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Demographic responses of shrews to removal of coarse woody debris in a managed pine forest

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Abstract

We trapped shrews at six 9.3 ha plots from which logs $\geq$10 cm diameter (coarse woody debris; CWD) had been manually removed and six control plots in managed loblolly pine (*Pinus taeda*) forests of the southeastern coastal plain, USA. Trapping was conducted seasonally between autumn 1997 and summer 2001. Capture rates of *Cryptotis parva* were lower at plots from which CWD was removed than at control plots ($P = 0.011$) and declined at all plots over the study period ($P < 0.001$). Capture rates of *Blarina carolinensis* ($P = 0.129$) and *Sorex longirostris* ($P = 0.432$) did not differ between removal and control plots, but declined over the study period ($P < 0.001$). Age distributions of *B. carolinensis* differed between removal and control plots ($P = 0.048$) with a smaller proportion of individuals in young age categories at removal plots. Sensitivity of *Cryptotis* to the removal of CWD may have been due to its sociality or low population density at the study area. A reduction in the abundance of young *B. carolinensis* after removal of CWD may reflect reduced reproduction and immigration of older individuals from outside the plot. Effect of removal of CWD on populations of these shrews was relatively weak compared to strong seasonal and multi-year variation in abundance. However, weak treatment effects may have been partly due to low ambient levels of CWD at control plots.

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1. Introduction

Management for timber production has been associated with a decrease in standing crop of coarse woody debris (CWD) in forests worldwide, including forests of the southeastern US (McMinn and Hardt, 1996). Mounting evidence suggests that reduction in abundance of CWD may lead to reduced diversity of birds (Lohr et al., 2002; MacNally et al., 2002), amphibians (Butts and McComb, 2000), and small mammals (Butts and McComb, 2000; Carey and Harrington, 2001; Carey and Johnson, 1995; Loeb, 1999) in managed ecosystems. There exist few studies, however, that separate the influence of CWD from the influences of factors that may covary with abundance of CWD, such as overstory vegetation (Carey and Harrington, 2001). Arguably, this can only be accomplished with large-scale, manipulative experiments.

Shrews may be particularly responsive to reductions in CWD because they are sensitive to changes in environmental moisture (Getz, 1961), which may be retained by decomposing wood (Jaeger, 1980).

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The abundance of CWD has been positively associated with population sizes of *Sorex trowbridgii* and *S. monticolus* in the Pacific Northwest (Butts and McComb, 2000; Carey and Johnson, 1995). However, *S. vagrans* was captured more frequently in Douglas-fir forests from which dead wood was removed than forests from which dead wood was not removed (Lee, 1995). Lee (1995) found that reproduction of *S. monticolus* and *S. trowbridgii* declined at plots from which CWD was removed, suggesting that demographic responses to the removal of CWD may not be limited to changes in abundance.

Volume of highly decomposed logs was an important predictor of *S. fumeus* abundance in hardwood forests of the southern Appalachian Mountains (Brannon, 2000). Similarly, McCay et al. (1998) found that capture rates of *S. fumeus* were correlated with abundance of CWD near traps in the southern Appalachian region. Capture rates of *S. cinereus* and *Blarina brevicauda* were not associated with amount of CWD in the southern Appalachians (Brannon, 2000; McCay et al., 1998), and Yahner (1982) found no association between abundance of *B. brevicauda* and CWD at farmstead shelterbelts.

Most studies of the importance of CWD to shrews have been conducted in the Pacific Northwest and southern Appalachian regions of North America, which are characterized by high environmental moisture and high abundance of dead wood (Harmon et al., 1986; McNab and Avers, 1994). Large amounts of CWD in these regions serve as important storage pools for nutrients and water (Harmon et al., 1986; Jaeger, 1980); whereas the relative nutritional importance of dead wood in other ecosystems may be much smaller (Busse, 1994; Prescott and Laiho, 2002). Perhaps because of these factors, forests of the Pacific Northwest and southern Appalachians support diverse shrew assemblages, including as many as five species in a single habitat (Nagorsen, 1996; Laerm et al., 1999).

