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Comparison of population characteristics of three species of shrews and the shrew-mole in habitats with different amounts of coarse woody debris

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Seasonal fluctuation and its causes for three species of *Sorex* shrews and the shrew-mole *Neurotrichus gibbsii* Baird, 1857 were investigated in three sites with high amounts of coarse woody debris (CWD) and three sites with low amounts of CWD in managed forests of western Washington, USA. *Sorex trowbridgii* Baird, 1857 was more abundant on sites with high amounts of CWD (captures per 100 trapping nights), and had higher reproductive rates than in sites with low amounts of CWD. *Sorex monticolus* Merriam, 1890 showed higher reproductive rates on sites with high amount of CWD. Population of *Sorex vagrans* Baird, 1857 fluctuated greater and abundance was higher in sites with low amounts of CWD. Most reproduction occurred from January to April and declined rapidly in May. Previous studies also have shown an early onset of breeding in Coastal California and Oregon. It seems that local species of soricids and *Neurotrichus gibbsii* gain reproductive benefits by breeding primarily in January through May.

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Introduction

In the Pacific Northwest shrew populations decline as a result of timber harvests (Sullivan and Sullivan 1982) although they were generally increasing after clearcutting (Kirkland 1990). The discrepancy is due to dense cover material, shrubs and increased insect abundance associated with slash decomposition (Terry 1981). Martell (1983) found that shrew abundance increased after clearcut harvesting. In Martell's studies, herb and shrub cover in clearcuts provided the necessary conditions for shrews. Hooven (1973) found that *Sorex trowbridgii* Baird, 1857 and *Sorex vagrans* Baird, 1857 decreased in abundance in slash-burn

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clearcuts due to the loss of woody debris. The availability and abundance of food following prescribed burning are important factors influencing occupation of clearcuts by shrews after timber harvesting (Gashwiler 1970, Hooven and Black 1976). Moisture conditions following timber harvest also limit the abundance of insectivores. Spencer and Pettus (1966) found that proximity to water, soil moisture or water-related microhabitat were important habitat features influencing the presence of *Sorex*.

Studies mentioned above describe population abundance. The abundance of shrews is extremely variable, and varies with the species, the time of year, and the nature of the habitat. Seasonal fluctuations are of considerable importance in the ecology of shrews. For example, *Sorex minutus* and *S. araneus* were observed to rapidly decline in numbers during autumn and winter (Shillito 1963, Churchfield 1980). Studies revealed high numbers of captures in summer, a drastic decline in autumn, low numbers in winter, and a sudden increase in spring. The authors did not discuss the cause of this fluctuation. In Finland, there was a remarkable population fluctuation and concurrently high variation of reproductive success of *S. araneus* (Henttonen *et al.* 1989). Similarly, Hanski (1989) reported the population dynamics of *S. caecutiens* were related to litter size. However, population fluctuation might also affect the litter size. There is still comparatively little information on the population dynamics of insectivores, and there has been little attempt to investigate seasonal fluctuations of populations of locally common species of *Sorex monticolus* Merriam, 1890, *S. trowbridgii*, *S. vagrans* and *Neurotrichus gibbsii* Baird, 1857.

This paper presents an investigation of seasonal fluctuation of shrew population and its causes in habitats with high amounts of coarse woody debris (CWD) and with low amounts of CWD. Coarse woody debris provided spatial and temporal continuity of habitat that could be important to the survival and migration of animals (Maser *et al.* 1979). It has been hypothesized that CWD is an important habitat component for small mammals, but, few studies have attempted to quantify its role. I hypothesized that populations in habitats with high amounts of CWD were higher in densities, more stable in population fluctuation, and higher in reproductive rate than those of populations in habitats with low amounts of CWD.

Study area and methods

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. Fort Lewis is located 100 m above sea level within the western hemlock *Tsuga heterophylla* vegetation zone (Franklin and Dyrness 1973). Six sites were chosen (three controls and three treatments). Each control (site with high amounts of CWD) and treatment (site with low amounts of CWD) was formed as a block within the distance of 5 km. Fallen logs were measured in detail. Length, diameter at both ends, decay stage (Maser *et al.* 1979), species, and location were recorded. Dead wood of 10 cm or greater at the small end was counted as fallen logs. I measured the circumference of the bottom end and height of all standing snags and diameter and height of stumps. I estimated CWD volume as follows:

Table 1. Summary of number (per ha) and volume (m^3 per ha) of coarse woody debris in each study site. * – denotes significant difference between treatments and controls ($p < 0.05$, paired t-test).

