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POPULATION DYNAMICS AND DEMOGRAPHY OF DEERMICE (*PEROMYSCUS MANICULATUS*) IN HETEROGENEOUS HABITAT: ROLE OF COARSE WOODY DEBRIS

ABSTRACT: I tested the hypothesis that habitat heterogeneity increases with increasing amounts of coarse woody debris (CWD) by comparing *Peromyscus maniculatus* populations in sites with high and low amounts of CWD. Sherman live-trapping technique was applied to monitor population fluctuation and to measure demographic parameters. In sites with high amount of CWD density was higher, populations fluctuated less, survivorship was better and residency time was longer. These results were in accordance with predictions of habitat heterogeneity and CWD played an important role for demography of *P. maniculatus* in managed coniferous forests.

KEY WORDS: *Peromyscus maniculatus*, coarse woody debris, habitat heterogeneity, population dynamics, demography, coniferous forests, Pacific Northwest

1. INTRODUCTION

Several theories suggest that habitat heterogeneity leads to increased carrying capacity and stability of small mammal populations (Hansson 1977, Anderson 1980, Łomnicki 1980, Stenseth 1980, Ostfeld *et al.* 1985, Bondrup-Nielsen 1987, Tallmon and Mills 1994, Loeb 1999). Stenseth (1980) states habitat heterogeneity in terms of the degree of structural diversity of the habitat. In a heterogeneous habitat populations are more stable due to more hiding places from predation. Łomnicki (1980) found populations to be more stable when resource partitioning is unequal and habitat is more structurally diverse. Bondrup-Nielsen (1987) found that population density and stability of *Clethrionomys gapperi* was positively correlated with high amounts of debris (fallen trees and dead branches) on the forest floor. Ims (1987) found higher population densities of *C. rufocanus* can be achieved by the addition of straw indicating the importance of cover. Studies above, however, did not compare demographic profiles with the suboptimal habitats (see Loeb 1999). Presumably, populations in the suboptimal habitats would show less stability, lower numbers and survival, and higher proportion of transients.

Presence of coarse woody debris (CWD) has been hypothesized as one of the most important habitat elements in forests of Pacific Northwest because it provides ground structural diversity (microenvironments) and increased food resources (Thomas 1979, Hunter 1990, Vickery and Rivest 1992, Carey and Johnson 1995, Carey and Harrington 2001). However, no one has carried out objective assessment based upon replicated fieldwork. Here I propose that habitat heterogeneity increases with increasing amount of CWD. Coarse woody debris, in turn, influence demographic features of *Peromyscus maniculatus*. Thus, I predicted more stability in density, higher survival and recruitment, and lower proportion of transients of *P. maniculatus* in sites with high amounts of CWD. The study objectives were 1) to describe the differences in population density and dynamics between sites with low and high amount of CWD in managed forests of western Washington, and 2) to identify the demographic parameters that play a key role in determining population density and its degree of variability.

2. STUDY AREA

The study was conducted on the Fort Lewis Military Reservation, located east of the southern tip of Puget Trough Province in Pierce County, WA USA. Ft. Lewis is located 100 m above sea level within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973). Six sites were chosen (3 controls and treatments). Controls are sites with high amount of coarse woody debris (CWD). Each site with high and low amount of CWD was formed as a pair within the distance of 5 km; site pairs of A, B and C were generally equal except for different amount of CWD. Pairing was intended to decrease variance among sites. Previous logging was done about 1910 after settlement except for low CWD site A where trees were invaded into prairie (forest inventory map from GIS lab in the Reservation). Sites of low amount of CWD were chosen without actual removal of CWD at the study time. However, different level of CWD was maintained due to two reasons: 1) Coarse woody debris, especially downed logs were removed as a part of forest management that viewed as hazardous of forest fire, 2) sites with high amount of CWD were designated as natural reserve. Downed log of 10 cm or greater at the small end were counted as downed logs. I estimated volume of CWD by measuring circumference of the base and height of all standing dead snags and diameter and height of all stumps. The volume of CWD was significantly higher in high CWD sites (average = 245.7 m^3/ha) than in low CWD sites (average = 33.3 m^3/ha) (paired t-test, $P < 0.05$) (Lee 1995a).

The study areas were relatively flat and homogeneous, and mostly Douglas fir (*Pseudotsuga menziesii*) dominated stands. Major understory vegetation was composed of salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and sword fern (*Polystichum munitum*). The annual precipitation was approximately 2000 mm and distributed bimodally (Lee 1995a). A winter rainy season occurred from approximately November through March, followed by a late spring-early summer drought. Temperature in winter was mild and the mean January temperature (the coldest month) was above 4°C as shown in the thirty year average data. Abundance and diversity of invertebrates and diversity for vegetation were not different between sites with high and low amounts of CWD (Lee 1995b).

