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THE IMPORTANCE OF SERAL STAGE AND COARSE WOODY DEBRIS TO THE ABUNDANCE AND DISTRIBUTION OF DEER MICE ON VANCOUVER ISLAND, BRITISH COLUMBIA

by

David William Carter

B.Sc. (Zoology), University of British Columbia, 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

SIMON FRASER UNIVERSITY

September 1993

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ISBN 0-315-91278-2

Canada

APPROVAL

Name: **DAVID WILLIAM CARTER**

Degree: **Master of Science**

Title of Thesis:

THE IMPORTANCE OF SERAL STAGE AND COARSE WOODY DEBRIS
TO THE ABUNDANCE AND DISTRIBUTION OF DEER MICE ON
VANCOUVER ISLAND, BRITISH COLUMBIA

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The Importance of Seral Stage and Coarse Woody Debris To The Abundance and Distribution of Deer Mice On Vancouver Island, British Columbia

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Sept 29, 1993

(date)

ABSTRACT

Abundance and demography of deer mice (*Peromyscus maniculatus*) in herb, shrub, young forest and mature forest seral stages of coastal forest were examined during 1988 and 1989. Deer mice were more abundant in herb and shrub seral stages than in young and mature forests. Deer mouse populations in younger seral stages produced more juveniles and had greater rates of juvenile recruitment, whereas the population in the mature forest had less immigration and higher adult survival. Deer mouse abundance was positively correlated with abundance of coarse woody debris in all 4 seral stages. Woody debris had greater influence on deer mouse abundance in the herb seral stage and mature forest than it did in the shrub seral stage and young forest. Fluorescent powder tracking was used to follow movements of deer mice and determine their habitat selection in the herb seral stage and mature forest. Travel routes of deer mice in both habitats were strongly associated with coarse woody debris. In the herb seral stage, deer mice usually travelled beside or under pieces of woody debris, whereas in mature forest, deer mice usually travelled on top of the woody debris. In coastal forest landscapes, coarse woody debris is an important habitat component which affects the abundance, distribution and behaviour of deer mice.

ACKNOWLEDGMENTS

Financial support for this project was provided by the B.C. Ministry of Environment, Natural Sciences and Engineering Research Council of Canada, and Simon Fraser University.

I thank the staff at B.C. Ministry of Environment in Nanaimo for logistical support and MacMillan Bloedel, Cowichan Woodlands Division for allowing me to work on their land.

Helpful editorial comments were provided by Dr. Brooke and Dr. Verbeek. I want to thank my senior supervisor, Alton Harestad, who put up with and encouraged me through this project.

I can not thank my wife Heather enough for the endless love and support she provided me with during this project. I do not know if I could have done it without you "Sweety".

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GENERAL INTRODUCTION

The deer mouse (*Peromyscus maniculatus*) is an important species in coastal forests at several levels of the community. Deer mice are prey for many avian and mammalian predators in British Columbia. Their consumption of seeds may slow succession and impede reforestation. Their consumption of mycorrhizal fungi disperses spores of root symbionts essential for survival of many higher plants including conifers (Maser et al. 1978). Deer mice also consume both pest and beneficial insects in forest habitats.

The impact of clearcut logging on deer mice has been studied in many areas of North America, including British Columbia. Some studies reported that deer mice are more abundant following logging (Tevis 1956, Gashwiler 1970, Hooven and Black 1976). Other studies have found that the abundance of deer mice is unaffected or declines after logging (Petticrew and Sadleir 1974, Harris 1968). Because of these conflicting results, the impacts of logging and forest succession on deer mice are unclear. Are deer mice more abundant following logging and if so, are recently logged areas better habitat than mature forests? It is possible that some seral stages have higher populations of deer mice because of immigration rather than increased reproduction or survival.

The abundance of deer mice within a particular macrohabitat (e.g. a seral stage) can vary greatly among different locations and it is suspected that factors such as food, water and cover determine microhabitat selection and thus the distribution and abundance of deer mice within the microhabitat (Bendell 1961). The importance of cover to small mammals is generally accepted (Elton 1939), but quantitative studies relating small mammal abundance and distribution to cover are lacking. Does the abundance and distribution of cover affect the abundance and distribution of deer mice, and if it does, is the effect of cover equal across habitat types?

In my study, I assess the importance of seral stage and coarse woody debris to deer mice. In Chapter 1, I examine the abundance and demography of deer mice in 4 seral stages. In Chapter 2, I compare variation in abundance and characteristics of coarse woody debris with variation in the abundance of deer mice. In Chapter 3, I examine the influence of coarse woody debris on microhabitat selection and travel routes of deer mice in recent cutovers and mature forests.

CHAPTER 1

ABUNDANCE AND DEMOGRAPHY OF DEER MICE IN SERAL STAGES OF COASTAL FOREST

INTRODUCTION

Deer mice (*Peromyscus maniculatus*) can occupy a variety of habitats within a landscape and their densities are often very different among habitat types. Some investigators have assumed that higher densities are indicative of better quality habitats (Hooven and Black 1976, Miller and Getz 1977). However, the validity of this assumption has been questioned (Sullivan 1979a, Van Horn 1981). The impact of logging on small mammal populations and the subsequent successional changes that follow have been studied throughout North America for the last 40 years (Orr-Ewing 1950, Tevis 1956, Gashwiler 1959, Ahlgren 1966, Hooven 1969, Petticrew and Sadleir 1974, Sullivan 1979a, Van Horn 1981). Changes to deer mouse populations following logging typically have been examined by comparing forested and recently cutover areas. Most investigators reported that deer mice were more abundant in cutovers than in forests (Tevis 1956, Hooven 1969, Gashwiler 1970, Krefting and Ahlgren 1974, Hooven and Black 1976, Martell 1983). Other investigators reported little difference in abundance of deer mice between forested and cutover habitats (Harris 1968, Petticrew and Sadleir 1974, Sullivan 1979a).

Studies that monitored both seasonal and annual variation of populations in different habitats suggested that densities of deer mice are influenced by both habitat quality and social factors (Petticrew and Sadleir 1974, Sullivan 1979a, Van Horn 1981). Van Horn (1981) proposed that density dependent regulation of breeding, survival, and dispersal may stabilize populations and keep densities below carrying capacity in high quality habitats. Sullivan (1979a), Van Horn (1983) and Pulliam (1988) have suggested that habitat specific demographic rates, such as reproduction and mortality, may be better indicators of habitat quality than is density. Pulliam (1988) argued that for many populations high numbers of subordinates immigrating into inferior "sink" habitats could make density a poor indicator of habitat quality.

Density dependent population regulation has been reported for deer mice (Healy 1967, Sadleir 1965). Demographic factors, such as reproduction (Terman 1984), dispersal (Fairbairn 1977), and juvenile survival (Wolff 1985a), are influenced by population density. Differences in habitat quality should therefore be associated with differences in demographic factors.

Intensive live trapping studies in coastal forest landscapes (Sadleir 1974, Sullivan 1979a, Van Horn 1981) indicated that densities and demographies of deer mouse populations are similar in cutovers and forests. However, all of these studies used a single live trapping grid in each habitat and thus only a single population was examined in each habitat type. My objectives were: (1) to test the hypothesis that early successional habitats support higher densities of deer mice than do later ones; (2) to monitor trends in the abundance of deer mice as succession progresses following clear-cutting; (3) to describe differences in the seasonal and annual population dynamics associated with different successional stages; and (4) to investigate the hypothesis that early seral habitats support less regulated populations of deer mice than do forested habitats

STUDY AREA

My study was conducted on Vancouver Island in the Nanaimo River Valley (49^{o} 1' N, 124^{o} 8' W), approximately 20 km southwest of Nanaimo, British Columbia, between May 1988 and November 1989 (Fig. 1). Forests in the area are typical of the Coastal Western Hemlock Biogeoclimatic Zone (Klinka et al. 1984). Plant names follow those used by Hitchcock and Cronquist (1973). Climax forest stands consist mainly of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). The most common species in the herb layer are hairy catsear (*Hypochaeris radicata*), pearly

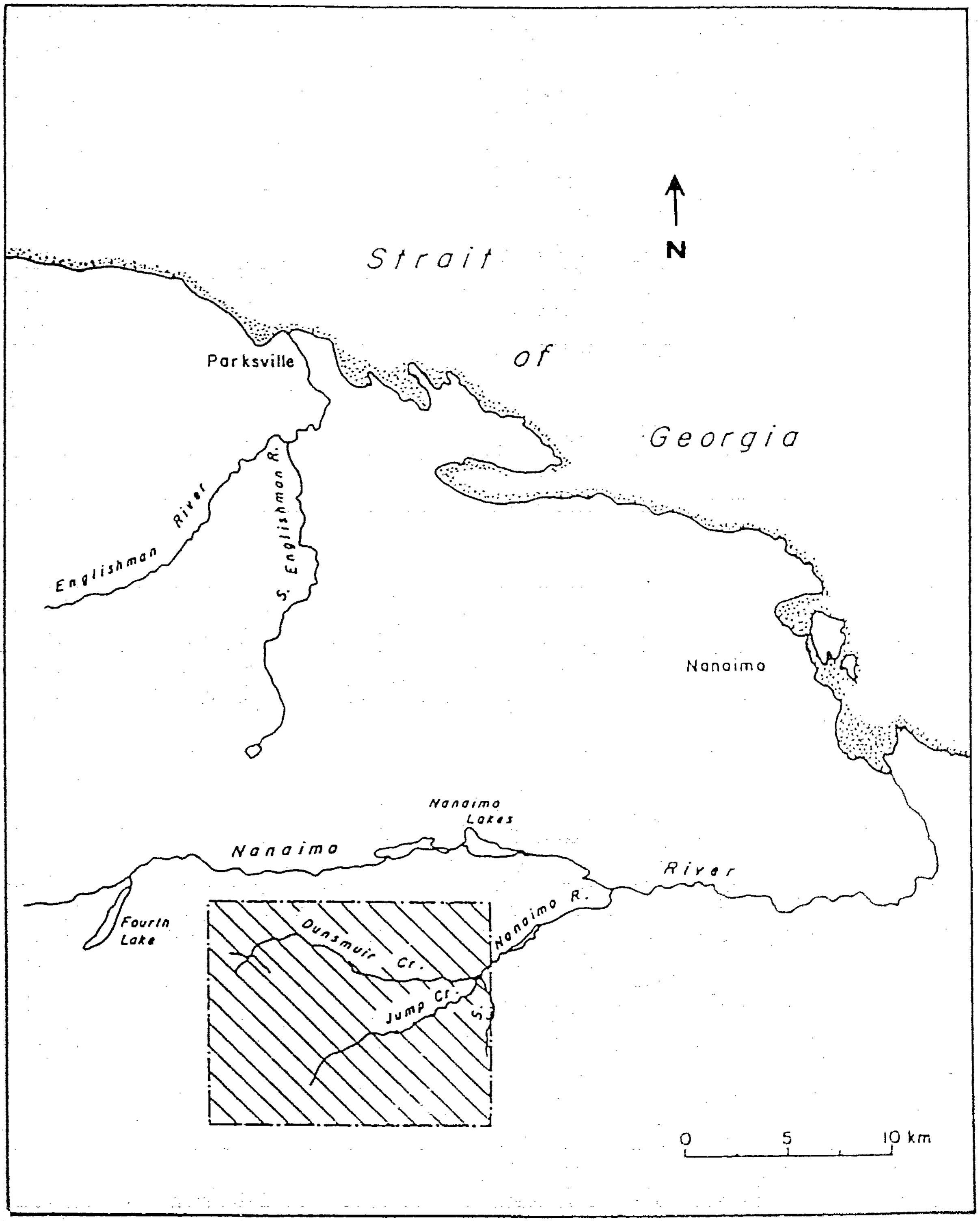

Fig. 1. Study area in the Nanaimo River watershed, British Columbia (after Baker 1992).

everlasting (*Anaphalis margaritacea*), vanilla leaf (*Achlys triphylla*), fireweed (*Epilobium angustifolium*), bracken fern (*Pteridium aquilinum*), and sword fern (*Polystichum munitum*). Common shrubs in the area are salal (*Gaultheria shallon*), trailing blackberry (*Rubus ursinus*), black raspberry (*Rubus leucodermis*), red huckleberry (*Vaccinium parvifolium*), and Oregon grape (*Berberis nervosa*). Characteristics of the forests and secondary succession on southeastern Vancouver Island are described by Mueller-Dombois (1959).

Clearcut logging has been conducted in the study area since the 1940's and has resulted in a mosaic of successional habitats. Cutovers in the area have been replanted exclusively with Douglas-fir. Some pole and sapling stands have been thinned to reduce stem density.

MATERIALS AND METHODS

Live-Trapping Grid Descriptions

To obtain detailed demographic data about deer mice, 1.0 ha live-trapping grids were established in 4 seral stages (herb dominated, shrub dominated, young forest, and mature forest). Each grid was live-trapped every second week from May to November during 1988 and 1989 and once in May 1990. The herb, shrub, and young forest grids were located in areas that had been logged and slash burned while the mature forest grid was located in a stand of mature forest that had not been logged previously. Locations of grids were selected so they would have similar slope, elevation, aspect and topography.

The herb grid was established within an area that was logged and slash burned in 1986. Vegetation in this 2-year-old cutover was dominated by herbaceous plants. Slash burning had reduced the abundance of most perennial species but salal and black raspberry were present and comprised the remainder of the vegetation cover. The burn was incomplete and substantial amounts of coarse woody debris remained.

The shrub grid was established in an area that had been logged and slash burned in 1978. The vegetation in this seral stage (10-yr-old) consisted mostly of salal, Douglas-fir saplings and minor herbaceous species. Coarse woody debris was abundant and consisted mainly of pieces that survived slash burning along with some smaller pieces produced by shrubs after the burn.

The young forest grid was in an area that had been logged and slash burned in 1960. The vegetation in this 28-yr-old forest was dominated by a dense stand of young Douglas-fir trees. Canopy closure was almost complete over much of the grid and the herb and shrub layer was very sparse beneath the dense canopy. Coarse woody debris was abundant and consisted mainly of debris produced when the stand was thinned in 1986, two years prior to my study.

The mature forest grid was located in a stand of Douglas-fir, western hemlock and western redcedar that was approximately 150-years-old and had not been previously logged. The canopy had multiple layers and was incomplete with sporadic openings. Ground level vegetation was patchy and consisted mainly of perennial shrubs, ferns, and mosses. The coarse woody debris on the grid consisted mostly of fallen branches and trees.

At each of the 49 trap locations in each grid, percentages of ground level vegetation (below 50 cm, 5 m diameter plot) and canopy closure were estimated with the aid of visual comparison charts (Walmsley et al. 1980). To estimate the abundance and describe the type of coarse woody debris in each seral stage, I established seven, 100-m transects along the grid lines of each grid. I recorded the diameter, height above ground and state of decay of each piece of woody debris > 1 cm in diameter that was intersected by the transects. The volume of debris present was estimated using the line intersect method (Van Wagner 1968).

Live Trapping

Each 1.0 ha live-trapping grid consisted of 49 trap stations distributed at approximately 15 m intervals in a checkerboard fashion. At each trap station, a single Sherman live trap was placed within 1 m of a marked stake. Traps were baited with peanut butter and rolled oats.

Polyester batting was provided as bedding material. Traps were prebaited for 3 days prior to the first trapping session each year and left locked open between bi-weekly trapping sessions. Traps were set in the afternoon of day 1 and checked each morning on days 2, 3, and 4.

All deer mice (*Peromyscus maniculatus austerus* Baird) captured were weighed with a Pesola spring scale and ear tagged with a numbered fingerling fish tag. The sex of each mouse was determined and the trap location was recorded. Testes of males and the vaginal openings and mammaries of females were examined for evidence of reproduction and to determine breeding condition. Mice were classified as juveniles if they were < 13 g, subadults if they were between 13-16 g, and adults if they were > 16 g (Sullivan 1977).

Direct enumeration of the minimum number of animals known to be alive (MNA) was used to estimate deer mouse abundance. I assumed that this technique would provide sufficiently accurate estimates for comparison among the different seral stages.

Live-Trapping Transects

Live-trapping transects were used to broaden my sampling of deer mouse populations in the different seral stages and to allow better comparisons among seral stages. Thirty, 100-m line transects were established and trapped in each seral stage at various locations that were similar in age and site characteristics. Each 100-m transect had 7 equally spaced trapping stations at each of which, a single live trap was placed. Live trapping was conducted for 3 consecutive nights (21 trap nights) on each of these transects during July and August of 1989, using the same 4 day trapping regime as the bi-weekly trappings on the grids.

