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Habitat use by the southern red-backed vole (Clethrionomys gapperi) : response of an old-growth associated species to succession

Dean E. Pearson
The University of Montana

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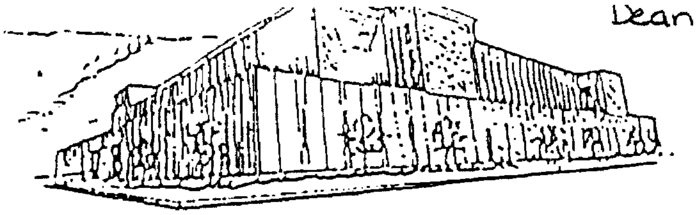

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HABITAT USE BY
THE SOUTHERN RED-BACKED VOLE (*CLETHRIONOMYS GAPPERI*): RESPONSE OF AN OLD-GROWTH ASSOCIATED SPECIES TO SUCCESSION

by

Dean E. Pearson

B.S. University of Montana, 1991

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for the degree of

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Approved by :

Chairperson

Dean, Graduate School

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Habitat Use by the Southern Red-backed Vole (*Clethrionomys gapperi*): Response of an Old-growth Associated Species to Succession

Director: Dr. Kerry R. Foresman KRF

Abstract: I examined populations of the southern red-backed vole (*Clethrionomys gapperi*) and deer mouse (*Peromyscus maniculatus*) in 4 successional stages (65, 138, 256, 457 Y) in cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests of Glacier National Park to determine macrohabitat selection among stands and microhabitat selection within stands. Abundance of *Clethrionomys gapperi* and *Peromyscus maniculatus* increased with increasing stand age. Microhabitat use differed from available habitat for both species within most age classes, but was not consistent for either species among age classes. The inconsistency in microhabitat use among successional stages and lack of correspondence between micro- and macrohabitat variables selected leads to the conclusion that macrohabitat associations determine microhabitat selection. In order to properly assess habitat use at either scale the difference between scales must be addressed in the design and analysis of habitat studies.

Peromyscus maniculatus behaved as a generalist at the macrohabitat scale, but exhibited stronger microhabitat selection than did *C. gapperi*. I suggest that *P. maniculatus* may exhibit "habitat switching" and respond to local site conditions by developing search images that manifest themselves as distinctive foraging patterns at the microhabitat scale. Such behavior would render *P. maniculatus* a potentially formidable competitor for resources and explain its tenacity for a wide variety of habitats.

Clethrionomys gapperi exhibits a strong positive linear relationship with stand age and old-growth conditions near the forest floor. If monitored in conjunction with other species such as the pine marten (*Martes americana*), pileated woodpecker (*Dryocopus pileatus*) and barred owl (*Strix asio*), *C. gapperi* could contribute significantly to an "indicator guild" for identifying and monitoring the old-growth condition.

I also compared fluorescent pigment tracking and live trapping to determine microhabitat use by *Clethrionomys gapperi*. The two methods generally agreed, but fluorescent pigment tracking may allow more sensitive analyses of microhabitat use.

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Finally, I wish to thank my wife Ellen and son Alex for their sufferance and understanding through the completion of this thesis.

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INTRODUCTION

Old-growth forests of western North America are unique ecosystems. Species that depend on these forests such as the northern spotted owl (*Strix occidentalis*), fisher (*Martes pennanti*), and northern flying squirrel (*Glaucomys sabrinus*) are an important part of the matrix we identify as old-growth ecosystems. Intensive harvest in recent decades has vastly reduced and fragmented existing old-growth stands (Harris, 1984) imperiling the northern spotted owl, marbled murrelet (*Brachyramphus marmoratus*) and numerous stocks of anadromous fish (Thomas et al., 1993). Conservation of these species necessitates an understanding of the requirements that link them to old-growth forests. By understanding old-growth dependent species, we will begin to understand what makes old-growth unique, allowing us to plan reasonable strategies for conserving these ecosystems and perhaps improve our ability to manage other forest lands.

The southern red-backed vole (*Clethrionomys gapperi*) is listed as an old-growth dependent species (Lumen and Nietro, 1980) and has been used by the United States Forest Service (USFS) as an indicator species for old-growth forests in the central Rocky Mountains (USDA Forest Service, 1985). Although this species is in no way in danger of extinction, its association with the old-growth condition is of interest in understanding old-growth dependence and the old-growth ecosystem.

Clethrionomys gapperi fulfills the role of consumer, supporting forest carnivores by transforming primary producers and decomposers into available biomass. Additionally, *C. gapperi* is a mycophagist (Maser et al., 1978). In consuming mycorrhizal fungi and incidental nitrogen-fixing bacteria found in sporocarps (Li et al., 1986a), *C. gapperi* and other small rodents act as vectors for spore dispersal. Nitrogen-fixing bacteria and mycorrhizal fungi aid nutrient uptake for plants and mycorrhizal symbiosis is obligatory for many plant species (Trappe, 1987; Sanders et al., 1975; Marks and Kozlowski, 1973). This fact is particularly important in old-growth forests where nutrients are locked up in the biomass (Sollins et al., 1980) possibly increasing competition and the demand for mycorrhizae. Because hypogeous mycorrhizal fungi lack access to wind dispersal, they require animals and possibly insects to disperse their spores (Maser et al., 1978). Animals which are lured to sporocarps by the odors they emit, consume the sporocarps and disperse viable spores in their feces as they travel (Li et al., 1986a, 1986b).

Until the last decade, comparatively little research had been conducted in old-growth forests (Schoen et al., 1981). Research since has focused on the Pacific Northwest, with few studies occurring in old-growth of the northern Rocky Mountains. Although cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests of Glacier National Park (GNP) are an eastern extension of Pacific Northwest forests, the two areas maintain distinct faunas resulting from isolation during the late Pleistocene (Harris, 1984). Old-growth forests of the Pacific Northwest boast a richer small mammal fauna than that of the northern Rocky Mountains (Harris, 1984). This is important, because the roles of mycophagist and primary consumer fall more heavily on fewer species in the northern Rocky Mountains. In the McDonald Valley of GNP, *C. gapperi* is an important mycophagist and is tied closely to the old-growth condition. These characteristics make *Clethrionomys* an excellent subject for research which explores the unique aspects of old-growth ecosystems. *Peromyscus maniculatus* is a sympatric species which is also an important forest rodent and potential competitor with *C. gapperi*. The role of *P. maniculatus* is considered in context of its relationship to *C. gapperi*.

LITERATURE REVIEW

Clethrionomys gapperi

Clethrionomys gapperi is a forest mammal. In GNP where spruce (*Picea engelmanii*) forest borders fen meadows in the McGee Meadow complex, the boundary of *C. gapperi*'s distribution sharply coincides with the forest boundary. Similar relationships have been observed elsewhere (Morris, 1969) and 4 general hypotheses can be formulated to explain local habitat selection by *C. gapperi*. Numerous authors have attributed *C. gapperi*'s restriction to cool moist forests as a physiological constraint due to poor water balance (Miller and Getz, 1977a, 1977b, 1973, 1972; Getz, 1968; Odum, 1944). Grant (1969), Morris and Grant (1972) and Morris (1979) attribute this pattern to competitive interactions with the meadow vole (*Microtus pennsylvanicus*). Tevis (1956a) and Gunderson (1959) suggest that *Clethrionomys* requires structural components such as logs and it is this microhabitat requirement that restricts *C. gapperi* to forest environments. Maser et al. (1978) and Martell (1981) reason that the absence of mycorrhizal sporocarps from clearcuts make these habitats unsuitable for *Clethrionomys* species.

Water balance

Odum (1944) reported high water requirements for *C. gapperi* in lab studies and determined that in the field, it was captured in mesic habitats and was most abundant near water. Butsch (1954) and Manville (1949) found *C. gapperi* near wet sites, and Butsch (1954) suggested that the local distribution of *C. gapperi* was controlled more by the availability of free water than food.

Getz (1962) concluded that *C. gapperi* required more water than *Microtus pennsylvanicus*, but was able to maintain its weight on lower rations (33% of normal) than *Microtus* (72%). Getz (1968) conducted studies on the water balance of *C. gapperi* and *Peromyscus leucopus* in Connecticut and northern Vermont where *C. gapperi* is restricted to lowland swamps and *P. leucopus* abounds in dry uplands. He found that the water turn-over rate for *C. gapperi* was 2.2 times that for *P. leucopus* due to greater water losses in the urine. McManus (1974) also reported high water requirements for *C. gapperi*. Getz (1968) compared temperature and humidity between the lowland swamps and uplands and concluded that microclimate was not a significant factor restricting *C. gapperi* to the moist swamps of southern New England. Although evaporative losses between the two sites could not account for the habitat separation, Getz (1968) suggested the moisture content of foods associated with the habitats might, and he showed *C. gapperi* could be maintained on mushrooms for 14 days without loosing weight.

In the McGee Meadow system of GNP, the fen meadows are the more mesic sites with wet soils and standing water. The forest-meadow ecotone results from a sharp moisture gradient with the forest on the dry end. Therefore, *C. gapperi* is unlikely restricted to the forest by moisture. Wywialowski and Smith (1988) measured distance to open water in microhabitat studies of *C. gapperi* and found non-capture sites were closer than capture sites.

In general, *C. gapperi*'s functional niche is limited by moisture availability and water losses associated with higher temperatures and lower humidity. This fact may explain the species' geographic distribution in the northern United States and Canada. However, within this range physiological constraints are unlikely to limit local populations of *C. gapperi*.

Competition

The forest-grassland ecotone often delineates the boundary between *Clethrionomys gapperi* and *Microtus pennsylvanicus*. Morris (1979) suggested this was the result of competitive interactions between *C. gapperi* and *M. pennsylvanicus*. Enclosure studies of aspen-grassland ecotones indicated that *C. gapperi* entered the grassland more in the absence of *M. pennsylvanicus* (Grant, 1969) and complimentary studies by Morris and Grant (1972) showed that *M. pennsylvanicus* may have used the forest more when *C. gapperi* was removed from aspen stands. Cameron (1964) found that *M. pennsylvanicus* could occupy *Clethrionomys* habitat on islands where *C. gapperi* was absent. He concluded that the presence of one or the other, but not both species, on ecologically similar islands, was the result of a beachhead phenomenon where a competitive advantage was established by the first arrival. In other studies, where *C. gapperi* and *P. maniculatus* were introduced to islands previously inhabited only by *M. pennsylvanicus*, *C. gapperi* displaced both *P. maniculatus* and *M. pennsylvanicus* from forested habitats (Crowell and Pimm, 1976), but did not expand beyond the forest even in high densities (Crowell, 1983, 1973).

Competition studies of *C. gapperi* have focused on interference competition between *C. gapperi* and *M. pennsylvanicus* (Grant, 1969; Morris and Grant, 1972), because of greater taxonomic and morphologic similarities between these species and because the distinct boundary between the two species suggests a competitive front. However, although *C. gapperi* and *M. pennsylvanicus* are often sympatric at the macrohabitat scale, they seldom overlap at the microhabitat scale except in peripheral habitats like shrubby bogs and savanna-like forest (Buckner, 1957; Smith and Foster, 1957). The same pattern of habitat separation exists for tree squirrels (*Tamiasciurus* spp.) and ground squirrels (*Spermophilus* spp.), but it is not attributed to competitive interactions. A similar case could be made for *C. gapperi* and *M. pennsylvanicus*. Although it could be argued that this habitat separation is the residual effect of historical competitive interactions, doing so would infer that competition no longer exists and that the distinct ecological separation observed is the ghost of competition past (Rosenzweig, 1979). For these reasons, I conclude that *M. pennsylvanicus* is generally unlikely to compete with *C. gapperi*.

Peromyscus maniculatus is commonly found in association with *C. gapperi*, but it is often regarded as an unworthy competitor because it is taxonomically and morphologically more distinct (Wolff and Dueser, 1986). This logic is faulty! Because *P. maniculatus* is sympatric with *C. gapperi* at the microhabitat scale, and its dietary niche encompasses that of *C. gapperi* (Gunther et al., 1983; Martell, 1981; and Macaulay 1981), it is far more likely to compete with *C. gapperi* than *M. pennsylvanicus*. It is well established that *P. maniculatus* is a generalist. As a generalist, its foraging behavior incorporates many habitats and includes foods encountered opportunistically. The great breadth of its niche does not mean that *P. maniculatus* does not compete with specialists such as *C. gapperi*; rather, this plasticity allows switching behavior which potentially confers a competitive advantage to *P. maniculatus*.

Studies of forest succession throughout the United States and Canada strongly infer competitive interactions between *C. gapperi* and *P. maniculatus* where the two not only replace each other on the successional gradient, but do so, at times, with a sharp temporal ecotone (Martell, 1982a, 1982b). That is, *C. gapperi* and *P. maniculatus* do not just reciprocally switch places when the habitat is altered, as would be predicted by a strict habitat hypothesis explaining distribution; rather, there is a time lag in which *C. gapperi* may increase in abundance over the first 1 to 2 years post-disturbance. *Peromyscus* does not make a significant entrance until after *Clethrionomys* relinquishes its hold on the site.

However, few studies have directly assessed competitive interactions between these two species. Of those that have, most have returned negative results (but see Vickery, 1981; Crowell and Pimm, 1976). For example, Wolff and Dueser (1986) looked for competitive interactions between *C. gapperi* and *Peromyscus* species in deciduous forests of Virginia where *C. gapperi* was restricted to rocky outcrops within the forest. They concluded that the 3 species "exhibit noncompetitive coexistence at this location." Barry et al. (1990) also found extensive overlap between *C. gapperi* and *P. maniculatus* in their use of rocky outcrops in deciduous forests of Maryland. Morris (1983) sought evidence of competitive interference for space between rodents in the Rocky Mountains of Alberta and concluded that *C. gapperi* and *P. maniculatus* were independently distributed as he found "no consistent relationship between the densities of the two species over a broad range of habitats." In laboratory studies, *C. gapperi* does not maintain aggressive relationships with *P. maniculatus* (Grant, 1970) or *P. leucopus* (Getz, 1969).

These results are consistent with the above discussion regarding competitive interactions between *C. gapperi* and *P. maniculatus* because they all examine interference competition for space, which is neither a necessary nor a very likely form of competition given the extensive spacial overlap between these two species. I found no studies examining dietary shifts that might result from resource competition. I believe this to be the most likely form of competition between these rodents.

Although competition has been suggested as important in structuring mainland small mammal communities (Crowell and Pimm, 1976), evidence suggests that habitat apportioning is more the result of habitat selection than contemporary competitive interactions between species. In island studies, *Clethrionomys gapperi* drove *M. pennsylvanicus* and *P. maniculatus* out of forest habitats, but was unable to expand populations beyond the forest edge (Crowell, 1983; Crowell and Pimm, 1976).

It should be noted that most studies of competitive interactions in small mammal communities have focused on interference competition for space. In doing so, these studies may have overlooked the more subtle, but more likely forms of indirect competition via resource exploitation. A comparison of the diet of *P. maniculatus* in *C. gapperi*'s habitat in the presence and absence of *C. gapperi* would provide a measure of competitive overlap for resources between the two species. It might also provide the most appropriate test for competitive interactions between the two.

Habitat structure

Physiological constraints due to poor water balance and interspecific competition for space are unlikely to explain local distributions of *C. gapperi*. Differences in habitat selection is better supported in the literature.

On the scale of macrohabitat, *C. gapperi* selects forests as opposed to grasslands or shrubby habitats, but is also found in swamps and other mesic, structurally more complex habitats where forest is lacking (Getz, 1968). When forest is present, *C. gapperi* favors coniferous over deciduous forests as shown for ecotone studies in the Adirondacks of New York (Kirkland and Griffin, 1974).

A number of microhabitat studies have linked *Clethrionomys* species to structural components of forest environments such as roots, stumps, logs, brushpiles and rocks (Tallmon and Mills, 1994; Barry et al. 1990; Hays and Cross, 1987; Wolff and Dueser, 1986; Miller and Getz 1977a, 1973, 1972; Gunderson, 1959; Tevis, 1956a). The importance of vegetative cover to *C. gapperi* microhabitats is variable. Wywialowski and Smith (1988) found *C. gapperi* positively associated with cover within 4 dm of the ground surface. Miller and Getz (1977a, 1973, 1972) also found *C. gapperi* associated with ground cover, and Nordyke and Buskirk (1991) found vegetative cover of young conifers very important to *C. gapperi* at the macrohabitat scale. However, *C. gapperi* was negatively associated with vegetative cover in mixed forest habitats of Quebec (Vickery and Rivest, 1992). Stock (1967) found that ground cover was not important to *C. gapperi* in northern Idaho grand fir (*Abies grandis*).

Early on, researchers noted that *Clethrionomys* species have an affinity for logs (Gunderson, 1959; Tevis, 1956a). This has led to studies directed specifically at the use of logs by *C. californicus* (Tallmon and Mills, 1994; Hays and Cross, 1987) and the inclusion of course woody debris in more recent habitat analyses for *Clethrionomys* species (Vickery and Rivest, 1992; Buskirk and Nordyke, 1991; Wywiakoski and Smith, 1988; Doyle, 1987; Morris, 1984). Tallmon and Mills (1994) used radio telemetry to determine that *Clethrionomys californicus* was strongly associated with logs and preferred logs in later stages of decay. Hays and Cross (1987) found *C. californicus* associated with large-diameter logs with wider overhanging edges, but did not find the state of decay to be important. In a habitat study in western Oregon, Doyle (1987) concluded that *C. californicus* abundance was correlated with "highly decayed logs", and lichen was important in separating *C. californicus* capture sites from noncapture sites. Wywialowski and Smith (1988) did not find distance, size or age-class to be significant in separating *C. gapperi* capture and noncapture sites, and Nordyke and Buskirk (1991) found cover and diameter of logs unimportant to *C. gapperi* at the macrohabitat level, but they determined that log decay explained 49% of the variation in capture success.

Although *C. gapperi*'s relationship to vegetative cover is not clear, evidence supports the contention that *Clethrionomys* species select microsites with abundant structure at ground level, though the type of structure may vary, and that logs are important microhabitat components for *Clethrionomys* species.

Succession

Early work relating small mammals to cutting and burning of forest stands clearly showed that *Clethrionomys* species were unable to survive the dramatic changes that resulted from these treatments (Gashwiler, 1970 and 1959; Tevis, 1956a). Studies since corroborate these findings (Scrivner and Smith, 1984; Martell, 1982a, 1982b; Sims and Buckner, 1973; Hooven, 1969) for much of North America. Western and eastern North America differ in that the vegetative communities are predominantly coniferous and deciduous respectively. As a result, the communities differ in many ways including the pattern of succession and the composition of small mammal and vegetative communities. In fact, *C. gapperi* seems to prefer coniferous forests over deciduous forests (Kirkland and Griffin, 1974). Despite arguments that small mammals respond similarly to succession in coniferous and deciduous forests (Kirkland, 1990), I treat eastern and western North America separately. I also divided the western half of North America into the Rocky Mountain and Cascade Regions.

Western North America

Rocky Mountain Region

In southeastern Wyoming, Nordyke and Buskirk (1991) studied the effects of succession on *C. gapperi* in spruce-fir (*Picea engelmannii-Abis lasiocarpa*) forests from 2300 to 2750 m in the Medicine Bow Mountains. From this study which focused on macrohabitat (differences between age-classes), they determined that 70% and 67% of the total variation in *C. gapperi* abundance was associated with understory cover (conifer regeneration) in 1986 and 1987 respectively. They also found that a positive correlation between mean log decay and *C. gapperi* abundance explained 49% of the variation in capture success in 1987, but found no correlation with cover and mean diameter of logs. *C. gapperi* was most abundant in old-growth spruce, followed by lodgepole pine (*Pinus contorta*) and least abundant in mature spruce stands. They found weights of adult males to be highest in the old-growth stands and lowest in the lodgepole pine stands and concluded that the early successional sites were dispersal sinks for *C. gapperi* during peak populations such as the one observed during their study. Raphael (1988) also found that *C. gapperi* was most abundant in mature *Picea engelmannii*, and *P. maniculatus* was most abundant in younger

Pinus contorta stands in southeastern Wyoming.

