RESPONSES OF SMALL MAMMALS TO COARSE WOODY DEBRIS IN A SOUTHEASTERN PINE FOREST

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The importance of coarse woody debris (CWD) to small mammals in a managed pine forest in South Carolina was tested experimentally during summer and autumn 1990 and winter and spring 1991-1994. Abundance and demographics of small mammals were compared between plots with abundant CWD created by a tornado (unsalvaged plots) and plots where tornado-created CWD had been removed (salvaged plots). Species composition was similar between unsalvaged and salvaged plots, but more small mammals were captured on unsalvaged plots. Cotton mice *(Peromyscus* gossypinus) were the most abundant species captured in all plots and were significantly more abundant in unsalvaged plots in every trapping period. Adult female *P.* gossypinus in unsalvaged plots had greater survival and were more likely to be in reproductive condition than adult females in salvaged plots. Southern short-tailed shrews (*Blarina carolinensis*) and cotton rats *(Sigmodon hispidus*) tended to be more abundant in unsalvaged plots. Fox squirrels *(Sciurus niger)*, the second most abundant species in salvaged plots, were never captured on unsalvaged plots. Large amounts of CWD improve habitat quality of pine forests for *P. gossypinus,* and CWD is probably an important habitat component for other species.

Key words: ***Peromyscus gossypinus, Blarina carolinensis, Sigmodon hispidus, Sciurus niger,*** coarse woody debris, reproduction

Coarse woody debris (CWD) is any standing dead tree (snag), downed bole, or downed large branch >10 cm in diameter (Harmon et al., 1986; Spies and Cline, 1988). Many mammals in forested ecosystems depend on CWD (Maser et al., 1979, 1988; Thomas et al., 1979). Cavities and loose bark of snags provide nesting and roosting sites; logs and large branches provide cover, nest sites, and travel routes. Invertebrates and fungi that invade logs and snags also may be important food sources for insectivores, omnivores, and mycophagists.

Several studies on the importance of CWD to small mammals have tested if small mammals selectively use logs over other substrates (Barnum et al., 1992; Graves et al., 1988; McMillan and Kaufman, 1995; Olszewski, 1968; Planz and Kirkland, 1992; Tallmon and Mills, 1994). For example, Tallmon and Mills (1994) found that 98% of radio-telemetry locations of California red-backed voles (*Clethrionomys californicus*) were associated with logs, although logs comprised only 7% of the home ranges of voles. Other investigators have tested if habitat use by and abundance of small mammals are correlated with presence or amount of CWD (Carey and Johnson, 1995; Goodwin and Hungerford, 1979; Gore, 1988; McComb and Rumsey, 1982; Nordyke and Buskirk, 1988; Seagle, 1985; Vickery and Rivest, 1992). Goodwin and Hungerford (1979) found that the abundance of deer ***mice (Peromyscus maniculatus)*** was almost perfectly correlated with abundance of CWD in ponderosa pine forests in Arizona. Carey and Johnson (1995) observed that abundance of CWD was a good predictor of the abundance of deer mice, Gapper's red-backed voles (C. *gapperi*), Trowbridge's shrews (*Sorex trowbridgii),* and shrew-moles *(Neurotrichus*

gibbsii) in the Olympic Peninsula, Washington.

Most studies of the importance of CWD to mammals have been conducted in the Pacific Northwest or the Northeast (e.g., Barry and Francq, 1980; Carey and Johnson, 1995; Corn et al., 1988; Gore, 1988; Graves et al., 1988; Planz and Kirkland, 1992; Tallmon and Mills, 1994). Little is known about the use or importance of CWD to mammals in the Southeast (Loeb, 1996). Further, although several studies have demonstrated a positive correlation between CWD and abundance of small mammals, population density is not an adequate indicator of habitat quality (Pulliam, 1988; Van Horne, 1983). Habitat quality can only be assessed by comparing survival and reproductive rates of animals in areas with different characteristics. Only Lee (1993, 1995) has examined the relationship between the abundance of CWD and demographic characteristics.

In September 1989, several tornados created large amounts of snags and downed logs in an extensive area of the Savannah River Site in South Carolina. Much of that CWD was salvaged within a short period of time. By comparing salvaged and unsalvaged areas, I was able to test experimentally if presence of large amounts of CWD significantly affected abundance and diversity of small mammals in maturing pine (*Pinus*) stands. I also compared reproduction and survival of the most abundant species, the cotton mouse (P. *gossypinus*), in areas with and without large amounts of CWD to fully assess the contribution of CWD to habitat quality.