Coarse woody debris	Site A		Site B		Site C	
	Control	Treatment	Control	Treatment	Control	Treatment
Number of logs	202	31	177	132	132	66
Volume of logs	233.98	12.12	181.37	45.21	137.82	18.42
Number of stumps	70	6	22	45	77	49
Volume of stumps	12.50	0.11	6.24	10.59	26.65	5.57
Number of snags	9	10	10	4	6	3
Volume of snags	77.79	5.29	55.56	1.02	5.60	4.77
Total volume of coarse woody debris*	324.27	17.51	243.17	56.82	170.07	27.76

Volume of logs = Length $\times \pi \times (A^2 + a^2) / 2$, where A = radius of large end, a = radius of small end,
Volume of stumps = Length $\times \pi \times A^2$, where A = radius of top end of stump,
Volume of snags = Length $\times \pi \times A^2 / 2$, where A = radius of bottom end of snag.

The total volume of all CWD was different between controls and treatments (Table 1).

Sites were dominated mostly by Douglas fir *Pseudotsuga menziesii* approaching stem exclusion stage (50–60 years old). Major understory vegetation composition is salal *Gaultheria shallon*, Oregon grape *Berberis nervosa*, and sword fern *Polystichum munitum*. Abundance and diversity of invertebrates and diversity for vegetation were not different between sites with high and low amounts of CWD (Lee 1995). Light penetration to the understory was measured taking five slides of the canopy (four corners and one center in each site) through a Nikon 8 mm fish eye lens, then analyzed into a computer program, 'OPTIMAS'. There were differences ($p < 0.001$) between controls and treatments (Lee 1995). Annual precipitation (approximately 200 cm) at these sites is distributed bimodally. A winter rainy season occurs from approximately November through March, followed by a late spring--early summer drought. Temperature in winter is relatively mild and the mean January temperature (the coldest month) was above 4°C as shown in the thirty year average data.

Previous logging was done about 1910 after settlement except for treatment in site A in which trees were invaded into prairie (forest inventory map from GIS in the Reservation). Sites of low amount of CWD were chosen without actual removal of CWD at the study time. Coarse woody debris, especially downed logs were removed as a part of forest management policy that viewed downed woody material as hazardous of forest fire (G. Dickey, pers. comm.).

Study sites were chosen late in the seral stage for two reasons. First, to clarify the elements of CWD the understory vegetation should be minimized. Ground dwelling small mammals may not differentiate thick understory vegetation from CWD for cover and food resources. For example, high quality habitat for *Clethrionomys gapperi* can be characterized by either extensive debris and/or high shrub diversity (Bondrup-Nielsen 1987). Secondly, small mammal communities tend to be stabilized around the canopy-closed stage. Rather minor changes in species composition and relative abundance among species take place in subsequent successional stage (West 1991).

Live trapping and pitfall trapping

Live trapping was conducted on one hectare grids in each of the six sites (three controls and three treatments). Each sampling grid consisted of a 10 × 10 array of trapping stations with 10 m spacing. A Sherman collapsible trap (7.6 × 8.9 × 22.9 cm) was placed within a 2-m radius of each station for a total of 100 traps per grid. In each trap synthetic bedding was used and replaced whenever it was wet. Rolled oats were used for another ongoing study of demography of *Peromyscus maniculatus*. A wooden cover was applied to each trap to prevent rain and snow and to provide shade.

Live trapping was carried out for two 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), animals were trapped only once a month. All trapped animals were identified, sexed, and weighed, and their reproductive condition was recorded. In January and February of 1993 trapping was unsuccessful due to an unusually cold winter.

A 5 × 5 array of pitfall traps, 10 m apart, (No 10 tin cans, 15 cm in diameter buried in the ground) was placed in the center of every one hectare live trapping grid so that pitfall traps were placed in between Sherman traps. Animals from pitfall traps were observed in the autopsy. Length and width of testes, presence of uterine scars, and length, width and number of embryos (pregnant females) were recorded. Pitfall traps were sunk flush with the soil layer and covered with a piece of wood cover that was propped one to several cm over the can lip with twigs or a nearby log. Traps were opened for two consecutive trap days and nights every two weeks. Beginning in July 1992, I extended the pitfall trapping period to ten consecutive days and nights per month to increase the sample size.

