E-C	E-F	E-C	E-F	E-C
D	0.01	0.18	-0.00	-0.01	-1.46	0.26	-0.63	0.23
t	0.15	0.61	-0.02	-0.06	-1.60	0.39	-1.49	0.48
df	13	8	9	8	6	7	5	8
$\bar{d}_i$	54.2	46.7	42.0	53.3	38.6	37.5	30.0	35.0

* E-F = edge and forest; E-C = edge and clearcut.

Table II.7. Number of individuals (n) and percentage of the total number per site (%) in one of seven habitat categories per small-mammal species, Buck Peak.

		Habitat categories*														
		C		E		F		EC		EF		FC		CEF		
Species	Site	n	%	n	%	n	%	n	%	n	%	n	%	n	%	Total
Tamias amoenus	SE	42	42.4	8	8.1	30	30.3	5	5.1	8	8.1	4	4.0	2	2.0	99
	SW	18	23.7	8	10.5	15	19.7	12	15.8	8	10.5	3	3.9	12	15.8	76
	West	18	22.0	15	18.3	22	26.8	7	8.5	11	13.4	2	2.4	7	8.5	82
	North	36	61.0	5	8.5	2	3.4	14	23.7	+	+	+	+	2	3.4	59
Tamias siskiyou	SE	1	1.7	12	20.0	28	46.7	1	1.7	16	26.7	+	+	2	3.3	60
	SW	1	2.0	9	18.4	15	30.6	+	+	23	46.9	+	+	1	2.0	49
	West	+	+	3	10.3	19	65.5	2	6.9	4	13.8	+	+	1	3.4	29
	North	1	1.2	22	26.2	22	26.2	4	4.8	30	35.7	1	1.2	4	4.8	84
Spermophilus lateralis	SE	26	41.9	7	11.3	10	16.1	7	11.3	7	11.3	2	3.2	3	4.8	62
	SW	30	33.0	25	27.5	14	15.4	15	16.5	3	3.3	1	1.1	3	3.3	91
	West	35	27.8	30	23.8	43	34.1	10	7.9	7	5.6	+	+	1	0.8	126
	North	16	22.9	14	20.0	18	25.7	10	14.3	6	8.6	2	2.9	4	5.7	70
Peromyscus maniculatus	SE	44	44.0	27	27.0	7	7.0	14	14.0	5	5.0	2	2.0	1	1.0	100
	SW	23	30.7	12	16.0	13	17.3	18	24.0	6	8.0	1	1.3	2	2.7	75
	West	28	32.9	11	12.9	20	23.5	14	16.5	7	8.2	1	1.2	4	4.7	85
	North	35	42.2	10	12.0	8	9.6	23	27.7	2	2.4	3	3.6	2	2.4	83
Clethrionomys californicus	SE	+	+	2	28.6	4	57.1	+	+	1	14.3	+	+	+	+	7
	SW	+	+	+	+	5	100.0	+	+	+	+	+	+	+	+	5
	West	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0
	North	+	+	3	21.4	8	57.1	+	+	3	21.4	+	+	+	+	14
Microtus longicaudus	SE	2	16.7	6	50.0	4	33.3	+	+	+	+	+	+	+	+	12
	SW	+	+	2	33.3	4	66.7	+	+	+	+	+	+	+	+	6
	West	2	66.7	1	33.3	+	+	+	+	+	+	+	+	+	+	3
	North	4	66.7	1	16.7	1	16.7	+	+	+	+	+	+	+	+	6

* C = captured in clearcut only; E = edge only; F = forest only; EC = edge and clearcut; EF = edge and forest; FC = forest and clearcut; CEF = clearcut, edge, and forest.
+ Not captured in this category.

Table II.8. Number of movements (n), average net distance per movement ($\bar{D}$), proportion of total distance traveled in the object habitat (P), and maximum distance traveled (d_{max}) for Spermophilus, Tamias amoenus, T. siskiyou, and Peromyscus in each site, Buck Peak.