Scrivner and Smith (1984) conducted a study of small mammal succession in spruce-fir forests in Idaho. Stands included 4 age-classes from early succession to "climax" (1-10, 11-39, 40-79, 80+ yrs) in two locations. They found that *C. gapperi* was more abundant in stands over 40 years old and that *P. maniculatus* generally increased with stand age and was more abundant in stands over 80 years old than in stands under 11 years old.

Ramirez and Hornocker (1981) examined small mammal response to forest succession in the Southfork drainage of the Flathead River, northwestern Montana. In the *Abies-Clintonia* habitat type (Pfister et al., 1977), *C. gapperi* favored uncut forest and partial cuts, occurring in extremely low numbers in clearcuts 5-15 years old. *C. gapperi* was also abundant in the uncut *Abies-Luzula* habitat type, but absent from 15 year old clearcuts. *P. maniculatus* was most common in the clearcut *Abies-Clintonia* habitat, but somewhat more abundant in the uncut *Abies-Luzula* habitat type.

Cascade Region

In western Oregon, Hooven and Black (1976) found that *C. californicus* was abundant in an unlogged forest, but was not present in recently logged forests up to 4 years old. For *P. maniculatus*, however, they found much higher abundance in the recently cut sites than on the control grid. *C. californicus* was very rare in clearcuts in Douglas-fir (*Pseudotsuga menziesii*) forests of northwestern California (Tevis, 1956a), but *P. maniculatus* was far more abundant on clearcut sites, both before and after fires, than on uncut sites (Tevis, 1956a, 1965b).

Gashwiler (1970) conducted the only study I found for the western United States that follows the temporal progression of small mammals on the same site after clearcutting. In this study, in the Cascades in western Oregon, *C. californicus* fluctuated, but remained relatively common in the virgin forest control. On the cut grid, *C. californicus* was more abundant than on the control grid before the cut and during the year of the cut, but no voles were captured the first year after or any subsequent years for the next 10 years of the study. *P. maniculatus* populations were initially similar on both grids, but after the cut and burn, *P. maniculatus* populations erupted and remained high, though erratic, on the clearcut grid. It should be noted that *P. maniculatus* populations on the control grid remained stable for the duration of the study. This may have resulted from more constant food sources, interspecific competition or dispersal from forest populations to clearcuts.

Near Vancouver, British Columbia, Walters (1991) compared small mammal abundance between burned and unburned clearcuts and old-growth forests of *Abies amabilis*, *Tsuga* *heterophylla* and *Tsuga mertensiana*. *Clethrionomys* abundance was similar between old-growth and unburned clearcuts, but was lower on the burned clearcut. *P. maniculatus* populations on both cuts were more than twice the forest population. Caution should be taken when interpreting these results regarding the effects of burning on small mammal abundance because all sites were adjoining and the unburned site was closest to the old-growth forest. Other studies in British Columbia found *P. maniculatus* either only slightly higher on clearcuts (Sullivan, 1979) or found no difference between clearcuts and mature forests of *Tsuga heterophylla*, *Thuja plicata* and *Pseudotsuga menziesii* (Petticrew and Sadleir, 1974).

Eastern North America

Comparisons between early seral stages and uncut stands in the deciduous forests of the eastern United States for *C. gapperi* and *P. maniculatus* produce more ambiguous results.

Clethrionomys gapperi is generally more abundant in early succession than in mature stands (Monthey and Soutiere, 1985; Ahlgren, 1966), but Kirkland (1977) found *C. gapperi* more abundant in early stages when he compared the data to stands > 25 years old. However, he clumped older clearcuts (> 25 yrs) and uncut stands, so it is unclear how *C. gapperi* responds to the successional gradient. Yahner (1992) concluded that *C. gapperi* and *P. leucopus* were favored by forest fragmentation in Pennsylvania. However, his data include only the first few years following harvest, and *C. gapperi* is known to increase initially in response to cutting, only to decline to extinction after the first few years (Martell, 1982a, 1982b). In other studies *C. gapperi* was more abundant in uncut stands or there was no difference between sites (Clough, 1987; Krull, 1970). Krefting and Ahlgren (1974) followed numbers of *C. gapperi* after two fires in coniferous forests of Minnesota. For the first 10 years for which data were collected after the burns, the unburned site produced more *C. gapperi* than either burned site.

P. maniculatus initially increases in response to clearcutting (Clough, 1987; Ahlgren, 1966). Afterward there is a subtle trend in which *P. maniculatus* declines through the sapling and pole stages of succession, then rises slightly and stabilizes at low numbers in mature forests (Clough 1987; Kirkland, 1977). Monthey and Soutiere's (1985) data show a similar trend, except *P. maniculatus* did not increase in the initial period after cutting. Data from natural fire succession for 10-15 years after the burns also suggest this trend (Krefting and Ahlgren, 1974). Sims and Buckner (1973) obtained classical results for *P. maniculatus* and *C. gapperi* on three sites in jack pine (*Pinus banksiana*) stands of southeastern Manitoba. Three years of trapping on each paired control and clearcut produced 241 *P. maniculatus* in clearcuts with 19 in mature stands and 4 *C. gapperi* in clearcuts with 153 in mature forest. However, in Nova Scotia hardwood forests neither *P. maniculatus* nor *C. gapperi* differed between clearcuts and controls (Swan et al., 1984). Results from New Brunswick for different aged spruce (*Picea mariana* and *P. glauca*) and jack pine plantations were ambiguous for *C. gapperi*, but showed a slight increase in numbers of *P. maniculatus* for naturally regenerating forest and spruce stands up to about 8 years (as compared to mature *Abies balsamea* stands) (Parker, 1989).

Changes in the small mammal community of boreal *Picea mariana* in forests of northcentral Ontario have been studied extensively. In mature forest, *C. gapperi* dominates and *P. maniculatus* is rare. However, both fire and clearcutting result in the decline of *C. gapperi* over the first few years followed by a complimentary increase in *P. maniculatus* that ultimately dominates the early successional community (Martell, 1984, 1982a, 1982b; Martell and Radvanyi, 1977).

Summary of Succession

Clethrionomys and *Peromyscus* are often the two most prominent players in the successional drama. In its simplest form, the relationship is one where *Clethrionomys* dominates the mature coniferous forest, but is replaced by *Peromyscus* after the canopy is removed. The persistence of

Clethrionomys after cutting depends on post-cutting treatment and the timing of treatment, but complimentary replacement ultimately occurs.

This relationship is strong in the western United States and boreal forests of northcentral Ontario, but is variable to ambiguous in eastern forests. This may be attributed to a number of causes. The primary distinction between the two regions is the dominance of deciduous forest in the east and coniferous forest in the west. Evidence provided by Kirkland and Griffin (1974) suggests that *C. gapperi* prefers coniferous forest. This is also apparent in western Montana, where *P. maniculatus* tends to dominate deciduous forest (pers. obs.). General differences in species composition between the two regions, especially the presence of *Peromyscus leucopus* in the east, also may account for the variable results. Finally, old-growth is less common in the intensively managed forests of the eastern United States and Canada, resulting in younger control grids and the use of plantations for numerous eastern studies.

Diet

Diet is an important aspect of an organism's interaction with its environment. As mycophagists and dispersers of hypogeous mycorrhizal spores, some small mammals help maintain the important symbiotic relationship between plants and their mycobionts (Maser et al., 1978). Many small mammals indulge in mycophagy to some extent, but certain species associated with old-growth forests are largely mycophagist (Maser et al., 1978). *Glaucomys sabrinus* is a specialist on fungi and lichens (Maser et al., 1985) and *C. californicus* obtains 90% -100% of its diet from fungi, particularly hypogeous mycorrhizal forms (Ure and Maser, 1982; Maser et al., 1978). *C. gapperi* is also strongly mycophagist (Maser et al., 1978; Hansson, 1985), though its diet is more variable, and the dominant component seems to depend on author and region.

Many studies indicate fungi and lichens are important to *C. gapperi's* diet (Ure and Maser, 1982; Martell, 1981; Maser et al., 1978; Merritt and Merritt, 1978; Schloyer, 1977; Dyke, 1971; Fisher, 1968; Whitaker, 1962). However, mycophagy is seasonal for *Clethrionomys*, peaking in the spring and fall (Hays et al., 1986; Ure and Maser, 1982; Martell, 1981, Merritt and Merritt, 1978; Williams and Finney, 1964) or summer and fall (Fisher, 1968) apparently resulting from the seasonal availability of sporocarps (Luoma, 1991; Luoma et al., 1991; Williams and Finney, 1964). Vegetation and insects, including Coleoptera and the larvae of Lepidoptera, have also been reported as important dietary components (Perrin, 1979; Schloyer, 1977). Seeds, fruits and other foods play a lesser, but variable role.

Between successional stages, *C. gapperi's* diet reportedly varies little (Martell, 1981; Schloyer, 1977), though Schloyer (1977) did find insects more abundant in the 16-20 year age-class. A lack of hypogeous sporocarps in clear cuts and early successional stages may contribute significantly to the decline of *Clethrionomys* species after the first few years following disturbance (Martell, 1981; Maser et al., 1978; Williams and Finney, 1964).

Although consumption of any mycorrhizal fungus and dispersal of spores will help in maintaining the symbiotic interplay, the focus of some mycophagists on hypogeous forms increases the significance of their role as dispersers, since these spores lack access to wind dispersal (Maser et al., 1978). Spore viability after passage through the digestive tract has been documented for at least some rodent species (Kotter and Farentinos, 1984). Additionally, *C. gapperi* and others have been shown to consume and presumably disperse nitrogen-fixing bacteria which are also viable after defecation (Li et al., 1986a, 1986b) and important for nutrient uptake in plants.

OBJECTIVES

In order to preserve old-growth ecosystems and maintain the viability of species requiring old-growth components, we must understand the relationships that link these organisms to their environment. It is hoped that the research presented here will contribute toward a greater understanding of small mammals and their roles in old-growth ecosystems.

This thesis is divided into 2 chapters. In the first chapter, I examined populations of *Clethrionomys gapperi* and *Peromyscus maniculatus* in 4 successional stages of cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests in the McDonald Valley, Glacier National Park, to determine macrohabitat selection between age classes and microhabitat selection within age classes. The following null hypotheses were tested: 1) Neither *C. gapperi* nor *P. maniculatus* differs in abundance between successional stages (i.e., there is no evidence of macrohabitat selection); 2) Measures of population health; over-winter survival, spring abundance, geometric growth rate, mean adult male body weight do not differ for *C. gapperi* or *P. maniculatus* between successional stages; 3) Microhabitat use does not differ from random for *C. gapperi* or *P. maniculatus* within successional stages; 4) Microhabitat selection does not correspond to macrohabitat selection for *C. gapperi* or *P. maniculatus*. That is, there is no evidence that microhabitat selection determines macrohabitat associations; 5) Habitat separation does not occur between *C. gapperi* and *P. maniculatus*.

In Chapter II, I compared fluorescent pigment tracking (Lemen and Freeman, 1985) with live trapping to examine the null hypothesis that potential biases associated with live trapping do not reduce its ability to assess microhabitat use by *Clethrionomys gapperi*.

CHAPTER I. HABITAT USE BY *CLETHRIONOMYS GAPPERI* AND *PEROMYSCUS MANICULATUS* ALONG A SUCCESSIONAL GRADIENT: THE IMPORTANCE OF SCALE

Abstract. I examined populations of the southern red-backed vole (*Clethrionomys gapperi*) and deer mouse (*Peromyscus maniculatus*) in 4 successional stages (65, 138, 256, 457 Y) in cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests of Glacier National Park to determine macrohabitat selection among stand age classes and microhabitat selection within stand age classes. Abundance of *Clethrionomys gapperi* and *Peromyscus maniculatus* increased with increasing stand age. Microhabitat use differed from available habitat for both species within most age classes, but was not consistent for either species among age classes. The inconsistency in microhabitat use among successional stages, and lack of correspondence between micro- and macrohabitat variables leads to the conclusion that macrohabitat associations determine microhabitat selection, although microhabitat variables may be limiting. In order to properly assess habitat use at either scale the difference between scales must be addressed in the design and analysis of habitat studies. The consistency with which the 2 species partitioned microhabitat was remarkable, yet habitat separation still occurred between species. These results suggest that competitive interactions may have

maintained a spatial barrier between *C. gapperi* and *P. maniculatus* in the McDonald Valley of Glacier National Park.

Peromyscus maniculatus behaved as a generalist at the macrohabitat scale, but exhibited stronger microhabitat selection than did *C. gapperi*. I suggest that *P. maniculatus* may exhibit "habitat switching" and respond to local site conditions by developing search images that manifest themselves as distinctive foraging patterns at the microhabitat scale. Such behavior would render *P. maniculatus* a potentially formidable competitor for resources and explain its tenacity for a wide variety of habitats.

Clethrionomys gapperi exhibits a strong positive linear relationship with stand age and old-growth conditions near the forest floor. If monitored in conjunction with other species such as the pine marten (*Martes americana*), pileated woodpecker (*Dryocopus pileatus*) and barred owl (*Strix asio*), *C. gapperi* could contribute significantly to an "indicator guild" for identifying and monitoring the old-growth condition.

INTRODUCTION

Research examining the relationship between small mammals and forest succession initially arose from concerns that rodent seed predation inhibited stand regeneration (Gashwiler, 1959; Tevis, 1956a). However, accumulating information on mycorrhizal symbiosis and rodent mycophagy indicates small mammals play important roles in forest ecosystems (Maser et al., 1978). By consuming sporocarps of mycorrhizal fungi, rodents disperse viable spores (Li et al., 1986a, 1986b), thereby facilitating mycorrhizal symbiosis which is essential to many higher plants (Trappe, 1987; Sanders et al., 1975; Marks and Kozlowski, 1973). In this capacity, small mammals may contribute significantly to the process of forest succession. Small mammals are also the food base for carnivores such as the pine marten (*Martes americana*) and barred owl (*Strix asio*), recognized by management agencies as important old-growth associated species (Thomas et al., 1993). Rodents, therefore, not only help maintain mycorrhizal symbiosis, they also bridge the gap between trophic levels allowing unique carnivores to persist in the forest environment.

The southern red-backed vole (*Clethrionomys gapperi*) and the deer mouse (*Peromyscus maniculatus*) occur sympatrically over much of their range (Vickery and Rivest, 1992; Miller and Getz, 1977a; Kirkland and Griffin, 1974) and predominate studies that attempt to assess the effects of forest management practices on small mammal populations (Walters, 1991; Gunther et al., 1983; Martell, 1982a, 1982b). *Peromyscus* is a habitat generalist, but is often associated with early seral stages and tends to increase after clearcutting (Walters, 1991; Martell, 1982a, 1982b;

Hooven and Black, 1976; Gashwiler, 1970; Tevis, 1956a, 1956b; but see Sullivan, 1979; Petticrew and Sadlier, 1974). *Clethrionomys gapperi* is a habitat specialist preferring mature forest environments. *Clethrionomys gapperi* is used as an indicator species for the old-growth condition in parts of the Rocky Mountains (USDA Forest Service, 1985) and is listed as an old-growth dependent species (Lumen and Nietro, 1980) and an old-growth associated species requiring old-growth components (Thomas et al., 1993).

Four hypotheses have been purposed by various authors to explain *C. gapperi*'s association with mature and old-growth forests. Odum (1944) reasoned that *C. gapperi* was restricted to mesic environments based on the high water requirements he found for this rodent in the lab and habitat associations he observed in the field. Getz (1962, 1968) confirmed Odum's laboratory results, and other researchers have reported similar associations with moist habitats in field studies (Miller and Getz, 1977a; Kirkland and Griffin 1974; Butsch, 1954). Tevis (1956) and Gunderson (1959) determined that logs were important components of *Clethrionomys*' habitat. Some evidence has been produced to support this conclusion for *C. californicus* (Tallmon and Mills, 1994; Doyle, 1987; Hays and Cross, 1987). Miller and Getz (1977a, 1973, 1972) found *C. gapperi* to associate with woody debris in Connecticut and Virginia. In Wyoming, Nordyke and Buskirk (1991) reported *C. gapperi* in sites with logs in early stages of decay. *Clethrionomys gapperi* was not associated with logs in a microhabitat study in Utah (Wywialowski and Smith, 1988). Competition has been purposed to explain *C. gapperi*'s restriction to forests in some areas (Morris and Grant, 1972; Grant, 1969; Morris, 1969). Maser et al. (1978) suggested the lack of sporocarps in early seral stages could account for the absence of *C. californicus* in these sites. A similar case was established for *C. gapperi* (Martell, 1981), which is also a mycophagist rodent (Ure and Maser, 1982; Martell, 1981; Merritt and Merritt, 1978; Maser et al., 1978; Whitaker, 1962). It is evident that *C. gapperi* is strongly tied to the old-growth condition. However, its relationship to old-growth conditions is not clearly understood.

Most research relating small mammals to forest succession has compared clearcutting or other management practices to controls (Walters, 1991; Clough, 1987; Monthey and Soutiere, 1985; Gunther et al., 1983; Martell, 1982a; Ramirez and Hornocker, 1980; Sullivan, 1979; Kirkland, 1977; Petticrew and Sadlier, 1974; Simms and Buckner, 1973; Gashwiler, 1970, 1959; Ahlgren, 1966; Tevis, 1956a). Surprisingly few studies have compared small mammal communities among a more complete range of successional stages (Nordyke and Buskirk, 1991; Morris 1984; Scrivner and Smith 1984). Scrivner and Smith (1984) found *P. maniculatus* was positively associated with stand age in spruce-fir

(*Picea engelmannii-Abies lasiocarpa*) forests of Idaho, and *C. gapperi* was most abundant in the mature forest, but they did not determine habitat associations. In *Picea glauca-Abies lasiocarpa* and mixed forests of Alberta and Ontario, *P. maniculatus* was most abundant in clearcuts and mature forest, and *C. gapperi* was least common in clearcuts (Morris, 1984). However, this study examined habitat separation among rodents, so microhabitat associations were relative, and no attempt was made to explain the macrohabitat associations reported. Nordyke and Buskirk (1991) studied habitat selection by *C. gapperi* in three successional stages in spruce-fir (*Picea engelmannii-Abies lasiocarpa*) forests in Wyoming and assessed the efficacy of using *C. gapperi* as an indicator species. They determined that *C. gapperi* was most abundant in old-growth spruce-fir and least abundant in mature spruce-fir. They found a strong correlation between *C. gapperi* abundance and old-growth condition and concluded that "populations of *C. gapperi* were not unambiguous indicators of old-growth condition." They suggested that lower numbers, combined with lower body weights of animals in lodgepole pine (*Pinus contorta*) stands, indicated these areas were dispersal sinks. Their results imply that abundance data combined with a qualitative measure of population health, such as body weights, might provide a better indicator for the old-growth condition than abundance alone.

Morris (1984) pointed out the importance of scale in habitat studies of small mammals, arguing that researchers must distinguish between macro- and microhabitat. He also recognized the potential inter-relationship between habitat selection at both scales and asked: "Do the patterns of microhabitat use lead to those at the macrohabitat scale?" I test the null hypothesis that macrohabitat associations are not the result of microhabitat selection.