Managed pine forests of the southeastern coastal plain, in contrast, support a lower diversity and abundance of shrews (Langley and Shure, 1980; Mengak et al., 1989; Mengak and Guynn, 2003). Shrews generally make up a smaller fraction of small mammal species at southern latitudes than northern latitudes in North America (Churchfield, 1990). Sandy soils of the coastal plain may retain less moisture and create conditions less suitable for members of this group (Getz, 1961). Pine forests of the Southeast also generally have lower abundances of dead wood than habitats of the Pacific Northwest or Appalachian regions (McMinn and Hardt, 1996). Because dead wood has the ability to retain moisture (Harmon et al., 1986; Jaeger, 1980), CWD may be more important to shrews in relatively dry habitats. We studied shrews at pine forests subjected to manual removal of CWD to better understand the importance of dead wood to shrews in managed forests of the southeastern US.

2. Methods

The study was conducted at the Savannah River Site, a National Environmental Research Park in the upper portion of the Coastal Plain Physiographic Province (Fenneman, 1938), South Carolina, USA (33°0–25′N, 81°25–50′W). Climate of the region is warm temperate, with long summers and mild winters. The study was conducted in upland areas supporting loblolly pine (*Pinus taeda*) plantations. Soils were well drained and sandy (Workman and McLeod, 1990). This study was part of a larger effort to better understand the ecological role of dead wood in managed southeastern pine forests (McCay et al., 2002).

2.1. Study areas

The study was designed as a randomized complete block with four treatments replicated in three blocks. Blocks were forest stands with the following characteristics: forested with approximately 45-year-old loblolly pine plantations; ≥ 76 m from nearest wetland, road, and power line; and able to accommodate four square 9.3 ha plots. Each plot consisted of a 6 ha core area, surrounded by a 3.3 ha buffer area (buffer width = 60 m) subjected to the same treatment as the core area. Buffer areas were not used for surveys to avoid edge effects. All plots were thinned to achieve a standing basal area of 14–21 $m^2\,ha^{-1}$ and intentionally burned on a uniform rotation.

Within each stand, each of the four plots was randomly assigned to one of the following treatments: removal of all snags and fallen logs, removal of fallen logs only, felling and girdling to simulate a catastrophic input of dead wood, and control. Snags and fallen logs considered in this study were $\geq$10 cm diameter at the large end and $\geq$60 cm long. A private crew under USDA Forest Service supervision removed dead wood in summer 1996 and each winter 1997–2000. The catastrophic input of dead wood was implemented following completion of the present study; thus, catastrophic plots were considered additional controls for the present analyses. Because the retention of snags in the log-removal treatment should have little effect on populations of shrews, which reside exclusively at the forest floor, we combined both removal treatments. One year after treatment, mean volume of logs $\geq$10 cm at control plots was 7.16 $m^3\,ha^{-1}$; whereas mean volume of logs at removal plots was 0.37 $m^3\,ha^{-1}$ (McCay et al., 2002).

2.2. *Shrew trapping*

We trapped shrews using a series of pitfall-drift-fence arrays, which remained stationary throughout the study period. Aluminum flashing ($\geq$35 cm) was used as drift fencing, and 19 l plastic buckets were used as pitfall traps. At each plot, we installed a single centrally located X-shaped array (Corn, 1994) with 30 m arms. Between the central array and each corner of the plot we installed a Y-shaped array (Kirkland and Sheppard, 1994) with 15 m arms. Traps were kept dry and supplied with a small amount of soil and forest debris during sample periods. Between sample periods traps were closed with fitted lids. Occasionally lids were opened by raccoons (*Procyon lotor*) between sample periods. Animals caught in traps between periods ($n = 6$) were not considered when calculating capture rates.

Trapping was conducted between autumn 1997 and summer 2001. Traps were opened during a 14-day period in each of winter (January), summer (July), and autumn (October), and during a 28-day period in spring (March). We designed longer trapping periods during spring to increase capture rates for amphibians pursuant to other aims of the project. Traps were checked daily between 0600 and 1200 h; large distances among plots and the remote nature of the study area precluded more frequent checking of traps. Shrews were identified, massed, and uniquely marked using toe clips. Shrews that died during trapping (68%) were removed to the laboratory for necropsy.