Data analysis

Analysis of variance (randomized complete block design) was used to compare differences in population abundance of each species between three controls and three treatments. The percentage of reproductive insectivores was estimated, and using the Wilcoxon test, compared between control and treatment sites. The percentage of reproductive animals was estimated in each month to examine any trends throughout the year.

Index of population abundance [monthly captures per 100 trapping nights (TN)] was estimated only for *Sorex trowbridgii* in each site due to the lack of sample size. I hypothesized that there was a higher capture rate and less fluctuation of the population (more stability) in control sites than in treatment sites due to the presence of CWD in control sites. The mean population number was compared with Hotelling-Lawley's T^2 test (Zar 1984). Mean population number was log-transformed and population fluctuation was tested using an F-test to compare the variance between control and treatment sites. Comparison of other species was not possible due to small sample size except for *Sorex vagrans* in site A.

Results

Total captures of insectivores all sites combined comprised *Sorex trowbridgii* (24.8%, n = 330), *S. monticolus* (7.0%, n = 93), *S. vagrans* (5.8%, n = 77) and *Neurotrichus gibbsii* (6.0%, n = 82). Total abundance of *S. vagrans* from live and pitfall traps was significantly higher in sites with low amounts of CWD than in sites with high amounts of CWD ($p < 0.05$) (Table 2). *Peromyscus maniculatus* was the predominant small mammal species in the community (45.6%, n = 605). Other species were caught included in the decreasing order: *Microtus oregoni* (n = 70), *Tamias townsendii* (n = 26), *Clethrionomys gapperi* (n = 22), *Tamias douglasii* (n = 7), *Mustela ernimea* (n = 3), and *Glaucomys sabrinus* (n = 2), but each species compromised less than five percent.

There was a higher percentage of reproductively active animals (scrotal for males, lactating or pregnant for females) in control sites than in treatment sites for *S. monticolus* (p = 0.04) and *S. trowbridgii* (p = 0.03) (Table 3). The presence

Table 2. Total number of insectivores from Sherman and pitfall (in parenthes) trappings in each site during June 1991 – June 1993 as well as results of comparison (paired t-test) of population totals in each species between treatment and control sites. * – denotes significant difference between controls and treatments ($p < 0.05$).

Species	Site A		Site B		Site C		Total	t-test	p-value
	Control	Treatment	Control	Treatment	Control	Treatment			
Neurotrichus gibbsii	5(4)	11(11)	22(16)	17(9)	11(6)	16(13)	82(59)	−0.32	0.78
Sorex monticolus	15(6)	3(2)	23(18)	11(2)	15(11)	26(4)	93(43)	0.57	0.63
Sorex trowbridgii	44(23)	15(3)	69(48)	69(45)	54(37)	79(47)	330(203)	0.04	0.97
Sorex vagrans	17(10)	35(13)	0	8(5)	0	17(7)	77(35)	−4.51	0.05*
Unidentified *Sorex*	1(0)	1(1)	1(1)	0	2(1)	4(3)	9(6)	–	–
Total	82(43)	65(30)	115(83)	105(61)	82(55)	142(74)	591(346)		

Table 3. Proportion of reproductively active shrew-moles and shrews in each site. * – denotes significantly different ratios between controls and treatments ($p < 0.05$, Wilcoxon test). F – female, M – male.

Species	Sex	Site A		Site B		Site C		p
		Control	Treatment	Control	Treatment	Control	Treatment	
Neurotrichus gibbsii	F	0.33	0.14	0.22	0.08	0.29	0.25	0.14
	M	1.00	0.50	0.40	0.40	0.25	0.33	
Sorex monticolus	F	0.43	0.00	0.50	0.33	0.30	0.23	0.04*
	M	0.50	0.00	0.60	0.60	0.40	0.23	
Sorex trowbridgii	F	0.24	0.20	0.29	0.19	0.33	0.22	0.03*
	M	0.28	0.20	0.53	0.31	0.44	0.43	
Sorex vagrans	F	0.07	0.26	–	0.40	–	0.29	–
	M	0.33	0.41	–	0.00	–	0.22	

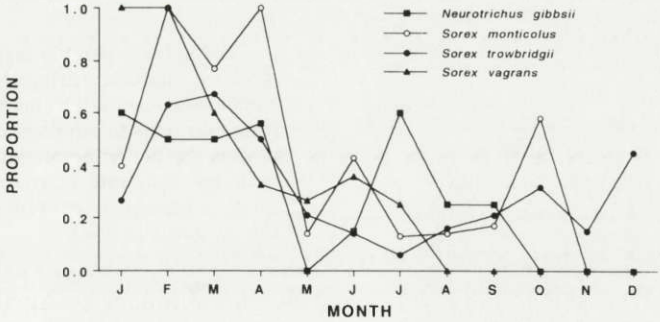

Fig. 1. Proportion of reproductively active the shrew-mole and shrews in each month during July 1991 – June 1993.