		Forest and edge into clearcut*				Clearcut and edge into forest**			
Species	Site	n	$\bar{D}_c$	P_c	d_{max}	n	$\bar{D}_f$	P_f	d_{max}
Spermophilus lateralis	SE	10	48.0	0.76	90	9	46.7	0.51	90
	SW	18	49.2	0.82	75	7	47.1	0.52	90
	West	7	49.3	0.96	90	7	38.6	0.75	60
	North	14	42.9	0.82	90	13	50.8	0.68	90
Tamias amoenus	SE	11	51.8	0.69	90	13	36.9	0.62	90
	SW	35	37.3	0.53	90	32	61.4	0.66	90
	West	17	58.2	0.67	90	22	38.2	0.58	90
	North	20	45.0	0.86	75	2	60.0	0.80	90
Tamias siskiyou	SE	4	22.5	0.75	30	34	46.8	0.89	90
	SW	++	++	++	++	28	48.2	0.92	90
	West	2	30.0	0.44	30	5	54.0	1.00	75
	North	11	38.2	0.49	90	48	50.9	0.89	90
Peromyscus maniculatis	SE	16	44.1	0.76	90	6	47.5	0.79	75
	SW	21	37.1	0.81	90	10	52.5	0.81	75
	West	16	54.4	0.84	75	13	39.2	0.58	90
	North	28	53.0	0.81	90	3	25.0	0.50	30

++ Not recorded for this category.
* Net distances from the edge and forest trap line segments into the clearcut are measured from the A line to the segment of capture.
** Net distances from the edge and clearcut trap line segments into the forest are measured from the B line to the segment of capture.

Table II.9. Total number of samples taken and percentage with ≥1 genera of fungi per site and habitat for *Tamias siskiyou*, *T. amoenus*, *Peromyscus*, and *Spermophilus*, Buck Peak. Frequency of occurrence (percentage) per observed fungal genus is given also.

	Tamias siskiyou						*Tamias amoenus*						*Peromyscus maniculatus*						*Spermophilus lateralis*					
	SE		West		North		SE		West		North		SE		West		North		SE		West		North	
Species	C*	F*	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
No. of samples	17	54	3	27	27	86	41	36	40	47	52	2	54	22	75	46	67	20	26	6	22	24	17	16
Percentage with fungi	88.2	96.2	100.0	85.2	100.0	100.0	36.6	44.4	50.0	34.0	53.8	100.0	35.2	45.5	28.0	37.0	38.8	85.0	96.2	100.0	90.9	100.0	100.0	100.0
Basidiomycetes																								
Rhizopogon**	70.6	79.6	33.3	55.6	74.1	91.9	9.8	19.4	12.5	4.3	15.4	50.0	25.9	27.3	10.7	21.7	26.9	65.0	30.8	66.7	31.8	66.7	70.6	87.5
Leucogaster	23.5	27.8	+	11.1	44.4	61.6	+	+	5.0	+	9.6	+	1.9	31.8	5.3	17.4	13.4	55.0	3.8	+	+	+	29.4	62.5
Gautieria	5.9	14.8	+	3.7	22.2	32.6	2.4	+	+	+	5.8	+	11.1	13.6	4.0	6.5	7.5	15.0	11.5	16.7	9.1	12.5	52.9	75.0
Melanogaster	35.3	31.5	+	11.1	44.4	60.5	+	5.6	+	+	3.8	50.0	9.3	13.6	2.7	4.3	14.9	35.0	30.8	50.0	4.5	20.8	52.9	50.0
Hysterangium	+	14.8	+	7.4	11.1	33.7	2.4	8.3	2.5	4.3	7.7	50.0	1.9	+	4.0	2.2	11.9	20.0	19.2	33.3	9.1	33.3	47.1	81.3
Thaxterogaster	+	+	+	+	+	4.7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	5.9	+
Martellia	+	+	+	+	+	+	+	+	+	+	+	+	1.9	+	1.3	+	+	+	+	+	+	+	5.9	6.3
Gastroboletus	+	3.7	+	3.7	+	5.8	+	+	+	+	+	+	+	4.5	+	4.3	1.5	+	+	+	+	12.5	5.9	+
Octavianina	17.6	9.3	+	3.7	14.8	2.3	+	+	+	+	+	+	+	9.1	+	2.2	1.5	+	3.8	+	18.2	41.7	5.9	31.3
Calvatia	+	+	+	+	+	+	+	+	7.5	4.3	1.9	+	+	+	1.3	4.3	1.5	+	19.2	+	45.5	16.7	+	6.3
Microthecium	+	+	+	+	+	+	+	+	2.5	+	+	+	+	+	6.7	+	+	+	+	+	+	+	+	+
Caprinus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3.8	+	+	+	+	+
Hymenogaster	+	+	+	+	+	1.2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6.3
Ascomycetes																								
Geopora	11.8	31.5	+	33.3	44.4	68.6	+	+	2.5	4.3	+	+	3.7	4.5	4.0	6.5	3.0	10.0	15.4	33.3	45.5	62.5	47.1	37.5
Balsamia	23.5	35.2	100.0	22.2	44.4	11.6	+	+	+	2.1	1.9	+	3.7	+	1.3	+	10.4	10.0	26.9	33.3	4.5	16.7	47.1	37.5
Hydnotrya	5.9	33.3	+	22.2	29.6	32.6	+	+	2.5	2.1	+	+	+	+	+	6.5	6.0	5.0	34.6	16.7	18.2	37.5	35.3	75.0
Elaphomyces	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	7.7	+	+	+	+	+
Tuber	+	+	+	+	+	+	+	+	+	+	+	+	1.9	+	+	+	+	+	+	+	+	+	+	+
Choiromyces	+	+	+	+	3.7	3.5	+	+	+	+	+	+	+	+	2.7	6.5	+	+	+	+	+	4.2	+	6.3
Phyomycetes																								
Glomus	35.3	59.3	100.0	77.8	18.5	19.8	75.6	52.8	55.0	51.1	71.2	100.0	35.2	40.9	37.3	30.4	23.9	20.0	100.0	100.0	63.6	91.7	94.1	50.0
Endogone	+	+	+	3.7	7.4	7.0	+	+	2.5	+	1.9	50.0	+	+	1.3	4.3	1.5	+	+	+	4.5	4.2	+	6.3
Sclerocystis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1.5	+	+	+	4.5	+	+	+