Shrews were weighed to the nearest 0.1 g in the lab after drying and cleaning of the pelage. Sex was determined by gross examination of the internal organs. Age was estimated using relative tooth wear. For each species, a 12-class (ranging 1− to 4+) aging system was devised based on Pearson (1945) for *Blarina carolinensis* and Rudd (1955) for *S. longirostris* and *Cryptotis parva*. For analyses presented here, classes were combined (e.g. 2−, 2, and 2+ were combined to 2), resulting in four age classes ranging 1–4. All specimens were accessioned into the zoological collections of the Georgia Museum of Natural History or Colgate University.

2.3. *Data analysis*

Capture rates were represented as unique captures per plot-day. Strong seasonal trends in capture rates prompted us to remove seasonal effects as a confounding factor in analyses. Seasonal effects were estimated for each plot and removed from the data following the procedure of Kendall (1976) for additive seasonal effects. The effect of removal of CWD on residuals was analyzed using repeated-measures ANOVA (Milliken and Johnson, 1992). Significance of temporally autocorrelated factors, including time and time × treatment interaction, was evaluated using the procedure of Greenhouse and Geisser (1959). Data were blocked by forest stand.

The influence of removal of CWD on shrew weight was examined using ANOVA. Shrew weight was blocked by age and sex because of the potential influence of these factors on shrew size (Baumgardner and McPherson, 1985). Age distributions at control and removal plots were compared using log-likelihood-ratio tests (Sokal and Rohlf, 1995). The proportions of captured shrews that died in traps and could be aged were approximately equal at removal (69%) and control (66%) plots, and we assumed that mortality occurred independent of age. Null hypotheses were rejected at $\alpha \leq 0.05$.

3. Results

During 280 plot-nights we captured 512 individual shrews, including 281 *B. carolinensis*, 70 *C. parva*, and 161 *S. longirostris*. Other insectivores