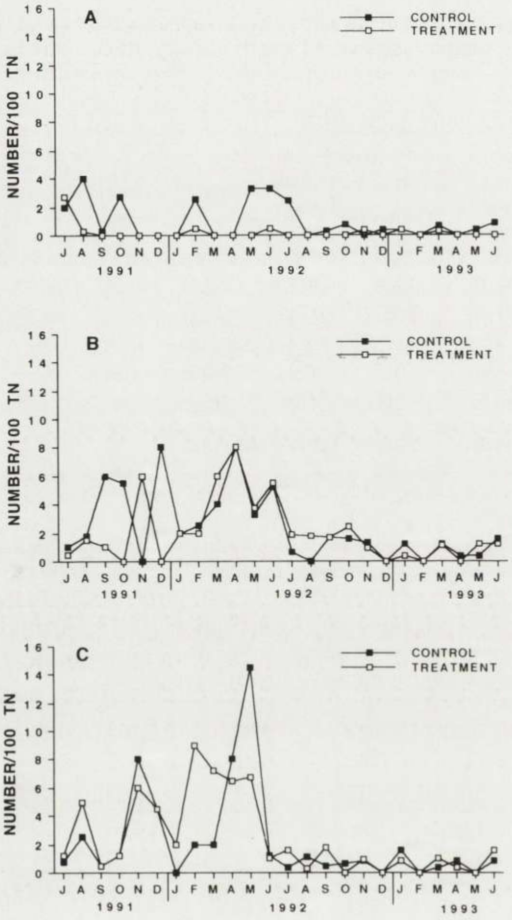

Fig. 2. Captures (both Sherman and pitfall trappings combined) per 100 trapping nights (TN) of *Sorex trowbridgii* during July 1991 – June 1993 in sites A, B, and C. Pitfall trapping periods changed from four days to ten days in July 1992.

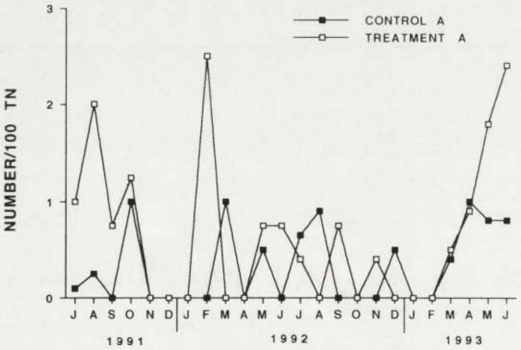

Fig. 3. Captures per 100 trapping nights (TN) of *Sorex vagrans* during July 1991 – June 1993 in site A. Pitfall trapping periods changed from four days to ten days in July 1992. Population fluctuated greater in treatment (sites with low amounts of coarse woody debris) than in control (sites with high amounts of coarse woody debris).

of reproductively active animals was greatest from January to April and declined rapidly in May (Fig. 1). Little variation in the percentage of reproductive animals was observed during the remaining months.

Population fluctuations were highly variable depending on species and season. The mean difference analysis of Hotelling-Lawley's T^2 test showed significant differences ($p = 0.05$) in *S. trowbridgii* captures (per 100 TN) between treatment and control sites (Fig. 2). The variation analysis of *S. trowbridgii* was non-significant for all sites indicating that population fluctuations were not higher in treatment than in control sites ($p > 0.05$). Population abundance index (per 100 TN) of *S. vagrans* was greater only in A treatment than in A control ($p = 0.05$). Population variation of *S. vagrans* was significant ($p < 0.05$) indicating that a higher population fluctuation occurred in A treatment than in A control (Fig. 3). Analysis of population fluctuations for *S. monticolus* and *Neurotrichus gibbsii* was not successful due to the lack of sample size.