I examined populations of *Clethrionomys gapperi* and *Peromyscus maniculatus* in 4 successional stages of cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests in the McDonald Valley, Glacier National Park, to determine macrohabitat selection among age classes and microhabitat selection within age classes. The following null hypotheses were tested: 1) Neither *C. gapperi* nor *P. maniculatus* differs in abundance between successional stages (i.e., there is no evidence of macrohabitat selection); 2) Measures of population health: over-winter survival, spring abundance, geometric growth rate, fecundity, and mean adult male body weight do not differ for *C. gapperi* or *P. maniculatus* between successional stages; 3) Microhabitat use does not differ from random for *C. gapperi* or *P. maniculatus* within successional stages; 4) Microhabitat selection does not correspond to macrohabitat selection for *C. gapperi* or *P. maniculatus* (i.e., there is no evidence that microhabitat selection determines macrohabitat associations); 5)

Microhabitat separation between *C. gapperi* and *P. maniculatus* does not occur.

METHODS

Study Area

The study was conducted in the *Tsuga heterophylla-Clintonia uniflora* (western hemlock-queen's cup) and *Tsuga heterophylla-Oplopanax horridum* (western hemlock-devil's club) habitat types (Pfister et al., 1977) of the McDonald Valley, Glacier National Park, Montana (Figure 1). These forests are an inland extension and the eastern boundary of Pacific Northwest western red-cedar (*Thuja plicata*) and western hemlock forests (Habeck, 1968), and they receive an average annual precipitation of 76 cm at West Glacier (Finklin, 1986). Sites included 3 replicates in each of 4 stand ages: ca. 65, 138, 256 and 457 y (Barrett et al., 1991) in the hemlock-queen's cup habitat with an additional 3 replicates in 1 hemlock-devil's club stand. Replicates (plots) were chosen for their similarity in representing stand ages (classes). Average distances between plot centers in each age class were 790, 538, 500, 299, and 264 m for classes 1-5 respectively (Figure 2).

Four distinct successional stages are included in this study. Since the most recent stand replacing fires in the hemlock habitat of the McDonald Valley took place 65 years ago, the early forb, shrub and sapling stages are absent.

Class 1 (65 y), is dominated by even-aged lodgepole pine (*Pinus contorta*) and has an open mid- and understory with a homogeneous species-rich herbaceous layer. Class 2 (138 y) is a structurally complex uneven-aged stand rich in tree species. The canopy is a mixture of seral and climax species: western larch (*Larix occidentalis*), western white pine (*Pinus monticolus*), Douglas-fir (*Pseudotsuga menziesii*), paper birch (*Betula papyrifera*), Engelman spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*), western red-cedar and western hemlock. The midstory is dominated by cedar and hemlock. Lodgepole pine occurs mostly as snags or logs. Ground vegetation is diverse and very heterogeneous ranging from lush patches of vegetation to bare ground. This class expresses old-growth conditions in pre-climax cedar-hemlock forest. Class 3 (256 y) represents the canopy closure phase of forest succession. The canopy is composed primarily of climax cedar and hemlock with some residual white pine and larch present. The midstory is mostly open with dense patches of regenerating hemlock and cedar and the understory is dominated by bryophytes with little herbaceous vegetation due to the heavy, even canopy cover.

The climax cedar-hemlock forest is apparent in classes 4 and 5. The fourth class (457 y) represents a stand entering climax for this habitat. The canopy is dominated by hemlock and cedar with some large diameter larch and white pine (mostly snags) present. Community dynamics in this phase are controlled by gap succession resulting in rich patches of vegetation where recent light gaps occur, a dense mid-story where tree regeneration fills in older gaps, and moss-covered to bare ground where canopy cover is nearly complete. Class 5 (hemlock-devil's club) stands are ca. 457 y. However, these are minimum estimates and conditions in this class suggest it is older than class 4. I treat this stand as a separate class. Class 5 is a moister phase of the hemlock habitat with larger average diameter trees and larger gaps in the canopy. This class has abundant devil's club and boasts greater fern (primarily *Athyrium filix-femina*) coverage and fewer, larger diameter logs.

Field Methods

Fifteen 1/4-ha grids were each divided into 25 10- by 10-m cells. Trapping was conducted for 3 days each month, June to September, 1992-93. One-hundred Sherman live traps were placed at 5-m intervals on each grid so that a cell contained 4 traps approximately equidistant from the center. Traps were baited with peanut butter and rolled oats and lined with cotton for bedding. Traps were checked each morning.

The 10- by 10-m cells provided the basic sampling unit for structure and vegetation data (Table 1). Cover was estimated for each species of vascular plant and for lichens and mosses by randomly placing a 0.2- by 0.5-m rectangular quadrat in each cell once each month June to September, 1992-93 and estimating percent cover for each species present (after Ecodata techniques, USFS). Cover percentages were pooled between months and between years producing 8 samples from each cell that were averaged by species and condensed into the categories listed in Table 1 by summing the mean covers. Quadrat sampling included shrubs and trees under 0.5 m. Shrubs > 0.5 m and trees > 0.5 m and < 3 cm diameter breast height (DBH) were sampled by randomly placing a 50 m^2 circular plot in each of the 4 quadrants of a trapping grid once each year 1992-93. Cover values were obtained similar to those for quadrat sampling by estimating the percentage of the circular plot covered by each species for 2 height classes (0.5-1.5 m and 1.5-2.5 m). DBH was measured for all trees and snags ≥ 3 cm DBH in the circular plots. Plots were sampled in this manner once in 1992 and once in 1993. Cover was averaged by species and summed for the categories SHRB1, REGEN1 and REGEN2 described in Table 1.

Woody debris was defined as stumps, logs and rootwads ≥ 3 cm diameter as measured parallel to the ground. Cells were sampled for woody debris by randomly placing a 10-m transect running north-south or east-west in each cell once each year, 1992-93. Data collected for debris (Table 1) intersecting these transects were averaged by transect and cell. All cell values for cover and woody debris were averaged by plot for macrohabitat analyses.

Data Analysis

Due to problems associated with estimating small mammal populations (Krebs and Meyers, 1974), I used the abundance of individuals present during a trapping period as a simple index of populations. This estimate is equivalent to removal trapping without opening habitat to dispersal, and is preferable to the commonly used ratio of captures per trap nights because it controls for trap response (see Pollock et al., 1990). I used a single factor analysis of variance (ANOVA) to test the null hypothesis that mean annual abundance of *C. gapperi* and *P. maniculatus* did not differ by stand age. Tukey's range test was applied to determine which comparisons were significant. Stepwise multiple regression was used to identify habitat variables correlated with the 2 species and with stand age to help explain macrohabitat selection. I used Pearson product-moment correlations to identify potentially important variables that were masked in the multiple regression analysis due to correlations among variables. Stepwise discriminant function analysis (DFA) (minimizing the overall Wilks' lambda) was used to identify variables important in discerning among age classes.

Five measures of population health were estimated and compared among age classes. I compared weights for adult males of each species, where adult males were defined as *C. gapperi* ≥ 16 g and *P. maniculatus* ≥ 15 g based on timing of reproductive maturity observed in the study area. Over-winter survival was defined as the number of individuals captured in June which weighed ≥ 16 g for *C. gapperi* and ≥ 15 g for *P. maniculatus*. Spring abundance was the total number of individuals captured on a plot in June. I calculated geometric growth rates (λ) for both species from spring and fall abundance after Ricklefs (1979) using

$$\lambda = \frac{N_o + \Delta N/\Delta t}{N_o}$$

where N_o is the initial population size and ΔN and Δt are the respective changes in population and time from N_o to $N_{t=i}$. For N_o=0, λ is undefined. In those cases, I defined λ as 0 for analytical purposes. Fecundity was estimated by summing all individuals appearing on a plot from June to September whose weight was < 15 g for *C. gapperi* and < 14 g for *P. maniculatus*. Multivariate analysis of variance (MANOVA) was used to test the null hypothesis that qualitative measures of population health did not differ among age classes. Adult male weights could not be analyzed with other estimates of population health in the MANOVA, because of empty cells. Weights were compared separately using ANOVA. Natural log transformations were made for abundance data and λ's were analyzed using their squareroots.

For assessing microhabitat use, cells were weighted by their total captures for each species during a 3-day trapping rotation and compared to cells randomly sampled from each plot. MANOVA was used to test the null hypothesis that microhabitat use by *C. gapperi* and *P. maniculatus* did not differ from random. Univariate tests were employed to identify habitat variables that differed in the MANOVA. I used stepwise DFA, minimizing Wilk's lambda (lambda=0.001), to determine microhabitat separation between the 2 species within age classes. Square-root and natural log transformations were used on habitat variables. SPSS® software was used for all analyses (Norušis, 1990). Alpha is 0.05 for all results reported.

RESULTS

Macrohabitat Analysis

Clethrionomys gapperi was more abundant than *Peromyscus maniculatus* in age classes 2, 3, and 4 in 1993 (F=5.28, df=4, P=0.001), but abundance did not differ between species in 1992 (F=1.67, df=4, P=0.161). Mean seasonal abundance did not differ between years by age class for *C. gapperi* (F=0.86, df=4, P=0.505) or *P. maniculatus* (F=1.20, df=4, P=0.343) (Table 2). These data were pooled for each species to analyze abundance among stand ages. Mean annual abundance of *C. gapperi* was lower in class 1 lodgepole pine than in all other classes ($F=11.93$, $df=4$, $P<0.001$) (Figure 3). Mean annual abundance of *P. maniculatus* was higher in class 5 than in class 1 ($F=2.98$, $df=4$, $P=0.039$). Both species increased in abundance with increasing stand age (Figure 3).

Stepwise multiple regression indicated *C. gapperi* was linearly correlated with DTREE and SHRUB ($R^2=0.67$; $P=0.001$), and *P. maniculatus* was linearly correlated with DTREE and #WOOD ($R^2=0.53$; $P=0.011$) at the macrohabitat scale. However, tree diameter is so strongly correlated with stand age and other variables like log diameter that these variables are masked in multiple regression analysis. Independent product-moment correlations identified DWOOD for *Clethrionomys* and LICHEN for *Peromyscus* as plausible causative variables driving macrohabitat selection (Table 3). Stepwise DFA assigned plots to age classes with 100% accuracy using a single discriminant function which, by incorporating 9 of the 13 habitat variables, explained 98% of the variability between age classes. The relative weights of the variables contributing to this function were given by their standardized discriminant function coefficients in Table 3.

DTREE, LOGHT, RNKWOOD and REGEN2 were important conjoining variables in discerning between age classes. Opposing variables, LICHEN, FORBS, SHRB1 and REGEN1, carried less weight in separating age classes. SHRUB and DWOOD were rejected in the stepwise DFA, but were independently correlated with age and *C. gapperi* indicating that they could still be important in explaining macrohabitat use by *C. gapperi*. Ordination of the age classes based on discriminant function scores indicated that class 1 was the most distinct and that classes 2 and 5 were most similar (Figure 4). The 2 classes separated by the greatest distance were classes 1 and 4. Class 3 was approximately equidistant from classes 2 and 5.

Abundance-related indices of population health, over-winter survival, spring abundance, λ and fecundity did not differ between years for *C. gapperi* (F=1.11; df=16, 80; P=0.363) (Table 4). Stand data were pooled across years for MANOVA and found to differ among age classes (F=2.57; df=16, 100; P=0.002). Univariate tests indicated over-winter survival, spring abundance, and λ were significant (P=0.035, 0.024, 0.001) (Figure 5). Adult male *C. gapperi* did not differ in weight between years for classes with sufficient data for comparisons (F=0.659; df=2; P=0.541) (Table 4). Pooled weights were similar among age classes (F=0.969; df=4; P=0.446).

For *P. maniculatus*, abundance-related indices of population health could not be pooled due to differences between years by class (F=1.05; df=16, 80; P=0.050) (Table 5). In 1992, indices were similar among age classes (F=1.70; df=16, 40; P=0.058)(Figure 5). There was insufficient data to test for differences in 1993. Adult male body weights could not be pooled for *P. maniculatus*, because they were higher in 1993 than in 1992 when compared by class (F=4.31; df=2; P=0.049) (Table 5). There was insufficient data to test for differences in weights among classes in 1993, but in 1992 *P. maniculatus* weights were similar among age classes (F=3.81; df=4; P=0.051).

Microhabitat Analyses

Summary statistics from randomly sampled cells provide a description of microhabitat availability and are compared with means for the 2 species (Table 6). Microhabitat use by *C. gapperi* differed from random samples of available habitat in class 1 (F=2.45; df=8, 73; P=0.021), class 4 (F=3.40; df=8, 180; P=0.001) and class 5 (F=2.42; df=8, 150; P=0.018). *Peromyscus maniculatus* differed from random for class 1 (F=3.33; df=8, 85; P=0.002), class 2 (F=2.56; df=8, 148 P=0.012), class 4 (F=3.66; df=8, 222; P<0.001) and class 5 (F=2.99; df=8, 264; P=0.003). Variables identified by ANOVA as important in MANOVA's are given as differences between the species' mean and the random mean in Table 7 and 8 for *Clethrionomys* and *Peromyscus* respectively.

Deviations from random samples of available habitat were remarkably similar for the 2 species. MANOVA's differed for the 2 species only in class 2 where microhabitat use by *P. maniculatus* deviated from random, but

C. gapperi did not. The actual variables driving the MANOVA results were the same for both species except in 2 cases where *P. maniculatus* selected on an additional variable. In class 1 both species were positively associated with MOSS and negatively associated with FORBS. *P. maniculatus* was also found in cells with greater SHRUB cover. In class 4 both species were found in cells with lower LICHEN and MOSS than random and lower RNKWOOD values than expected. LOGHT was higher for *P. maniculatus* in this class. Both species selected sites with lower LICHEN cover and larger structure diameters (DWOOD). In class 2, *P. maniculatus* was found in microhabitats with less FORBS and more LICHEN and #WOOD.

Manova results comparing microhabitat use with available habitat strongly suggested overlap between the 2 species' microhabitats. However, stepwise DFA indicated that habitat separation occurred between the 2 species in class 1 (Wilks' lambda=0.617; $P=0.005$), class 2 (Wilks' lambda=0.802; $P<0.001$) and class 4 (Wilks' lambda=0.935; $P=0.013$). Cover of FORBS was a strong discriminating variable in classes 2 and 4 and LICHEN was of lesser importance for the same classes, but other variables were inconsistent in separating the 2 species (Table 9).

DISCUSSION

This study examined populations of *Clethrionomys gapperi* and *Peromyscus maniculatus* in 4 successional stages

(65-457 y) of cedar-hemlock forests in the McDonald Valley of Glacier National Park to determine macrohabitat selection between age classes and microhabitat selection within age classes. Both species increased in abundance with increasing stand age. High abundance, fecundity and λ in class 4 suggested this was optimal habitat for *C. gapperi* in the McDonald Valley and may have been a source population. Classes 2, 3 and 5 seemed to support *C. gapperi* in moderate numbers and class 1 was likely a sink for this species. Abundance, over-winter survival, spring abundance and fecundity were highest in class 5 (hemlock-devil's club) for *P. maniculatus* indicating this was optimal habitat for this species in the McDonald Valley. Classes 3 and 4 support *Peromyscus* populations in moderate numbers. In classes 1 and 2 *Peromyscus* were uncommon to rare, but it was difficult to assess the quality of these habitats. Microhabitat selection differed for each species between habitats, but was remarkably similar between species within habitats. However, microhabitat separation occurred in most age classes.

Macrohabitat Selection

That macrohabitat selection occurred for *Clethrionomys gapperi* and *Peromyscus maniculatus* was not surprising. However the positive linear association with stand age has not been reported elsewhere for *Clethrionomys* and has only been reported once for *Peromyscus* (Scrivner and Smith, 1984). These results suggest both species shared a preference for older stands, yet abundance alone can be a misleading index of habitat quality (Van Horne, 1983), and other population parameters should also be considered. Nordyke and Buskirk (1991) found *C. gapperi* to be abundant in both early and late successional stages, but found lower body weights associated with animals in early stages of succession and suggested this seral stage was a dispersal sink. I found no differences in adult male body weights for either species between age classes. Adult male body weights may provide additive information for determining population health when higher weights are correlated with higher densities, but high body weights associated with low numbers proves inconclusive, and weights are likely to vary significantly only under extreme conditions of crowding due to stress or resource depletion.

Sullivan (1979) determined that high populations of deer mice commonly reported in clearcuts were probably the result of juvenile dispersal to suboptimal habitats. He found fall populations of deer mice to be over-inflated by the presence of juvenile recruits and suggested spring censusing would circumvent this bias. Because winter is the population bottle-neck for temperate zone rodents, over-winter survival should provide an estimate of population health which indicates the critical carrying capacity for a habitat. Van Horne's (1982) results imply over-winter survival may give good estimates of habitat quality.

Spring abundance is closely related to over-winter survival, but may provide a better measure of habitat quality by including the initial reproductive output of a population. Neither spring abundance nor over-winter survival indicated inequalities among habitats other than the lack of individuals in class 1 for *Clethrionomys*. For *Peromyscus* in 1992, spring abundance and over-winter survival were higher in classes 4 and 5 than in classes 1 and 2. This suggests optimal habitat for *P. maniculatus* was in the oldest 2 age classes. Abundance results supported this conclusion for class 5, but not class 4 where abundance of *Peromyscus* was similar to other age classes.

Spring abundance and over-winter survival were highly variable for both species in class 3. This may have been caused by unpredictable resource availability in this age class resulting in a fluctuating carrying capacity. The lack of under-story vegetation precluded any buffering affect vegetation might have offered against the vagaries of weather or predation. Fungal sporocarps may have been the primary food source here, and sporocarp production is reportedly seasonal and variable between years (Luoma, 1991; Luoma et al., 1991).

Clethrionomys reached their highest numbers in classes 4 and 5 where the old-growth condition and climax overlap.

Population geometric growth rates were well above 1 in class 4 and generally near or below 1 elsewhere. Fecundity was also highest there. This suggested that class 4 produced beyond its critical carrying capacity and was both a core habitat for *C. gapperi* and a source population. Populations 2, 3 and 5 exhibited λ's at or near 1 and so probably supported *C. gapperi*, but did not function as source populations. Class 1 seemed overall to produce only vagrant animals and was likely a sink. Population geometric growth rates were highest in class 3 for *P. maniculatus*, but abundance and fecundity were much higher in class 5 suggesting that class 3 could have been a sink and the high λ a result of immigration, whereas class 5 was optimal habitat.

The population geometric growth rate relates spring numbers to fall abundance in an attempt to estimate the geometric increase of a population. However, as with general population models, the problem lies in controlling for immigration and emigration. For this reason, λ is also problematic in that it can produce inconclusive results. A sink population with low over-winter survival, but high immigration will achieve high λ's. To overcome this deficiency, I presented λ's with a measure of on-site fecundity. Fecundity results were not significant, but they helped to interpret λ's. For *C. gapperi*, fecundity was highest in classes 2, 4 and 5 which most strongly expressed the old-growth condition and somewhat lower in class 3 which contained abundant logs, but lacked the rich patches of vegetative cover associated with classes 2, 4 and 5.

Two explanations may account for the general lack of significant results in estimates of population health for *Clethrionomys* among age classes 2, 3, 4 and 5. These habitats all exhibit old-growth characteristics and as a result, habitat quality may vary within the limits of *Clethrionomys'* requirements. Alternatively, the small area sampled by the 1/4 ha grids in this study may not have provided a sufficiently sensitive measure of spring populations.

Habitat selection only becomes interesting when the habitat features potentially driving selection can be identified. In this study, tree diameter was correlated with abundance of both species, but was also highly correlated with stand age and so its importance is difficult to assess. I suspect that tree diameter was only indirectly recognized by these animals, perhaps as canopy cover and eventually as logs. In Minnesota, Gunderson (1959) found *C. gapperi* positively associated with woody debris and negatively associated with herbaceous cover. Nordyke and Buskirk (1991) reported log decay and vegetative cover (primarily conifers) were correlated with *C. gapperi* abundance among stand ages in Wyoming. I found diameter of woody structure (primarily logs) was strongly correlated with *C. gapperi* and decreasing shrub cover up to 0.5 m was also correlated, although not as strongly. Results presented here are consistent with a habitat-requirement hypothesis explaining *C. gapperi*'s association with mature and old-growth forest. Shrub and herbaceous cover may also be important in determining *Clethrionomys*' habitat, but the relationship appears less consistent.