3. METHODS

Capture-mark-recapture program was used to monitor animals in one hectare trapping grid. Each grid was consisted of a 10 × 10 array of trapping stations with 10 m spacing. A Sherman collapsible trap was placed within a 2-m radius of each station for a total of 100 traps per grid. Each trap contained synthetic bedding and was baited with rolled oats. Traps were baited in the late afternoon and checked in the early mornings. A wooden cover was applied to each trap to prevent rain and snow from entering and to provide shade from direct sun.

I trapped live deermice for three consecutive days twice a month from June 1991 to June 1993. Traps were set on day 1 and checked on days 2 and 3. During the winter months (November through February), I live-trapped only once a month. In January and February of 1993 trapping was not done due to an unusually cold winter. All trapped animals were uniquely marked by toe-clipping and their sex, weight, and reproductive condition were recorded. Deermice were weighed on Pesola spring balances, to the nearest 0.5 g. Males were described as either breeding (testes descended) or nonbreeding (testes abdominal). Females were described as nonreproductive, reproductive, or postreproductive depending on perforate, pubic symphysis, pregnant, and size of nipples. Age classes were estimated using body mass (juveniles <12 g, subadults <13–16 g, and adults >17 g) (Sullivan 1979, Martell 1983), and reproductive condition.

The population of *P. maniculatus* was followed throughout the study period using Jolly-Seber methods with constant sampling efforts (Seber 1982). Within each trapping period I was able to estimate percentage of survivorship, and recruitment (number of animals), and population numbers. Survivorship and recruitment were compared using a paired t-test between low and high CWD sites. The same test was applied for winter survivorship during non-breeding season.

Population numbers were compared using Hotelling-Lawley T^2 test (Zar 1984). The null hypothesis was that there are no population differences among sites with different amount of CWD. Population stability was compared using the variance between two populations (Zar 1984). Population parameters were log transformed and variance was compared using a one-tailed F-test. The alternative hypothesis states that population fluctuates more in low CWD sites than in high CWD sites.

Resident animals live on the grid for an extended period of time and may reproduce and raise young. They also travel through the grid but do not remain there. As inferred from low resident adult population I expected that animals in poor quality habitat would result in a high proportion of transient. This should be particularly apparent for juvenile. Animals in poor habitat could be expected to continue searching for better habitat and would gain little advantage from the long term staying in home range within poor habitat (Van Horne 1981, Teferi and Millar 1993). In this study I defined transient animals as those that were captured in only one trapping period on a grid. Animals captured ≥ 2 periods were defined to be residents. A paired t-test was applied for the percentage of transients in each grid, average time of residency, and number of new adult recruits.

Mean travel distance between each capture point was calculated for all animals caught more than once. In most cases, animals did not return immediately to the same trap after a release during a trapping period. Therefore, I treated all subsequent captures independently. I did not differentiate between subsequent captures within a trapping period and those between trapping periods. The paired t-test was used to examine differences in distance traveled between sites with high and low amount of CWD. I separated animals into different age classes (subadults and adults) based on their reproductive condition. Breeding and non-breeding mean travel distance was tested in the different age classes.

3. RESULTS

Most of the animals caught belong to deermice (45.6%, n = 579). Other animals caught less often belong to: *Sorex trowbridgii* (13.5%, 127), *Microtus oregoni* (6.2%, 58), *S. monticolus* (5.3%, 50), *S. vagrans* (4.5%, 42), *Tamias townsendii* (2.7%, 26), *Neurotrichus gibbsii* (2.4%, 23), and *C. gapperi* (2.3%, 22). *T. douglasii*, *Glaucomys sabrinus*, and *Mustela erminea* were visitors (<8 individuals).

Population numbers in high CWD sites were significantly higher than those in low CWD sites (P <0.001) (Fig. 1), and the populations were more stable in high CWD sites than in low CWD sites. Comparing the variance of population in high and low CWD sites, I failed to reject the alternative hypothesis. Deermice population was more stable in high CWD sites than in low CWD sites (Table 1).

Table 1. The variance of population numbers of *Peromyscus maniculatus* was higher in high coarse woody debris (CWD) than in low CWD sites. Sites with different amount of CWD were formed as pairs of grids (A, B, C). The one-tailed F-test was applied.