MATERIALS AND METHODS

Study area and experimental design.-The study was conducted on the Savannah River Site, a National Environmental Research Park in Aiken and Barnwell counties, South Carolina. The ca. 80,000-ha site is in the Upper Coastal Plain Physiographic Province (Myers, 1986). Study plots were located on uplands and ridges where soils are generally sandy, well-drained, and infertile (Batson et al., 1985; Workman and McLeod, 1990). Study plots were within a 121-ha managed pine stand that was regenerated in 1958. The stand was predominantly longleaf pine (*P. palustris*), although loblolly pine (*P. taeda*) was found throughout.

Two 4-ha plots in each of two blocks were established in an area of the stand that received considerable tornado damage. The two plots in block 1 were adjacent to each other but separated by a dirt road. The two plots in block 2 were ca. 250 m apart. Salvage crews removed all the logs, snags, and debris created by the tornado from one randomly selected plot in each block (salvaged plots), and no material was removed from the other plot (unsalvaged plots). Downed logs or snags that were in the salvaged plots before the storm were not removed. Salvage operations were completed by January 1990. Much of the surrounding area was salvaged completely, burned in November 1990, and regenerated.

Small-mammal trapping.-Within each plot, one 7 by 7 trapping grid with 20-m spacing between traps was established. The grids were 40 m from borders of plots. One folding aluminum Sherman live trap (7.5 by 9.0 by 25.5 cm) and one Mosby wooden box trap (19 by 19 by 61 cm) were placed at each station in lines 1, 3, 5, and 7. A 19-1 pitfall trap was placed at each station on lines 2, 4, and 6. Because drift fences leading to the pitfalls could not be placed in unsalvaged plots due to the large amounts of debris, no drift fences were used in any of the plots.

Trapping was conducted for 8 consecutive nights in August and November 1990, February and May 1991, and January-February 1992 and for 9 consecutive nights in May 1992, January and April 1993, and February and May 1994. Trap sessions were centered on the new moon phase. Sherman traps and pitfall traps were baited with sunflower seeds, and box traps were baited with corn. Traps were checked each morning, and all captured animals were identified to species and sex, weighed, and toe-clipped for individual identification (Clemson University Animal Use Protocol No. 597, Clemson, SC). Age, reproductive condition, location and type of trap also were recorded. *Peromyscus* were considered adults if they had completed their post-juvenile molt (Layne, 1968) and cotton rats (*Sigmodon hispidus*) were classified as adults if they weighed >80 g (Chipman, 1965). Age classes of other species were based on a combination of body mass and pelage characteristics.

Five measures of persistence or survival were used: number of captures per individual, number of trapping periods in which each individual was captured, minimum number of trapping periods in which an animal was present (including periods when it was not captured), days between first and last capture, and resident versus transient (captured during ≥2 or <2 trapping periods, respectively). Animals first captured in May 1994 were not included in analyses.

Vegetative and CWD sampling.-Circular plots with 8-m radii (200 m^2) were established at each trap station. Species, diameter at breast height (dbh), crown layer (canopy or midstory), and stage of decomposition of all trees were recorded. Stages of decomposition followed those of Thomas et al. (1979) and ranged from 1 (healthy trees) to 9 (highly decomposed stumps). The length class (<2 m, 2-4 m, >4 m), diameter class (<20 cm, 20-30 cm, >30 cm), stage of decomposition (Maser et al., 1979), and presence or absence of a root mass were recorded for each log or large branch >1 m in length. Diameters of logs were measured at the midpoint.

Statistical analysis.-Captures of small mammals were too few, particularly in the beginning of the study, to allow statistical estimation of population abundance. However, because I was more concerned with differences in relative abundance between treatments than with actual abundance, I used number of individuals captured to evaluate importance of CWD. That method is valid for comparisons if probabilities of capture are equal between treatments (Lancia et al., 1994; Skalski and Robson, 1992). Homogeneity of capture probabilities was tested using methods of Skalski and Robson (1992:67-68). Further, number of trap nights for each grid and each trapping period were adjusted for number of sprung traps and non-target (non-mammal) captures (Nelson and Clark, 1973) and adjusted number of trap nights was used to verify that number of traps available was equal between treatments. The two trap sessions in 1990 were excluded from analyses because only two cotton mice and two eastern cottontails (*Sylvilagus floridanus*) were captured.