* C = clearcut + A line samples; F = forest + B line samples.
** Includes several other closely related genera with similar spores.
+ Not present in this category.

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SUMMARY AND CONCLUSIONS

For Little Chinquapin Mountain and Buck Peak, small-mammal community structure was shown to vary with differing habitat structure. Microhabitat preferences were hypothesized to help determine community structure. As habitat structure varies across these sites, less common species were observed in communities when structural heterogeneity and complexity increased. As preferred microhabitat of less common species became abundant, e.g. T. siskiyou in the North forest, species diversity declined, and overall common species declined in relative abundance.

Differential mycophagy among species was observed at both sites. For all species, population-wide occurrence of fungi in fecal samples was highly correlated with spore abundance when paired by species and site per habitat. Observed patterns of mycophagy and dispersal were thought to be directly related to variation in habitat structure. Species exhibiting the greatest spore abundances, e.g. chipmunks, occurred at sites of presumably greater sporocarp concentrations.

The degree of habitat alteration determines both the small-mammal and fungal communities. Therefore, minimal disturbance in habitats that act as fungal reservoirs is necessary to increase the inocula potential of adjacent, disturbed sites. Maximum inocula potential is inversely related to the degree of disturbance within the logged area. Species that exhibit extensive mycophagy and are habitat generalists, e.g. Spermophilus lateralis, may mitigate disturbance effects to some unknown degree, however.

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APPENDIX

Appendix 1. Characteristics of 1981 and 1982 study sites.

Year and site	Elevation (m)	Slope aspect	Forests			Clearcuts		
			Location	Past management	Present condition	Location	Year cut	Site preparation
1981								
Little Chinquapin 3-West	2050	20-40, NE	T39S, R4E, S17 SE 1/4	1/3 PC*: 1966	O*: OF*, WF*, OG*	T39S, R4E, S16 SW 1/4	1978	WBSS*: 1978
Little Chinquapin 3-south	1900	25, E	T39S, R4E, S31 NW 1/4	1/2 PC: 1969	MC*, OF, WF, OG	T39S, R4E, S16 SW 1/4	1978	WBSS: 1978
Little Chinquapin 5	1900	40, NW	T39S, R4E, S17 NW 1/4	PC: 1966	O: OF, WF, OG	T39S, R4E, S18 NE 1/4	1977-1979	None
Soda Creek	1710	40, NW	T39S, R4E, S19 NW 1/4	PC: 1967	O: OF, WD, OG	T39S, R4E, S8 NE 1/4	1979	None
1982								
Southeast	1803	10, SW	T38S, R6E, S17 NE 1/4	SC*: 1973-1974. OR*: 1980	P*; SS-PS*: WF, OF	T38S, R6E, S8 SE 1/4	1976	WBSS: 1977, HS*: 1978-80, GB*: 1979-80
Southwest	1720	10, SW	T38S, R6E, S17 NW 1/4	SC: 1973-74 DR: 1980	P; SS-PS: WR, OF	T38S, R6E, S8 SW 1/4	1976	WBSS: 1977, HS: 1980, GB: 1979-80
West	1700	10, W	T38S, R6E, S7 NE 1/4	SC, IP*: 1978	EA*: OG, WF, OF	T38S, R6E, S8 NW 1/4	1976	WBSS: 1977, HS: 1978, GB: 1979-80
North	1770	10, W	T38S, R6E, S5 SW 1/4	PRC*: 1978	UA*; M* - OG, WF, OF, SRF*	T38S, R6E, S8 NW 1/4	1976	WBSS: 1977, HS: 1978, GB: 1979-80