To ensure that estimates of relative abundance obtained using the transects were representative of the grid determined estimates, I established 100 m transects (7 traps/transect) between the grid lines on each of the 4 grids during July 1989. I used 5 different transects within each grid during the periods between the bi-weekly grid trappings. These data allowed transect determined abundance to be calibrated with abundance determined by trapping entire grids.

RESULTS

Seral Stage Characteristics

The percent cover of ground level vegetation was 13.6% in the herb seral stage, it increased to 29.5% in the shrub seral stage, then declined to 7.7% in young forest, followed by an increase to 26.6% in mature forest (Table 1). The herb and shrub seral stages lacked large trees and so lacked a canopy. Canopy closure was greatest in young forest and then decreased in mature forest (Table 1).

Table 1. Mean percent cover of ground level vegetation and canopy closure at grid sites in 4 seral stages during July 1988.

Seral Stage	n	Percent Ground Cover (SE)	Percent Canopy Closure (SE)
Herb	49	13.6 (1.1)	0.0
Shrub	49	29.5 (1.3)[a]	0.0
Young Forest	49	7.7 (0.8)	89.0 (2.6)
Mature Forest	49	26.6 (1.6)[a]	62.1 (6.0)

[a] Within a column means with the same superscript are not significantly different ($P > 0.05$), Tukey HSD test for multiple comparisons.

The number of pieces of coarse woody debris in different size classes and the total volume of debris differed among seral stages (Table 2). Small coarse woody debris (1-5 cm diameter) was most abundant in the shrub seral stage and mature forest. It was least abundant in young forest. Medium sized coarse woody debris (> 5-25 cm diameter) was most abundant in the shrub seral stage and least abundant in mature forest. Large woody debris (> 25 cm diameter) was most abundant in young forest and least abundant in mature forest. Total volume of debris was greatest in the shrub seral stage and least in the herb seral stage. The relative importance of different size classes and amounts of debris to deer mice within each seral stage is examined and discussed in Chapter 2.

Trappability

My comparison of deer mouse populations in different seral stages assumes that most of the mice residing in each grid were captured. Minimum unweighted trappability (Krebs and Boonstra 1984) was used to estimate how successful trapping was in each grid. This method ignores all first and last captures for each individual and thus it is not influenced by mice captured only once or twice. It provides a single value for each animal so it is not influenced by animals with long capture histories (Hilborn et al. 1976). Minimum unweighted trappability was above 74% for all 4 grids during 1988 and 1989 (Table 3).

Table 2. Mean number of pieces and volume of coarse woody debris along 100 m transects through 4 grids. n = 7 transects/seral stage. SE is given in brackets beneath the mean.

Seral Stage	Mean Number of Pieces/100 m 1-5 cm diameter	 >5-25 cm diameter	 >25 cm diameter	Total Volume (m^3/m^2)
Herb	184.12 (9.3)	24.52[a] (1.2)	2.83 (0.1)	0.12[a] (0.02)
Shrub	257.91[a] (15.5)	30.40 (1.5)	7.74 (0.5)	0.17[a] (0.03)
Young Forest	154.56 (9.8)	26.14[a] (1.3)	12.19 (0.7)	0.16[a] (0.02)
Mature Forest	243.14[a] (13.2)	19.29 (0.8)	1.57 (0.1)	0.13[a] (0.01)

[a] Within a column, means with same superscript are not significantly different ($P > 0.05$), Tukey HSD test for multiple comparisons.

Table 3. Minimum unweighted trappability estimates of deer mice on each live-trapping grid. Sample size (n) is the number of individual deer mice and is given in parentheses. There were no significant differences between males and females, seral stages or years (Chi-squared tests, $P > 0.05$).

	Minimum Unweighted Trappability			
Seral Stage	1988		1989	
	Males	Females	Males	Females
Herb	0.83 (28)	0.85 (26)	0.80 (22)	0.79 (17)
Shrub	0.84 (36)	0.82 (21)	0.84 (32)	0.81 (28)
Young Forest	0.79 (21)	0.80 (18)	0.74 (19)	0.78 (16)
Mature Forest	0.88 (23)	0.81 (16)	0.82 (17)	0.79 (14)

Trappabilities were not significantly different between males and females on any of the grids during either year (Chi-squared tests, $P > 0.05$).

Transect Captures and Abundance

To determine if transects could be used to estimate the relative abundance of mice at other locations, I plotted numbers of individual deer mice captured during 21 trap nights (7 traps/transect for 3 nights) on live-trapping transects conducted on each grid against population estimates determined from data gathered while trapping the entire grid. The linear regression of single transect captures versus estimates made using enumeration on the grids reveals a strong correlation between these methods of estimating deer mouse abundance ($r^2 = 0.77$, $P < 0.01$, $n = 20$, Fig. 2).

Abundance and Seasonal Population Changes

To avoid complications caused by seasonal variation and repeated trapping of individual mice on the grids, deer mouse abundance in the various seral stages was compared using data from live-trapping transects. Data from live-trapping grids were used to compare seasonal population changes and trends among the 4 seral stages.

Relative abundance of deer mice in the 4 seral stages was determined from the 30 live-trapping transects conducted once in each seral stage during July-August 1989

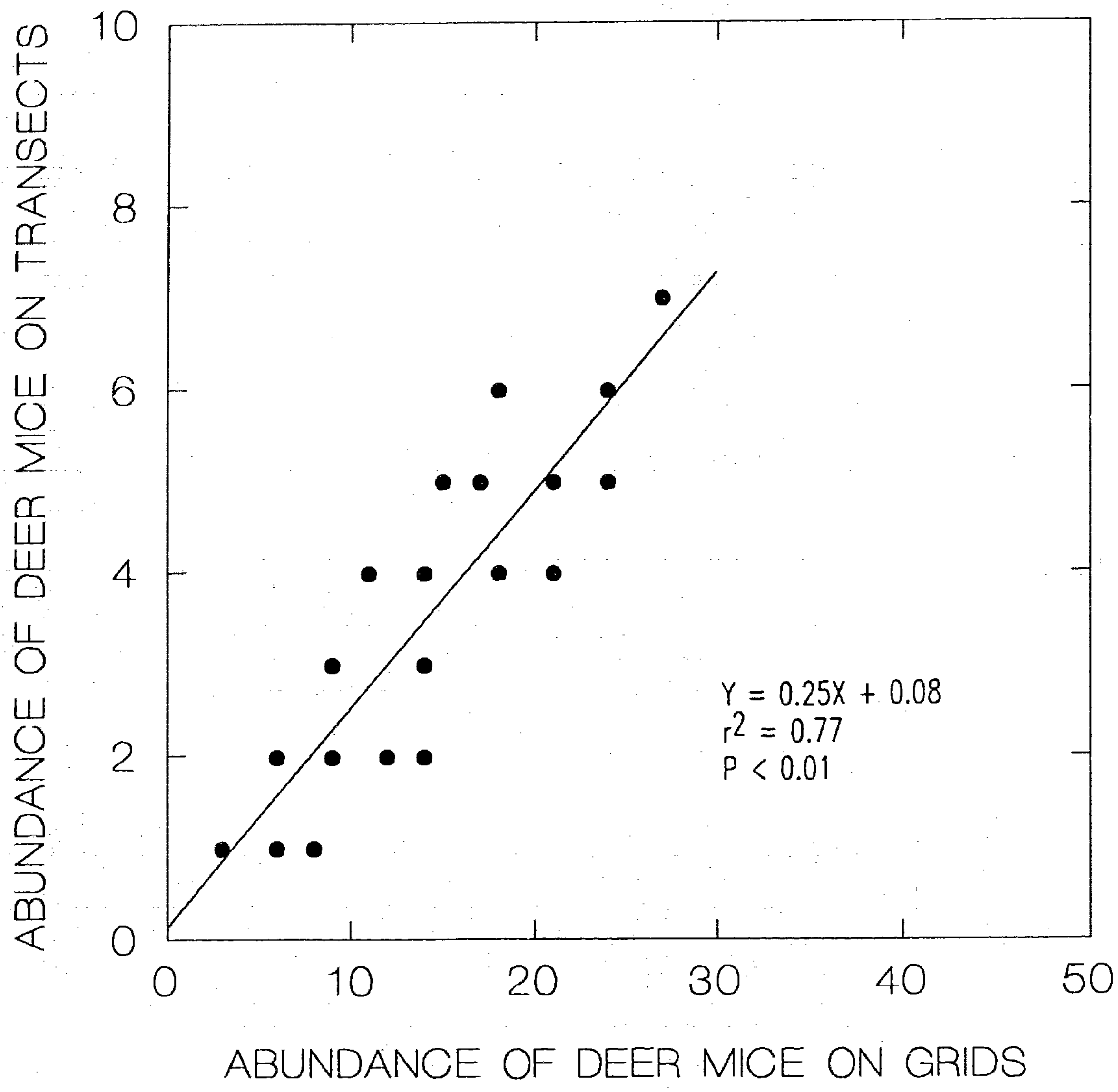

Fig. 2. Linear regression of abundance of deer mice captured on each of 20 transects (mice/100 m) and abundance of deer mice determined from 4 live-trapping grids (MNA) during July 1989.

(Fig. 3). Analysis of variance reveals that deer mice were not equally abundant in the different seral stages ($F = 12.38$, $df = 3$, $P = 0.001$). There were no significant differences between herb and shrub seral stages ($P = 0.66$, Tukey HSD) and between the young and mature forest ($P = 0.90$, Tukey HSD). Deer mice were more abundant in the 2 younger seral stages than in the 2 older seral stages ($P < 0.05$, Tukey HSD).

Seasonal changes in deer mouse abundance were not always similar in the 4 seral stages during 1988 and 1989 (Fig. 4). The major differences in seasonal abundance among the seral stages occurred during spring and fall. During spring, deer mouse abundance in the herb seral stage and mature forest remained low while that in the shrub seral stage decreased and that in the young forest increased. All 4 seral stages showed substantial population increases during September and early October 1988. However, deer mouse abundance in the young forest began to decrease by late October. Overall, deer mouse abundances in the different habitats were similar throughout most of the breeding season during 1988. All 4 populations declined over winter 1988-1989 and were substantially lower when trapping began again in the spring of 1989.

During the summer of 1989, abundances of mice in the herb, shrub, and young forest seral stages were similar to those observed in 1988. Populations on the grids increased

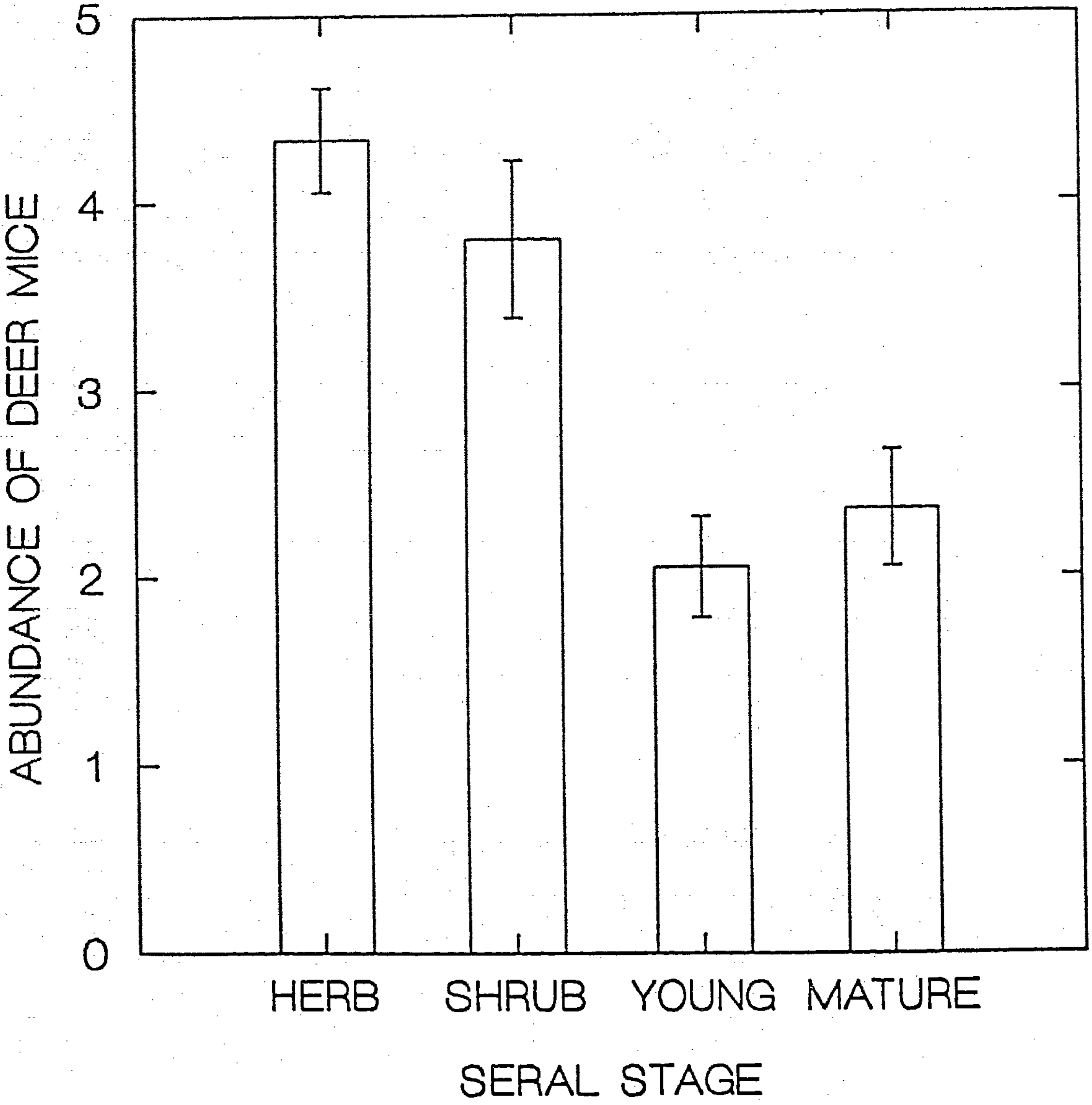

Fig. 3. Mean (± SE) relative abundance of deer mice in each seral stage during July-August 1989. Number of individual mice captured (individuals/21 trap nights) on 100-m transects is indicated. n = 30 transects in each seral stage.

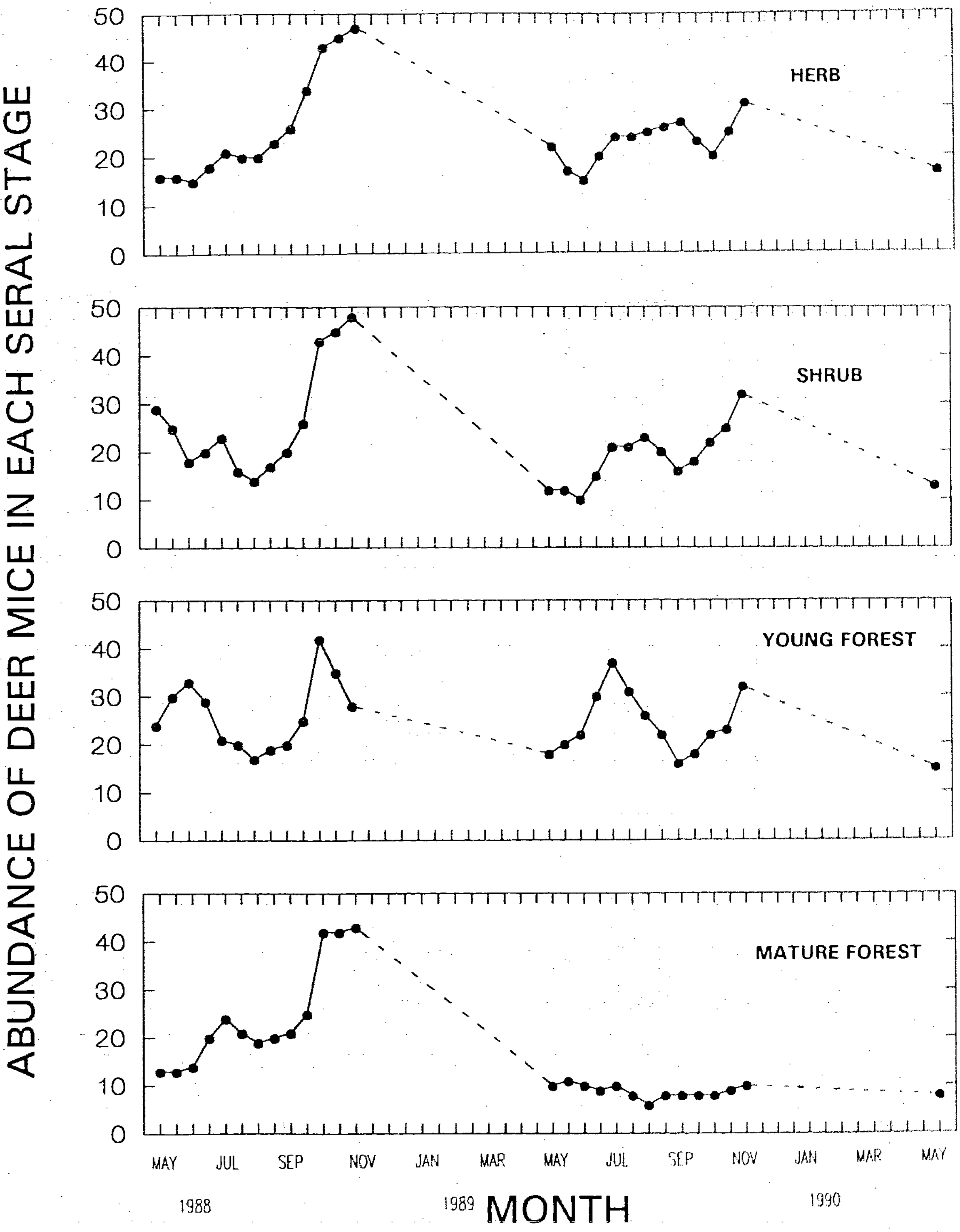

Fig. 4. Abundance (MNA) of deer mice on live-trapping grids in each seral stage from May 1988 to May 1990.

during the fall of 1989 but none reached abundances as high as those recorded in 1988. The population in the young forest increased during early spring as it did during 1988, but instead of stabilizing during the summer, the population decreased until September. During 1989, the population in the mature forest remained low during the entire trapping season. A single live-trapping session conducted in May 1990 revealed that deer mouse populations in the herb, shrub and young forest seral stages had again declined over the winter months. The population in the mature forest also declined but the relative decrease was much smaller than those in the other seral stages.