A two-way analysis of variance was used to test for differences between treatments in density of the overstory, midstory, snags, and logs; diameter of snags; and stage of decomposition of snags. Because data for each plot consisted of 49 subsamples, preliminary tests of significance were performed to determine the appropriate error term to use for hypothesis testing (Ostle, 1963). The sampling error term was used to test for treatment effects when it was greater than the experimental error term. In contrast, the experimental error term was used to test for treatment effects when it was greater than the sampling error term (i.e., there was a significant treatment by block effect). Two-way analysis of variance with treatment and trapping period as main effects was used to test for differences in number of available traps (adjusted trap-nights), body weight, and number of individuals captured per trapping period. A least significant difference (LSD) test (SAS Institute Inc., 1990) was used to test for specific differences among trapping periods. Differences in the total number of animals captured were examined with t-tests. Treatment means ± 1 ***SE*** are presented.

I used G-tests of independence (SAS Institute Inc., 1990) to test for differences between treatments in distribution of logs among length and diameter classes, distribution of logs among stages of decomposition, and number of logs with root masses. G-tests of independence also were used to test if age ratios, sex ratios, number of residents, and reproductive activity of cotton mice differed between treatments. Data were pooled across plots within treatments after examination to determine if pooling was justified. There were only two cases in which there were significant differences between plots within treatments, and because sample sizes prior to pooling were small, these differences probably had little influence on pooled results. Age and sex ratios were based on first captures only. Chi-squared tests were used to test if sex ratios of cotton mice in each treatment differed significantly from a 1:1 ratio. Wilcoxon two-sample tests were used to determine if measures of survival varied between treatments. A significance level of $P \leq 0.05$ was used for all tests.

RESULTS

Characteristics of canopy, midstory, and CWD.—Pines **were the dominant canopy trees in all plots, and density of canopy pines did not differ significantly between**

TABLE *1.-Density (number of stems per 200 m^2) of live trees >10 cm diameter at breast height (dbh); density, dbh, and decomposition stage of snags >10 cm dbh; and density of logs >1 m in length and >10 cm in diameter at the midpoint in salvaged and unsalvaged plots on the Savannah River Site, South Carolina. Means ± 1* SE, *the F-statistic comparing differences between treatments, and the probability* (P) *of a greater* F *are presented.*

Habitat characteristic	Salvaged	Unsalvaged	*F*	*d.f.*	*P*
Density of canopy pines	3.70 ± 0.18	3.89 ± 0.26	1.39	1,192	0.24
Density of canopy hardwoods	0.16 ± 0.09	0.19 ± 0.95	0.07	1,192	0.79
Density of midstory pines	0.20 ± 0.06	0.52 ± 0.11	6.38	1,192	0.01
Density of midstory hardwoods	0.24 ± 0.08	0.02 ± 0.01	1.21	1,1	0.57
Density of total midstory	0.45 ± 0.10	0.54 ± 0.11	0.40	1,192	0.53
Density of snags	0.40 ± 0.08	1.19 ± 0.13	4.69	1,1	0.27
Diameter of snags (cm)	25.04 ± 1.25	26.08 ± 0.66	0.42	1,192	0.52
Mean stage of decomposition	5.24 ± 0.16	5.66 ± 0.13	4.06	1,192	0.04
Density of logs	2.04 ± 0.18	6.55 ± 0.31	7.26	1,1	0.23

treatments (Table 1). Longleaf pine constituted 97.8%, 94.0%, and 85.1% of the canopy pines in salvaged plot 1, salvaged plot 2, and unsalvaged plot 1, respectively. In unsalvaged plot 2, loblolly pine was the dominant pine and constituted 63.5% of the canopy pines. Hardwood species found in the canopy were black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), sweet gum (*Liquidambar styraciflua*), and black jack oak (*Quercus marilandica*); the density of canopy hardwoods did not differ between treatments (Table 1). The midstory was relatively sparse in all plots. Density of midstory pines was significantly greater in unsalvaged plots than in salvaged plots, but density of midstory hardwoods and total midstory density did not differ between treatments (Table 1). Hardwood species found in the midstory were black cherry, black gum, sweet gum, mockernut hickory (*Carya tomentosa*), and white oak (*Quercus alba*). Eastern red cedar (*Juniper-us virginiana*) also was found in the midstory.