Peromyscus was associated with higher lichen cover and a greater abundance of woody structure at the macrohabitat scale. However, *P. maniculatus* was both positively and negatively associated with lichen within habitats, suggesting that lichen is probably not causal in determining *P. maniculatus* habitat selection. Wywialowski and Smith (1988) also found *P. maniculatus* in sites with more woody debris when in deciduous habitat, but found no microhabitat selection for either *P. maniculatus* or *C. gapperi* in adjacent coniferous forest.

Although succession results from continuous changes in communities over time, the rate of change is not continuous. Distinct plateaus occur along the continuum until a dynamic equilibrium is established in the climax. Response of animals to succession will likely be most detectable when measured at these stages rather than at the interfaces or transitions between stages. In treating a fuller range of successional stages that includes old-growth this study presents a more complete picture of succession. This may explain the positive linear relationship observed here for both *C. gapperi* and *P. maniculatus* which has not been reported elsewhere. Other studies in the Rocky Mountains corroborate the findings reported here (Nordyke and Buskirk, 1991; Scrivner and Smith, 1984; Ramirez and Hornocker, 1980). The composite created for *C. gapperi* when data are overlaid suggests that although sink populations may exist in younger stands with lower old-growth ratings (Nordye and Buskirk, 1991), *C. gapperi* exhibits a positive linear response to stand age and old-growth condition.

Clethrionomys gapperi is a small mammal of the forest floor and as such may be a reliable indicator of old-growth conditions near ground level, but may poorly indicate old-growth components above the shrub layer. Nordyke and Buskirk (1991) described a second degree polynomial relationship between C. *gapperi* and the old-growth condition. However, their old-growth rating system included canopy components which are unlikely to be recognized by *C. gapperi*. *Clethrionomys* may provide a stronger more linear correlation with old-growth conditions at ground level. In conjunction with species like the barred owl, pine marten and pileated woodpecker (*Dryocopus pileatus*) the potential exists for *Clethrionomys gapperi* to contribute significantly to an "indicator guild" for identifying and monitoring the old-growth condition in the Rocky Mountains. This hypothesis could be tested by comparing population parameters for such a guild to a measure of old-growth condition (Nordyke and Buskirk, 1991).

For Peromyscus, Scrivner and Smith (1984) also reported a positive linear relationship with stand age. *Peromyscus* is reportedly most abundant in early seral stages (Martell and Radvanyi, 1977; Hooven and Black, 1976; Gashwiler, 1970; Ahlgren, 1966; Tevis, 1956a), but Petticrew and Sadleir (1974) found *P. maniculatus* only slightly more abundant in clearcuts and Sullivan (1979) challenged this notion with data that indicated early seral stages were dispersal sinks for *P. maniculatus*. *Peromyscus'* relationship to stand age is not clear, but it is safe to conclude that in the Rocky Mountains *P. maniculatus* is far more common in early seral stages than *C. gapperi*. This fact may increase the importance of *P. maniculatus'* role in succession.

Spores are thought to be destroyed by fire and high temperatures in newly disturbed sites (Maser et al., 1978), but mycorrhizae are important for conifer regeneration (Trappe, 1987). *Peromyscus maniculatus* consumes mycorrhizal sporocarps (Li et al., 1986a, 1986b; Maser et al., 1978; Williams and Finney, 1964; Whitaker, 1962), and through its use of early seral stages may act as a critical disperser of hypogeous mycorrhizal spores and a catalyst for stand regeneration. Whereas, *C. gapperi* and the northern flying squirrel (*Glaucomys sabrinus*) are stronger mycophagists (Maser et al., 1985; Ure and Maser, 1982; Maser et al., 1978; Whitaker, 1962), their restriction to mature forest renders them poorly suited to disperse spores into regenerating forest.

Microhabitat Use

Microhabitat use between species within macrohabitats was more consistent than microhabitat use by either species among habitats. Within microhabitats species differed from random in the same direction using the same variables except in 2 instances where *P. maniculatus* selected on an additional variable. However, selected microhabitat variables differed considerably among sites for both species. In fact, in 2 cases associations with a variable was opposite among macrohabitats. This occurred once with MOSS for *Clethrionomys* and once with LICHEN for *Peromyscus*.

Vickery and Rivest (1992) found no microhabitat selection for *P. maniculatus* or *C. gapperi* in coniferous forest of Quebec. Miller and Getz (1977a, 1973, 1972) found *C. gapperi* in micro-sites with greater cover of shrubs, herbaceous vegetation and woody debris. They also reported *C. gapperi* was associated with saturated substrates. Wywialowski and Smith (1988) found *C. gapperi* in sites with higher ground cover and farther from water than noncapture sites. Caution is advised in interpreting Wywialowski and Smith's (1988) data. Their trapping grid contained more than one habitat, but they do not distinguish between habitats in their analysis of microhabitat use (see discussion below).

Specialist Verses Generalist

Clethrionomys was less selective at the microhabitat scale than was *Peromyscus* which differed from random in more age classes and differed for more variables within age classes. These results seem incongruous given the restricted range of habitats used by *Clethrionomys* and the ubiquity of *Peromyscus*. However, an examination of microhabitat use by *Peromyscus* across all age classes shows that it was associated with every measured variable in one age class or another. At the macrohabitat scale *Clethrionomys* was correlated with more variables and showed stronger correlations than did *Peromyscus*. Additionally, higher *Peromyscus* numbers in class 1 indicated its greater ability to invade what appeared to be suboptimal habitat for both species.

These results confirm that *Peromyscus* is a habitat generalist as defined by its ability to use a variety of habitats, but they also establish that within habitats *Peromyscus* is a strong microhabitat selector. This ability to use a variety of habitats and still maximize use of specific local habitat components suggests *Peromyscus* is capable of a form of "habitat switching" similar to prey switching (Murdoch, 1969). Such behavior would allow *P.*

maniculatus to respond to resource depletion by changing habitats. Once in a habitat, general foraging patterns and opportunistic feeding could quickly result in establishing search images and altering foraging patterns to target abundant or high-reward resources. Holling's (1959) work indicates that *Peromyscus* is capable of a numerical response to increasing prey populations, and McShea and Gilles (1992) observed *Peromyscus leucopus* altered its foraging patterns in response to mast fall. Such behavior renders *Peromyscus maniculatus* a potentially formidable competitor for resources and explains its tenacity for a wide range of habitats.

The consistency with which the 2 species selected and partitioned microhabitat relative to habitat availability was remarkable. Habitat overlap should have resulted. However, the 2 species maintained habitat separation in 2 of the 3 classes (classes 1 and 4) where MANOVA results suggested overlap and in class 2 where only *Peromyscus* differed from random. These results suggest competitive interactions may have been maintaining a barrier between *Clethrionomys gapperi* and *Peromyscus maniculatus* at the microhabitat level.

The habitat separation found here is in accordance with results reported by Vickery (1981) who, by using tracking stations, found microhabitat separation between *P. maniculatus* and *C. gapperi*. Crowell and Pimm (1976) reported macrohabitat separation between these rodents on a 0.8 ha island where the two species had been introduced. This study has been cited as evidence for the importance of competitive interactions in shaping temperate forest communities (see Morris, 1983). Nonetheless, results reported by Crowell and Pimm (1976) are anomalous. *Clethrionomys gapperi* and *P. maniculatus* are sympatric at the macrohabitat scale throughout most of North America (Barry et al., 1990; Vickery et al., 1989; Clough, 1987; Monthey and Souteire, 1985; Fuller, 1985; Morris, 1984, 1983; Gunther et al., 1983; Martell, 1982a, 1982b; Vickery, 1981; Mihok, 1979; Kirkland, 1977; Krefting and Ahlgren, 1974; Simms and Buckner, 1973; Ahlgren, 1966), and microhabitat separation is uncommon for this pair.

In deciduous forests of Virginia (Wolff and Dueser, 1986) and Maryland (Barry et al., 1990) where *C. gapperi* is associated with rocky outcrops, extensive spacial overlap was found between *C. gapperi* and 2 species of *Peromyscus* including *P. maniculatus*. Morris (1983) concluded that *P. maniculatus* and *C. gapperi* were independently distributed within macrohabitats sampled in Alberta.

Vickery et al. (1989) reported microhabitat separation between *C. gapperi* and *P. maniculatus* for 12 of 14 years that the 2 species were monitored. However, their transects included upland dry deciduous forest and spruce bogs and they did not distinguish between macrohabitat and microhabitat in their analyses. Macrohabitat separation almost surely occurred between these sites, but whether microhabitat selection did can not be determined.

If competition is responsible for the habitat partitioning observed here, resource competition for food is most plausible. Interspecific aggression did not result between *C. gapperi* and *P. leucopus* (Getz, 1969) or *C. gapperi* and *P. maniculatus* (Grant, 1972) in lab tests, and it is unlikely that *C. gapperi* and *P. maniculatus* exhibit interference competition for space given the extensive sympatry and limited microhabitat separation reported for these species. Furthermore, diets of *C. gapperi* and *P. maniculatus* overlap extensively when examined from the same location (Gunther et al., 1983; , 1981; and Macaulay 1981; but see Wolff and Dueser [1986] who argue otherwise).

Comparison of Scale

Comparisons of variables implicated in macrohabitat selection with those that differed from random for microhabitat use indicate that there was little correspondence between the 2 scales. DWOOD and SHRUB were associated with greater abundance of *Clethrionomys* at the population level, but no association was found with SHRUB within habitats, and DWOOD was important within only one of 5 locations. *Peromyscus* abundance was positively associated with LICHEN among age classes, but microhabitat associations within sites were contradictory. *Peromyscus* trap sites were correlated with greater LICHEN cover in class 2, but in classes 4 and 5 individuals were found in sites with lower LICHEN cover.

These results indicate that macrohabitat associations determine microhabitat selection. That is, microhabitat use is contingent upon the spacial distribution and quality of resources present on a site. For example, DWOOD was highly correlated with *Clethrionomys* abundance between age classes, but was only identified as a significant microhabitat variable in class 5. This may be explained by the different scale of log availability in this class. Class 5 has fewer logs with larger mean diameters, but greater variability in diameter than classes 2, 3, and 4 (Table 6). Class 1 logs are perhaps too small to be of value to *Clethrionomys*. In this scenario, microhabitat selection may determine the overall habitat use, but selection within habitats is determined by the distribution or availability of resources. In this case greater variability in DWOOD results in selection for the preferred resource in class 5, but the lack of sufficient resource in class 1 results in avoidance of this habitat.

Morris (1984) reported discrepancies in macro- and microhabitat separation between species in Alberta and Ontario, and argued that habitat studies of small mammals must discern between the two scales. Because small mammals use a very finite space in their movements and habitat variables are generally measured at the trapsites, researchers analyze data by trapsite and draw conclusions about "microhabitat use". This is appropriate when the trapping grid and replicates encompass only a single habitat, but when different habitats exist on a grid or when grids lie in different habitats, this approach can result in bias. Results presented here indicate that microhabitat selection depends on macrohabitat. Therefore, samples drawn from different habitats do not represent independent samples between habitats. If an animal selects a macrohabitat on a grid, which is likely for most species, then a random sample of trapping stations will present a biased view of habitat availability. Even greater bias may result from use of noncapture sites for the null dataset. This condition will tend to produce significant results for microhabitat analyses, because differences in macrohabitats have been ignored.

The appropriate unit of comparison for macrohabitat analyses is the macrohabitat. Data can still come from trapsites (and should if microhabitat analyses are also intended), but the statistics compared should be those that reflect the conditions on the grid or in the respective habitats within the grid. These data can be obtained by summarizing data from trapsites.

A number of otherwise well designed studies have succumbed to this error (Nordyke and Buskirk, 1991; Vickery et al., 1989; Wywialowski and Smith, 1988; Doyle, 1987; Gunderson, 1959). I suggest the reason is that the distinction between microhabitat and macrohabitat have not been clearly defined. Whereas macrohabitat analyses should identify patterns of use among different habitats, microhabitat analyses should identify the habitat components animals associate with within a habitat. These variables will describe the manner in which a species uses a habitat, or individuals use habitat components within their home ranges. Significant results will tend to occur less often at the microhabitat scale, because greater sensitivity will be required to detect differences in patterns of use. In a heterogeneous habitat matrix such as that described by Lemen and Freeman (1986) for the Nebraska sandhills, macrohabitat and microhabitat become synonymous because the fine scale of the habitat mosaic places different habitats within individual home ranges. This is the exception, however, and not the rule. Morris' (1984) results and data presented here clearly indicate the importance of distinguishing between macro- and microhabitat scales in small mammal studies of habitat selection and habitat separation.

Conclusions

Abundance of *Clethrionomys gapperi* and *Peromyscus maniculatus* increased with increasing stand age. Microhabitat use differed from available habitat for both species within most successional stages, but was not consistent for either species among age classes. The inconsistency in microhabitat use among age classes and lack of correspondence between micro- and macrohabitat variables leads to the conclusion that macrohabitat associations determine microhabitat selection. In order to properly assess habitat use at either scale the difference between scales must be acknowledged in the design and analysis of habitat studies. The consistency with which the 2 species selected microhabitat relative to habitat availability was remarkable, yet habitat separation still occurred. These results suggest that competitive interactions may have maintained a spatial barrier between *C. gapperi* and *P. maniculatus* in the McDonald Valley.

Peromyscus maniculatus behaved as a generalist at the macrohabitat scale, but exhibited stronger microhabitat selection than *C. gapperi*. I suggest that *P. maniculatus* may exhibit "habitat switching" and respond to local site conditions by developing search images that manifest themselves as distinctive foraging patterns at the microhabitat scale.

Clethrionomys gapperi exhibits a strong positive linear relationship with stand age and old-growth components near the forest floor. If monitored in conjunction with other indicator species such as the pine marten, pileated woodpecker and barred owl, *C. gapperi* could contribute significantly to an "indicator guild" for identifying and monitoring the old-growth condition.

Table 1. Vegetative and structural habitat variables used in analyses.

Habitat variable	Definition
LICHEN	% cover of lichen.
MOSS	% cover of moss.
FORBS	% cover of grasses and forbs.
SHRUB	% cover of shrubs < 0.5 m.
SHRUB1	% cover for shrubs, deciduous trees and conifers from 0.5-1.5 m not included in REGEN1 and 2.
REGEN1	% cover for *Tsuhet*, *Thupli*, *Piceng* and *Abilas** 0.5-1.5 m.
REGEN2	% cover for *Tsuhet*, *Thupli*, *Piceng* and *Abilas** 1.5-2.5 m.
AGE	Estimated stand age.
DTREE	Mean diameter of trees ≥ 3 cm DBH.
DWOOD	Mean diameter of logs, stumps and rootwads ≥ 5 cm measured parallel to the ground.
#WOOD	Mean # of logs, stumps and rootwads as defined above.
LOGHT	Height from the ground to the bottom of logs.
RNKWOOD	Decay class for logs, stumps and rootwads ranging from 1-5, where 1 is freshly fallen and 5 is nearly duff.

* *Tsuhet* (*Tsuga heterophylla*), *Thupli* (*Thuja plicata*), *Piceng* (*Picea engelmanii*), *Abilas* (*Abis lasiocarpa*).

Table 2. Mean annual abundance of *Clethrionomys gapperi* (*Clegap*) and *Peromyscus maniculatus* (*Peoman*).

		Stand age class				
		1	2	3	4	5
Species	Year	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se
Clegap	1992	0.2 ±0.1	1.9 ±0.4	1.9 ±0.9	4.2 ±0.9	4.3 ±0.7
	1993	0.3 ±0.1	1.3 ±0.6	1.4 ±0.5	3.2 ±1.1	1.8 ±0.4
	pooled	0.2 ±0.1	1.6 ±0.4	1.7 ±0.5	3.7 ±0.7	3.0 ±0.7
Peoman	1992	0.5 ±0.3	1.6 ±1.3	2.8 ±0.7	2.1 ±1.2	4.6 ±1.3
	1993	0.3 ±0.3	0.3 ±0.1	0.3 ±0.2	0.0	1.5 ±0.0
	pooled	0.4 ±0.2	0.9 ±0.7	1.6 ±0.7	1.0 ±0.7	3.0 ±0.9

Table 3. Standardized discriminant function coefficients and Pearson product-moment correlations. Discriminant function coefficients are from the first discriminant function which explained 98% of the variability between age classes using the 9 variables indicated. Product-moment correlations are reported for correlations where $\alpha \leq 0.05$ in independent comparisons between the habitat variables and age class, *Clethrionomys gapperi* (*Clegap*) and *Peromyscus maniculatus* (*Peoman*). Asterisks indicate significance levels.

Variables	Discriminant function coefficients	Stand Age	*Clegap* abundance	*Peoman* abundance
LICHEN	-6	+0.57*		+0.55*
MOSS				
FORBS	-5			
SHRUB		-0.59*	-0.58*	
SHRB1	-5			
REGEN1	-3			
REGEN2	+10			
DTREE	+15	+0.80***	+0.72**	+0.58*
DWOOD		+0.73**	+0.66**	
#WOOD	+8			
LOGHT	+13			
RNKWOOD	+12	+0.59*		

* P<0.05, ** P<0.005, *** P<0.0005, **** P<0.00005

Table 4. Indices of population health for *Clethrionomys gapperi*. Indices are defined in the methods.

		Indices of population health				
Age class	Year	Over-winter survival $\bar{x}$ ±se	Spring abundance $\bar{x}$ ±se	λ $\bar{x}$ ±se	Fecundity $\bar{x}$ ±se	Adult ♂ weights $\bar{x}$ ±se
1	1992	0.0	0.0	0.0	0.0	19.6 ±3.8
	1993	0.0	0.0	0.0	0.3 ±0.3	16.0 ±0.0
	pooled	0.0	0.0	0.0	0.2 ±0.2	18.5 ±2.5
2	1992	1.7 ±0.3	2.7 ±0.7	1.2 ±0.1	2.3 ±0.3	20.7 ±0.9
	1993	1.0 ±0.6	1.0 ±0.6	0.4 ±0.2	0.7 ±0.7	20.8 ±1.1
	pooled	1.3 ±0.3	1.8 ±0.5	0.8 ±0.2	1.5 ±0.5	20.8 ±0.7
3	1992	1.3 ±0.9	1.3 ±0.9	1.0 ±0.5	1.0 ±1.0	22.3 ±1.5
	1993	2.0 ±1.0	2.0 ±1.0	0.9 ±0.1	0.0	19.5 ±1.1
	pooled	1.7 ±0.6	1.7 ±1.5	1.0 ±0.2	0.5 ±0.5	21.1 ±1.1
4	1992	1.3 ±0.3	1.3 ±0.3	3.2 ±0.3	2.7 ±1.2	20.1 ±1.6
	1993	0.7 ±0.3	0.7 ±0.3	2.1 ±1.4	2.3 ±1.5	20.1 ±0.9
	pooled	1.0 ±0.3	1.0 ±0.6	2.6 ±0.7	2.5 ±0.5	20.1 ±0.8
5	1992	2.0 ±1.0	2.7 ±0.9	1.3 ±0.5	1.3 ±0.9	21.9 ±0.5
	1993	0.3 ±0.6	0.3 ±0.3	0.3 ±0.3	1.3 ±1.3	20.9 ±1.2
	pooled	1.2 ±0.6	1.5 ±0.7	0.8 ±0.4	1.3 ±0.7	21.4 ±0.6

Table 5. Indices of population health for *Peromyscus maniculatus*. Indices are defined in the methods.