Breeding Season

Because the average gestation period for non-lactating female deer mice is 22-25 days (Millar et al. 1979), I assumed that the breeding season started 23 days prior to the first appearance of pregnant or lactating females in each seral stage. The end of the breeding season was taken as the date of the last capture of a lactating female. Males in all 4 seral stages had scrotal testes and were in breeding condition during the first trapping sessions in 1988 and 1989. Testes regressed before the end of lactation in all seral stages and males were not in breeding condition prior to the end of the breeding season for females.

During 1988, the breeding season commenced in mid-April in all seral stages and it ended in mid-October in the shrub, young forest, and mature forest; it was thus about 28 weeks long. In the herb seral stage, the breeding season lasted approximately 30 weeks, ending in early November (Fig. 5).

During 1989, the breeding season commenced in mid-May in the herb, young forest, and mature forest seral stages, about 4 weeks later than in 1988. In the shrub seral stage, breeding began in mid-April as it had in 1988. In the shrub seral stage and mature forest, breeding ended by mid-October. In the herb seral stage and young forest breeding ended in early October. Thus, the breeding season lasted approximately 22 weeks in the herb seral stage and young forest, 24 weeks in the mature forest, and 28 weeks in the shrub seral stage. Breeding season length varied between years and habitats. No particular habitat had consistently longer or shorter breeding seasons.

Reproduction

I used the number of juveniles entering the trappable population as an index of reproductive rate. Juvenile deer mice first enter the trappable population at approximately 20 days-of-age (Millar et al. 1979). Trappable juveniles are assumed to be independent and successfully weaned (Millar et al. 1979). Use of juveniles as an index of reproduction ignores differences in survival of juveniles

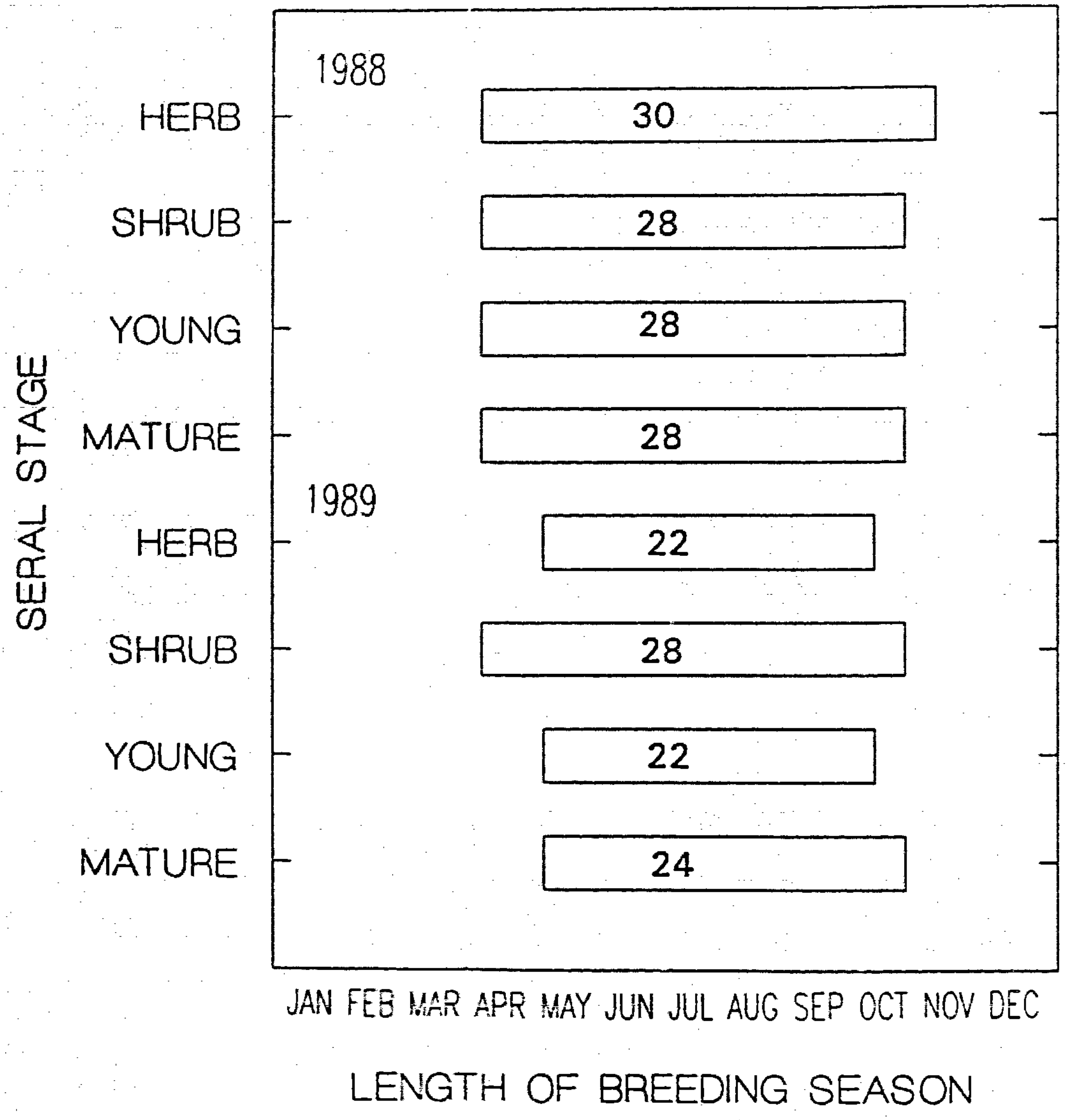

Fig. 5. Approximate length of the breeding seasons in each each seral stage during 1988 and 1989. Number of weeks is given inside bars.

prior to independence and thus underestimates reproduction in areas with poor juvenile survival. However, this method provides an estimate of how many individuals were successfully weaned and available for recruitment.

During 1988, more juveniles were observed in the herb and shrub seral stages than in young and mature forests (Table 4). During 1989, the number of juveniles observed in all of the seral stages was significantly lower than in 1988 (paired t-test, P = 0.01). During 1989, there were no pronounced differences in the number of juveniles among the herb, shrub and young forest seral stages whereas in the mature forest no juveniles were captured. Reproductive rate varied more between trapping seasons than between seral stages.

During 1988, the first appearance of juveniles and the number of juveniles observed each month followed similar trends in the different seral stages (Fig. 6). The first juveniles appeared in June. The number of juveniles present each month increased throughout the summer and peaked in October.

During 1989, recruitment of juveniles did not follow the pattern exhibited in 1988. In all of the seral stages, juveniles appeared later and in lower numbers. Juvenile recruitment in the herb, shrub, and young forest seral stages was low through the summer and did not peak in the fall. Juveniles were not captured in the mature forest during 1989. During 1988, all of the grids had similar

Table 4. Total number of individual juveniles captured on the live-trapping grids during 1988 and 1989.

Seral Stage	1988	1989
Herb	42	9
Shrub	40	10
Young Forest	19	11
Mature Forest	29	0

Significantly more juvenile deer mice were observed during 1988, paired t-test 1988 vs 1989, $t = 4.36$, $P = 0.01$.

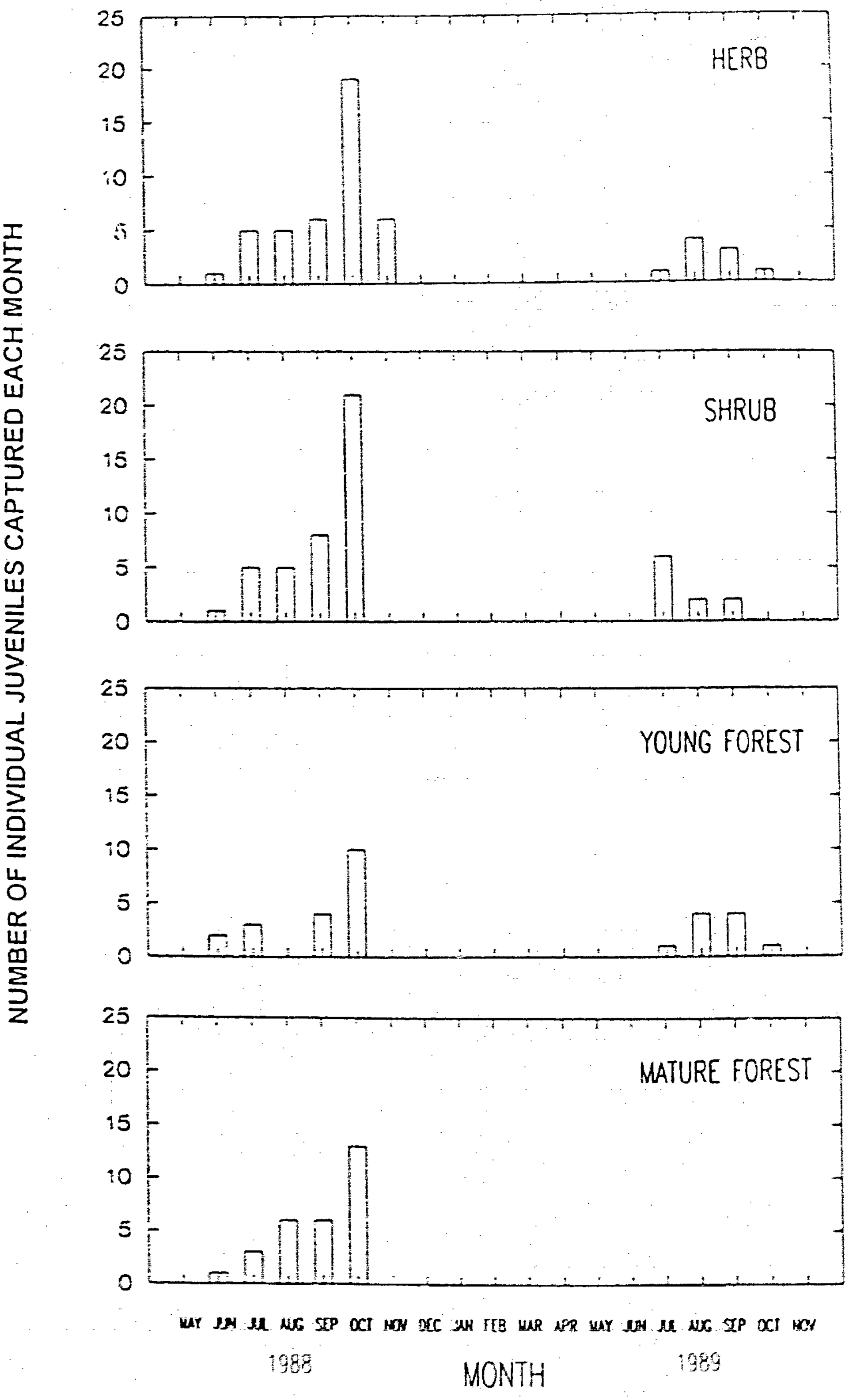

Fig. 6. The number of individual juveniles captured each month in 4 seral stages.

seasonal trends in juvenile recruitment although there were differences in the total number of juveniles captured. During 1989, all of the grids had reduced levels of juvenile recruitment with no consistent seasonal increase. There were differences in the magnitude of juvenile recruitment between grids and between years but, within each year, most of the grids followed similar patterns of juvenile recruitment.

Juvenile Recruitment and Survival

To determine the proportion of juveniles born which enter the trappable population, the number of young expected to be born on each grid was estimated and compared with the number of juveniles observed. The average litter size for deer mice in southwestern British Columbia is approximately 4.5 pups (Sadleir 1974). Assuming there were no differences in mean litter sizes among seral stages, the number of births was calculated by multiplying the mean litter size of deer mice by the number of successful pregnancies observed. A pregnancy was assumed successful if the female remained on the grid and showed evidence of weight loss and lactation. The total number of juveniles observed divided by the expected number of births gives the proportion of pretrappable juveniles entering the population. Pretrappable juveniles may be lost through mortality or emigration and I did not attempt to separate these factors. The numbers of pregnancies, expected births, juveniles, and juveniles entering the population were estimated for each seral stage (Table 5).

During 1988, the herb and shrub seral stages had more pregnancies and greater juvenile survival than did the forested seral stages. These factors contributed to the greater numbers of trappable juveniles in the younger seral stages during 1988. During 1988 and 1989, juveniles born in the herb and shrub seral stages were more likely to enter the trappable population than were juveniles born in the young forest and mature forest (Chi-squared, $P < 0.05$). The early seral stages had greater numbers of juveniles recruited in October or November 1988, near the end of the breeding season.

The number of pregnancies and the recruitment of juveniles were lower on 3 of the 4 grids during 1989 (Chi-squared, $P < 0.01$) than during 1988. During 1989, the herb seral stage, shrub seral stage and mature forest had less than half the number of pregnancies observed in 1988 and juvenile survival was lower than in 1988. More pregnancies occurred in the young forest relative to the other seral stages during 1989, but few juveniles entered the trappable population. There was no increase in juvenile recruitment at the end of the 1989 breeding season.

The number of pregnancies was not consistently higher in any particular seral stage during my study. The proportion of juveniles born that survived and entered the trappable population was consistently higher in the herb

Table 5. Number of pregnancies observed, number of juveniles, and survival of juveniles on live-trapping grids in each seral stage.

	Pregnancies Observed	Juveniles Expected	Juveniles Observed	Juvenile Survival
<u>1988</u>				
Herb	29	131	42	0.32
Shrub	26	117	40	0.34
Young Forest	17	77	19	0.25
Mature Forest	23	104	29	0.28
<u>1989</u>				
Herb	11	50	9	0.18
Shrub	13	59	10	0.17
Young Forest	27	122	11	0.09
Mature Forest	8	36	0	0.00

and shrub seral stages than in the forested seral stages (Wilcoxon signed-ranks test, P = 0.03).

Subadult Recruitment

The number of subadults entering a population in an area depends on the number of juveniles successfully weaned that remain in the area and the number of subadults that immigrate into the area. To separate reproduction from immigration, subadults that were tagged as juveniles on a grid were assumed to have been born on that grid, while individuals first tagged as subadults were assumed to be immigrants. Using these criteria, the total number of subadults observed and the proportion of immigrants was estimated for each seral stage (Table 6). In 1988 and 1989, subadults were more abundant in the herb and shrub seral stages than in the young forest and mature forest. The proportion of subadults that immigrated was lowest in the herb seral stage and highest in the mature forest during both years of the study. The herb seral stage had the greatest number of subadults observed each year and the lowest proportion of immigrants. Subadult numbers were significantly lower in all seral stages, in 1989 than in 1988 (Wilcoxon signed-ranks test, P = 0.01). The decreases in subadult numbers were accompanied by increases in the proportion of subadults that were immigrants.

The number of juveniles in an area that remain in the area long enough to be observed as subadults is influenced

Table 6. Number of subadults and percent of immigrant subadults observed on each grid during 1988 and 1989.