There were significant treatment by block effects in density of both snags and logs. Consequently, although densities of snags and logs in unsalvaged plots were about three times greater than in salvaged plots, they did not differ statistically (Table 1). Mean snag densities per 200 m^2 were 0.41 ± 0.11, 0.39 ± 0.10, 0.84 ± 0.15, and 1.55 ± 0.19, and mean log densities per 200 m^2 were 2.37 ± 0.26, 1.71 ± 0.25, 5.20 ± 0.42, and 7.90 ± 0.36 in salvaged plot 1, salvaged plot 2, unsalvaged plot 1, and unsalvaged plot 2, respectively. Snags in unsalvaged plots were in a greater stage of decomposition than those in salvaged plots (Table 1) primarily because number of snags with broken tops (stage 6) was greater in unsalvaged plots. Only 4 of 37 snags (9.8%) in salvaged plots had cavities, and only 2 of 115 snags (1.7%) in unsalvaged plots had cavities.

Although density of logs did not differ between treatments, distribution of logs among various size classes differed significantly between salvaged and unsalvaged plots. Salvaged plots were dominated by logs in the mid-length class; unsalvaged plots were dominated by logs in the largest length class (G = 152.83, *d.f.* = 2, P < 0.001; Fig. 1a). Similarly, most logs in salvaged plots were in either the <20 cm diameter class or the 20-30 cm diameter class and most logs in unsalvaged plots were in the 20-30 cm class and the >30 cm class (G = 81.60, *d.f.* = 2, P < 0.001; Fig 1b). More logs in salvaged plots were in the later stages of decomposition; logs in unsalvaged plots were primarily in the first and second stages of decay (G = 199.42, *d.f.* = 3, P < 0.001; Fig. 1c). Fewer logs in salvaged than unsalvaged plots had root mass-

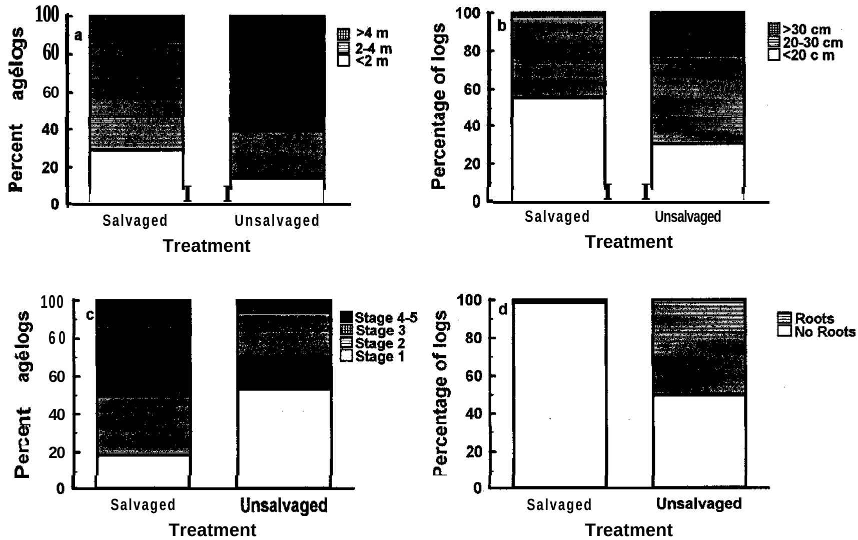

FIG. 1.-Percentage of logs in salvaged and unsalvaged plots in each a) length class, b) diameter class, c) stage of decomposition, and d) with and without root boles.

es ($G = 202.88$, *d.f.* = 1, $P < 0.001$; Fig. 1d).

Trappability-Trappability of all mammals and of cotton mice did not differ between treatments in any trapping period or for all trapping periods combined (all $P > 0.35$). Further, number of adjusted trap nights did not vary between treatments (Sherman traps, $F = 0.41$, *d.f.* = 1,16, $P = 0.53$; box traps, $F = 0.00$, *d.f.* = 1,16, $P = 0.98$). Number of available Sherman traps ($F = 3.59$, *d.f.* = 7,16, $P = 0.02$) and box traps ($F = 25.63$, *d.f.* = 7,16, $P = 0.0001$) varied with trapping period. However, the trapping period by treatment interactions were not significant for either Sherman traps ($F = 0.49$, *d.f.* = 7,16, $P = 0.83$) or box traps ($F = 0.67$, *d.f.* = 7,16, $P = 0.70$). Therefore, capture data were not adjusted for number of available traps or trappability. Mean number of adjusted Sherman trap nights per trapping period was 223.8 ± 3.1 for salvaged grids and 227.2 ± 3.1 for unsalvaged grids. Mean number of adjusted box trap nights per trapping period was 232.5 ± 1.9 for salvaged grids and 232.6 ± 1.9 for unsalvaged grids.