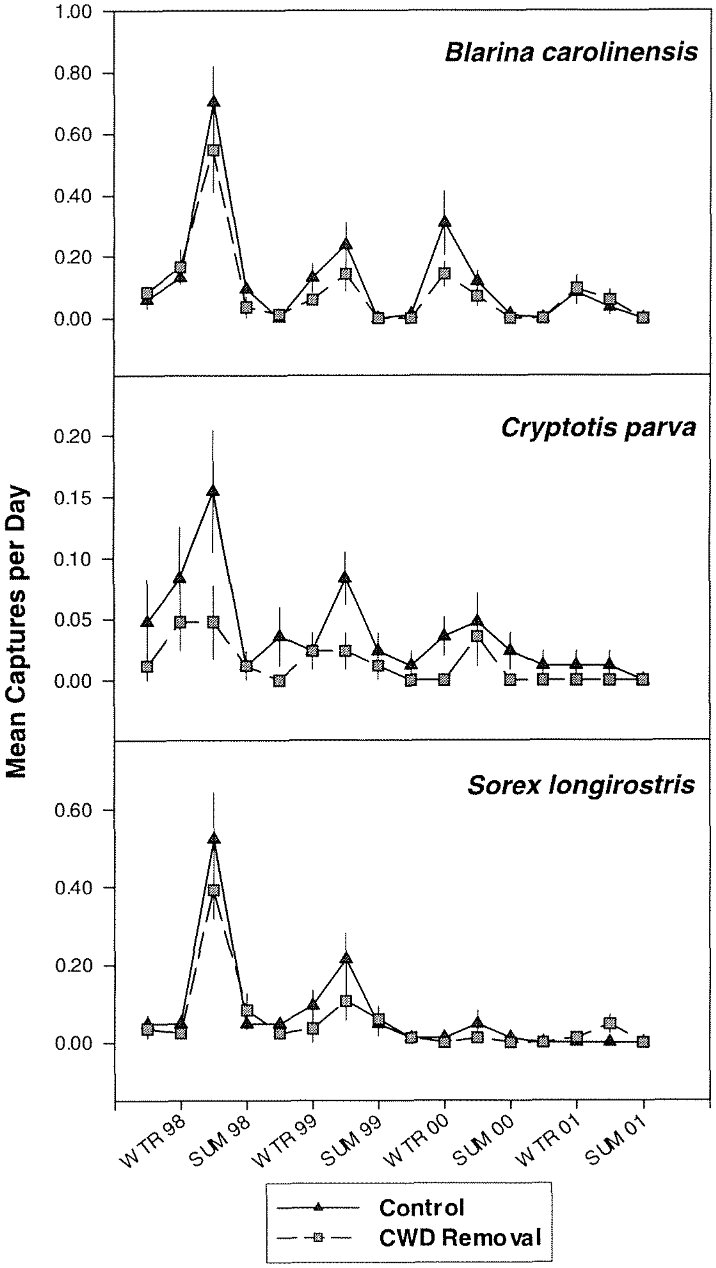

Fig. 1. Capture rates of three shrews at 9.3 ha plots from which CWD (logs ≥ 10 cm) was removed (CWD removal; $n = 6$) and plots from which CWD was not removed (control; $n = 6$). Capture rates were mean daily shrew captures across the entire plot, including 40 pitfall traps and 350 m of aluminum drift-fencing.

included one *Scalopus aquaticus* and two *Condylura cristata*.

The capture rate of *B. carolinensis* exhibited a strong seasonal trend, with an annual peak during winter–spring and an annual low during summer–autumn (Fig. 1). Capture rates of *B. carolinensis* at removal plots did not differ from those on control plots ($F = 2.87$; d.f. $= 1, 8$; $P = 0.129$). Capture rates