Site	Log-transformed coefficient of variation	Variance	F-value	*P*-value
High CWD A	0.27	0.09	1.84	P <0.05
Low CWD A	0.58	0.16		
High CWD B	0.25	0.07	8.64	P <0.05
Low CWD B	1.70	0.57		
High CWD C	0.24	0.05	2.13	P <0.05
Low CWD C	0.38	0.12		

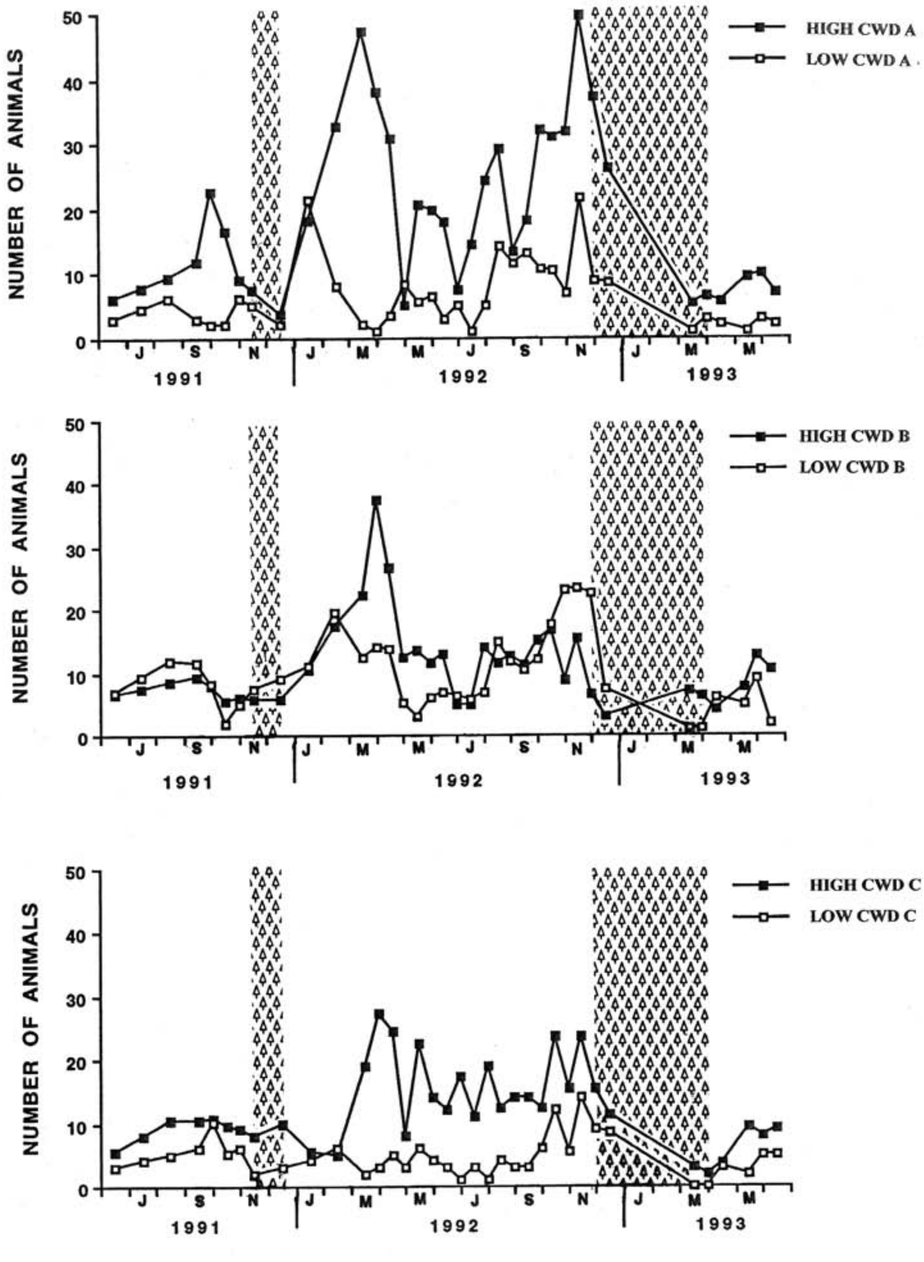

Fig. 1. Population number of deermice (*Peromyscus maniculatus*) per one hectare grid (100 × 100 m) estimated by Jolly-Seber method with constant sampling efforts. Trapping periods were from June 1991 to June 1993, and the number was based on each trapping period. Three pairs of sites with high coarse woody debris (CWD) and low CWD (A, B, C) were used. Shading indicated non-breeding season. Population number was significantly higher ($P < 0.001$) in high CWD sites than in low CWD sites.