Species composition and *abundance of small mammals*.-A total of 289 small mammals was captured during the study. Cotton mice were most numerous and accounted for the majority of individuals captured on each plot (Table 2). Fox squirrels (*Sciurus niger*) were the second most common species in salvaged plots but made up only 7.3% of the individuals captured in these plots. Cotton rats were the second most common species found in unsalvaged plots and comprised 11.3% of the individuals in those plots. Species richness was similar between treatments (10 for salvaged plots and 9 for unsalvaged plots). All species except three were captured in both treatments; fox squirrels and golden mice (*Ochrotomys nuttalli*) were captured only in salvaged plots, and the long-tailed weasel (*Mustela frenata*) was captured only in an unsalvaged plot. Captures of short-tailed shrews (*Blarina carolinensis*) were few in both treatments but were greatest on one of the unsalvaged plots (Table 2). Seven individuals (6 cotton mice and 1 fox squirrel) were captured in more than one plot. Five of the cotton mice were captured originally in unsalvaged plots and moved to salvaged plots, and the sixth cotton mouse moved

TABLE 2.—*Number (and percentage) of individuals by species captured on salvaged (SI and S2) and unsalvaged (Ul and U2) plots from February 1991 through May 1994 on the Savannah River Site, South Carolina. Some individuals (I S.* niger *and 6 F! gossypinus) were captured on more than one plot.*

Species	Plot			
	S1	s2	U1	u2
Blarina carolinensis	1 (2.1)	3 (4.8)	10 (10.1)	3 (3.4)
Cryptotis parva	1 (2.1)	2 (3.2)	1 (1.0)	0 (0.0)
Sylvilagus floridanus	2 (4.2)	0 (0.0)	3 (3.0)	1 (1.1)
Glaucomys volans	0 (0.0)	2 (3.2)	1 (1.0)	1 (1.1)
Sciurus niger	6 (12.5)	3 (4.8)	0 (0.0)	0 (0.0)
Neotoma floridana	1 (2.1)	3 (4.8)	0 (0.0)	3 (3.4)
Ochrotomys nuttalli	0 (0.0)	3 (4.8)	0 (0.0)	0 (0.0)
Peromyscus polinotus	2 (4.2)	1 (1.6)	1 (1.1)	1 (1.2)
Peromyscus gossypinus	35 (72.9)	42 (67.7)	75 (75.8)	64 (73.6)
Sigmodon hispidus	0 (0.0)	3 (4.8)	8 (8.1)	13 (14.9)
Mustela frenata	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.1)
Total	48	62	99	87

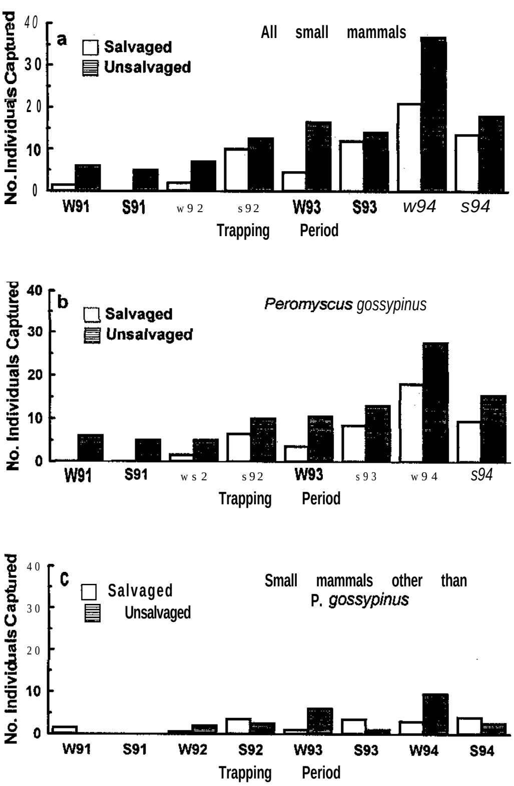

FIG. 2.-Mean number of a) all small mammals, b) cotton mice, and c) mammals other than cotton mice captured on salvaged and unsalvaged plots from winter 1991 through spring 1994.

from a salvaged to an unsalvaged plot. The fox squirrel moved from salvaged plot 1 to salvaged plot 2.