	Total Number Subadults	Percentage of Subadults That Were Immigrants
1988		
Herb	71	60.6^{a}
Shrub	46	63.0^{ab}
Young Forest	32	71.9^{ab}
Mature Forest	43	79.1^{b}
1989		
Herb	32	78.1^{a}
Shrub	20	80.0^{a}
Young Forest	11	81.8^{a}
Mature Forest	4	100.0

[a,b] Within a year, proportions followed by the same superscript are not significantly different, Fisher exact probability test, $P > 0.05$.

by both survival and emigration. The proportion of juveniles tagged on each grid that were later observed as subadults and the percentage of subadults remaining at least one month on each grid were calculated (Table 7). A significantly greater proportion of local juveniles entered the subadult population in the herb seral stage than the other seral stages during both 1988 and 1989. The mature forest had the lowest proportion of local juveniles entering the subadult population in 1988; in 1989, all of the subadults on this grid were immigrants. The shrub seral stage and young forest had intermediate proportions of local juveniles entering the subadult population during both years of the study. There were no significant differences among the proportions of subadults remaining for one month or more in the herb seral stage, shrub seral stage or young forest during either year. During 1988, significantly fewer subadults remained for a month or more in the mature forest than did those in other seral stages.

Survival

In an open population, the disappearance of individuals includes losses from both emigration and mortality. I did not attempt to separate these factors but treated them collectively regarding on-site survival. Survival rates were calculated for the breeding season and the nonbreeding season (Table 8). The breeding season survival rate was estimated as the proportion of tagged

Table 7. Percentages of subadults tagged as juveniles and subadults remaining at least one month on each grid.

	N	Percent Tagged as Juvenile	Percent Remaining 1 Month
<u>1988</u>			
Herb	71	66.7	53.8^{a}
Shrub	46	42.5^{a}	66.7^{a}
Young Forest	32	47.5^{a}	63.6^{a}
Mature Forest	43	31.0	36.4
<u>1989</u>			
Herb	32	77.8	42.9^{a}
Shrub	20	40.0^{a}	61.3^{a}
Young Forest	11	18.2^{a}	77.8^{a}
Mature Forest	4	0.0	50.0^{a}

[a] Within a column and year proportions followed by the same superscript are not significantly different, Fisher's exact probability test, $P > 0.05$.

Table 8. Breeding (summer) season and nonbreeding (winter) season survival rates for the 4 seral stages. The sample size (n) is the number of tagged adults present at the beginning of each season.

Seral Stage	n	Survival Breeding	n	Survival Nonbreeding
<u>1988</u>				
Herb	20	0.40[a]	24	0.21[a]
Shrub	22	0.32[a]	22	0.18[a]
Young Forest	20	0.35[a]	14	0.29[a]
Mature Forest	22	0.68	20	0.25[a]
<u>1989</u>				
Herb	24	0.38[a]	13	0.23[a]
Shrub	20	0.25[a]	15	0.27[a]
Young Forest	34	0.41[a]	13	0.31[a]
Mature Forest	10	0.60	9	0.56

[a] Within a column and year, values followed by the same superscript are not significantly different, Fisher exact probability test, $P > 0.05$.

adults surviving from 1 July to 31 August of each year. This period was chosen to avoid increased emigration and immigration at the beginning and end of the breeding season. Breeding season survival was significantly higher in the mature forest during both years of the study.

Nonbreeding season survival was estimated as the proportion of tagged mice remaining on each grid over the nontrapping period (31 November and 1 May). During 1988, nonbreeding season survival rates were not significantly different among seral stages. During 1989, the nonbreeding season survival rate was significantly greater in mature forest. Nonbreeding season survival rates were consistently lower in the herb and shrub seral stages but the differences were small and the rates in some seral stages varied considerably between years.

Sex Ratios

Sex ratios were calculated monthly for each grid from the minimum number of males and females known to be alive each month (Fig. 7). Sex ratios fluctuated seasonally in all of the seral stages. To avoid bias caused by individuals being captured in more than one trapping session on the grids, sex ratios for each seral stage were also calculated during the breeding season from the number of males and females captured on the 30 transects trapped in each seral stage during July and August of 1989. The deer mouse populations in the herb seral stage (n = 135,

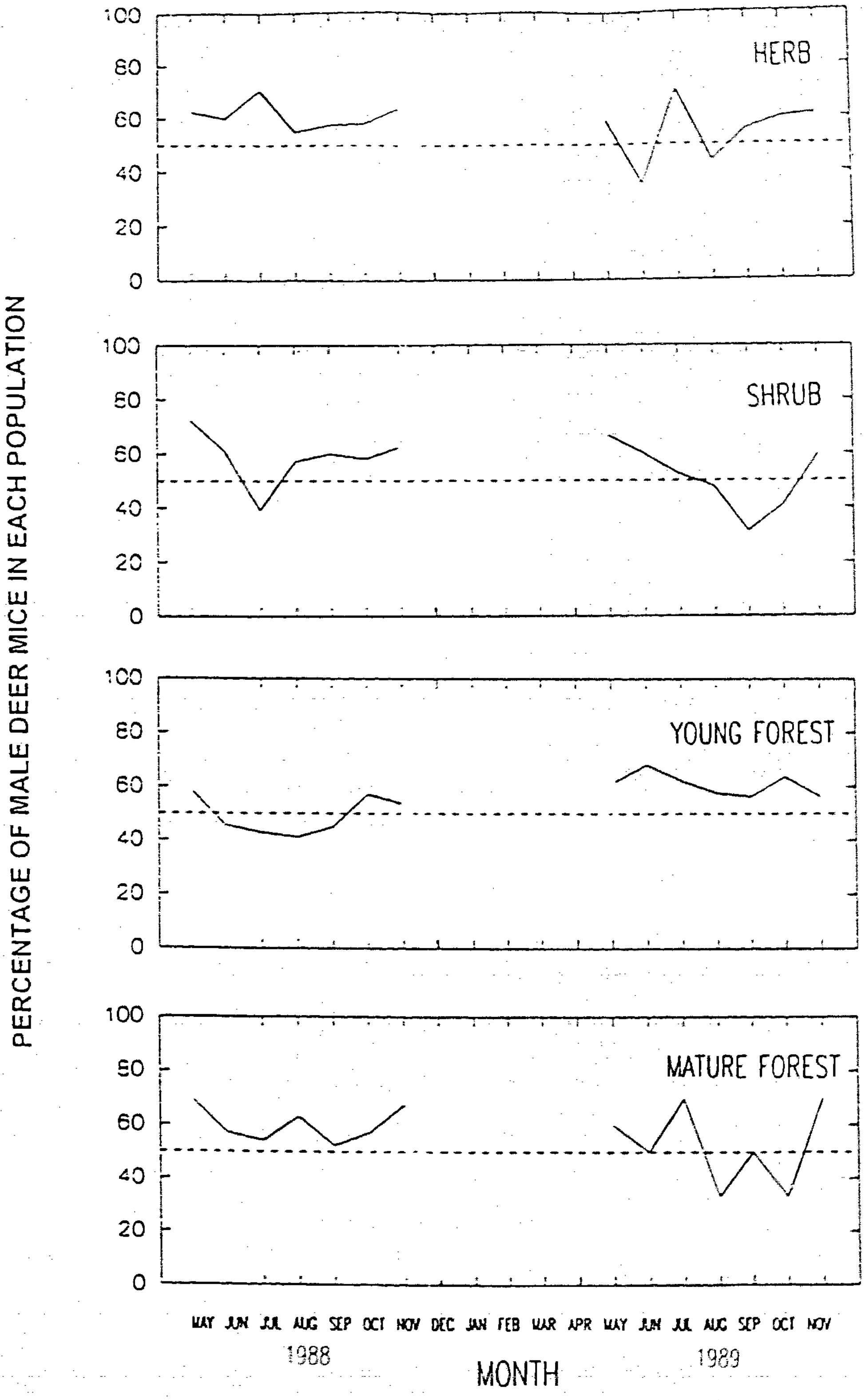

Fig. 7. Monthly sex ratio in each seral stage between May 1988 and November 1989. The sex ratio is expressed as the percentage of males in the total population on each grid.

male/total = 0.54) and mature forest (n = 66, male/total = 0.56) did not differ significantly from a 50:50 sex ratio. The shrub seral stage (n = 114, male/total = 0.70) and young forest (n = 72, male/total = 0.73) populations did have a significant male bias (Wilcoxon signed-ranks test, P = 0.05).

Proportion of Transients

Adults captured in only one trapping session were considered transient. This definition of transient is not completely independent of mortality but high mortality would also be indicative of poor habitat or high levels of predation. The average number of transients observed per month was calculated for each seral stage (Table 9). During 1988, there were no significant differences among seral stages. The mature forest population had significantly fewer transients during 1989 than during 1988 and it also had significantly fewer transients than did other seral stages during 1989.

DISCUSSION

Investigations of the effects of logging and forest removal on *Peromyscus* spp. have typically only considered the first few years following cutting. Results of these studies have been mixed. Most investigators reported an increase in *Peromyscus* spp. populations following cutting

Table 9. Mean number (± SE) of transients captured per month during 7, 1-month trapping sessions ($n = 7$ / yr) conducted in each seral stage during 1988 and 1989.

Seral Stage	1988	1989	Significance of Interannual Difference (P)
Herb	11.7^a(3.2)	11.4^a(2.1)	> 0.05
Shrub	13.3^a(2.0)	7.4^a(2.4)	> 0.05
Young Forest	10.3^a(1.8)	7.3^a(1.2)	> 0.05
Mature Forest	10.7^a(2.1)	2.4 (0.5)	< 0.05

[a] Within a column, values followed by the same superscript are not significantly different, $P > 0.05$, Tukey HSD test for multiple comparisons.

(Trousdell 1954, Gashwiler 1959, Ahlgren 1966, Tevis 1956, Sims and Buckner 1973, Krefting and Ahlgren 1974, Hooven and Black 1976, Martell and Radvanyi 1977). Other investigators have found little difference in deer mouse abundance between cutover and forest habitats (Krull 1970, Lovejoy 1975) or that deer mice were more abundant in forest habitats (Harris 1968). Intensive monthly or biweekly live-trapping studies in British Columbia, such as those of Petticrew and Sadleir (1974) and Sullivan (1979a), concluded that the average abundance of deer mice was similar in forest and logged areas. Van Horn (1981) trapped intensively throughout most of the year in Alaska and found there was only a slight increase in deer mouse densities following cutting.

My results indicate that there can be much seasonal and interannual variation in the abundance of deer mice within and among seral stages. This variation makes it difficult to identify differences among seral stages if average abundance is calculated with numbers gathered in more than one season or year. To avoid this problem, I compared the relative number on multiple live-trapping transects conducted in each seral stage during the breeding season (July-August). Previous studies have reported that deer mice maintain exclusive home ranges and stable numbers only during the breeding season (Sadleir 1965, Fordham 1971, Metzgar 1971, Wolff et al. 1983). I assumed that the breeding season would be the best time to compare densities of deer mice among seral stages because the abundance during the breeding season would best indicate how many individuals were maintaining home ranges at each site. During my study, populations on the live-trapping grids in all 4 seral stages were relatively stable during the summer months. This suggests that individuals were maintaining exclusive home ranges in each seral stage during the summer.

My results agree with most other investigators; in that deer mice are more abundant in early seral habitats. Significantly more deer mice were captured on the transects in the herb and shrub seral stages than were captured in young forest and mature forest.

Most studies have compared only new cutovers and mature forests, fewer studies have examined the intermediate seral stages. The studies which investigated deer mouse populations in intermediate seral stages have had mixed results. Deer mouse populations in northern California increased for the first 3 years following cutting then stabilized between 4 and 10 years, after which they declined and remained low (Tevis 1956). Kirkland (1977) reported no increase immediately after cutting but found that numbers of white-footed mice (*Peromyscus leucopus*) began to decline 6 to 15 years after cutting. Probst and Rakstad (1987), working in aspen forests, found that densities of deer mice decreased for the first 10 years after cutting. Gashwiler (1970) reported that deer mice numbers increased immediately after cutting in Oregon, but he found no consistent trend during the first 10 years after cutting. In Alaska, deer mouse populations increased slightly after cutting and continued to increase until the area reached the stage of maximum understory production at 23-25 years of age. The population then declined as canopy closure increased (Van Horn 1981). Krefting and Ahlgren (1974) found that deer mice were most abundant during the first 7 years following a burn and they suggested that this was due to increases in herbaceous vegetation and thus seed and berry availability during this period.

On southeastern Vancouver Island, herbaceous plants reach peak percent cover about 3 years after burning and then decline gradually until 15 years after burning when they are of minor abundance (Gates 1968). Shrubs dominate the low stratum from 3-15 years post-cutting and then decline as they are shaded by coniferous trees (Gates 1968). In my study area, deer mouse abundance was highest in the herb seral stage. Numbers of mice then declined moderately in the shrub seral stage and were substantially lower in young forests. Deer mouse abundance increased slightly in the mature forest. This trend broadly follows the abundance of herbaceous plants. However, deer mouse abundance in the herb and shrub seral stages was not significantly different nor was mouse abundance in young and mature forests.

The lack of a strong correlation between percent cover of herbs and shrubs and abundance of deer mice was not unexpected. Many population studies of deer mice suggest that adults (both males and females) are territorial or limit their numbers through mutual avoidance (Sadleir 1965, Healey 1967, Fordham 1971, Petticrew and Sadleir 1974, Fairbairn 1977, Metzgar 1971, Wolff et al. 1983, Wolff 1985a). Intrinsic regulation of population density may keep densities stable at low levels in areas that could otherwise support higher numbers. Metzgar (1971) showed that resident animals familiar with their home range have a survival advantage because transient mice are more susceptible to predators.

Densities of deer mice may not be positively correlated with habitat quality or suitability (Van Horn 1983) because survival or reproduction may be low in particularly high density populations. Adler and Wilson (1987) found that some populations of white-footed mice regulate numbers intrinsically while other high density populations do not and thus grow in an unregulated manner during the breeding season, only to decline during the nonbreeding season. Adler and Wilson (1987) suggested that intrinsic regulation of population density may increase with habitat suitability and stability. If this is the case, more suitable habitats should support stable populations that are regulated, while less suitable habitat should have patterns of demography that exhibit little or no regulation. Although there are problems of circularity relating density or population stability to habitat quality, demographic characteristics indicative of higher individual survival, productivity or intrinsic population regulation are likely associated with superior habitat. Density along with survival, productivity, and population stability should be considered when assessing habitat suitability.

One hectare will contain approximately 17 average sized (590 m^2) home ranges of male and female deer mice (with male ranges overlapping female ranges). Wolff (1985b), using behavioural trials, found that the density threshold for aggression is between 25-30 mice/ha. Below this level, aggression could be avoided through mutual avoidance. Above this level, home ranges were compressed resulting in increased aggressiveness of resident animals and subsequent exclusion of intruders.

If early seral stages are acting as dispersal or behavioural "sinks" (Sullivan 1979a), it should be possible to detect differences in productivity, survival or population regulation. I hypothesized that "sink" habitats will support less aggressive adult populations that may have higher rates of reproduction and juvenile recruitment but lower rates of adult survival. Higher quality habitats will support more self-regulated populations with reduced but more stable numbers, lower rates of reproduction and juvenile recruitment, and higher rates of adult survival.

If only abundance is considered, more mice occur in the younger seral stages but, are the numbers higher because early seral stages are more suitable habitat or because the populations in early seral stages are less regulated and kept high through immigration? Seasonal population patterns in the seral stages indicate that some populations may be more regulated than others. During 1988, populations in all seral stages broadly followed similar seasonal fluctuations and all of the populations experienced increased recruitment in fall. An autumn increase in recruitment at the end of the breeding season is typical for this species (Sullivan 1979a). Sadleir (1965) suggested that these peaks result from increased juvenile recruitment because adult aggression ceases with the end of the breeding season. In 1989, seasonal patterns were not as evident, populations in the herb, shrub and young forest fluctuated seasonally, but the mature forest population remained low during the entire trapping season.

I attempted to compare levels of reproduction among the different seral stages to determine if deer mice were more productive in some seral stages than in others. There were no consistent differences in the length of breeding seasons among the different seral stages, nor were there any consistent differences in the number of pregnancies observed. However, more of the juveniles produced in the younger seral stages entered the trappable population each year than did those in the older seral stages. High rates of juvenile survival and low rates of juvenile emigration may be indicative of better quality habitats (Van Horn 1981), a less aggressive adult population (Sadleir 1965) or a population well below carrying capacity for the habitat (Metzgar 1971).

The herb and shrub seral stages had consistently higher proportions of local juveniles entering the subadult population. This may indicate that the younger seral stages are better quality habitats or that adults in younger seral stages do not force subadults to emigrate. During 1988 and 1989, the numbers of juveniles observed and the proportions of juveniles surviving were higher in the younger seral stages than in the older ones, although juvenile numbers and survival declined during 1989 on all of the grids. It is difficult to determine whether higher juvenile numbers and survival indicates that younger seral stages are better habitats for reproduction or that the adults in the younger seral stages are less aggressive and allow more juveniles to remain.