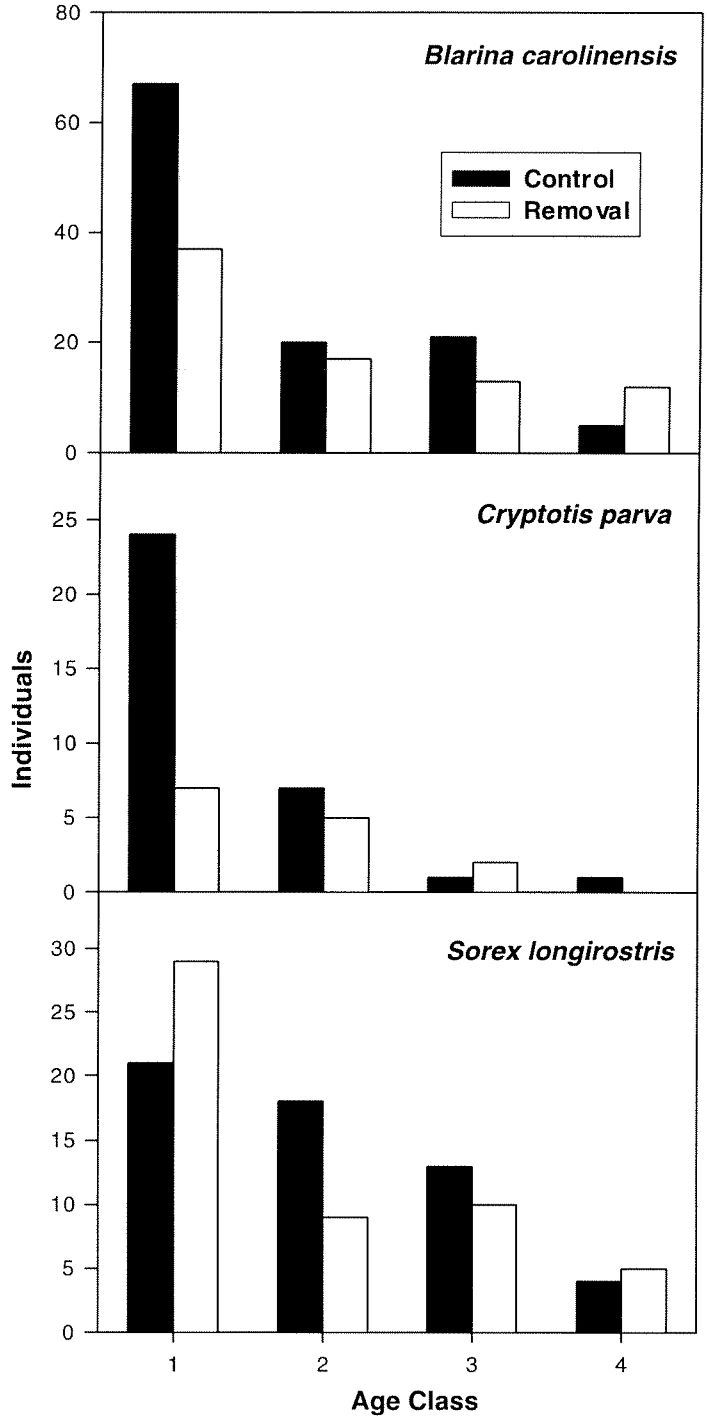

Fig. 2. Age distributions of three shrews captured at plots from which CWD (logs ≥ 10 cm) was removed (CWD removal; $n = 6$) and plots from which CWD was not removed (control; $n = 6$). Data were pooled across plots within a treatment. Age classification system was based on relative tooth wear.

declined during the 4-year study period ($F = 23.53$; d.f. $= 15, 120$; $P < 0.001$), but declined similarly at removal and control plots (time × treatment: $F = 1.23$; d.f. $= 15, 120$; $P = 0.322$). Capture rates of *Cryptotis* exhibited a weak seasonal trend. Capture rates of *C. parva* at removal plots were lower than capture rates at control plots ($F = 10.83$; d.f. $= 1, 8$; $P = 0.011$). Capture rates declined over the study period ($F = 3.39$; d.f. $= 15, 120$; $P = 0.031$), but declined similarly at removal and control plots ($F = 0.93$; d.f. $= 15, 120$; $P = 0.445$). Capture rates of *S. longirostris* exhibited a moderate seasonal trend, with greatest capture rates in spring. Capture rates of *S. longirostris* at removal plots did not differ from capture rates at control plots ($F = 0.69$; d.f. $= 1, 8$; $P = 0.432$). Capture rates strongly declined during the study period ($F = 19.43$; d.f. $= 15, 120$; $P < 0.001$), but declined similarly at removal and control plots ($F = 0.86$; d.f. $= 15, 120$; $P = 0.378$).

Mass of *B. carolinensis* did not vary by removal treatment when sex and age were accounted for ($F = 0.45$; d.f. $= 1, 31$; $P = 0.504$). Age distributions of *Blarina* differed between removal and control plots ($G^2 = 7.84$; d.f. $= 3$; $P = 0.049$), with a smaller proportion of shrews at removal plots consisting of young individuals (Fig. 2). Weights of *C. parva* did not differ by removal treatment ($F = 0.43$; d.f. $= 1, 31$; $P = 0.518$). Age distributions of *Cryptotis* were similar at removal and control plots ($G^2 = 4.01$; d.f. $= 3$; $P = 0.260$). Weights of *S. longirostris* did not differ between removal and control plots ($F = 0.04$; d.f. $= 1, 89$; $P = 0.847$). Age distributions of *Sorex* were similar at removal and control plots ($G^2 = 4.76$; d.f. $= 3$; $P = 0.189$).

4. Discussion

Although descriptions of high-quality habitat for shrews often include logs, many studies have shown little association between capture rates of shrews and dead wood in forests of eastern North America. Yahner (1982) found no evidence of microhabitat selection by *B. brevicauda*. Microhabitat selection had little influence on the distribution of *B. brevicauda* and *S. cinereus* in southern Michigan (Getz, 1961). McCay et al. (1998) found only weak ($r^2 \leq 0.02$) associations between capture rates of *Sorex* spp. and logs and rocks at the forest floor in the southern Appalachians. Similarly, we found that shrew responses to drastic decreases in the abundance of large logs were small or absent.