Survivorship of deermice was significantly different between high and low CWD sites. Survivorship in high CWD site B was the highest (0.80) during breeding season whereas survivorship in low CWD site B was the lowest (0.42) during non-breeding season (Table 2). Survivorship in non-breeding season was significantly higher ($P = 0.04$) in high CWD site (mean = 0.67) than in low CWD site (mean = 0.28). Coupled with mild winter temperature (mean = 6.8 °C) the number of animals in all high CWD sites were the highest in March during the study period followed by a rapid decline in spring (Fig. 1).

Table 2. Number of trapping periods (N), mean, and standard deviation (SD) of percentage survivorship in breeding and non-breeding season. *Survivorship of deermice was significantly higher ($P < 0.001$) in sites with high CWD than in sites with low CWD throughout trapping periods. **Survivorship in non-breeding season was significantly higher ($P = 0.04$) in high CWD site than in low CWD site.

Site*	Breeding			Non-Breeding**		
	N	Mean	S.D.	N	Mean	S.D.
High CWD A	29	0.74	0.21	6	0.62	0.23
Low CWD A	29	0.59	0.29	6	0.64	0.32
High CWD B	29	0.80	0.19	6	0.75	0.26
Low CWD B	29	0.65	0.28	6	0.42	0.24
High CWD C	29	0.73	0.21	6	0.68	0.25
Low CWD C	29	0.59	0.27	6	0.59	0.32

The percentage of residents was not significantly different between high CWD and low CWD sites ($P > 0.05$) (Table 3). Due to high proportion of transients (mean=53.5% for high CWD sites; 63% for low CWD sites) separation of age groups was unsuccessful. There were no differences in the number of animals that were caught as juveniles and those that remained within the grids as adults ($P > 0.05$). The number of new adult recruits was compared among animals in high and low CWD sites, but no significant difference was found ($P > 0.05$). However, a significant difference was detected in average residency time when the resident animals were considered ($P < 0.05$).

Table 3. Comparison of % of resident animals (total number), and mean residency time ± SD. Resident animals were defined as animals caught >=2 times. Sites with different amount of coarse woody debris (CWD) were formed as pairs of girds (A, B, C). *Residency time was longer in high CWD sites than in low CWD sites ($P < 0.001$).

Site	% of residents (number)	Residency Time* (months)
High CWD A	47.8 (154)	3.84 ± 2.90
Low CWD A	41.7 (59)	3.11 ± 1.37
High CWD B	29 (106)	3.72 ± 2.78
Low CWD B	29 (95)	3.24 ± 2.41
High CWD C	29 (104)	3.55 ± 2.27
Low CWD C	29 (70)	2.61 ± 1.94

Mean travel distance of adult female deermice was significantly lower ($P = 0.008$) in high CWD sites (mean = 19.8 m) than in low CWD sites (mean = 29.9) (Table 4). When considering only adult animals mean travel distance in breeding season (mean = 33.6) was significantly greater ($P < 0.001$) than in non-breeding season (mean = 18.0).

Table 4. Mean travel distance (m) between captures in breeding and non-breeding season in each site. *Mean travel distance (m) between captures was significantly higher ($P < 0.001$) in breeding season than in non-breeding season when only considering adult animals. **Mean travel distance is significantly lower ($P = 0.008$) in high coarse woody debris (CWD) sites than in low CWD sites when only considering adult females. Number of captured animals in parentheses. B – breeding season, NB – non-breeding season.

	High CWD A		Low CWD A	
	B*	NB	B*	NB
Male, Adult	27.5(22)	7.7(5)	43.9(3)	22.3(2)
Male Sub-adult	22.9(13)	20.7(12)	29.4(4)	20.0(3)
Female, Adult**	21.8(12)	14.0(8)	56.9(3)	26.1(2)
Female, Sub-adult	21.4(17)	17.8(4)	27.8(4)	18.8(3)
	High CWD B		**Low CWD B**	
	B*	NB	B*	NB
Male, Adult	37.9(7)	17.6(3)	40.9(6)	24.0(3)
Male Sub-adult	27.4(14)	27.6(10)	24.9(12)	12.8(12)
Female, Adult**	35.2(4)	15.3(2)	24.9(6)	20.8(2)
Female, Sub-adult	22.8(4)	20.9(9)	25.9(9)	16.9(5)
	High CWD C		**Low CWD C**	
	B*	NB	B*	NB
Male, Adult	22.6(14)	6.0(2)	45.0(2)	24.2(2)
Male Sub-adult	21.9(15)	17.7(11)	29.4(6)	25.0(2)
Female, Adult**	17.0(14)	15.5(3)	29.1(2)	22.1(2)
Female, Sub-adult	24.3(8)	14.7(6)	22.3(5)	11.9(4)