It has been suggested that the numbers of transients in a population may be used to judge habitat suitability (Van Horn 1982). Poor quality habitat is expected to have a high proportion of transients because individuals would gain little advantage if they established a home range in these areas (Van Horn 1981). During 1988, there were no significant differences in the number of transients among the seral stages; but in 1989, significantly fewer transients were observed in the mature forest.

Survival of adults in each habitat should give an indication of habitat suitability. I assumed that dominant adults would benefit by establishing and maintaining home ranges in better habitats. Thus, I expected better habitats to have higher rates of adult survival because of both reduced mortality and reduced emigration. During both years of my study, breeding season survival was significantly higher in the mature forest than in any of the other seral stages. This suggests that the mature forest may be better deer mouse habitat at least during the breeding season. Non-breeding season survival was not significantly different among seral stages during 1988, but in 1989, survival was higher in the mature forest. Nonbreeding season survival seems to be variable between years and seral stages. This suggests that the habitat quality may vary among seral stages both seasonally and annually.

All of the deer mouse populations decreased to similar numbers over winter, suggesting that carrying capacity is lower during winter than in other seasons. Higher numbers of deer mice in the younger seral stages during summer and fall may occur because the younger seral stages are more productive and have higher carrying capacities in summer and fall but not during the winter. Although populations in the younger seral stages may be higher in the summer and fall, nonbreeding season survival ultimately determines population abundance the following spring. Seasonal variation in plant productivity, food availability, and carrying capacity among seral stages could occur because herb and shrub seeds and insects would be more abundant in the early seral stages only during summer and fall, while conifer seeds offer a winter food source in forested areas. Depending on winter conditions and conifer seed production, it may be advantageous to produce large numbers of offspring in the younger seral stages during years of high winter survival but during years of low winter survival this advantage will be lost.

My results indicate that habitat suitability for deer mice varies among seral stages. Herb and shrub seral stages have higher summer populations while mature forest populations tend to have higher survival. My results suggest that there may be substantial seasonal and interannual variation in the suitability of the different seral stages.

CHAPTER 2

INFLUENCE OF COARSE WOODY DEBRIS ON THE ABUNDANCE OF DEER MICE IN SERAL STAGES OF COASTAL FOREST

INTRODUCTION

Cover has long been recognized as an important component of small mammal habitats. Small mammals rely on cover to avoid detection by predators, escape predators, and provide suitable microclimates, feeding and nesting sites (Elton 1939). In forest ecosystems, this cover is provided primarily by coarse woody debris such as logs, fallen branches, and stumps. Although coarse woody debris is assumed to be important cover for small mammals (Bendell 1961, Maser et al. 1979), very little quantitative information has been published regarding the influence of coarse woody debris on abundance and distribution of small mammals. Information that has been published is equivocal. Goodwin and Hungerford (1979) found that capture success of deer mice (*Peromyscus maniculatus*) was positively correlated with the density of logs and stumps in Ponderosa pine (*Pinus ponderosa*) forests. This contrasts with Baker (1968), who observed that deer mice were common in habitats that had little or no coarse woody debris. In other studies, the abundance of white-footed mice (*Peromyscus leucopus*) in various habitats was not related to density of coarse woody debris (Getz 1959) or was negatively associated (Meierotto 1967). Thus, the importance of coarse woody debris to the abundance of *Peromyscus* spp. is unclear and may vary among habitats. The influence of coarse woody debris must be quantified if deer mouse habitat preference and abundance are to be compared among different habitats.

During past forest management regimes, coarse woody debris has typically been left on site after logging and is often the most abundant type of cover present in recently cutover habitats. However, modern forestry practices prescribe increased utilization standards and less coarse woody debris is being left on site. The impact of increased utilization standards on small mammal populations needs to be assessed.

Characteristics of coarse woody debris, such as abundance, diameter, decay, length and height above the ground, affect the value of woody debris as cover by influencing the level of security it offers to small mammals. Cover characteristics (such as exposure, continuity and distance to cover) have been shown to affect use of space by small mammals (Harestad and Shackleton 1990). The real or perceived risk of predation varies with these cover characteristics and tradeoffs in foraging and habitat selection are made accordingly (Anderson 1986, Merkens et al. 1991).

Very few studies have considered the influence of woody debris characteristics on the abundance and distribution of small mammals. Hayes and Cross (1987) examined micro-habitat selection by deer mice and western red-backed voles (*Clethrionomys californicus*) in old-growth mixed conifer forest by measuring live trap capture success near logs of various diameters. Western red-backed voles were captured more often near logs that provided greater amounts of overhead cover. However, Hayes and Cross (1987) showed no correlation between deer mouse capture and log diameter.

The amount and characteristics of woody debris in an area determine the availability of cover which in turn contributes to the site's quality. I hypothesize that if deer mice make habitat selection decisions based on real or perceived security from predators, then they should be more abundant in areas with greater quantities and quality of cover. I also hypothesize that the availability of other types of cover, e.g. ground level vegetation, will affect the importance of coarse woody debris as cover for deer mice.

My objectives were to: 1) measure the effect of coarse woody debris availability on deer mouse abundance, 2) determine whether specific features of coarse woody debris influence deer mouse abundance, and 3) determine if relationships between coarse woody debris and deer mouse abundance vary among different seral stages.

MATERIALS AND METHODS

Seral Stages

During July-August 1989, thirty 100-m live-trapping transects were ramdomly established in each of 4 seral stages: herb, shrub, young forest, and mature forest. Transects were located within a 10 km radius of each other. I selected locations for the transects that had similar slope, elevation, aspect and topography.

The first 30 transects were established within herb dominated cutovers that had been logged and slash burned 1 to 2 yr previously. Vegetation in these cutovers was dominated by herbaceous plants and low growing salal (*Gaultheria shallon*).

The second set of 30 transects was placed in shrub dominated cutovers that had been logged and slash burned 10 to 12 yr previously. Vegetation consisted mostly of salal with Douglas-fir (*Pseudotsuga menziesii*) saplings and few herbaceous species.

The third set of 30 transects was placed in young forest stands that had been logged and slash burned 28 to 30 yr previously. In these dense stands of young Douglas-fir, canopy closure was almost complete and ground level vegetation was very sparse.

The last set of 30 transects was located in mature Douglas-fir, western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) forest stands (> 150 yr old) that had not been previously logged. There were frequent openings in the canopies of most of the stands. Ground level vegetation was patchy and consisted mainly of salal, ferns, and mosses.

Live-Trapping

Each 100-m transect consisted of 7 trap stations at approximately 15 m intervals. At each trap station, a single live trap was placed within 1 m of a marked stake. Traps were baited with peanut butter and rolled oats. Polyester batting was provided as bedding material. Traps were prebaited for 3 days prior to trapping. Traps were set on the afternoon of day 1 and checked each morning on days 2, 3, and 4.

All deer mice captured were weighed with a Pesola spring scale and ear-tagged with a numbered fingerling fish tag. Their sex was determined and the trap location was recorded. The mice were classified as juveniles if they were < 13 g, subadults if they were between 13-16 g and, adults if they were > 16 g (Sullivan 1977).

Direct enumeration of individually tagged deer mice captured on the transects was used to estimate relative abundance. Enumeration was used rather than total number of captures so that deer mice captured more than once would not bias population estimates.

To ensure that the relative abundance obtained from the transects were representative of actual abundance, I also established transects within live-trapping grids (see Chapter 1). Transect determined abundance was calibrated with abundance determined from the more intensive bi-weekly trappings conducted on grids.

Escape Routes

To assess the ability of deer mice to use the cover provided by each seral stage, escape routes of 28 individual mice in each seral stage were recorded. Each mouse was released at the trap location where it was captured and no attempt was made to pursue it. The route followed upon release was noted in terms of distance and type of cover where the mouse disappeared from view.

Site Description

During July 1989, the percent cover of ground level vegetation (< 50 cm high) within a 5 m radius of each trap was estimated with the aid of visual comparison charts (Walmsley et al. 1980). The amount and characteristics of the coarse woody debris present at each of the 30 sites in the 4 seral stages was estimated along each 100 m transect. Along these transects, I counted and measured all pieces of woody debris $\geq$ 1 cm in diameter (Van Wagner 1968). I measured the diameter, length, and height above the ground of each piece of debris that intersected the transect. I also classified its state of decay as: 1) solid (bark attached, solid throughout), 2) partially decayed (loose bark, punky at surface), 3) moderately decayed (punky at surface and core), or 4) very decayed (punky throughout and falling apart).

RESULTS

Comparison of Seral Stages

The herb and shrub dominated seral stages both lacked a forest canopy. Percent cover of ground level vegetation (< 50 cm high) was greater in the shrub seral stage than in the herb seral stage (Fig. 8). The young and mature forest seral stages both had a tree canopy. The canopy in the young forest was nearly complete while the mature forest's canopy had frequent openings. Ground level vegetation was very sparse in the young forest. In the mature forest, percent cover of ground level vegetation was greater than in the herb seral stage and young forest (Fig. 8).

The mean number of pieces of coarse woody debris ≥ 1 cm in diameter varied significantly among the different seral stages (analysis of variance, $F = 12.15$, $df = 3$, $P < 0.005$, Fig. 9). The shrub seral stage had the most pieces while mature forest had the fewest. There was considerable variation in the diameter distribution of debris in each seral stage (Fig. 10). The herb and shrub seral stages had greater densities of debris ≤ 20 cm in diameter than did

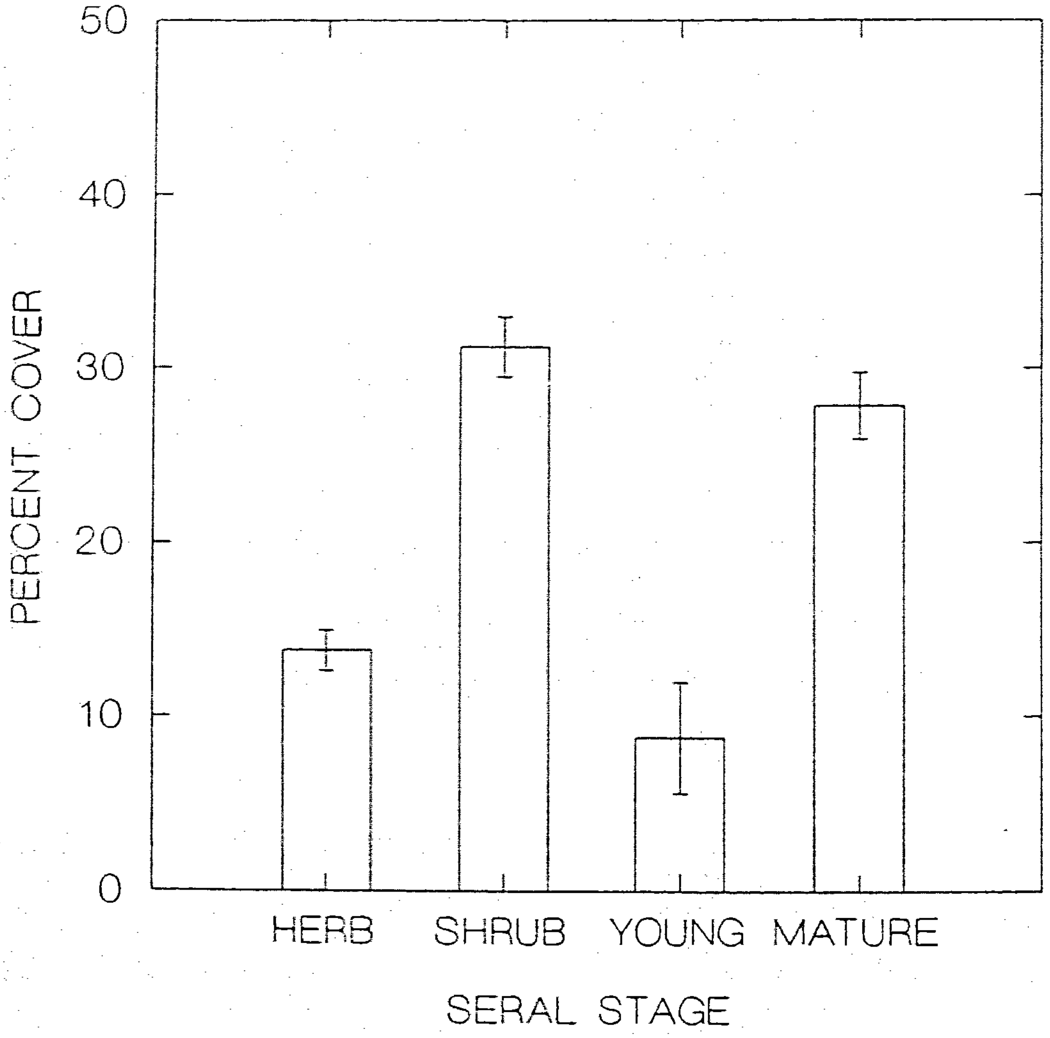

Fig. 8. Mean (± SE) percentage cover of ground level vegetation (< 50 cm) along transects in the 4 seral stages. n = 30 in each seral stage.

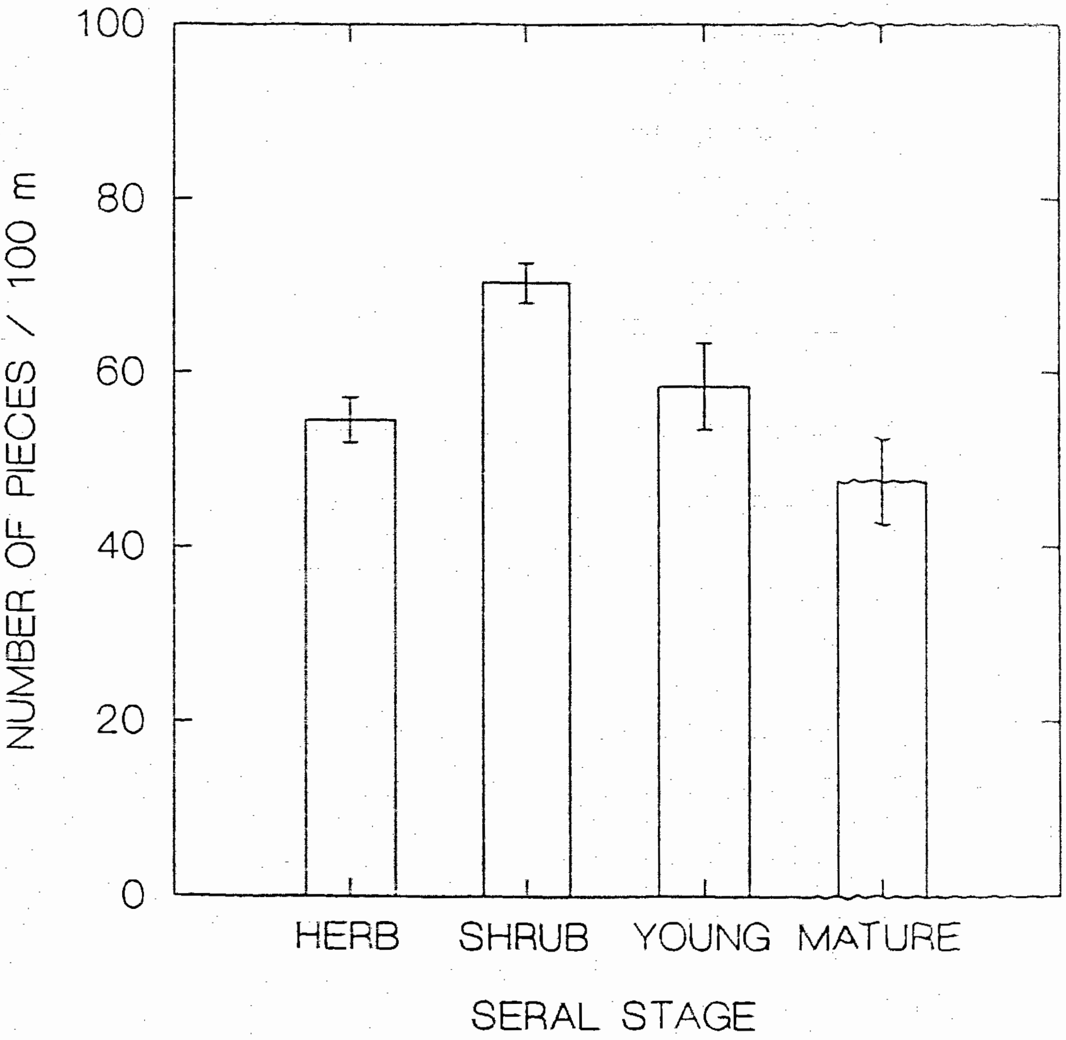

Fig. 9. Mean (+ SE) number of pieces of coarse woody debris pieces (≥ 1 cm diameter) intersected by 100 m transects in each seral stage. n = 30 transects in each seral stage.