Mean number of small mammals captured per grid was greater in unsalvaged (93.0 ± 6.0) than salvaged plots (55.0 ± 7.0; t = 4.12, *d.f.* = 2, *P* = 0.05). The greater number of cotton mice in unsalvaged plots (69.5 ± 5.5) than salvaged plots (38.5 ± 3.5; t = 4.75, *d.f.* = 2, *P* = 0.04) was the primary reason for that difference. Total number of mammals (*F* = 13.12, *d.f.* = 7, 15, *P* = 0.0001) and number of cotton mice (*F* = 10.08, *d.f.* = 7, 15, *P* = 0.001) captured per trapping period varied among trapping periods (Fig. 2). However, total number of small mammals (*F* = 14.71, *d.f.* = 1,15, *P* = 0.002) and number of cotton mice (*F* = 13.96, *d.f.* = 1,15, *P* = 0.002) captured per trapping period were greater in unsalvaged than in salvaged plots and that difference was consistent among trapping periods (i.e., the interaction terms were not significant, *F* = 1.07, *d.f.* = 7,15, *P* = 0.43 and *F* = 0.22, *d.f.* = 7,15, *P* = 0.97; Fig. 2).

Demographics of populations of cotton mice.-Twelve (15.6%) of the cotton mice in salvaged plots and 14 (10.1%) of the cotton mice in unsalvaged plots were subadults

TABLE 3.—*Indices of survival for* F! gossypinus *on salvaged and unsalvaged plots.*

	Males				Females			
	Salvaged		Unsalvaged		Salvaged		Unsalvaged	
Index of survival	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Total no. captures	2.64	0.37	3.10	0.26	2.77	0.35	2.71	0.28
No. periods captured	1.42	0.12	1.38	0.06	1.14	0.06	1.29	0.07
Total no. periods present	1.61	0.18	1.39	0.08	1.14	0.06	1.35	0.07
Days between first and last capture	75.9	25.2	59.4	13.5	15.4	5.6	36.1	8.6

when first captured, and the ratio of adults to subadults did not differ between treatments (G = 1.38, *d.f.* = 1, *P* = 0.24). Sex ratio (M:F) of adults in salvaged plots was 1:0.97 (*n* = 65) and did not differ from a 1:1 ratio (χ^2 = 0.015, *d.f.* = 1, *P* = 0.90). Sex ratio of adults in unsalvaged plots was 1:0.62 (*n* = 125) which was marginally different from 1:1 (χ^2 = 3.36, *d.f.* = 1, *P* = 0.07). However, sex ratios of adults did not differ significantly between treatments (G = 2.05, *d.f.* = 1, *P* = 0.15).

Because no cotton mice were captured on salvaged plots in 199 1, only data from 1992 through 1994 were included in the analysis of body mass, and only body masses of individuals at first capture as adults were included. Data for males and females were combined because body masses of males and females did not differ in salvaged (*F* = 0.27, *d.f.* = 1, 52, *P* = 0.60) or unsalvaged (*F* = 0.18, *d.f.* = 1, 97, *P* = 0.67) plots. Mean body mass was 24.8 ± 0.6 g in unsalvaged plots and 23.6 ± 0.8 g in salvaged plots and ranged from 22.2 ± 0.9 g in spring 1993 to 26.6 ± 1.1 g in winter 1993. Body mass of cotton mice did not differ between treatments (*F* = 2.04, *d.f.* = 1, 161, *P* = 0.15) but differed among trapping periods (*F* = 3.03, *d.f.* = 5, 161, *P* = 0.01). Body mass in winter 1992 and winter 1993 was greater than body mass in spring 1992 and spring 1993 ($P < 0.05$). Body mass in spring 1994 did not differ from any other trapping season, and body mass in winter 1994 was significantly lower than body mass of animals captured in winter 1993 but did not differ from any other trapping period.