4. DISCUSSION

This study demonstrated that the amount of coarse woody debris (CWD) is important habitat characteristics for *P. maniculatus* and its demographic parameters. Population is less stable in sites with low amount of CWD indicating that populations in low amount of CWD tend to be opportunistic showing high fluctuations in density. Suboptimal habitats are temporarily unstable so that density soon declines to low levels (Adler and Wilson 1987, Bowman *et al.* 2000). Kaufman *et al.* (1985) found no differences between male and female *P. leucopus* population associated with trees, trees of different sized, and microsites associated with shrubs. However, they did not directly measure the habitat variable of CWD. Van Horne (1981) indicated that population density is not an adequate indicator of habitat quality. Survival and reproductive rates of animals should be assessed to measure habitat quality and found overwinter survival of *P. maniculatus* in both sex and age group was higher in relation to ground structure of coniferous forests in Alaska. Recently the number of logs and snags on the forest floor improved the quality of habitat for *P. gossipinus* in pine forests (*Pinus palustris* and *P. taeda*) of South Carolina (Loeb 1999). In her study adult females in sites with high amount of CWD had greater survival and were more likely to be in reproductive condition than adult females in sites with low amount of CWD. In my study high CWD sites proved to be a better quality habitat for *P. maniculatus* so that population in high CWD sites was more stable and better rerproductive condition.

A spring decline is common among populations of small mammals for *Microtus* species by Krebs and Boonstra (1978), *Apodemus* species by Gurnell (1978), and *Clethrionomys* species by West (1982). The decline is density dependent, being more severe in years with good over-winter survival, and small or non-existent in years of poor overwinter survival (Petticrew and Sadleir 1974). Although I did not directly measure the cause of decline in spring the results support the observation of Petticrew and Sadleir (1974). The high CWD sites, which exhibited higher winter survival, reflect a severe spring decline whereas the low CWD sites showed a mild or nonexistent one.

I expected a greater percentage of transient animals in low CWD sites than in high CWD sites. But, I failed to confirm the hypothesis due to large proportion of transients. Lack of differences may be attributed to the unsuccessful separation of age class. Greater proportion of young age class would bring higher proportion of transients in poorer habitats. However, mean residency time was significantly higher in high CWD sites among resident animals. The differences in stability, survivorship, recruitment, and mean residency time reflect that the habitat quality differs between low and high CWD sites. Overall, the sites with high amount of CWD supported better population performances. The high amount of CWD in the site can be regarded as "survival" habitat in landscape configuration. "Survival" habitats are always favorable and populations in "survival" habitats are expected to have high and stable density, high survivorship, and long residency time (Anderson 1980, Merriam and Lanoue 1990). Populations in less quality habitats will often be extinguished and show a short residency time. In my study, habitat resources may be increased in sites with high amount of CWD. The CWD provided *P. maniculatus* with better cover from predation and food resources due to increased accumulation of nutrients surrounding the cumulated CWD (Sollins 1982, Sittonen *et al.* 2000). In accordance with these results I thus conclude that the sites with high amount of CWD represent preferred habitats by *P. maniculatus* in managed coniferous forests so that in future forest management CWD should be included as important habitat components.

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4. SUMMARY

Live trapping technique was applied to monitor population dynamics and demography of deermice (*Peromyscus maniculatus*). Sites with high amount of coarse woody debris (CWD) were considered as better quality habitat and this study tested habitat matrix in landscape configuration. Populations in high CWD habitat are expected to have stable population fluctuation and are better in demographic performance. Population fluctuation was stable in sites with high amounts of CWD presumably due to more hiding places and abundant resources (Fig. 1). Variation of population density was higher in sites with low amount of CWD indicating population was highly fluctuated (Table 1). Survivorship was also compared and animals in sites with high amount of CWD have higher survivorship (Table 2). Although percentages of resident animals (caught more than 2 times) were insignificant, residency time by months was higher in sites with high amount of CWD (Table 3). Mean travel distance between each capture point was estimated and animals in sites with low amount of CWD was found to travel more frequently (Table 4). This result may indicate that population travels long distance to search for food or hiding places. The results mostly are in accordance with the prediction of the importance of habitat heterogeneity. The study showed that CWD is an important habitat characteristic for small mammals.

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