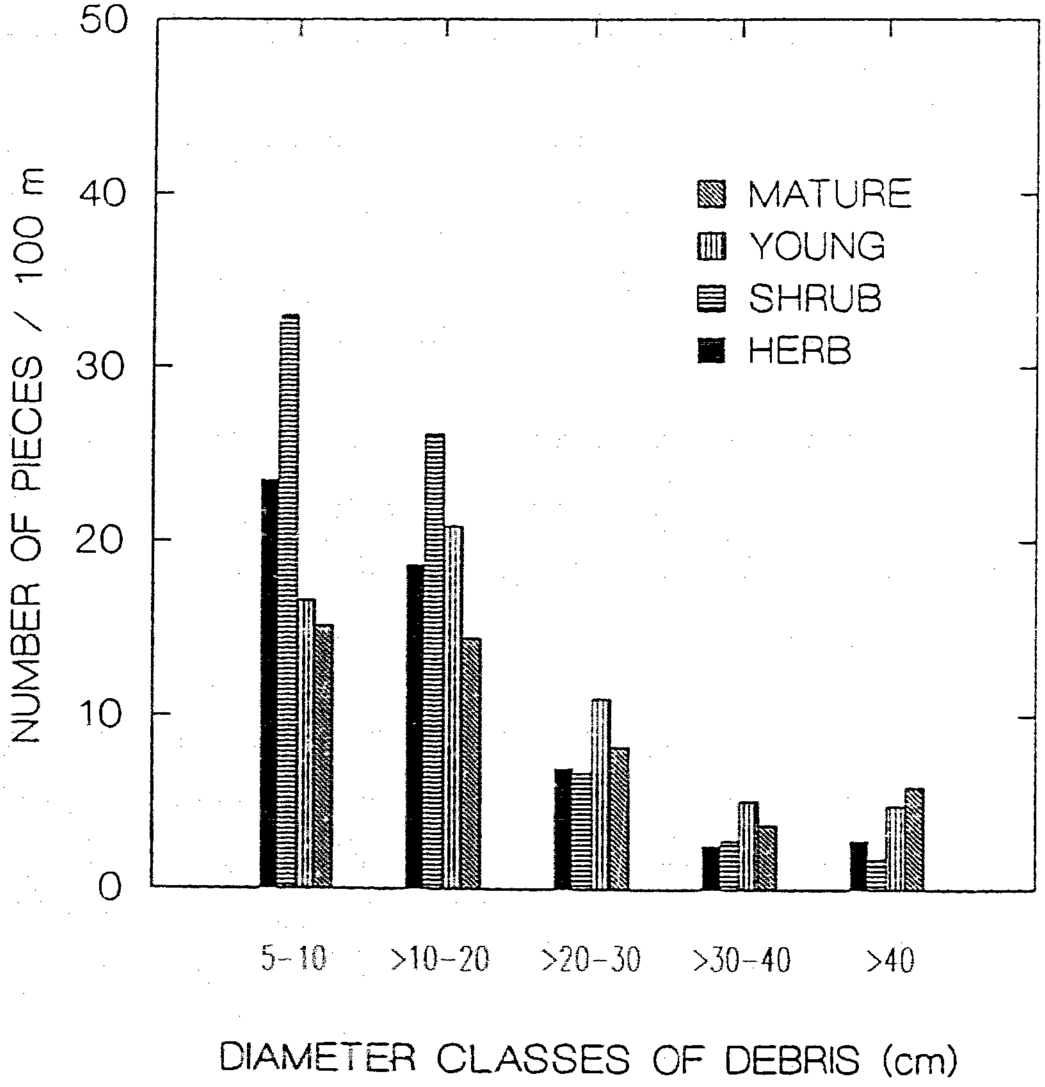

Fig. 10. Distribution of diameter classes of pieces of coarse woody debris in the 4 seral stages.

the young and mature forests. The young and mature forests had greater densities of debris > 20 cm in diameter than did the herb and shrub seral stages. The mean diameter of debris in the two forested stages was greater than those in the herb and shrub seral stages (Fig. 11).

Mean lengths of pieces of coarse woody debris were not significantly different among the various seral stages (analysis of variance, $F = 1.43$, $df = 3$, $P > 0.05$). Mean height above the ground of debris was significantly different among seral stages (analysis of variance, $F = 16.21$, $df = 3$, $P < 0.005$, Fig. 12). Debris was highest above the ground in mature forest and lowest in the herb seral stage. The mean height above ground of debris in the shrub and young forest seral stages did not differ significantly from each other (student's t-test, $P > 0.05$).

In all of the seral stages, the mean state of decay of the coarse woody debris ranged from partial to moderate (Fig. 13). The only significant difference in states of decay occurred between the herb and shrub seral stages where decay was greater in the herb seral stage (Mann-Whitney U-test, $P = 0.05$).

Escape Routes

Escape distances were significantly different among the seral stages (Table 10). Escape distances were shortest in the shrub seral stage and longest in the herb seral stage. The type of cover into which mice disappeared

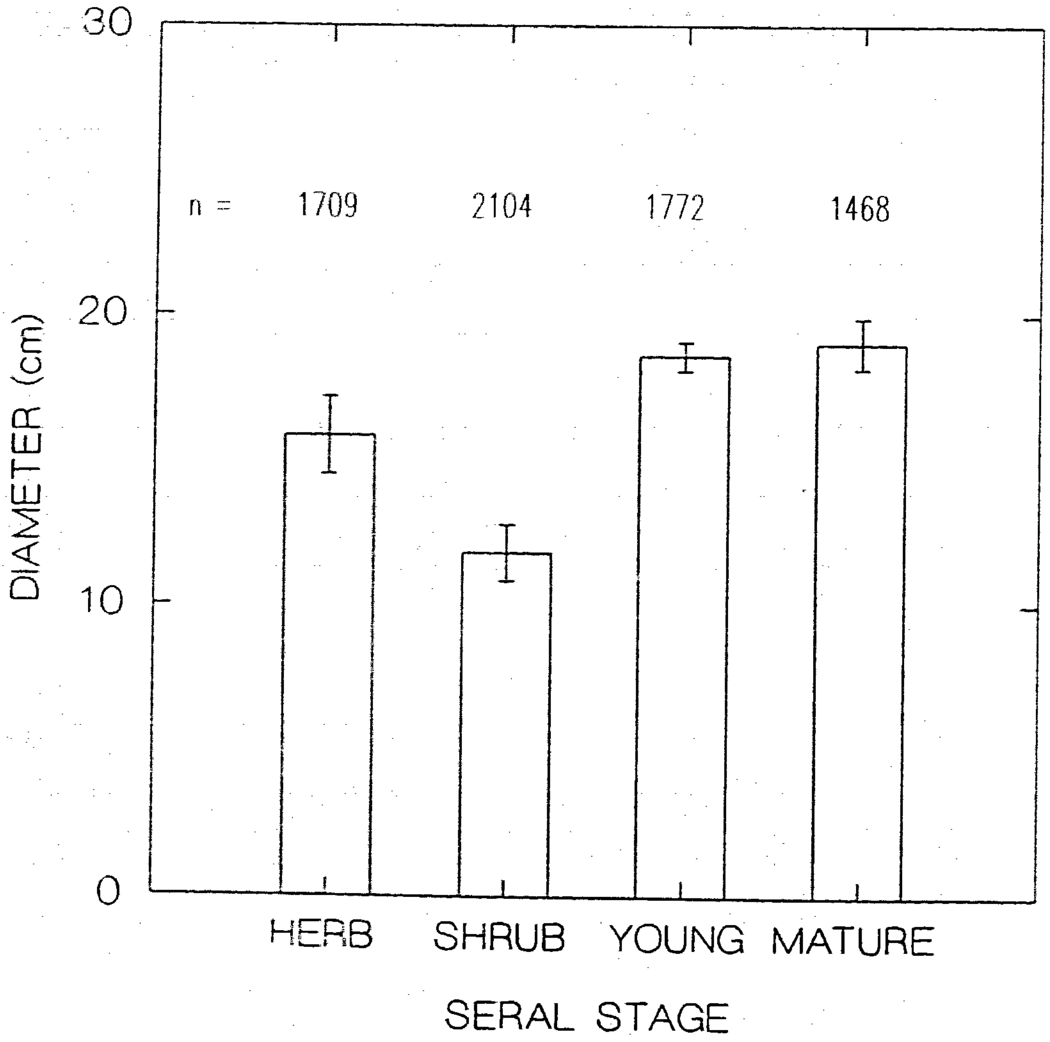

Fig. 11. Mean (± SE) diameter of pieces of coarse woody debris (≥ 1 cm diameter) in the 4 seral stages.

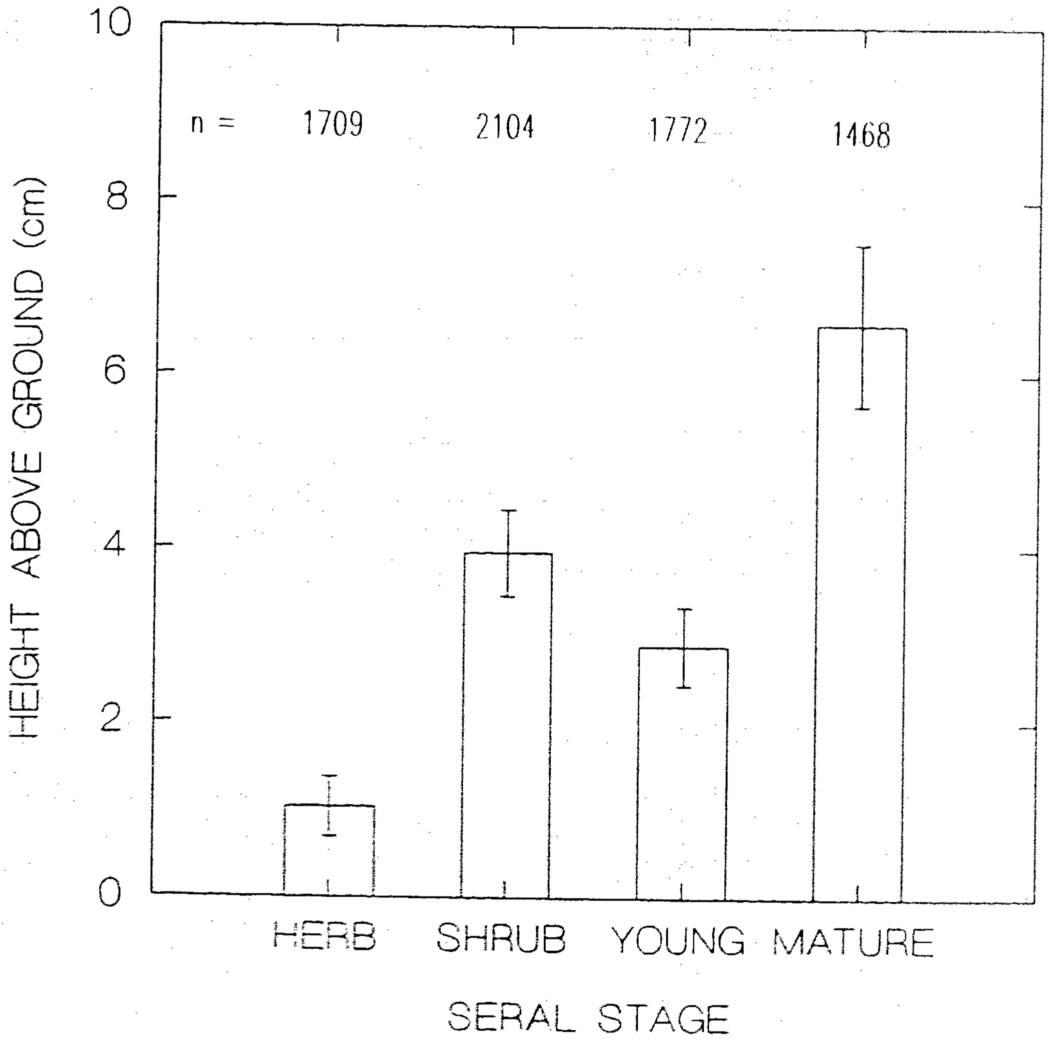

Fig. 12. Mean (± SE) height above the ground of pieces of coarse woody debris (≥ 1 cm diameter) in the 4 seral stages.

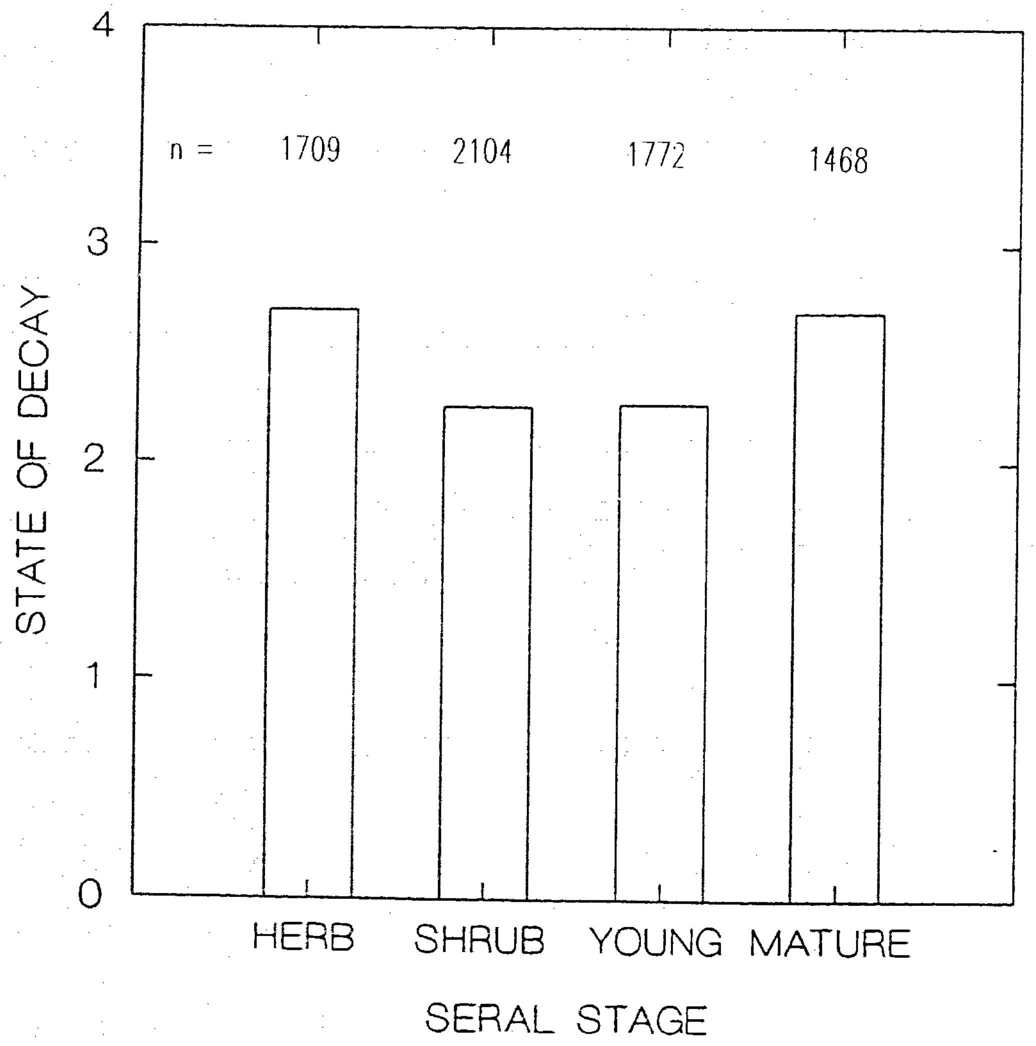

Fig. 13. Mean rank state of decay of pieces of coarse woody debris ($\geq$ 1 cm diameter) in the 4 seral stages.

Table 10. Escape distance of deer mice and percentage of different types of cover that blocked the view of observer in each seral stage.

Seral Stage	n	Mean Distance (SE) (m)
Herb	28	5.30 (0.72)
Shrub	28	1.34 (0.24)
Young	28	2.75 (0.35)
Mature	28	3.41 (0.44)

One-way Anova, F = 12.21, df = 3, $P < 0.05$

		Percentage of Times Cover Type Blocked View			
Seral Stage	n	Burrow	Woody Debris	Vegetation	Other
Herb[a]	28	39.3	46.4	10.7	3.6
Shrub	28	7.1	28.6	57.1	7.2
Young[a]	28	32.1	42.9	17.9	7.1
Mature	28	57.2	32.1	10.7	0.0

[a] Seral stages not significantly different, Chi-squared test, $P > 0.05$.

also varied significantly among seral stages. In the herb and young forest seral stages, I lost sight of the mice most often because of coarse woody debris and burrows. In the shrub seral stage, I lost sight of the mice most often because of vegetation. Burrows were the most common destination for deer mice in the mature forest (Table 10).