		Indices of population health				
Age class	Year	Over-winter survival $\bar{x}$ ±se	Spring abundance $\bar{x}$ ±se	λ $\bar{x}$ ±se	Fecundity $\bar{x}$ ±se	Adult ♂ weights $\bar{x}$ ±se
1	1992	0.7 ±0.7	0.6 ±0.7	0.3 ±0.3	0.3 ±0.3	16.8 ±0.8
	1993	0.0	0.0	0.0	0.0	22.9 ±0.0
2	1992	0.0	0.0	0.0	2.7 ±2.7	16.4 ±0.4
	1993	0.7 ±0.3	0.7 ±0.3	0.4 ±0.2	0.0	21.4 ±0.0
3	1992	2.7 ±1.7	2.7 ±1.7	1.8 ±0.4	1.7 ±0.7	19.2 ±0.7
	1993	0.3 ±0.3	0.3 ±0.3	0.3 ±0.3	0.0	21.5 ±0.0
4	1992	1.7 ±0.9	2.3 ±0.3	1.0 ±0.2	1.3 ±0.3	19.8 ±1.7
	1993	0.0	0.0	0.0	0.0	
5	1992	3.3 ±0.3	3.7 ±0.3	0.7 ±0.1	4.0 ±1.5	21.1 ±0.9
	1993	1.0 ±0.6	1.0 ±0.6	0.7 ±0.4	0.3 ±0.3	18.7 ±2.3

Table 6. Means and standard errors of structure and vegetation data from random samples of available habitat and from *Clethrionomys gapperi* (*Clegap*) and *Peromyscus maniculatus* (*Peoman*) trap sites in each age class.

		Stand age class									
		1		2		3		4		5	
Variable	Species	$\bar{x}$	±se	$\bar{x}$	±se	$\bar{x}$	±se	$\bar{x}$	±se	$\bar{x}$	±se
LICHEN	Random	1.7	±0.1	1.2	±0.1	2.3	±0.2	3.1	±0.4	2.7	±0.3
	Clegap	1.1	±0.4	1.5	±0.1	2.7	±0.3	2.1	±0.1	2.0	±0.2
	Peoman	3.7	±0.9	2.4	±0.4	2.4	±0.2	2.5	±0.3	2.2	±0.2
MOSS	Random	22.3	±1.8	19.5	±1.7	49.2	±2.2	20.3	±1.8	26.9	±1.6
	Clegap	35.1	±7.0	16.9	±1.6	42.2	±2.8	15.8	±0.9	30.4	±1.5
	Peoman	30.5	±3.7	22.7	±2.2	46.3	±2.2	14.6	±1.7	30.1	±1.1
FORBS	Random	57.5	±2.2	61.9	±2.7	7.9	±0.8	33.9	±2.0	60.6	±2.2
	Clegap	41.3	±5.0	55.7	±2.9	6.9	±0.6	30.7	±1.4	57.2	±1.5
	Peoman	39.7	±2.4	34.3	±3.3	7.7	±0.7	34.8	±2.2	58.8	±1.3
SHRUB	Random	11.9	±1.0	12.4	±0.9	3.7	±0.5	2.1	±0.3	6.5	±0.8
	Clegap	12.5	±3.8	12.5	±0.9	3.8	±0.5	2.0	±0.3	8.6	±0.8
	Peoman	21.9	±2.1	11.6	±1.4	4.3	±0.5	0.8	±0.2	9.6	±0.8
DWOOD	Random	13.5	±1.1	17.2	±1.0	17.6	±1.1	19.7	±0.6	26.7	±2.7
	Clegap	11.1	±2.1	19.0	±1.4	17.5	±0.9	20.5	±0.4	31.5	±1.9
	Peoman	10.3	±1.2	16.8	±0.7	17.6	±1.1	21.3	±0.8	34.8	±2.0

Table 6 (cont). Means and standard errors of structure and vegetation data from random samples of available habitat and from *Clethrionomys gapperi* (*Clegap*) and *Peromyscus maniculatus* (*Peoman*) trap sites in each age class.

		Stand age class				
		1	2	3	4	5
Variable	Species	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se
#WOOD	Random	7.3 ±0.6	4.6 ±0.3	6.4 ±0.3	4.7 ±0.3	3.0 ±0.2
	Clegap	4.9 ±1.9	5.1 ±0.4	6.8 ±0.3	5.1 ±0.2	3.2 ±0.2
	Peoman	8.5 ±1.1	6.1 ±0.3	6.7 ±0.4	5.1 ±0.3	2.8 ±0.1
LOGHT	Random	6.8 ±0.6	13.3 ±1.1	7.9 ±0.8	8.6 ±1.0	4.9 ±0.7
	Clegap	4.3 ±1.3	12.9 ±1.2	8.6 ±1.0	10.3 ±0.7	5.5 ±0.7
	Peoman	10.0 ±1.2	15.3 ±1.4	10.8 ±1.3	11.5 ±1.3	5.4 ±0.7
RNKWOOD	Random	3.2 ±0.1	2.8 ±0.1	3.4 ±0.1	3.6 ±0.1	3.3 ±0.1
	Clegap	3.2 ±0.3	3.0 ±0.1	3.4 ±0.1	3.4 ±0.0	3.6 ±0.1
	Peoman	2.7 ±0.1	2.9 ±0.1	3.3 ±0.1	3.4 ±0.1	3.6 ±0.1

Table 7. Microhabitat variables associated with *Clethrionomys gapperi* which differed from random samples of available habitat using MANOVA. Significant variables are given as differences from random. Univariate p-values are presented below the differences.

	Stand age class				
Variables	1	2	3	4	5
LICHEN				-1.0 P=0.001	-0.7 P=0.024
MOSS	+12.8 P=0.041			-4.5 P=0.012	
FORBS	-16.2 P=0.020				
SHRUB					
DWOOD					+4.8 P=0.021
#WOOD					
LOGHT					
RNKWOOD				-0.2 P=0.015	
Multivariate significance	F=2.45 df=8,73 P=0.021*	F=0.76 df=8,115 P=0.635	F=0.81 df=8,104 P=0.596	F=3.40 df=8,180 P=0.001*	F=2.42 df=8,150 P=0.018*
Eigenvalues	0.268	0.053	0.062	0.151	0.129

* indicates multivariate significance.

Table 8. Microhabitat variables associated with *Peromyscus maniculatus* which differed from random samples of available habitat using MANOVA. Significant variables are given as differences from random. Univariate p-values are presented below the differences.

	Stand age class				
Variables	1	2	3	4	5
LICHEN		+1.2 P=0.019		-0.6 P=0.002	-0.5 P=0.029
MOSS	+8.2 P=0.013			-5.7 P=0.004	
FORBS	-17.8 P<0.001	-27.6 P<0.001			
SHRUB	+10.0 P=0.013				
DWOOD					+8.1 P=0.001
#WOOD		+1.5 P=0.024			
LOGHT				+2.9 P=0.033	
RNKWOOD				-0.2 P=0.007	
Multivariate significance	F=3.33 df=8,85 P=0.002*	F=2.56 df=8,148 P=0.012*	F=0.71 df=8,164 P=0.685	F=3.66 df=8,222 P<0.001*	F=2.99 df=8,264 P=0.003*
Eigenvalues	0.313	0.138	0.034	0.132	0.091

* indicates multivariate significance.

Table 9. Microhabitat separation between *Clethrionomys gapperi* and *Peromyscus maniculatus* and significant variables contributing to separation in stepwise discriminant function analyses.

Age class	Wilks' lambda	P-value	Significant variables in order of importance
1	0.617	P=0.005	LOGHT
2	0.802	P<0.001	FORBS MOSS #WOOD LICHEN RNKWOOD
3	0.951	P=0.147	
4	0.935	P=0.013	SHRUB FORBS LICHEN
5	0.977	P=0.185	

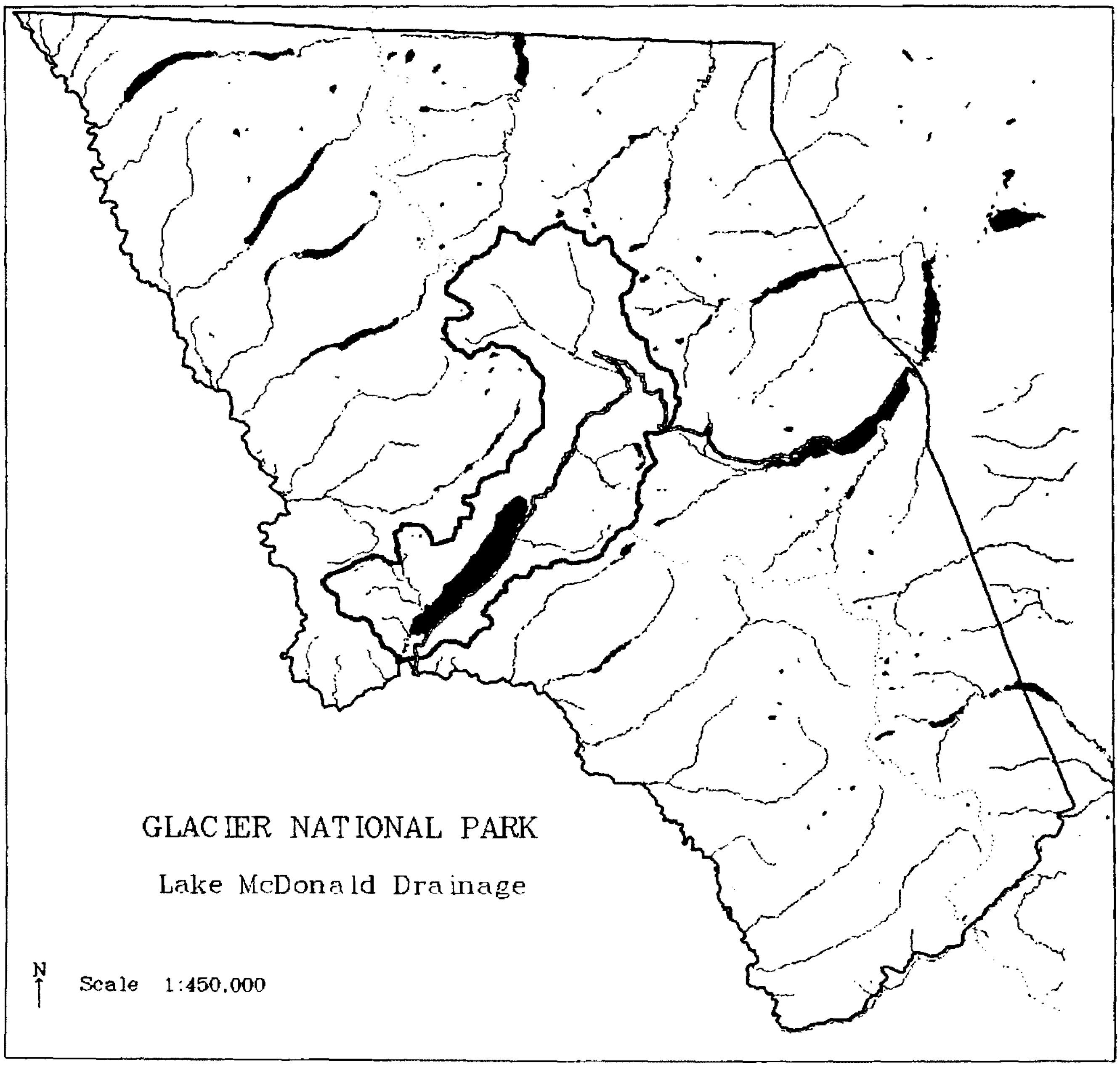

Figure 1. Map showing Glacier National Park and the Lake McDonald Drainage (outlined in bold). Going To The Sun Road is shown for reference.

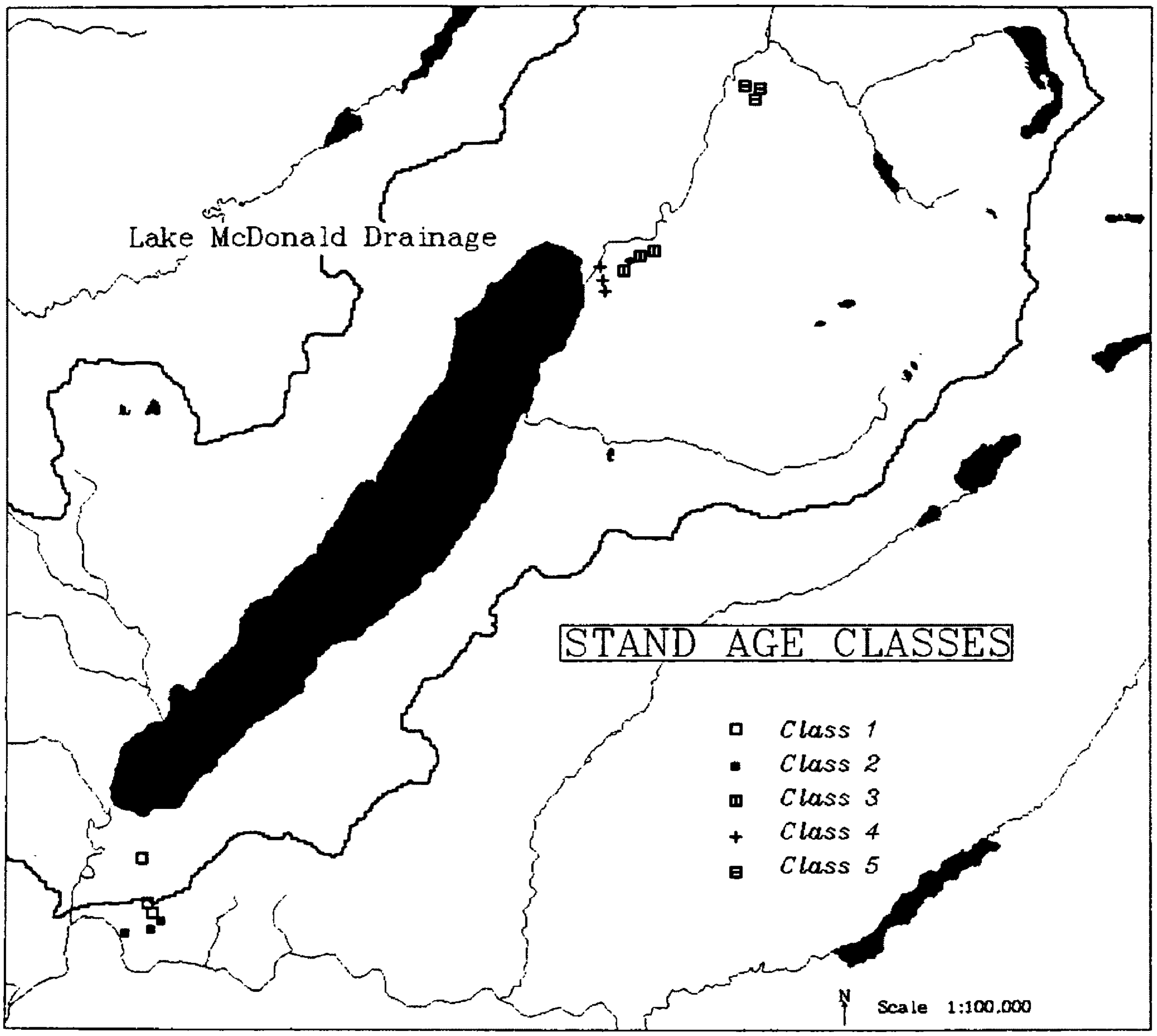

Figure 2. Map of the Lake McDonald Drainage showing the relative positions of age classes and replicates. Symbols are enlarged for clarity.

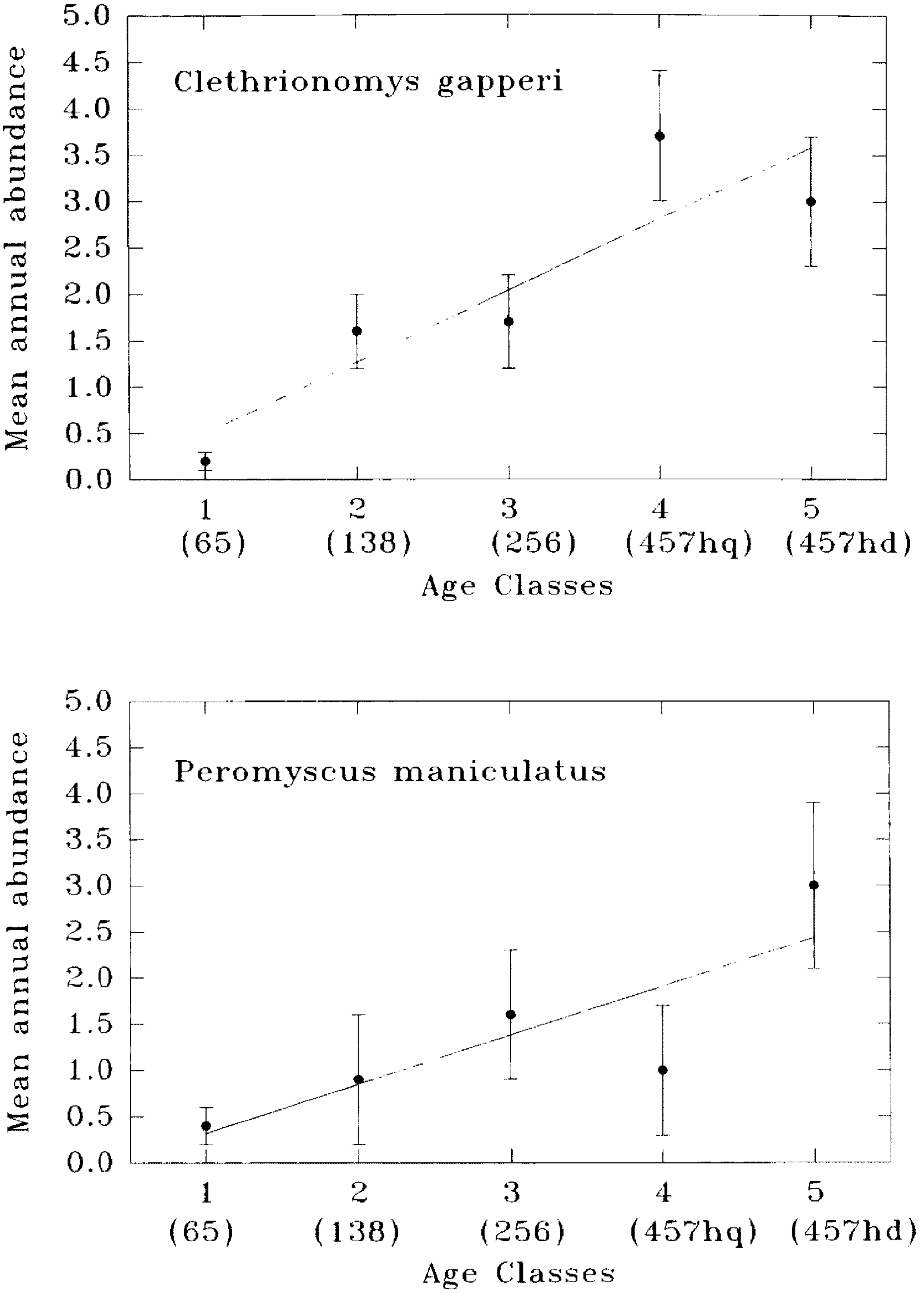

Figure 3. Comparison of mean annual abundance between stand age classes for *Clethrionomys gapperi* and *Peromyscus maniculatus*. Data represent pooled means from 1992 and 1993. Regression lines are displayed. Estimated stand ages are in parentheses. hq and hd denote hemlock-queen's cup and hemlock-devil's club habitat types.