Median number of captures per individual, median number of trapping periods in which an animal was captured, and median number of days between first and last captures did not differ between treatments for either males or females (Wilcoxon two-sample tests, $P > 0.10$; Table 3). However, median number of trapping periods in which a female was assumed to be present on a grid (whether she was captured or not) was greater in unsalvaged than salvaged plots (*Z* = 1.94, *P* = 0.05). Median number of trapping periods in which males were assumed to be present did not differ between treatments (*Z* = 0.63, *P* = 0.53). Proportion of males classified as residents did not differ between salvaged and unsalvaged plots (G = 0.016, *d.f.* = 1, *P* = 0.90). Thirty-four percent of males (26 of 76) in unsalvaged plots and 35.5% of males (11 of 31) in salvaged plots were residents. More females were classified as residents in unsalvaged plots (17 of 52, 32.7%) than in salvaged plots (5 of 35, 14.3%; G = 3.96, *d.f.* = 1, *P* = 0.05).

When only first captures of animals on a plot were used in the analysis, reproductive activity among females in unsalvaged plots (16 of 48, 33.3%) tended to be greater than reproductive activity of females in salvaged plots (5 of 32, 15.6%; G = 3.26, *d.f.* = 1, *P* = 0.07). When first captures for each trapping period were used in the analysis, reproductive activity among females in unsalvaged (20 of 54, 37.0%) plots was greater than reproductive activity in salvaged plots (6 of 37, 16.2%; G = 4.90, *d.f.* = 1, $P = 0.03$). Reproductive activity among males did not differ significantly between treatments when either first captures (G = 0.02, *d.f.* = 1, $P = 0.89$) or monthly captures (G = 0.02, *d.f.* = 1, $P = 0.90$) were considered. Reproductive activity among males was 27.3% (9 of 33) in salvaged plots and 26.0% (20 of 77) in unsalvaged plots for first captures and 34.8% (16 of 46) and 33.7% (32 of 95) for monthly captures.

DISCUSSION

Study plots used to test effects of CWD on small mammals differed primarily in the treatment that they received (salvaged or unsalvaged) following the tornado. Because the study was conducted within one large stand, defined as an aggregation of trees or other vegetation that was relatively homogenous in terms of composition, age structure, arrangement, and conditions (Anderson and Smith, 1976), composition and structure of the live vegetation, management history, natural disturbance history, and soil type were similar between treatments. Although densities of logs and snags were three times higher in unsalvaged plots than salvaged plots, those differences were not statistically significant due to the significant block by treatment effects, probably caused by spatial variability in damage by the tornado. However, differences in CWD between treatments were likely biologically significant, particularly because logs in unsalvaged plots were larger in diameter and length (i.e., volume of CWD in unsalvaged plots was likely greater). While differences in responses of small mammals to treatments could have resulted from disturbance caused by salvage crews and not differing levels of CWD, removal of CWD was completed 6 months before the first trapping period and 4.5 years before the end of the study. Populations of small mammals were very low in all study plots during 1990 suggesting that large-scale disturbances created by the tornados may have had a negative effect on small mammals throughout the area but those in areas with larger amounts of CWD appeared to recover more quickly.

Presence of large amounts of CWD affected species composition of plots. Although cotton mice were the dominant species in both treatments and most other species also were captured in both salvaged and unsalvaged plots, fox squirrels, the second most abundant species in salvaged plots, were never captured in unsalvaged plots. Fox squirrels in the southeastern United States prefer areas with little or no understory and avoid areas with a brushy understory because of their relatively large body size and low agility (Taylor, 1973; Weigl et al., 1989). Fox squirrels also spend a considerable amount of time on the ground, and a brushy understory makes detection and evasion of predators more difficult (Taylor, 1973). Thus, the large amount of downed logs and branches in unsalvaged plots may have made movement and visibility more difficult for fox squirrels, resulting in their apparent avoidance of those plots.

Abundance of small mammals was significantly greater in unsalvaged plots than in salvaged plots. Most of that difference resulted from a strong positive response of cotton mice to abundant CWD, although cotton rats and short-tailed shrews also contributed to that difference. Almost twice as many cotton mice were captured on unsalvaged plots, and cotton mice were more abundant in unsalvaged plots in every trapping period. Although no other studies have examined specifically the relationship between cotton mice and CWD, Pournelle (1952) noted that cotton mice in Florida were more abundant in moist hammock habitats with many logs and hollow trees than in other types of habitats. In addition, Bigler and Jenkins (1975) noted that cotton mice are more abundant in mature hammocks with many snags and logs than in younger hammocks with fewer logs and snags.