Coarse Woody Debris and Deer Mouse Abundance

Regression analysis was used to examine relationships between coarse woody debris and deer mouse abundance. All data were plotted and examined for non-linear relationships. Characteristics of coarse woody debris included: total number of pieces of debris ≥ 1 cm in diameter, ≥ 1-10 cm, > 10-20 cm, > 20-30 cm, > 30-40 cm, and > 40 cm; mean height of debris above ground; mean state of decay; and mean length of debris pieces.

The total number of pieces of coarse woody debris was positively correlated to deer mouse abundance in all seral stages (Table 11). The strongest correlations and steepest slopes were observed in the herb seral stage and mature forest. In the shrub seral stage and young forest, the total numbers of pieces of coarse woody debris was positively and significantly correlated to deer mouse abundance but it did not explain the bulk of the variation in deer mouse numbers observed in these seral stages.

The influence of different diameter classes of coarse woody debris varied between seral stages (Table 12). In

Table 11. Results of linear regressions between deer mouse abundance (number of individuals captured / 100 m) and abundance of coarse woody debris (pieces / 100 m). n = 30 transects / seral stage. The Y intercept (a) and slope (b) are provided for each regression equation.

Seral Stage	a	b	r^2	P
Herb	0.9	0.07	0.55	< 0.01
Shrub	1.1	0.04	0.26	< 0.01
Young Forest	0.8	0.02	0.26	0.02
Mature Forest	0.2	0.10	0.88	< 0.01

Table 12. Results of linear regressions between deer mouse abundance (number of individuals captured / 100 m) and abundance of coarse woody debris (pieces / 100 m) in different size classes. n=30 transects in each seral stage. The Y intercept (a) and slope (b) are provided for each regression equation.

Debris Diameter (cm)	a	b	r^2	P
Herb				
≥ 1-10	0.8	0.2	0.27	0.02
> 10-20	0.4	0.3	0.24	< 0.01
> 20-30	0.6	0.5	0.39	< 0.01
> 30-40	1.1	1.1	0.19	0.04
> 40	0.3	1.0	0.13	0.07
Shrub				
≥ 1-10	2.0	0.1	0.04	0.27
> 10-20	0.7	0.5	0.28	< 0.01
> 20-30	0.6	0.1	0.12	0.57
> 30-40	1.5	0.3	< 0.01	0.75
> 40	1.7	0.2	< 0.01	0.95
Young Forest				
≥ 1-10	0.8	0.1	0.03	0.42
> 10-20	0.9	0.1	0.11	0.14
> 20-30	0.3	0.4	0.20	0.05
> 30-40	1.1	0.2	0.29	0.02
> 40	0.7	0.1	0.16	0.08
Mature Forest				
≥ 1-10	0.3	0.2	0.65	< 0.01
> 10-20	0.4	0.2	0.52	< 0.01
> 20-30	0.1	0.3	0.23	0.01
> 30-40	0.2	0.6	0.59	< 0.01
> 40	0.1	0.4	0.78	< 0.01

the herb seral stage, deer mouse abundance had stronger correlations with some diameter classes of debris than with others. Deer mouse abundance was most closely correlated with debris in the > 20-30 cm diameter class and least correlated with the abundance of debris in the > 40 cm diameter class. In the shrub seral stage, deer mouse abundance was positively correlated only with the abundance of coarse woody debris in the > 10-20 cm diameter class. All other diameter classes of debris were not significantly correlated with deer mouse abundance. Deer mouse abundance in the young forest was significantly correlated only with the abundance of debris greater than > 20 cm diameter classes. The strongest correlation occurred with the > 30-40 cm diameter class. In the mature forest, deer mouse abundance was positively correlated with the abundance of debris in all diameter classes. The strongest correlations occurred with the abundance of debris in the > 40 cm diameter class and small debris in the > 1-10 cm diameter size class. The weakest correlation was with the > 20-30 cm diameter class. The slopes of the regression equations for the seral stages were significantly different (analysis of covariance, $F = 4.16$, $P < 0.05$). In the herb seral stage and the mature forest increased abundances of larger pieces of woody debris influenced deer mouse abundance more than it did in the shrub seral stage and young forest (Tukey HSD $P < 0.05$).

The mean height of coarse woody debris above the ground was negatively correlated with deer mouse abundance in all seral stages except the young forest (Table 13). Deer mouse abundance was not significantly correlated with the mean state of decay of coarse woody debris in any of the seral stages (Table 14). Mean length of debris pieces was not significantly correlated with deer mouse abundances in any of the seral stages ($P > 0.10$). The percent cover of ground level vegetation was not correlated to deer mouse abundance except in the shrub seral stage where greater amounts of ground level vegetation were indicative of lower deer mouse abundance (Table 15).

Interaction Between Vegetation and Coarse Woody Debris

The shrub seral stage was the only stage in which both vegetation and coarse woody debris had significant linear regressions with the abundance of deer mice. I chose this seral stage to examine the interaction between vegetation, coarse woody debris and deer mouse abundance. A multiple regression of deer mouse abundance against percent cover of ground level vegetation and total abundance of coarse woody debris did explain more of the variation (multiple $r^2 = 0.36$, $P = 0.03$) than did either of the two factors separately. Examination of this regression suggests that these habitat factors do interact in this seral stage. In areas with low abundances of coarse woody debris, increased amounts of ground level vegetation corresponded to

Table 13. Linear regressions for deer mouse abundance (individuals captured / 100 m) and mean height above ground of coarse woody debris (cm) for each seral stage. n = 30 transects in each seral stage. The Y intercept (a) and slope (b) are provided for each regression equation.

Seral Stage	a	b	r^2	P
Herb	5.7	-0.3	0.13	< 0.01
Shrub	4.3	-0.2	0.16	0.03
Young Forest	3.1	-0.2	0.05	0.28
Mature Forest	5.2	-0.5	0.20	< 0.01

Table 14. Spearman rank correlations for deer mouse abundance (individuals captured / 100 m) and mean rank state of decay for coarse woody debris in each seral stage. n = 30 transects in each seral stage.

Seral stage	R_s	$R_{critical}$ (P = 0.05)
Herb	0.06	0.31
Shrub	0.02	0.31
Young Forest	0.01	0.31
Mature Forest	0.13	0.31

Table 15. Linear regressions for deer mouse abundance (individuals captured / 100 m) and mean percent cover of ground level vegetation (< 50 cm tall) in each seral stage. n = 30 transects in each seral stage. The Y intercept (a) and slope (b) are provided for each regression equation.

Seral Stage	a	b	r^2	P
Herb	2.8	0.3	0.04	0.40
Shrub	4.7	-0.2	0.15	0.04
Young Forest	1.6	0.1	0.07	0.27
Mature Forest	2.4	0.0	0.03	0.43

increased deer mouse abundance. In areas with greater amounts of coarse woody debris, deer mouse abundance was greatest at moderate percent cover of ground level vegetation but declined in areas with high percent cover of ground level vegetation.

DISCUSSION

A wide variety of factors have been reported to explain local distribution patterns of small mammals. The importance of specific microhabitat features such as food, water, and cover have been examined by many authors (e.g. Bendell 1961, Getz 1961, Myton 1974, Barry and Francq 1980). Cover is an important habitat feature and some investigators have observed that small mammals are more abundant in areas with greater amounts of vegetation or coarse woody debris (Hansson 1977, Van Horne 1982). However, few studies have tried to quantify the importance of coarse woody debris to the abundance of small mammals over a range of different habitats.

Previous studies have often lumped together distinctly different habitat types in their investigation of specific habitat factors. In my study, various habitat types were considered separately although deer mice were abundant in all of the habitat types. *Peromyscus* spp. are generally regarded as habitat generalists and their broad habitat requirements have been blamed for a lack of association between mouse densities and specific habitat factors (Seagle 1985).

Adler and Wilson (1987) observed that densities of white-footed mice occupying early successional habitats in Massachusetts were associated with specific microhabitat factors in some habitats but not in others. Some investigators have reported *Peromyscus* spp. to be microhabitat specialists in some habitats and microhabitat generalists in other habitats (Seagle 1985). This variation in the influence of habitat factors between differing habitat types suggests that the importance or influence of specific habitat factors may vary between habitats.

In my study, the abundance of deer mice was positively correlated to the abundance of coarse woody debris in all 4 seral stages. The strength of these relationships, however, varied greatly among seral stages, suggesting that the importance of coarse woody debris is variable among seral stages. Coarse woody debris was most important in the herb seral stage and the mature forest, where relationships were stronger and regression slopes were steeper, and least important in the shrub seral stage and young forest. This variation in the importance of coarse woody debris may be due to the different characteristics of the 4 seral stages. I suspect that dense vegetation cover in the shrub seral stage and the low, dense canopy in the young forest reduced the reliance of deer mice on coarse woody debris as protection from avian predators. The weak relationships between the abundance of coarse woody debris and the abundance of deer mice in the shrub seral stage and young forest may occur because woody debris offers more than just protection to small mammals, it also offers food (such as insects and fungi that feed on the woody debris; Maser et al. 1979) and nest sites (Bendell 1961). In these seral stages, increased amounts of coarse woody debris may influence deer mouse numbers by increasing the availability of other resources besides cover.

The importance of different diameter classes of woody debris to deer mouse abundance varied among the different seral stages. It is difficult to compare the importance of different diameter classes of debris among the seral stages because the distribution of debris diameter classes varied among seral stages. Some differences in the importance of different diameter classes of debris among seral stages may have more to do with seral stage characteristics rather than the utility of some debris diameter classes. For example, large diameter pieces of debris were abundant in the mature forest but uncommon in the herb seral stage. This may explain why the importance of debris > 40 cm in diameter was different in these two habitats.

In the herb seral stage and mature forest, deer mouse abundance was positively correlated with all diameter classes of woody debris. It should be noted that some of these correlations may be due to autocorrelations between debris size classes rather than the influence of specific size classes. In the shrub seral stage, woody debris > 10-20 cm in diameter is weakly correlated to deer mouse abundance and in the young forest debris > 20-40 cm in diameter is weakly correlated with deer mouse abundance. The lack of consistent effect for some debris diameter classes in these two intermediate seral stages suggests that aspects of debris other than its quality as cover may contribute to the correlations in these habitats.

In the mature forest and the herb seral stage, the relative importance of different diameter classes of debris is not the same. Pieces of debris > 40 cm diameter are very important in the mature forest but relatively unimportant in the herb seral stage. This seems counter intuitive because the lack of a tree canopy in the herb seral stage should increase the deer mouse's need for overhead cover that is provided by large diameter debris. Perhaps, as mentioned previously, the low abundance of large diameter debris in the herb seral stage may reduce its effect. It is also possible this difference occurs because deer mice use the debris differently in the two habitats. Powder tracking (Chapter 3) revealed that deer mice do use debris differently in different seral stages. In the herb seral stage, deer mice usually travel under debris and use it as overhead cover. In the mature forest, deer mice almost always travel on top of debris and use it as an above ground travel route. Because deer mice use woody debris differently in the two seral stages, it is understandable that the importance of different diameter classes varies among seral stages.

The height above ground of debris showed weak negative correlations with deer mouse abundance in the herb, shrub, and mature forest seral stages. The negative nature of the correlations suggests that the higher debris is above the ground, the less important it is to deer mice. This seems reasonable in the herb seral stage where mice are using the debris as overhead cover and increased height would increase the exposure of mice to predators. However, it makes little sense in the mature forest, where deer mice travel on top of the debris, unless the increased height above ground inhibits the ability of deer mice to climb on top of debris.

The average state of decay for woody debris in all of the seral stages was similar. In all of the seral stages, the state of decay had no effect on deer mouse abundance. This suggests that greater decay does not increase the availability of resources such as insects and cavities for nest sites, which seems unlikely, or that the range of variation in levels of decay that I examined was too limited in each seral stage. It was also surprising that the mean length of woody debris pieces did not influence deer mouse abundance. I expected that longer pieces would offer more continuous cover to deer mice and thus provide greater security for traveling.

The percent cover of ground level vegetation influenced the importance of coarse woody debris to deer mice in only one seral stage. In the shrub seral stage, multiple regression of woody debris abundance and percent vegetative cover showed that ground level vegetation interacted with coarse woody debris to influence abundance of deer mice. In this seral stage, vegetation cover was negatively correlated with deer mouse abundance. In areas with abundant coarse woody debris, high percent cover of ground level vegetation reduced deer mouse numbers. These results agree with previous studies (Miller and Getz 1977) that found a weak negative correlation between deer mouse density and ground level vegetation cover.

Coarse woody debris was positively correlated to deer mouse numbers in all 4 seral stages confirming that woody debris is an important habitat feature for deer mice. Because woody debris was more important to deer mice in some seral stages than in others, differences between seral stages, such as canopy closure, may influence the utility of woody debris to deer mice. Studies that attempt to measure the suitability of different habitats for deer mice should examine the abundance of woody debris and consider its importance to deer mice in each habitat.

CHAPTER 3

INFLUENCE OF COARSE WOODY DEBRIS ON MICROHABITAT SELECTION AND MOVEMENTS OF DEER MICE

INTRODUCTION

Elton (1939) recognized that coarse woody debris is an important habitat feature for small mammals. The influence of coarse woody debris on movements and microhabitat selection by small mammals is evident from several studies. White-footed mice (*Peromyscus leucopus*) orient toward microhabitats that offer cover in the form of woody debris (Bendell 1961, Sheppe 1965, and Stormer 1968) and use logs as travel routes (Barry and Francq 1980, Plantz and Kirkland 1992). Small mammals often exhibit an affinity for coarse woody debris and particular attributes of coarse woody debris, such as diameter, are important in determining its quality as cover and thus its use by small mammals. Kaufman et al. (1983) reported that deer mice (*Peromyscus maniculatus*) were more likely to be captured near large diameter pieces of woody debris and postulated that large pieces were used more than small pieces. Large pieces of debris provide more overhead cover and thus offer greater protection from predators (Maser et al. 1979).

The state of decay of coarse woody debris is another characteristic which is thought to affect its utility to small mammals. Small mammals should use decayed pieces of coarse woody debris more than undecayed woody debris because it is easier to burrow into decayed pieces (Maser et al. 1979). The interiors of decayed pieces of coarse woody debris provide protection from both predators and weather, as well as access to invertebrates and fungi living in the rotting wood. Cavities in woody debris are often used by small mammals as nest and refuge sites (Wolff and Hurlbutt 1982) and the availability of suitable nest sites can limit the distribution of small mammals (Bendell 1961). There is ample evidence supporting the importance of coarse woody debris as a microhabitat feature for small mammals, however, more information about which features of coarse woody debris are important to small mammals and the utility of coarse woody debris in different habitats would be useful when trying to judge the quality of different habitats for small mammals.

Fluorescent pigment tracking (Lemen and Freeman 1985) has been used to examine associations between microhabitats and small mammals (Getz and Hofmann 1986). This method produces a continuous record of movements of small mammals and thus allows assessment of the influence habitat variables have on those movements. Powder tracking avoids assumptions and problems associated with relating live-trapping success to habitat preferences. Livetraps can bias results because *Peromyscus* spp. explore their home ranges and are attracted to novel objects placed in their environments (Sheppe 1965). Powder tracking allows investigators to determine which microhabitats are being used by small mammals without the possibility that the animals were lured into a normally unused microhabitat by the novel trap or bait.

My objectives were: (1) to determine if coarse woody debris influences the movements of deer mice, (2) to identify which features of coarse woody debris are involved in microhabitat selection, and (3) to determine if the utility of coarse woody debris changes in different habitats.

MATERIALS AND METHODS

Powder Tracking

Powder tracking was conducted at two locations within the study area during July and August of 1988 and 1989. The first location was in a herb dominated cutover that had abundant coarse woody debris. The second location was in a mature forest stand (> 150 yrs old) that also had abundant coarse woody debris (see Chapter 2). The fluorescent pigment method (Lemen and Freeman 1985) was used to track movements of adult deer mice in each habitat.

Two transects with 5 livetraps placed approximately 15 m apart were used to capture mice for powder tracking at each location. The prebaited traps were set in the afternoon of day one and checked approximately 6 hr later at 22:00 PDT. Traps were then locked open and set the next afternoon for the second night of trapping. During each trapping session, only one male and one female mouse were selected for powder tracking. The trapping transects were moved approximately 50 m between trapping sessions to ensure the capture of different mice and to avoid confusion of overlapping powder tracks from different animals.