*Acronyms: PC = precommercially thinned; O = Open canopy; OF = Douglas-fir; WBSS = windrow burnning, soil scarification; WF = white fir; OG = old growth forest; MC = mostly closed canopy; SC = shelterwood cut; P = patchy; OR = overstory removal; SS-PS = shrub seedling, pole sapling; HS = herbicide spraying; GB = Gopher baiting; IP = intensive site preparation, piling and burning slash; EA = even aged stand; PRC = partial cut; UA = uneven-aged stand; M = mature; SRF = Shasta red fir.

Appendix 2. Habitat variables sampled per sampling scheme, 1980-1982.

Sampling scheme	Habitat variables	Definitions		
		1980	1981	1982
15 m transects for coverage calculations	Herbaceous vegetation	Any herbaceous vegetation (Hitchcock and Cronquist 1978)	NM*	NM
	Woody vegatation	Any woody vegetation (Hitchcock and Cronquist 1978)	NM	NM
	Rocks	Any exposed rock surface	NM	NM
	Bare ground	Bare humus or mineral soil, with or without a single layer of conifer needles.	+ with rocks.	+
	Stumps	Rooted remains of any tree, >7.5 cm diam.	NM	NM
	Logs	Any woody dead and down material ≥25 cm diam.	+ but ≥ 10 cm diam.	+
	Woody litter	Any woody material <25 cm diam.	+ but <10 cm diam.	+: twigs and limbs, naturally intact litter; chips, not intact but broken, often with angular edges.
	Wood piles	≥2 units of woody dead and down >1 m high.	+	+
	Herbaceous layer	NM	Any vegetation ≤25 cm from ground.	+ but ≤35 cm.
	Shrub layer	NM	Any vegeataion >25 cm from ground.	+ but >35 cm.
	Canopy cover	NM	Any overstory foliage sighted vertically through a cardboard tube.	+
	Thickness of woody vegetation		Any shoulder height contact with woody vegetation.	+
16 m^2 plot	Number of herbaceous species	NM	Total number of herbaceous species (Hitchcock and Cronquist 1978).	+
	Cover per herbaceous species	NM	Cover class (1-6) of each species.	+
	Number of woody species	NM	Total number of woody species (Hitchcock and Cronquist 1978).	+
	Cover per woody species	NM	Cover class (1-6) of each species.	+
	Foliage height density	NM	Proportion of a 5 x 10 cm board coverd by vegetation at 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140 and 160 cm above ground level. Read at 3 points, each 1 m from sample point.	+ but read at 10, 20, 30, 40, 60, 80, 100 and 140 cm above ground level.
	Mat depth	NM	Depth, cm of organic litter plus partially decayed organic matter at 3 points, each 1 m from sample point.	+
	Duff depth	NM	Depth, cm, of humus layer at mat readings.	+

Appendix 2
(continued)

Sampling scheme	Habitat variables	Definitions		
		1980	1981	1982
Each of four	Log distance	Distanct from trap stake to nearest log, m.	+	+
	Log diameter	Diameter to nearest log, cm.	+	+
	Log length	Length of nearest log, m.	+	+
	Log decomposition class	Stage of decay of nearest log (1-5).	+	+
	Woodpile distance	Distance to nearest woodpile, m.	NM	NM
	Woodpile number	Number of woodpiles, any portion of which in the quarter.	+	+
	Overstory tree distance	NM	Distance to nearest tree >7.5 cm dbh, >2 m tall.	+
	Understory tree distance	NM	Distance to nearest tree ≤7.5 cm dbh, ≤2 m tall.	+
	Number of stumps	NM	Number of stumps in each quarter.	+
	Number of boulders	NM	Number of rocks >50 cm in diameter.	NM
	Snag distance	NM	NM	Distance to nearest solidly rooted, dead woody vegetation >2 m tall.
	Number of snags	NM	NM	Number of snags in each quarter.

*Not measured.
+see previous years definition.