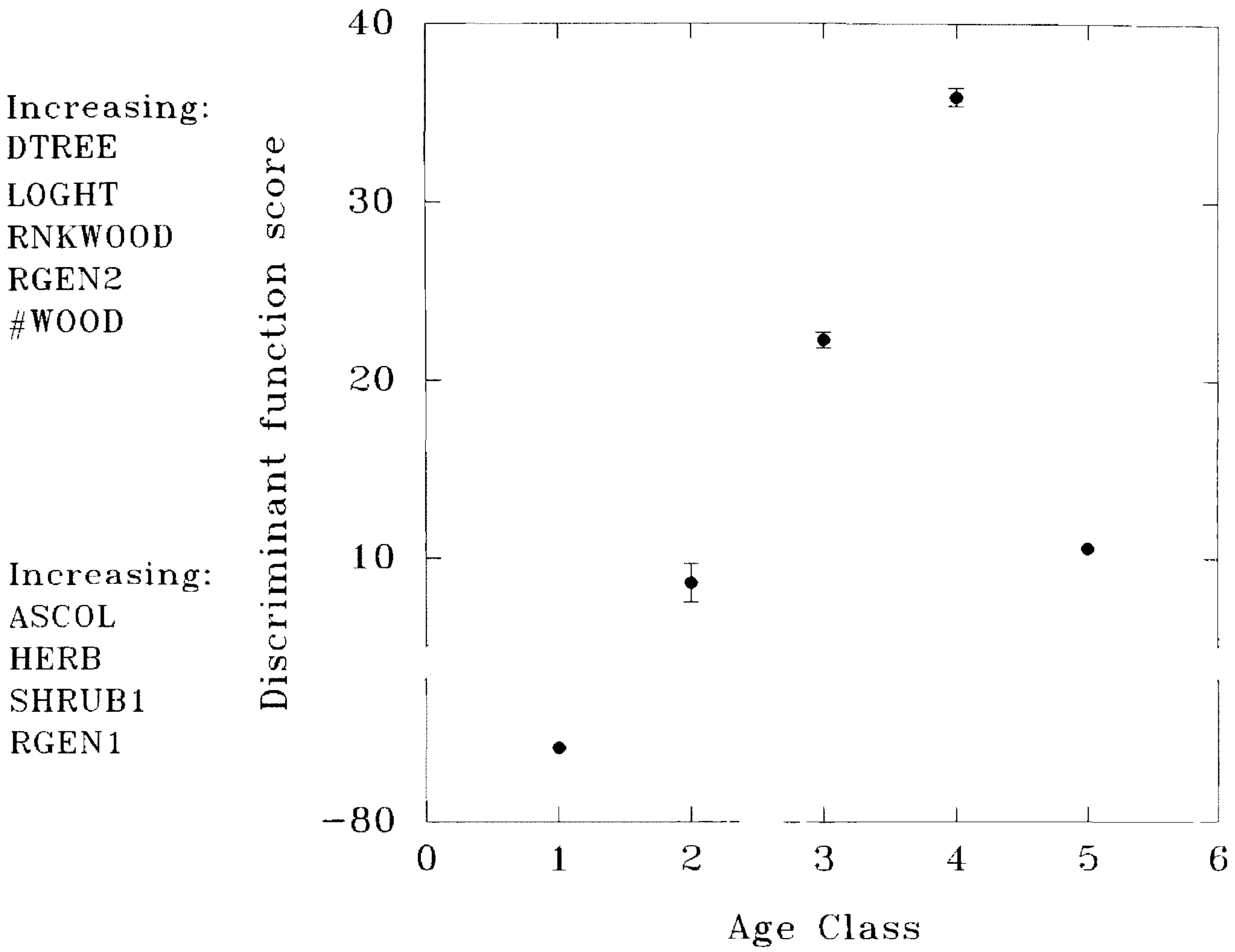

Figure 4. Ordination of stand age classes (65, 138, 256, 457hq*, 457hd) based on discriminant function scores from stepwise discriminant function analysis. All plots were correctly assigned to age classes and 98% of the variability between plots was described using this discriminant function. * hc and hd denote hemlock-queen's cup and hemlock-devil's club habitat types.

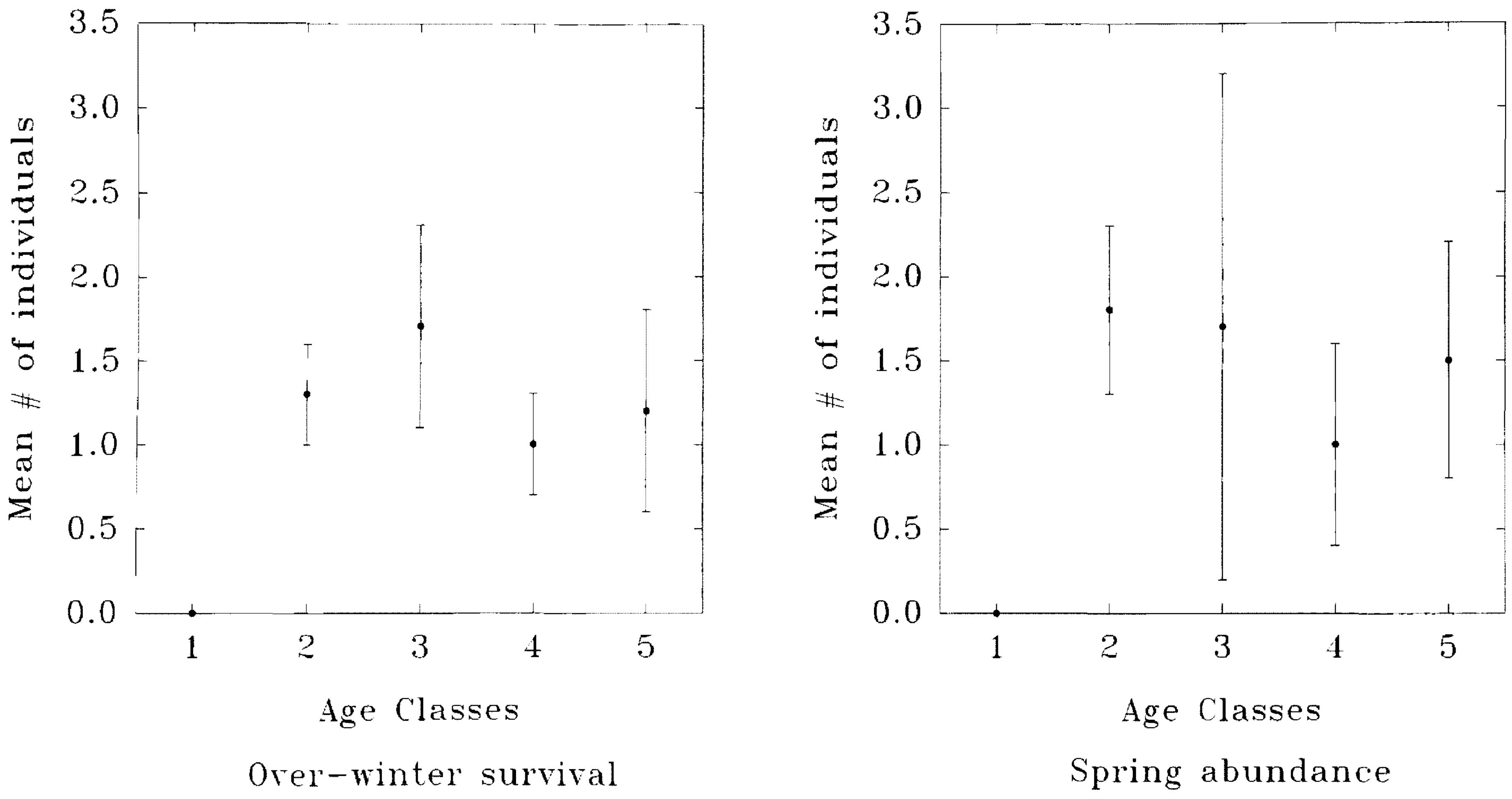

Figure 5. Comparison of means and standard errors for over-winter survival and spring abundance for *Clethrionomys gapperi*. Indices are defined in Methods. Age classes correspond to the following stand ages: 1 = 65 y; 2 = 138 y; 3 = 256 y; 4 = 457 y hemlock-queen's cup habitat type; 5 = 457 y hemlock-Devil's club habitat type.

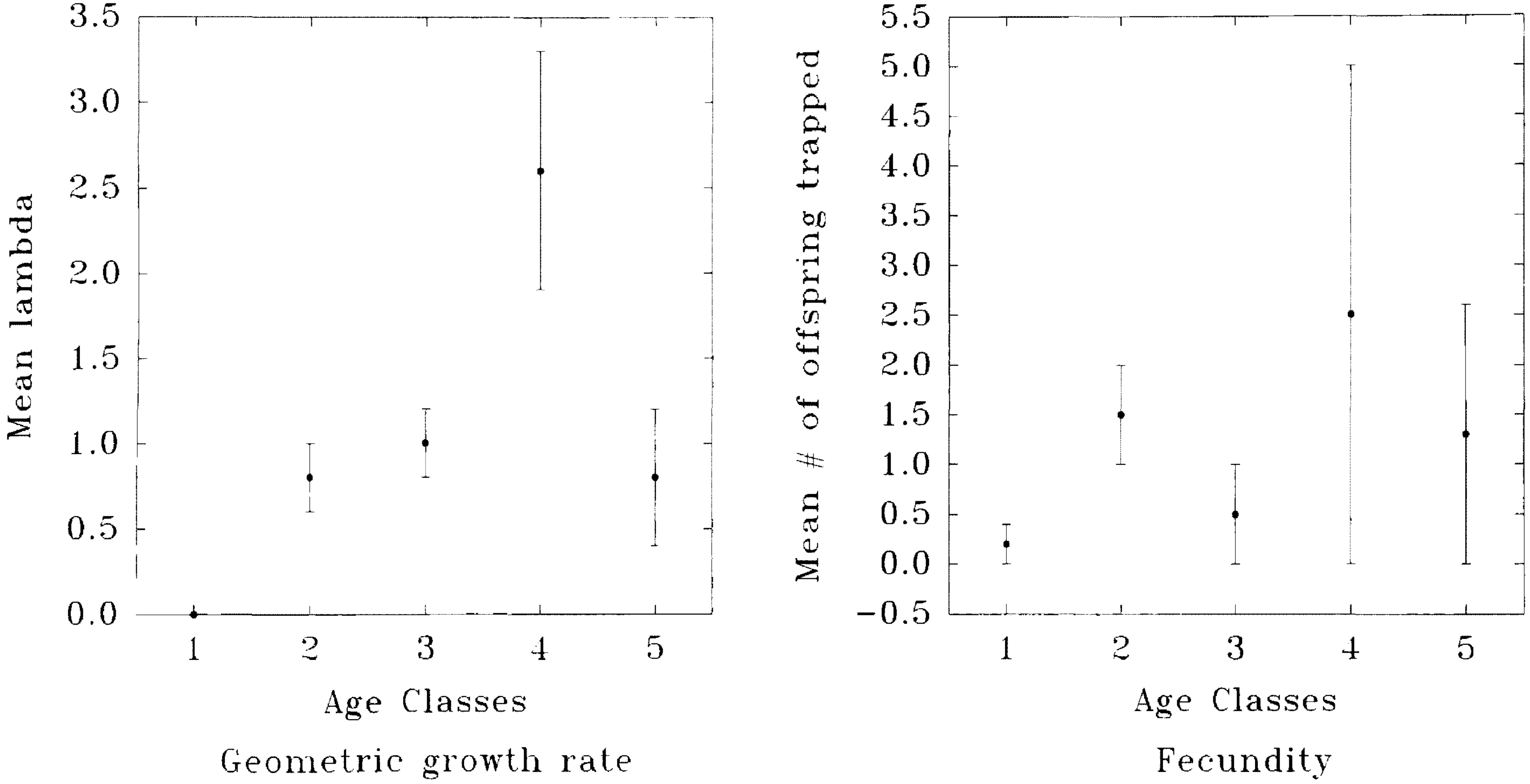

Figure 6. Comparison of means and standard errors for geometric growth rate and fecundity for *Clethrionomys gapperi*. Indices are defined in Methods. Age classes correspond to the following stand ages: 1 = 65 y ; 2 = 138 y; 3 = 256 y; 4 = 457 y hemlock-queen's cup habitat type; 5 = 457 y hemlock-Devil's club habitat type.

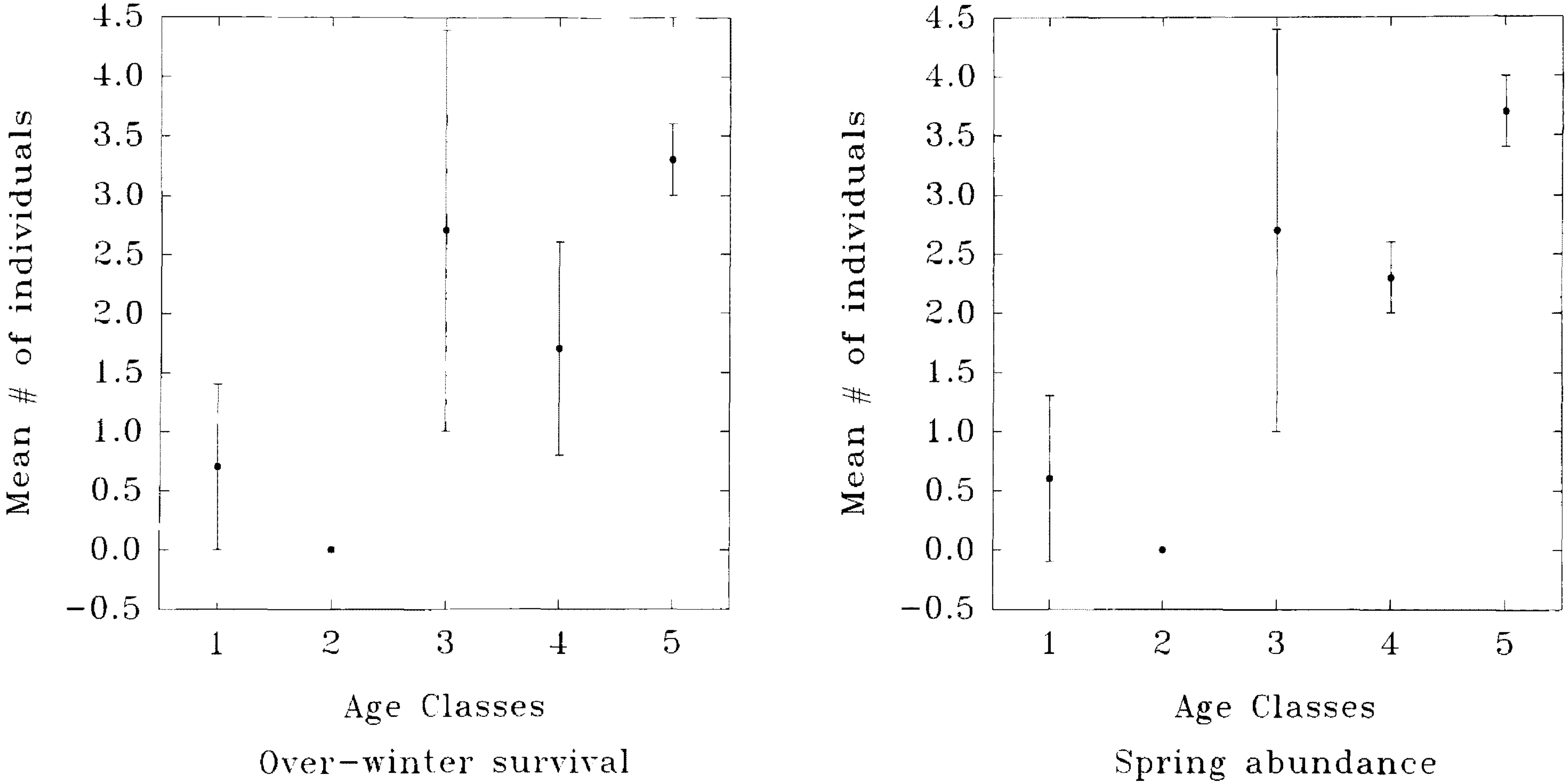

Figure 7. Comparison of means and standard errors for over-winter survival and spring abundance for *Peromyscus maniculatus*. Indices are defined in Methods. Age classes correspond to the following stand ages: 1 = 65 y; 2 = 138 y; 3 = 256 y; 4 = 457 y hemlock-queen's cup habitat type; 5 = 457 y hemlock-Devil's club habitat type.

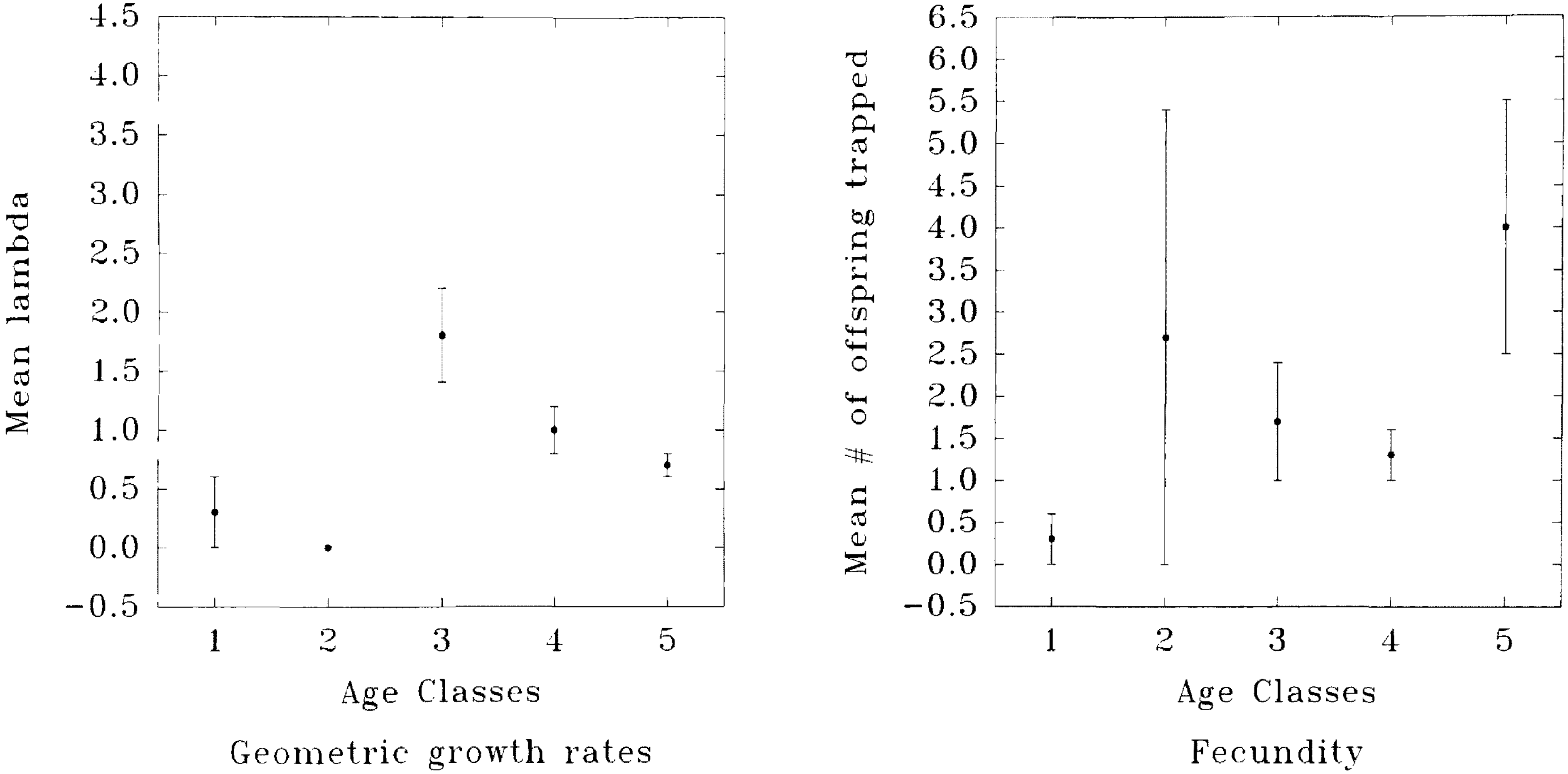

Figure 8. Comparison of means and standard errors for geometric growth rate and fecundity for *Peromyscus maniculatus*. Indices are defined in Methods. Age classes correspond to the following stand ages: 1 = 65 y; 2 = 138 y; 3 = 256 y; 4 = 457 y hemlock-queen's cup habitat type; 5 = 457 y hemlock-Devil's club habitat type.