Red and green ultraviolet pigments (Radiant Color Inc.) were used for powder tracking with all males dusted in red and all females dusted in green. A mouse selected for powder tracking was placed in a plastic bag containing a small amount of the powder, gently shaken, and released at the point of capture. I returned to the release site approximately 2 hr after the release and used an ultraviolet (black light) lamp to follow the trail of powder as far as possible. I used small stakes to mark the path at each change of direction. Twenty deer mice were captured and powder tracked in both the herb dominated cutover and the mature forest. An equal number of males and females were tracked in each of the two habitats.

Path and Debris Mapping

Within two days of marking the powder track, I returned to the release site during the day and used a measuring tape, starting at the release point, to measure the entire path length and the distance between each change of direction. The entire path was mapped by recording distances and changes of direction.

After mapping the path, diameter, length, height above the ground, state of decay, distance from the path and orientation to the path were recorded for each piece of coarse woody debris $\geq$ 5 cm in diameter that intersected or was within 1 m of the path. After recording the debris, a linear transect of equal length to the powder track was established from the release site in the same general direction as the powder track so I could compare debris along the powder track with debris along a linear transect. As with the powder track, all pieces of debris $\geq$ 5 cm in diameter that intersected or were within 1 m of the transect were recorded and described.

The initial response of deer mice to a piece of debris along the powder track was classified as either cross (if the path crossed the piece), follow (if the path traveled along the debris for a distance greater than twice the piece's diameter), or turn (if the path turned away from the debris). If the initial response was either cross or follow, how the mice traveled across or followed the debris was classified as either "on top" (if the path went over the top of the debris), "under" (if the path was under the debris), or "beside" (if the path was within 10 cm of the edge of the debris).

RESULTS

Paths selected by deer mice in each of the habitats were closely associated with coarse woody debris (Table 16). The proportions of total path length associated with woody debris for males and females were not significantly different in either seral stage (Mann-Whitney U-test, $P > 0.05$). Therefore, I treated males and females as one group and combined their data for further analyses.

The lengths of powder tracks associated with coarse woody debris were not significantly different between the two habitats (Mann-Whitney U-test, $P > 0.05$). I compared the amount of woody debris along mouse powder tracks to that along straight line transects in the same direction of travel. Mice in both habitats used coarse woody debris more than would be expected relative to its availability (Table 16; Mann-Whitney U-tests; herb, $P < 0.05$; mature forest, $P < 0.05$).

I examined the importance of coarse woody debris diameter to routes chosen by deer mice in each habitat. Responses of deer mice to small ($\geq$ 5- < 10 cm), medium ($\geq$ 10- < 20 cm), and large ($\geq$ 20 cm) diameter pieces of woody debris along the powder tracks were tabulated (Table 17).

Deer mice in the herb seral stage reacted differently to different size classes of debris (Table 17). Small diameter pieces along the path were usually crossed and the

Table 16. Mean (± SE) lengths of path associated with coarse woody debris (≥ 5 cm in diameter) along powder tracks of male and female deer mice and linear transects in each habitat.

Seral Stage	n	Length of powder track with debris (cm/m)	Length of linear transect with debris (cm/m)
<u>Herb</u>			
Males	10	56.7 (2.3)	
Females	10	50.8 (3.2)	
Total	20	53.75 (2.1)	9.41 (1.2)
<u>Mature Forest</u>			
Males	10	58.3 (3.0)	
Females	10	55.1 (2.1)	
Total	20	56.7 (1.8)	9.60 (0.8)

Table 17. Percentage of different responses deer mice had to different diameters of coarse woody debris in the herb seral stage.

Response	Diameter < 10 cm	Diameter 10- ≤ 20 cm	Diameter > 20 cm
<u>Encounters</u>			
	n = 200	n = 200	n = 100
Cross	86.5	66.5	22.0
Follow	13.5	30.5	78.0
Turn	0.0	3.0	0.0
<u>Pieces crossed</u>			
	n = 173	n = 133	n = 22
On top	77.5	44.36	0.0
Under	22.5	55.64	100.0
<u>Pieces followed</u>			
	n = 27	n = 61	n = 78
On top	85.2	42.6	0.0
Under	3.7	18.0	42.3
Beside	11.1	39.4	57.7

mice usually traveled over the debris. Medium sized pieces of debris were also usually crossed but mice traveled over and under these pieces about equally. Few large diameter pieces of debris were crossed but when they were, deer mice always crossed under them.

Deer mice in the herb seral stage were far more likely to cross rather than follow small pieces of debris, but when they did follow smaller pieces they tended to travel on top of them. Medium sized pieces of debris were crossed more often than followed. When medium sized pieces were followed, deer mice usually followed beside or under the piece, but 43% of the time deer mice traveled on top of the piece. Large diameter pieces of debris were usually followed rather than crossed and deer mice always traveled beside or under large pieces of debris.

In the mature forest, deer mice tended to cross small and medium diameter pieces and to follow larger diameter pieces of woody debris (Table 18), similar to their behaviour in the herb seral stage. However, the way they followed the debris was very different. In the mature forest, rather than traveling under or beside large pieces of woody debris, they usually traveled on top of the pieces. The powder tracks were often observed to follow logs from end to end along the upper surface. The logs they traveled on were often more than 2 m above the ground.

The mean state of decay (see Chapter 2) for pieces of coarse woody debris along the powder tracks was compared to

Table 18. Percentage of different responses deer mice had to different diameters of coarse woody debris in the mature forest.

Response	Diameter < 10 cm	Diameter 10- ≤ 20 cm	Diameter > 20 cm
<u>Encounters</u>			
	n = 200	n = 200	n = 100
Cross	82.0	54.5	12.0
Follow	18.0	45.5	88.0
Turn	0.0	0.0	0.0
<u>Pieces crossed</u>			
	n = 164	n = 109	n = 12
On top	82.3	71.5	75.0
Under	17.7	28.4	25.0
<u>Pieces followed</u>			
	N = 36	N = 91	N = 88
On top	75.0	39.5	78.5
Under	13.8	21.2	11.4
Beside	11.2	39.3	10.1

the mean state of decay for coarse woody debris along the linear transects. No significant differences between the mean state of decay for debris along powder tracks and those along linear transects were found in either habitat (Wilcoxin signed ranks test, $P > 0.05$). Although the amount of decayed woody debris along the powder tracks did not differ from availability, powder tracks were observed to enter the interior of decayed pieces of debris in both habitats.

Length of debris pieces had little influence on route selection by deer mice in the herb seral stage (Fisher exact probability test, $P > 0.05$, Table 19). In the mature forest, length did influence route selection. Deer mice in the mature forest were more likely to follow long pieces ($\geq$ 5 m) of woody debris than short pieces (Fisher exact probability test, $P = 0.05$).

To determine if the height of debris above the ground influenced the travel routes selected by deer mice, the responses of mice to debris (> 20- ≤ 30 cm diameter) < 10 cm above the ground and debris ≥ 10 cm above the ground were compared in each seral stage (Table 20). In mature forest, height of debris above the ground had little effect on whether mice followed a specific piece of debris. In the herb seral stage, the height above the ground of a piece of debris did affect whether deer mice followed that piece. Deer mice in the herb seral stage were more likely to follow pieces of debris < 10 cm above the ground than

Table 19. Number of times deer mice followed or crossed long and short pieces of debris. Pieces of debris used for comparison were > 20- ≤ 30 cm in diameter. Percentages are given in brackets.

Seral Stage	Length < 5 m		Length ≥ 5 m	
	Follow	Cross	Follow	Cross
Herb	54 (79.4)	14 (20.6)	43 (81.1)	10 (18.9)
Mature Forest	39 (81.3)	9 (18.8)	37 (94.9)	2 (5.1)

Table 20. Number of times deer mice followed or crossed debris < 10 cm above the ground and debris ≥ 10 cm above the ground. Percentages are given in brackets.

Seral Stage	Height < 10 cm		Height ≥ 10 cm	
	Follow	Cross	Follow	Cross
Herb	75 (91.5)	7 (8.5)	28 (71.8)	11 (28.2)
Mature Forest	49 (87.5)	7 (12.5)	25 (83.3)	5 (16.7)

they were to follow pieces $\geq$ 10 cm above the ground (Fisher exact probability test, P = 0.05).

DISCUSSION

Cover is a habitat component that can influence habitat use and behaviour of small mammals. Movements of small mammals tend to be associated with cover, thus the abundance and distribution of cover can influence where small mammals conduct their activities (Harestad 1991). Anderson (1986) reported that the addition of cover to areas lacking it, allowed deer mice to forage in areas not previously used. Studies on various species have suggested that movements and microhabitat selection may be influenced by predation risk (Milinski and Heller 1978, Krebs 1980). Prey species have been found to prefer areas with cover (Kaufman et al. 1983) and to rarely cross spaces where cover is absent (Wilkins 1982).

Coarse woody debris is accepted as an important habitat feature for deer mice (Bendell 1961, Barry and Francq 1980). Investigations that treat woody debris in general terms, have determined that *Peromyscus* spp. are usually more abundant in areas with abundant woody debris (Kaufman et al. 1983). They suggest that one of the reasons why deer mice are more abundant in areas with abundant woody debris is because deer mice use logs and stumps as cover to avoid detection by predators.

Most investigations of microhabitat selection by small mammals have relied on live-trapping. Habitat factors at capture and noncapture sites are compared, with the assumption that the live-traps do not influence the movements of the animals (Dueser and Shugart 1978, Kaufman et al. 1983, Morris 1987). These studies have concluded that *Peromyscus spp.* are generalists in microhabitat selection (Dueser and Shugart 1978, Barry and Francq 1980, Hayes and Cross 1987) in some habitats but not in others (Seagle 1985). This variation in results makes it difficult to clearly assess the importance of coarse woody debris and other habitat factors to deer mice abundance.

There are several problems with using trapping to measure microhabitat selection. Firstly, the spacing of traps may measure habitat differences at a scale irrelevant to the species. Secondly, it is difficult to determine if animals visited a particular site because it provided some requirement or because the animals were lured there by the trap or bait. Thirdly, variation in population density may influence results by increasing or decreasing the proportion of non-capture sites. Douglas (1989) reported that trap-revealed microhabitat selection differed from microhabitat selection determined through radio-telemetry, indicating that live-trapping does influence movements of deer mice. If movements of deer mice are influenced by placement of traps, then as Douglas (1989) suggested, live-trapping is not an appropriate method for determining microhabitat selection. Instead, methods such as radio-telemetry and powder tracking should be used, which allow animals to roam freely and thus provide a better measure of the influence of different habitat factors on microhabitat preferences.

In my study, I used powder tracking to determine the importance of coarse woody debris to movements and microhabitat selection of deer mice in 2 habitats. I found that travel routes of deer mice in the herb seral stage and mature forest were strongly influenced by coarse woody debris. In both habitats, deer mice selected routes that had far more woody debris along them than would be expected from the availability of woody debris. My results indicate that deer mice prefer microhabitats that have coarse woody debris. They travel near woody debris and orient their routes to increase their association with this habitat structure. This preference for debris and the greater abundances of deer mice in areas with increased amounts of woody debris (Chapter 2) indicates that coarse woody debris is important to deer mice. I conclude that the abundance and distribution of woody debris influences the abundance and distribution of deer mice.

The attributes of cover that affect the value of cover to an animal's security at a specific location are exposure, continuity, and how distant the cover is (Harestad 1991). Distance to cover is a function of availability. The farther animals must venture from cover the greater the risk of predation (Krebs 1980). Thus, habitats with abundant coarse woody debris or other forms of cover should reduce the distances that animals must venture unprotected from predators. The level of exposure that a particular piece of cover offers to an animal is a function of its structural characteristics. The more the structure conceals or protects an animal, the lower the exposure to predators. Continuity is a function of both structure and distribution of cover. I expect that prey species will select areas with abundant cover because they offer low exposure and high continuity, other habitat factors being equal, and the actual or perceived risk of predation will be lower.

In the herb seral stage, deer mice seem to use coarse woody debris as security cover. They preferred to travel near or under large diameter pieces of woody debris that were close to the ground and offered overhead cover and thus low exposure. I expected that long pieces of debris would offer greater continuity of cover and thus deer mice would be more likely to follow long pieces than short pieces. This was not supported by my observations in the herb seral stage. Perhaps from the ground level perspective of a mouse, the length of a piece of debris has little to do with its decision to follow the piece of debris. If a piece of debris is large enough to offer overhead cover, travelling along it may be the safest strategy regardless of the piece's length. Deer mice in the herb seral stage almost always traveled under or beside pieces of debris. In this habitat with no forest canopy, overhead cover provided by woody debris is probably the reason why mice elect to travel under or beside debris.

In the mature forest, deer mice prefer to follow large diameter woody debris, but how they followed the debris was very different from that in the herb seral stage. In the mature forest, deer mice usually travelled on top of the debris in a completely exposed manner. Several investigators have reported the use of the tops of logs as escape paths to avoid predators (Bendell 1961, Kaufman et al. 1983). This reason does not adequately explain deer mouse behaviour in my study. Mice travelled on top of the logs for distances greater than needed to escape and often returned to travelling on the top of logs after entering a burrow or cavity. If mice are only using the tops of logs to escape after release in the forest, why don't they use this tactic in the herb seral stage?

Two hypotheses which provide better explanations for this behaviour are that deer mice normally travel along the tops of logs in forested habitats because the threat of avian predators is reduced in these areas or that using the tops of logs is quieter than moving about on the forest floor. Fitzgerald and Wolff (1988) reported that *Peromyscus* spp. prefer to travel on damp rather than dry forest floors presumably because it was quieter and many of their predators used sound to locate them. Alternatively, travelling on the tops of logs would be faster and less obstructed than the forest floor, which may reduce their time of exposure to predators. Planz and Kirkland (1992) reported that white-footed mice commonly travelled on woody debris and that removal of debris reduced travel through the area.

In the mature forest, deer mice preferred to follow larger diameter logs and, unlike in the herb seral stage, they preferred longer logs. It is difficult to explain why deer mice selected longer logs in one habitat and not in the other. It may be because in the forest, diameter and length of logs are correlated, whereas among logging debris in the herb seral stage they may not be correlated.

Unlike in the herb seral stage, in the mature forest, height of a piece of debris above the ground did not influence the choice of whether or not to follow a piece of debris. If the canopy in the mature forest reduces the threat of avian predators it may be more important to select quieter or faster routes in this habitat, rather than selecting routes that provide overhead cover.

The lack of preference by deer mice for decayed pieces of debris in both habitats was unexpected. Increased levels of decay would allow access to the interiors of the debris and thus provide better cover. Because powder tracks were observed to occur through the interior of decayed woody debris in both habitats, it suggests that deer mice use the interiors of decayed debris but decayed debris does not strongly influence selection of routes by deer mice.

The results of my study indicate that the abundance and characteristics of woody debris influence microhabitat selection of deer mice. Woody debris is important in both habitats but debris is used differently in each habitat. I suspect that the lack of a forest canopy in the herb seral stage forced deer mice to trade-off faster and quieter travel routes on top of the woody debris in preference for more secure routes under or beside pieces of coarse woody debris.

SUMMARY

My study was conducted in the Nanaimo River Valley on southern Vancouver Island during 1988 and 1989. My objectives were to assess the importance of seral stage and coarse woody debris to deer mice in coastal forests.

In Chapter 1, I examined the influence of seral stage on the abundance and demography of deer mouse populations in 4 seral stages. There were significant differences in the abundance of deer mice among the different habitats. Deer mice were more abundant in herb and shrub seral stages during summer than in the young and mature forest. I found that deer mouse abundance fluctuated both seasonally and annually in all 4 seral stages. Reproduction and juvenile recruitment tended to be higher in younger seral stages while immigration was lower and adult survival was higher in mature forest.

I used live-trapping transects (Chapter 2) to examine the importance of coarse woody debris to deer mice in each of the 4 seral stages. Deer mouse numbers were positively correlated with the abundance of woody debris in all 4 seral stages. The effect of woody debris abundance on deer mouse abundance varied among seral stages. Deer mouse abundance had stronger correlations to woody debris abundance in the herb seral stage and mature forest than it did in the shrub seral stage and young forest. Debris

diameter, length, and height above the ground influenced the abundance of deer mice in some seral stages but not in others. The importance of coarse woody debris as a habitat factor is variable and depends on the habitat in which it occurs.

I used powder tracking to follow movements of deer mice in the herb seral stage and mature forest (Chapter 3). Deer mice used woody debris in both habitats. They oriented toward and travelled along woody debris in both habitats but their use of the debris differed between habitats. In the herb seral stage, deer mice travelled beside or under woody debris while in the mature forest, deer mice usually travelled on top of woody debris. The differences in how deer mice use woody debris in each seral stage indicate that generalizations about the importance of woody debris to deer mice need to consider the habitat context in which the debris occurs.

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