Discussion

I assumed that there were greater population abundance and less fluctuation in sites with high amounts of CWD due to increasing structural diversity or habitat complexity. Theoretically, heterogeneous habitats appeared to support superior demographic performance (eg high density, reproductive rate, stability) than adjacent habitats that supported inferior demographic performance (Anderson 1980). In my study, population of *Sorex trowbridgii* was abundant in control sites, and its stability was greater. *S. trowbridgii* supposedly favored areas with a dense forb of component (Morrison and Anthony 1989), where better moisture contents were associated with high amounts of CWD. The greater abundance of *S. vagrans* was found in treatment sites (Table 2). In addition, *S. vagrans* populations in treatment A site fluctuated more than in control A site. This site contained least amounts of woody debris and provided more open habitats. Terry (1981) found non-burrowing *S. vagrans* was at a disadvantage in dry areas where the burrowing species *S. trowbridgii* and *Neurotrichus gibbsii* were present. However, in this study the higher abundance of *S. vagrans* on treatment sites did not correspond to Terry's findings. *S. vagrans* might well adapt to dry sites where ground cover was lacking. A similar result was reported in ponderosa pine *Pinus ponderosa* of eastern Washington where *S. vagrans* was found to be the most common shrew in dry ponderosa pine habitat (Stinson 1987).

The three species of shrews captured were short-lived and the annual population turnover was completed by late summer. Life spans could extend 12–18 months with breeding initiated by late April and May and complete by autumn at the latest in most northern regions (Churchfield 1990). Surprisingly, the breeding period in this region peaked in January–April and declined rapidly in May for the three species of *Sorex* and *Neurotrichus gibbsii*. The early onset of breeding raises interesting points.

In California, Jameson (1955) examined 388 *S. trowbridgii* over three years by dissection and determined breeding periods to begin in January, peak in March and April, and decline in May. Notes on the natural history of the Oregon Coast showed the onset of breeding in January followed by a decline in May (Hooven *et al.* 1975, Maser *et al.* 1981). Hawes (1977) also noted in forests of British Columbia the signs of reproductive activity of males in mid-winter. The earlier onset of breeding in Coastal California, Oregon Coast, British Columbia and Washington (in this study) contrasts sharply with patterns in studies from other regions. For example, Skarén (1973) noticed captures of pregnant *S. araneus* in late April when a rise in ambient temperature and the winter snow melt occurred in Finland. Moore (1949) reported breeding seasons of *S. cinereus* beginning in April and ending in October in the Appalachians. Winter weather in West Coast is less severe when compared with weather in other northern regions, and does not constrain on early onset of the breeding season. Second, summer weather influences survival rates of small mammals on the West Coast. The lack of rainfall plus hot temperatures make survival very difficult. The breeding season apparently can be extended from January until November if weather is favorable (Dalquest 1948). Shrews are organisms selected for their high reproductive rates, equipping well for exploitation of habitats when conditions are favorable (Vickery and Bider 1978, Churchfield 1990), thus suggesting that environmental conditions (water and vegetation) determine the length of the breeding season. Thus it seems that local species of *Sorex* gain reproductive benefits by breeding primarily in January through May.

Several recent models have stressed the importance of habitat heterogeneity in small mammal population dynamics (Hansson 1977, Myllymaki 1977, Anderson 1980, Rosenzweig and Abramsky 1980, Stenseth 1980). Most of these theories were developed with species of microtine rodents with known cyclic population dynamics. In this study, I measured the quantitatively different amounts of CWD as an indication of increasing habitat heterogeneity. Habitat heterogeneity appears to be important for non-cyclic as well as cyclic species in most patchy environments, especially when habitat that supports superior demographic performance is adjacent to habitat that supports inferior demographic performance. It is proposed that the presence of poorer (sparsely populated) areas facilitates emigration from superior areas (Hansson 1977, Anderson 1980). A high degree of habitat heterogeneity is characteristic of high density and increased reproductive rate in studies of *C. gapperi* (Bondrup-Nielsen 1987) and in *P. maniculatus* (Lee 1993). A high degree of habitat heterogeneity as measured by quantitatively different amounts of CWD is correlated with higher reproductive rates in *S. trowbridgii* and *S. monticolus* than in sites with low amounts of CWD. Coupled with a higher mean number of *S. trowbridgii* captures in control sites these data could support the hypothesis that sites with high amounts of CWD were superior to sites with low amounts of CWD.

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