CHAPTER II. A COMPARISON OF FLUORESCENT PIGMENT TRACKING AND LIVE TRAPPING TO EXAMINE MICROHABITAT USE BY *CLETHRIONOMYS GAPPERI* IN GLACIER NATIONAL PARK, MONTANA.

A quantitative method developed for microhabitat analysis of fluorescent pigment trails was compared with live trapping. Microhabitat variables, measured along pigment trails and at trapping stations, were compared to corresponding random samples of available habitat in forests of 4 different age classes (65, 138, 256, 457 y). Data from random samples and *C. gapperi* were also directly compared between methods in each age class. Data collected in age class 2 differed between methods. Furthermore, fluorescent pigment tracking indicated that the microhabitat used by *C. gapperi* differed from random in class 2, but this habitat selection was not detected by live trapping. I conclude that live trapping can result in misleading conclusions about microhabitat use by small mammals due to trap bias or the gross scale at which associations are made between microhabitat variables and small mammals. Fluorescent pigment tracking, as described here, provides a more accurate and more sensitive means of assessing microhabitat use by and microhabitat separation between small mammals.

INTRODUCTION

Trapping is the primary technique employed in habitat studies of small rodents (Doyle, 1987; Morris, 1984; Crowell, 1983, 1973; Van Horne, 1982; Dueser and Shugart, 1979; Miller and Getz, 1977a; Crowell and Pimm, 1976; Grant, 1969; Gunderson, 1959). However, assessing microhabitat use with trapping is inferential; based on the assumption that capture sites are indicative of normal animal movements. Although this assumption should hold at the macrohabitat scale, its validity for microhabitat analysis is questionable (Goodyear, 1992, 1989; Douglass, 1989, 1977; White and Garrott, 1986; Lemen and Freeman, 1985). Because most trapping involves baiting which lures animals into traps, trap locations may not represent normal movement patterns (Douglass, 1989, 1977; but see Price, 1977). Residual odors left in traps from previous captures may also bias trap results due to inter- or intraspecific social interactions (Heske, 1987; Daly et al., 1980; Mazdzer et al., 1976; Boonstra and Krebs, 1976; Summerlin and Wolff, 1973). Trap placement is another factor which may affect results (Price and Kramer, 1984), especially when traps are placed to maximize captures, as is often the case (eg. Mullican and Baccus, 1990; Wywialowski and Smith, 1988). Trapping small mammals to examine microhabitat use involves collecting habitat data within a defined region around trapping stations (Lemen and Freeman, 1986; Rebar and

Conley, 1983; Van Horne, 1982). This method provides a gross approximation of microhabitat associations that may lead to irrelevant correlations. It also introduces ambiguity into the design, because it requires the researcher to define the scale at which variables will be measured.

Historically, trapping techniques monopolized spatial analyses of small mammals as the only reliable means of obtaining habitat information. More recently, radio-telemetry (Brooks and Banks, 1971; Sanderson and Sanderson, 1964), and fluorescent pigments (Lemen and Freeman, 1985) have been applied in habitat studies of small mammals. Radio-telemetry avoids many trapping biases, but introduces other potential biases such as observer presence and radio-transmitters. Although many telemetry users argue that animals are not affected by their presence (Tallmon and Mills, 1994; Mullican, 1988; Madison, 1978), I found no studies to verify this and results presented by Mullican (1988) indicated that home ranges using telemetry were generally larger than those for FPT. This could be interpreted as avoidance behavior resulting from the presence of an observer. Radio-transmitters have been shown to reduce animal activity for the first 1 to 2 days and increase winter mortality (Webster and Brooks, 1979; Hamley and Falls, 1975). Additionally, radio-telemetry does not give precise locations (White and Garrott, 1986; Lee et al., 1985). This reduces its effectiveness for microhabitat analysis and may result in a tendency for researchers to approach animals too closely to obtain more accurate locations.

Fluorescent pigment tracking (FPT) provides exact locations without the biases that may result from observers, radio transmitters or inferential use of traps as locations. Because scale is defined by the animal's movements, the ambiguity of defining scale is also reduced. Since its introduction in 1985 (Lemen and Freeman), FPT has been used primarily in microhabitat and homerange studies (McShea and Gilles, 1992; Mullican and Baccus, 1990; Etheredge et al., 1989; Mullican, 1988; Jike et al., 1988; Lemen and Freeman, 1986). Habitat studies using FPT have capitalized on qualitatively assessing habitat features important to small mammals and on FPT's obvious advantages for detecting 3-dimensional use of space (Goodyear, 1992, 1989; Mullican and Baccus, 1990; Etheredge et al., 1989; Lemen and Freeman, 1985), but have largely ignored its potential for precisely quantifying microhabitat use. Goodyear (1992) developed a method which effectively quantifies fluorescent pigment trails, but this method was not compared to trapping data for microhabitat analysis. Comparisons of FPT with radiotelemetry for home-range estimates indicated that FPT gave as good or better estimates of home-ranges than radio tracking (Jike et al., 1988; Mullican, 1988). Comparisons of FPT and trapping have proven less conclusive. Lemen and Freeman (1986) reported no difference in microhabitat results obtained with FPT and trapping for either *Dipodomys ordii* or *Perognathus flavescens*. However, McShea and Gilles (1992) determined they could distinguish between foraging areas and non-foraging areas of *Peromyscus leucopus* during mast-fall with FPT, but not with trapping, and therefore, concluded that FPT was a more sensitive means of estimating shifts in microhabitat. Although the results of McShea and Gilles (1992) suggest that FPT may be more sensitive than live trapping for estimating microhabitat use, contradictory results presented by Lemen and Freeman (1986) indicate further studies are needed. To my knowledge no further studies have been conducted.

I present here a quantitative method for measuring microhabitat variables directly associated with FPT locations for *Clethrionomys gapperi*. I assume that FPT, as applied here, is a more accurate, less biased method for determining microhabitat use by small mammals and compare FPT to live trapping to examine the null hypothesis that potential biases associated with live trapping do not reduce its ability to assess microhabitat use.

METHODS

Study area.—The study was conducted in the *Tsuga heterophylla-Clintonia uniflora* (western hemlock-queen's cup) habitat type (Pfister et al., 1977) of the McDonald Valley, Glacier National Park, Montana. Trapping grids include 4 stand ages: 65, ~138, ~256 and ~457 years old (Barrett et al., 1991).

Field methods.—Twelve 1/4-ha grids were each divided into 25 10- by 10-m cells. Trapping was conducted for three days each month, June to September, 1992-93. One-hundred Sherman live traps were placed at 5-m intervals on each grid so that a cell contained 4 traps approximately equidistant from the center. Traps were baited with peanut butter and rolled oats and lined with cotton for bedding. Traps were checked each morning. *Clethrionomys* were dusted with fluorescent pigments (Lemen and Freeman, 1985) and released at the trap site. Tracking was conducted at night using an ultraviolet light, and flags were placed in the trail center at 2-m intervals starting with the trap entrance. Trails often led immediately to dens where animals entered and apparently re-emerged later (trails leaving dens were fainter), but in some cases trails meandered extensively before entering a den or disappearing. I contend both diurnal and nocturnal activity was recorded even though animals were released in the mornings and that diurnal activity was representative of normal behavior, as untreated animals were observed to be active during the day.

In this study, I wished to make a direct comparison of variables measured by both methods using multivariate analyses. Because multivariate analyses take into account interactions between variables and can be greatly influenced by a comparison of nonparallel data sets, it was necessary to exclude variables not measured by both methods. The following variables were measured: diameter of woody structure; rank of decay; height to the bottom of logs; % cover of shrubs, herbaceous vegetation and moss. Cover of shrubs and herbaceous vegetation were strongly correlated so these categories were merged. Woody structure consisted of logs, stumps and rootwads ≥ 5 cm diameter (measured parallel to the ground). Height from the ground to the bottom of logs was determined by subtracting the diameter from the overall height and setting negative values to zero. A decay rank, ranging from 1-5 (freshly fallen to nearly duff), was assigned to woody structure (Thomas, 1971).

In measuring woody debris for trapping data, 2 10-m transects were randomly placed in each cell and the above variables were averaged within and between transects. Data for logs, stumps and rootwads were condensed into one general category of woody debris for each cell by averaging their values. For FPT, woody structure was the nearest log, stump or rootwad to a flag. The distance was measured and variables treated as described above. Data from location points along trails were averaged for each animal.

For trapping, vegetation was sampled with 0.5- by 0.2-m quadrats randomly placed in each cell once per month, June to September, 1992-93. Percent cover was estimated for each species and averaged for samples within a cell. The groups MOSS, SHRUB and herbaceous vegetation were obtained by summing percent cover for all species assigned to a category. For FPT, I quantified vegetation by counting the number of contacts along a 2-m by 4-cm rod in each category using a 2-dm interval for the first meter and a 1-m interval for the second meter (modified from Weins and Rotenberry, 1981).

Random sampling.—I determined microhabitat availability for trapping by randomly sampling, with replacement, from all trap sites collectively. For each FPT trail, a random trail (10-11 points or ~20 m long) was assigned to the same grid by randomly selecting a trapping station as a starting point. The first flag was placed at the trap entrance and a direction from 0-359 degrees was randomly chosen for the second flag. The remaining flags were placed at 2-m intervals by randomly selecting one of 5 directions; 288, 324, 0, 36, 72 degrees, using 0 degrees as straight ahead. This design approximated forward and lateral movements of actual trails and allowed trails to double back. Data were collected and treated like actual FPT trails.

Data analysis.—The first flag was excluded from analyses for random trails and FPT trails, because it was the trap site. For FPT trails, the second and third flags were also excluded to allow animals to resume normal behavior patterns. I averaged trails into a single observation for individuals tracked more than once. The practice of using multiple trails from a single individual as independent samples (McShea and Gilles, 1992; Etheredge et al., 1989) results in pseudoreplication (Hurlbert, 1984). Quadrat sampling included vegetation up to 0.5 m, so only the first 4 dm of vertical FPT data were analyzed. Data sets were pooled for 1992 and 1993 to increase FPT sample size.

I used multivariate analysis of variance (MANOVA) for each method to test the null hypothesis that habitat use did not differ significantly from random. I then compared the 2 methods in the same MANOVA to determine whether results differed between methods. Only diameter of woody debris, rank of decay and height to the bottom of logs were used when comparing the 2 methods within the same MANOVA, because these variables were measured exactly the same for both techniques. I felt differences in the way vegetative cover was measured between methods (point verses quadrat sampling) compromised a comparison of their statistics in the same analysis. Analyses were conducted for each age class separately due to differences in microhabitat use between age classes and the importance of distinguishing between the 2 scales (Morris, 1984; this thesis, CHAPTER I). Only age classes with ≥ 4 FPT trails were used. Univariate tests were examined to determine the importance of individual habitat variables. Alpha is 0.05 for all values reported. The SPSS® software (Norušis, 1990) was used for all analyses.

RESULTS AND DISCUSSION

Clethrionomys gapperi was captured 325 times in 28,800 trap nights from 1992 to 1993. Thirty-one individuals had fluorescent pigment trails long enough for analysis (≥ 20 m). For FPT, microhabitat use by *Clethrionomys gapperi* differed from random only in age class 2 (F=4.47; d.f.=5,6; P=0.048) due to lower moss cover associated with *Clethrionomys* trials (P=0.005) (Table 1). However, trap sites used by *C. gapperi* did not differ from random in any age class (Table 2). Data collected at *C. gapperi* and random trap sites differed from data collected along *C. gapperi* and random transects in class 2 (F=2.80; d.f.=3, 93; P=0.044) for diameter of woody structure (P=0.011) (Table 3).

Fluorescent pigment tracking and trapping led to different conclusions regarding microhabitat use by *C. gapperi*. Fluorescent pigment tracking indicated *C. gapperi* selected microhabitats which differed from random in class 2, but live trapping did not detect this habitat use. These differences may result from trap bias or a lack of sensitivity associated with the gross manner in which trapping relates microhabitat to capture sites.

Lemen and Freeman (1986) determined that FPT and live trapping gave similar results for microhabitat analysis of *Perognathus flavescens* and *Dipodomys ordii* in the sandhills of central Nebraska. McShea and Gilles (1992) found FPT more sensitive than trapping to shifts in foraging areas of *Peromyscus leucopus* during mast fall in Virginia hardwood forests. Results from this study are consistent with those from McShea and Gilles (1992) and indicate that trapping is not sufficiently sensitive to microhabitat use. Where microhabitat selection is strong, both methods should produce similar results unless trap bias is dramatic. However, when habitat selection is subtle or when detecting a shift in microhabitat use is the goal, greater sensitivity will be required to identify non-random associations between animals and habitat components.

In order to assess the limitations of live trapping and evaluate the appropriateness of using this technique for determining microhabitat use by small mammals, the factors undermining the effectiveness of live trapping must be identified. Although bias brought on by trap placement or residual odor can not be ruled out, I feel the gross scale by which trapping associates small mammals to components within their environments is a major weakness of this method. Arbitrary correlations can result in misleading conclusions about microhabitat selection. Researchers may be led to conclude microhabitat selection occurs when, in fact, it does not. The same loose associations between animals and microhabitat may result in overlooking habitat selection (this study) or important shifts in habitat use (McShea and Gilles, 1992). To some degree the sensitivity of trapping can be increased by using smaller sampling areas around traps, instead of the 10 m cells commonly used (McShea and Gilles, 1992; Rebar and Conley, 1983, Van Horne, 1982), but baiting still may draw animals into microhabitats they do not normally use.

Scale is particularly important when microhabitat use is compared between sympatric species and trap bias will likely increase due to differential trap use. FPT avoids the biases described for trapping and radiotelemetry and measures movement at a scale defined by the animal. Therefore, FPT is a less-biased more accurate method for determining microhabitat use by small mammals. For examining microhabitat use or microhabitat separation between species, fluorescent pigment tracking as described here (for structurally complex environments) or by Goodyear (1992) (for more open habitats) should prove more accurate and more discerning than live trapping.

Table 1.–Comparison of fluorescent pigment tracking data among *Clethrionomys gapperi* (*Clegap*) and random locations. Sample sizes and results from MANOVA are given below means and standard errors. Asterisks indicate significant variables identified by ANOVA.

		Stand Age Classes			
		1	2	3	4
Variables	Group	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se	$\bar{x}$ ±se
DIAMETER	Random	36.9 ±6.8	38.5 ±10.1	19.1 ±2.6	23.7 ±2.4
	Clegap	22.0 ±4.3	18.3 ±4.2	25.8 ±1.5	27.9 ±3.7
RANK	Random	3.7 ±0.2	3.3 ±0.4	3.5 ±0.1	3.6 ±0.2
	Clegap	3.2 ±0.1	2.8 ±0.4	3.2 ±0.4	3.6 ±0.1
HEIGHT	Random	3.2 ±0.9	7.1 ±2.6	10.7 ±4.0	6.7 ±2.0
	Clegap	4.4 ±1.6	10.5 ±1.3	8.0 ±2.9	9.7 ±2.6
SHRUB/HERB	Random	3.6 ±0.4	4.4 ±0.9	0.5 ±0.1	4.0 ±1.4
	Clegap	2.8 ±0.4	5.7 ±1.2	0.3 ±0.1	2.8 ±0.9
MOSS	Random	0.3 ±0.1	0.4 ±0.0	0.7 ±0.1	0.4 ±0.1
	Clegap	0.1 ±0.1	0.1 ±0.1**	0.3 ±0.2	0.3 ±0.1
Sample size	Random *Clegap*	n=7 n=7	n=6 n=6	n=4 n=4	n=13 n=13
Multivariate significance		F=1.74 d.f.=5,8 P=0.232	F=4.47 d.f.=5,6 P=0.048*	F=2.49 d.f.=5,2 P=0.311	F=0.82 d.f.=5,20 P=0.550

* $\alpha \leq 0.05$, ** $\alpha \leq 0.005$

Table 2.—Comparison of live trapping data among *Clethrionomys gapperi* (*Clegap*) and random locations. Sample sizes and results from MANOVA are given below means and standard errors.

		Stand age classes			
Variables	Group	1 $\bar{x}$ ±se	2 $\bar{x}$ ±se	3 $\bar{x}$ ±se	4 $\bar{x}$ ±se
DIAMETER	Random	16.7 ±2.8	18.0 ±1.3	17.6 ±1.3	20.3 ±0.5
	Clegap	19.0 ±3.7	20.7 ±2.0	17.0 ±0.7	20.5 ±0.4
RANK	Random	2.5 ±0.2	2.9 ±0.1	3.4 ±0.1	3.5 ±0.0
	Clegap	2.5 ±0.2	3.0 ±0.1	3.4 ±0.1	3.4 ±0.0
HEIGHT	Random	10.4 ±2.5	12.4 ±1.2	7.4 ±0.6	10.1 ±0.8
	Clegap	8.2 ±2.3	11.7 ±1.3	8.1 ±0.9	10.3 ±0.7
SHRUB/HERB	Random	76.2 ±3.5	78.3 ±2.9	10.0 ±1.2	35.1 ±1.6
	Clegap	79.8 ±3.5	75.1 ±3.0	8.7 ±0.9	31.7 ±1.4
MOSS	Random	4.6 ±0.9	15.8 ±1.6	45.1 ±2.6	21.3 ±1.5
	Clegap	3.2 ±0.6	16.8 ±1.7	39.1 ±3.1	15.8 ±0.9
Sample size	Random	n=30	n=46	n=44	n=119
	Clegap	n=23	n=41	n=41	n=120
Multivariate significance		F=0.47 d.f.=5,45 P=0.796	F=0.33 d.f.=5,81 P=0.893	F=0.59 d.f.=5,79 P=0.706	F=1.83 d.f.=5,233 P=0.108

Table 3.—Comparison of means and standard errors for microhabitat variables measured at random and *Clethrionomys gapperi* (*Clegap*) locations using fluorescent pigment tracking (FPT) and live trapping (traps) techniques. MANOVA results are given below. Asterisks indicate groups of variables identified as significant by ANOVA.

			Stand age classes			
Variables	Method		1 $\bar{x}$ ±se	2 $\bar{x}$ ±se	3 $\bar{x}$ ±se	4 $\bar{x}$ ±se
DIAMETER	FPT	Random	36.9 ±6.8	38.5 ±10.1*	19.1 ±2.6	23.7 ±2.4
		Clegap	21.8 ±4.3	18.3 ±4.2*	25.8 ±1.5	27.9 ±3.7
	Traps	Random	16.7 ±2.8	18.0 ±1.3*	17.6 ±1.3	20.3 ±0.5
		Clegap	19.0 ±3.7	20.7 ±2.0*	17.0 ±0.7	20.5 ±0.4
RANK	FPT	Random	3.7 ±0.2	3.3 ±0.4	3.5 ±0.1	3.6 ±0.2
		Clegap	3.2 ±0.1	2.3 ±0.4	3.2 ±0.4	3.6 ±0.1
	Traps	Random	2.5 ±0.2	2.4 ±0.1	3.4 ±0.1	3.5 ±0.0
		Clegap	2.5 ±0.2	3.0 ±0.1	3.4 ±0.1	3.4 ±0.0
HEIGHT	FPT	Random	3.2 ±0.9	7.1 ±2.6	10.7 ±0.4	6.7 ±0.2
		Clegap	4.4 ±1.6	10.5 ±1.3	8.0 ±2.9	9.7 ±2.6
	Traps	Random	10.4 ±2.5	12.4 ±1.2	7.4 ±0.6	10.1 ±0.8
		Clegap	8.2 ±2.3	11.7 ±1.3	8.1 ±0.9	10.7 ±0.7
Multivariate significance			F=0.86 d.f.=3,59 P=0.467	F=2.80 d.f.=3,93 P=0.044*	F=1.82 d.f.=3,87 P=0.149	F=0.89 d.f.=3,259 P=0.446

* $\alpha \leq 0.05$

Literature Cited

Algren, C. E. 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry 64:614-618.