Like Brannon (2000), Carey and Johnson (1995), and Lee (1995), we found that the importance of CWD varied among shrew species. Specifically, *C. parva* was the most sensitive species in this assemblage to the removal of logs. *Cryptotis* is the most social of the shrews in this assemblage, frequently found in communal nests (Whitaker, 1974). Large logs may be necessary to house communal nests or may serve some other role in social interactions of this species. Alternatively, low density and sociality may have combined to make *C. parva* particularly sensitive to negative changes in its environment. Slight reductions in the sizes of small populations may have disrupted behaviors related to reproduction (i.e. Allee effect; Allee, 1931).

Populations of *B. carolinensis* at removal plots were skewed toward older individuals. This likely reflects a decrease in reproduction at plots from which CWD was removed, though the small number of pregnant shrews in our sample ($n = 8$) prevented a direct test of this hypothesis. Lee (1995) found reproduction of *S. monticolus* and *S. trowbridgii* to decrease after removal of dead wood. Coarse woody debris is often associated with sites, such as dens and roosts, used for reproduction by wild rodents (McCay, 2000) and bats (Menzel et al., 2001) in similar habitats.

The shift in age distribution of *B. carolinensis* also is consistent with the notion that removal plots were acting as population sinks in the landscape, receiving older immigrants from areas of greater reproduction outside the plot (Pulliam, 1988; Van Horne, 1983). *B. carolinensis* frequently moves >100 m in this environment (Faust et al., 1971) making possible the immigration of individuals from outside of our plots. If so, this immigration may have compensated for population decreases within the removal plots. These results suggest that if the abundance of CWD was reduced more widely across the landscape that the local abundance of *B. carolinensis* would likely decrease.

Types of dead wood other than logs ≥10 cm may have been important to these shrews. We did not consider decomposing root systems, which are important to other small mammals in this environment (McCay, 2000). Similarly, we did not consider small

(<10 cm) logs. Fine woody debris is important in the maintenance of invertebrate diversity (Kruys and Jonsson, 1999) and may be important to small vertebrate animals. Although we manipulated the abundance of large logs, changes in the abundance of other types of woody debris were not studied. Thus, our estimate of the importance of dead wood to these species should be viewed as conservative.

There were large seasonal and multi-year fluctuations in shrew capture rates during the study period. Seasonal trends were probably a consequence of reproductive patterns. Reproduction of these shrews is concentrated during the fall, winter, and early spring in this region (O'Farrell et al., 1977; McCay, unpublished data), resulting in the recruitment of young during winter and late spring. The multi-year decline in the abundance of all three species may have been due to an extended drought at the study area during this period. A similar decline in *B. carolinensis* and *S. longirostris* was documented at this study area during a drought in 1967–1970 (Smith et al., 1974).

Our sampling, which removed individuals from plots as mortalities occurred, may have contributed to the long-term decline in these populations and obscured treatment effects. Because our capture rates were low, however, our sampling resulted in the removal of relatively few individuals from these populations. For example, an average of four *B. carolinensis* died in traps each year at each of our plots. Although Sullivan et al. (2003) found that removal of captured animals disrupted the nature of small mammal communities in British Columbia, they found that the shrews (*Sorex* spp.) at their plots increased in abundance following removal. A pitfall-drift-fence protocol, similar to the one we employed, did not affect abundance of shrews within an African assemblage (Nicolas et al., 2003). Thus, we believe that trap mortality likely had a small influence on multi-year population changes at our plots.

Our control plots had a very low standing crop of CWD, even compared to other pine plantations in this region (McMinn and Hardt, 1996). For example, the mean volume of CWD on our control plots was 1.9% of the mean of 26 values reported for various temperate coniferous forests (Harmon et al., 1986). It is possible that both treatment and control plots contained an amount of CWD below a threshold amount necessary for population response by these small mammals. If so, manipulations that involve additions of dead wood, rather than removals, may produce greater faunal responses in this ecosystem. Loeb (1999) found that the addition of dead wood to pine forests of our study area led to drastic increases in the abundance of cotton mice (*Peromyscus gossypinus*). Because the associations between animals and CWD are likely dependent on forest context (Bowman et al., 2000), we encourage experimental studies of faunal responses to a range of ambient amounts of dead wood in other ecosystems.

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