Barrett, S. W., S. F. Arno, and C. H. Key. 1991. Fire regimes of western larch-lodgepole pine forests in Glacier National Park, Montana. Canadian Journal of Forest Research 21:1711-1720.

Barry, R. E. Jr., A. A. Heft, and T. E. Baummer. Spatial relationships of syntopic white-footed mice, *Peromyscus leucopus*, deer mice, *Peromyscus maniculatus*, and red backed voles, *Clethrionomys gapperi*. Canadian Field Naturalist 104(3):387-393.

Boonstra, R., and C. J. Krebs. 1976. The effect of odour on trap response in *Microtus townsendii*. Journal of Zoology 180:467-476.

Brooks, R. J., and E. M. Banks. 1971. Radio-tracking study of lemming home range. Communications in Behavioral Biology 6:1-5.

Buckner, C. H. 1957. Populations studies on small mammals of southeastern Manitoba. Journal of Mammalogy 38:87-97.

Bustch, R. S. 1954. The life history and ecology of the red-backed vole, *Clethrionomys gapperi* Vigors, in Minnesota. Ph.D. dissertation, Univ. of Mich.

Cameron, A. W. 1964. Competitive exclusion between the rodent genera *Microtus* and *Clethrionomys*. Evolution 18:630-634.

Clough, G. C. 1987. Relations of small mammals to forest management in northern Maine. Canadian Field-Naturalist 101(1):40-48.

Crowell, K. L. 1973. Experimental zoogeography: introductions of mice to small islands. American Naturalist 107:535-558.

Crowell, K. L. 1983. Islands--insight or artifact? Population dynamics and habitat utilization in insular rodents. Oikos 41:442-454.

Crowell, K. L. and S. L. Pimm. 1976. Competition and niche shifts of mice introduced onto small islands. Oikos 27:251-258.

Daly, M., M. I. Wilson, and P. Behrends. 1980. Factors affecting rodents' responses to odours of strangers encountered in the field: experiments with odour-baited traps. Behavioral Ecology and Sociobiology 6(4):323-329.

Douglass, R. J. 1989. The use of radio-telemetry to evaluate microhabitat selection by deer mice. Journal of Mammalogy 70(3):648-652.

Douglass, R. J. 1977. Population dynamics, home ranges and habitat associations of the yellow-cheeked vole, *Microtus xanthognathus*, in the Northwest Territories. Canadian Field-Naturalist 91:237-247.

Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus*, *Microtus oregoni* and *M. richardsoni*. The American Midland Naturalist 118(2):258-265.

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

Dyke, G. R. 1971. Food and cover of fluctuating populations of northern cricetids. Ph.D. dissertation, Univ. of Alberta, Edmonton, Alberta.

Etheredge, D. R., M. D. Engstrom, and R. C. Stone. 1989. Habitat discrimination between sympatric populations of *Peromyscus attwateri* and *Peromyscus pectoralis* in west-central Texas. Journal of Mammalogy 69:825-828.

Finklin, A. L. 1986. A climatic handbook for Glacier National Park-with data for Waterton National Park. United States Department of Agriculture, Forests Service. Intermountain Research Station, GTR Int-204.

Fisher, R. L. 1968. An ecological study of the red-backed vole, *Clethrionomys gapperi gapperi* (Vigors), in central New York. Ph.D. dissertation, Cornell Univ., Ithica, New York.

Fuller, W. A. 1985. Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus* in northern Canada. Annales Zoologici Fennici 22:229-241.

Gashwiler, J. S. 1959. Small mammal study in West-central Oregon. Journal of Mammalogy 40(1):128-139.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51(6):1018-1026.

Getz, L. L. 1962. Notes on the water balance of the red-backed vole. Ecology 43:565-566.

Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology 49(2):276-286.

Getz, L. L. 1969. Laboratory studies of interaction between White-footed Mouse and Redback Vole. Canadian Field-Naturalist 83:141-146.

Goodyear, N. C. 1989. Studying fine-scale habitat use in small mammals. Journal of Wildlife Management 53(4):941-946.

Goodyear, N. C. 1992. Spacial overlap and dietary selection of native rice rats and exotic black rats. Journal of Mammalogy 73(1):186-200.

Grant, P. R. 1969. Experimental studies of competitive inter-actions in a two-species system. I. *Microtus* and *Clethrionomys* species in enclosures. Canadian Journal of Zoology 47:1059-82.

Grant, P. R. 1970. Colonization of islands by ecologically dis-similar species of mammals. Canadian Journal of Zoology 48:545-553.

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

Gunderson, H. L. 1959. Red-backed vole habitat studies in central Minnesota. Journal of Mammalogy 40(3):405-412.

Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57(1):32-44.

Habeck, J. R. 1968. Forest succession in the Glacier Park cedar-hemlock forests. Ecology 49(5):872-880.

Hamley, J. M., and J. B. Falls. 1975. Reduced activity in transmitter carrying voles. Canadian Journal of Zoology 53:1476-1478.

Hansson, L. 1985. *Clethrionomys* food: generic, specific and regional characteristics. Annales Zoologici Fennici 22:315-318.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, IL. Pp. 211.

Hays, J. P. and S. P. Cross. 1987. Characteristics of log use by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. Canadian Field-Naturalist 101(4):543-546.

Hays, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northwest Science 60(4):250-256.

Heske, E. J. 1987. Responses of a population of California voles, *Microtus californicus*, to odor-baited traps. Journal of Mammalogy 68:64-72.

Holling, C. S. 1959. "The components of predation as revealed by a study of small mammal predation of the European pine sawfly." Canadian Entomology 91:293-320.

Hooven, E. F. 1969. The influence of forest succession on populations of small animals in western Oregon. Pp 30-34 in Wildlife and reforestation in the Pacific Northwest (H. C. Black ed.). Oregon State University, Corvallis, OR.

Hooven, E. F. and H. C. Black. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. Northwest Science 50(4):189-208.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54(2):187-211.

Jike, L., G. O. Batzli, and L. L. Getz. 1988. Home ranges of prairie voles as determined by radiotracking and by powder-tracking. Journal of Mammalogy 69(1):183-186.

Kirkland, G. L. Jr. 1977. Responses of small mammals to the clearcutting of northern Appalachian forests. Journal of Mammalogy 58(4):600-609.

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

Kirkland, G. L., Jr., and R. J. Griffin. 1974. Microdistribution of small mammals at the coniferous deciduous forest ecotone in northern New York. Journal of Mammalogy 55:417-427.

Kotter, M. M., and R. C. Farentinos. 1984. Formation of ponderosa pine ectomycorhizae after innoculation with feces of tassel-eared squirrels. Mycologia 76:758-760.

Krebs, C. J., and J. H. Meyers. 1974. Population cycles in small mammals. Advances in Ecological Research 8:267-399.

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

Krull, J. N. 1970. Small mammal populations in cut and uncut northern hardwood forests. New York Fish and Game Journal 17(2):128-130.

Lee, J. E., G. C. White, R. A. Garrott, R. M. Bartmann, and A. W. Alldredge. 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. Journal of Wildlife Management 49:658-663.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescents: a new technique. Journal of Mammalogy 66(1):134-136.

Lemen, C. A., and P. W. Freeman. 1986. Habitat selection and movement patterns in sandhill rodents. The Prairie Naturalist 18(3):129-141.

Li, C. Y., C. Maser, Z. Maser, and B. A. Caldwell. 1986a. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. Great Basin Naturalist 46(3):411-414.

Li, C. Y., C. Maser, and H. Fay. 1986b. Initial survey of acetylene reduction and selected microorganisms in the feces of 19 species of mammals. Great Basin Naturalist 46(4):646-650.

Lumen, I, and A. Nietro. 1980. Preservation of Mature forest seral stages to provide wildlife habitat diversity. Trans 45th North American Wildlife and Natural Resources Conf. 271-277.

Luoma, D. L. 1991. Annual changes in seasonal production of hypogeous sporocarps in Oregon Douglas-fir forests.

In Wildlife and vegetation of unmanaged Douglas-fir forests (Eds. L. F. Ruggiero, K. B. Aubry, A. B. Carey and M. H. Huff). USDA Forest Service, PNW-GTR-285. Pacific Northwest Research Station, Portland, OR. Pp. 83-89.

Luoma, D. L., R. E. Frenkel, and J. M. Trappe. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. Mycologia 83(3):335-353.

Madison, D. M. 1978. Movement indicators of reproductive events among female meadow voles revealed by radiotelemetry. Journal of Mammalogy 59:835-843.

Manville, R. H. 1949. A study of small mammal populations in northern Michigan. Miscellaneous Publications Museum of Zoology, University of Michigan 73:1-83.

Marks, G. C., and T. T. Kozlowski. 1973. Ectomycorrhizae: their ecology and physiology. Academic Press, New York, USA.

Martell, A. M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in Northern Ontario. Canadian Field-Naturalist 95(3):325-328.

Martell, A. M. 1982a. Changes in small mammal communities after logging in north-central Ontario. Canadian Journal of Zoology 61:970-980.

Martell, A. M. 1982b. Demography of southern red-backed voles (*Clethrionomys gapperi*) after logging in north central Ontario. Canadian Journal of Zoology 61:958-969.

Martell, A. M. 1984. Changes in small mammal communities after fire in Northcentral Ontario. Canadian Field-Naturalist 98(2):223-226.

Martell, A. M., and A. L. Macaulay. 1981. Food habits of deer mice (*Peromyscus maniculatus*) in northern Ontario. Canadian Field-Naturalist 95(3):319-324.

Martell, A. M. and A. Radvanyi. 1977. Changes in small mammal populations after clearcutting of Northern Ontario black spruce forest. Canadian Field-Naturalist 91:41-46.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59(4):799-809.

Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habitats of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084-1088.

Mazdzer, E., M. R. Capone, and L. C. Drickamer. 1976. Conspecific odors and trapability of deer mice (*Peromyscus leucopus noveboracensis*). Journal of Mammalogy 57:607-609.

McShea, W. J., and A. B. Gilles. 1992. A comparison of traps and fluorescent powder to describe foraging for mast by *Peromyscus leucopus*. Journal of Mammalogy 73(1):218-222.

McManus, J. J. 1974. Bioenergetics and water balance of the red-backed vole, *Clethrionomys gapperi*. Journal of Mammalogy 55(1):30-44.

Merritt, J. F., and J. M. Merritt. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. Journal of Mammalogy 59:576-598.

Mihok, S. 1979. Behavioral structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus maniculatus*. Canadian Journal of Zoology 57:1520-1535.

Miller, D. H., and L. L. Getz. 1972. Factors influencing the local distribution of the red-backed vole, *Clethrionomys gapperi*, in New England. University of Connecticut Occasional Papers (Biol. Sci. Ser.) 2:115-138.

Miller, D. H., and L. L. Getz. 1973. Factors influencing the local distribution of the red-backed vole, *Clethrionomys gapperi*, in New England II. University of Connecticut Occasional Papers (Biol. Sci. Ser.) 2:159-180.

Miller, D. H., and L. L. Getz. 1977a. Factors influencing local distribution and species diversity of forest small mammals in New England. Canadian Journal of Zoology 55:806-814.

Miller, D. H., and L. L. Getz. 1977b. Comparisons of population dynamics of *Peromyscus* and *Clethrionomys* in New England. Journal of Mammalogy 58(1):1-16.

Monthey, R. W., and E. C. Soutiere. 1985. Responses of small mammals to forest harvesting in northern Maine. Canadian Field-Naturalist 99(1):13-18.

Morris, R. D. 1969. Competitive exclusion between *Microtus* and *Clethrionomys* in the aspen parkland of Saskatchewan. Journal of Mammalogy 50(2):291-301.

Morris, D. W. 1979. Microhabitat utilization and species distribution of sympatric small mammals in southwestern Ontario. American Midland Naturalist 101:373-384.

Morris, D. W. 1983. Field tests of competitive interference for space among temperate zone rodents. Canadian Journal of Zoology 61:1517-1523.

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

Morris, R. D. and P. R. Grant. 1972. Experimental studies of competitive interaction in a two-species system. IV. *Microtus* and *Clethrionomys* species in a singe enclosure. Journal of Animal Ecology 41:275-290.

Mullican, T. R. 1988. Radio telemetry and fluorescent pigments: a comparison of techniques. Journal of Wildlife Management 52(4):627-631.

Mullican, T. R., and J. T. Baccus. 1990. Horizontal and vertical movements of the white-ankled mouse (*Peromyscus pectoralis*) in central Texas. Journal of Mammalogy 71(3):378-381.

Murdoch, W. W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecological Monograph 39:335-354.

Nordyke, K. A., and S. W. Buskirk. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Canadian Field-Naturalist 105(3):330-334.

Norušis, M. J. 1990. SPSS® advanced statistics student guide. SPSS Inc. Chicago, IL. Pp 506.

Odum, E. P. 1944. Water consumption of certain mice in relation to habitat selection. Journal of Mammalogy 25:404-405.

Parker, G. R. 1989. Effects of reforestation upon small mammal communities in New Brunswick. Canadian Field-Naturalist 103(4):509-519.

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

Perrin, M. R. 1979. Seasonal variation in the growth, body composition and diet of *Clethrionomys gapperi* in spruce forest. Acta Theriologica 23:299-318.

Petticrew, B. G., and R. M. F. S. Sadleir. 1974. The ecology of the deer mouse, *Peromyscus maniculatus*, in a coastal coniferous forest. I. Population dynamics. Canadian Journal of Zoology 52:107-118.

Pfister, R. D., B. L. Kovalchick, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA Forest Service GTR INT-34:1-174.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107. Pp 97.

Price, M. V. 1977. Validity of live-trapping as a measure of foraging activities of heteromyid rodents. Journal of Mammalogy 58:107-110.

Price, M. V., and K. A. Kramer. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos 42:349-354.

Raphael, M. G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. Pp. 359-367 in Management of amphibians, reptiles and small mammals in north america. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Forest Sciences Laboratory, Laramie, Wyoming.

Ramirez, P., and M. Hornocker. 1980. Small mammal populations in different aged clearcuts in northwest Montana. Journal of Mammalogy 62:400-403.

Rebar, C., and W. Conley. 1983. Interactions in microhabitat use between *Dipodomys ordii* and *Onochomys leucogaster*. Ecology 64(5):984-988.

Ricklefs, R. E. 1979. Ecology. Chiron Press, New York. Pp. 966.

Rosenzweig, M. L. 1979. Optimal habitat selection in two-species competitive systems. Fortschr. Zoologica

25:283-293.

Sanderson, G. C., and B. C. Sanderson. 1964. Radio-tracking rats in Malaya - a preliminary study. Journal of Wildlife Management 28:752-768.

Sanders, F. B., B. Mosse, and P. B. Tinker. 1975. Endomycorrhizas. Academic Press, London, England.

Schloyer, C. R. 1977. Food habits of *Clethrionomys gapperi* on clearcuts in West Virginia. Journal of Mammalogy 58(4):677-679.

Schoen, J. W., O. C. Wallmo, and M. D. Kirchhoff. 1981. Wildlife forest relationships: is a re-evaluation of old-growth necessary. Transactions of the North American Wildlife and Natural Resource Conference 46:531-544.

Scrivner, J. H., and H. D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce-fir in Idaho. Northwest Science 58(3):171-176.

Sims, H. P., and C. H. Buckner. 1973. The effect of clear cutting and burning of *Pinus banksiana* forests on the populations of small mammals in southeastern Manitoba. The American Midland Naturalist 90(1):228-231.

Smith, D. A., and J. B. Foster. 1957. Notes on the small mammals of Churchill, Manitoba. Journal of Mammalogy 38:98-155.

Sollins, P., C. C. Grier, F. M. McCorrison, K. Cromack, Jr., R. Fogel, and R. L. Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monograph 50(3):261-285.

Stock, M. K. 1967. Successful changes in small mammal species diversity on clearcuts in the grand fir forest of northern Idaho. M.S. thesis, University of Idaho, Moscow, ID.

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

Summerlin, C. T., and J. L. Wolfe. 1973. Social influences on trap response in the cotton rat, *Sigmodon hispidus*. Ecology 54:967-981.

Swan, D., B. Freedman, and T. Dilworth. 1984. Effects of various hardwood forest management practices on small mammals in central Nova Scotia. Canadian Field-Naturalist 98(3):362-364.

Tallmon, D. and L. S. Mills. 1994. Use of logs within home ranges of california red-backed voles on a remnant of forest. Journal of Mammalogy 75(1):97-101.

Tevis, L. Jr. 1956a. Responses of small mammal populations to logging of Douglas-fir. Journal of Mammalogy 37(2): 189-196.

Tevis, L. Jr. 1956b. Effect of a slash burn on forest mice. Journal of Wildlife Management 20(4):405-409.

Thomas, J. W. 1971. Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook 553. 512 pp.

Thomas, J. W., M. G. Raphael, R. G. Anthony, E. D. Forsman, A. G. Gunderson, A. G. Holthausen, R. S. Marcot, B. G. Reeves, J. R. Sedell, D. M. Solis. 1993. Viability and management assessment considerations for species associated with late-successional and old-growth forests of the Pacific Northwest: the report of the scientific analysis team. USDA forest Service. Pp 530.

Trappe, J. M. 1987. Phylogenetic and ecological aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In Ecophysiology of V A Mycorrhizal plants, G. R. Safir (Ed.). CRC Press Boca Raton, FL. Pp. 5-25.

Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307-3315.

USDA Forest Service. 1985. Final environmental impact statement for the Medicine Bow National Forest and Thunder Basin National Grassland land and resource management plan. USDA Forest Service, Laramie, Wyoming.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (Peromyscus maniculatus) in seral stages of coniferous forest. Ecology 63(4):992-1003.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:898-901.

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

Vickery, W. L., S. L. Iverson, S. Mihok, and B. Schwartz. 1989. Environmental variation and habitat separation among small mammals. Canadian Journal of Zoology 67:8-13.

Vickery, W. L., and D. Rivest. 1992. The influence of weather on habitat use by small mammals. Ecography 15:205-211.

Walters, B. B. 1991. Small mammals in subalpine old-growth forest and clearcuts. Northwest Science 65(1):27-31.

Webster, A. B., and R. J. Brooks. 1979. Effects of radiotransmitters on the meadow vole, *Microtus pennsylvanicus*. Canadian Journal of Zoology 58:997-1001.

Weins, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51(1):21-41.

Whitaker, J. O. Jr. 1962. Endogone, Hymenogaster, and Melanogaster as small mammal foods. The American Midland Naturalist 67(1):152-156.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. Journal of Wildlife Management 50(3):509-513.

Williams, O., and B. A. Finney. 1964. Endogone-food for mice. Journal of Mammalogy 265-271.

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

Wywialowski, A. P., and G. W. Smith. 1988. Selection of microhabitat by the red-backed vole, *Clethrionomys gapperi*. Great Basin Naturalist 48(2):216-223.

Yahner, R. H. 1992. Dynamics of a small mammal community in a fragmented forest. American Midland Naturalist 127:381-391.