Demographic characteristics of cotton mice in salvaged and unsalvaged plots indicate that presence of large amounts of CWD significantly improves quality of pine stands as habitat for cotton mice. While persistence or reproductive potential of adult males did not differ between the two treatments, adult females were more likely to be residents and more likely to breed in unsalvaged than salvaged plots. At the onset of the study, number of cotton mice was low in all plots, and none were captured in salvaged plots until winter 1992. Although number of mice captured in all plots increased steadily throughout the study, the increase in abundance of cotton mice was greater and more rapid in unsalvaged plots than salvaged plots, perhaps as a result of the greater persistence and reproduction of females in those plots.

The large number of logs and snags in unsalvaged plots likely improved quality of the pine forest for cotton mice by increasing number of nest sites, amount of cover, number of travel routes, and food supply, particularly invertebrates. Under laboratory conditions, cotton mice nest in elevated sites (Taylor and McCarley, 1963), but in natural conditions, nest-site selection may depend on habitat. In mesic and hydric hammocks and hardwood swamps in Florida, cotton mice primarily nest in logs (Ivey, 1949; Pearson, 1954), but in upland slash pine-turkey oak (*P. elliottii/Q. laevis*) communities, cotton mice primarily nest in tortoise burrows and ground holes (Frank and Layne, 1992). The longleaf-pine stand where my study was conducted was similar to slash-pine stands studied by Frank and Layne (1992). However, gopher tortoises were not present on the Savannah River Site; thus logs, snags, and root masses created by the tornado probably greatly increased number of high-quality nest sites in unsalvaged plots.

Logs in unsalvaged plots also may have provided needed cover from predators and elements to cotton mice because ground cover in managed pine stands is typically scarce and consists mostly of a thick layer of pine needles. Thus, mice in unsalvaged plots may have been able to forage more efficiently and over a wider area while decreasing their risk of predation. Others have hypothesized that the similar white-footed mice (P. *leucopus*) use logs and other ground structures, such as rocks, as travel routes to reduce predation risk because traveling on these structures is quieter (Barnum et al., 1992; Fitzgerald and Wolff, 1988; Planz and Kirkland, 1992) and faster (McMillan and Kaufman, 1995).

Logs and snags also are important structures for a wide variety of invertebrates (Caldwell, 1996; Hanula, 1996; Hendrix, 1996). Cotton mice are omnivores (Wolfe and Linzey, 1977), but Calhoun (1941) found that 68% of the diet of cotton mice in Tennessee was animal matter, primarily Coleoptera, Lepidoptera, and Araneida. Large amounts of CWD in unsalvaged plots probably increased populations of invertebrates, thus increasing availability of a high-quality food source. Data on effects of additional food on populations of cotton mice are limited; however, McCarley (1954) found that 80% of the cotton mice living near a pile of dumped grain in eastern Texas were in reproductive condition but reproduction was at low levels in nearby populations. Young and Stout (1986) also found that reproduction of cotton mice in Florida was somewhat elevated compared with controls when food was added in experimental plots.

Logs in unsalvaged plots were larger in both length and diameter, in earlier stages of decomposition, and more likely to have their root masses attached than logs in salvaged plots. Those differences probably influenced suitability of unsalvaged sites for cotton mice. For example, white-footed mice prefer to travel along larger diameter logs (Barnum et al., 1992), and captures of California red-backed voles are correlated positively with log length, diameter, and overhang area (Hayes and Cross, 1987). Although white-footed mice in hardwood forests of Minnesota and Maryland (Barnum et al., 1992) and California red-backed voles in a southwestern Oregon Douglas-fir forest (Tallmon and Mills 1994) preferred logs in late stages of decay, deer mice and California red-backed voles showed no preference based on stage of decomposition in conifer forests of Oregon (Hayes and Cross, 1987). Thus, it is difficult to determine how state of decomposition of logs might have affected use of treatment plots by cotton mice in my study. However, abundance of root masses in unsalvaged plots likely improved habitat quality for mice because recent work on white-footed mice in the southern Appalachians Mountains and cotton mice on the Savannah River Site indicate that root masses and holes created by their uprooting may be important nest sites and escape areas for both species (C. Greenberg and T. McCay, pers. comm.).

Southern short-tailed shrews and cotton rats tended to be more abundant in unsalvaged than salvaged plots, but small numbers of captures of those species precluded making conclusions about their responses to treatments. Although a few studies reported a positive relationship between density of logs and abundance of and habitat use by northern short-tailed shrews (B. *brevicauda*—McComb and Rumsey, 1982; Seagle, 1985), few data are available on the relationship between CWD and southern short-tailed shrews. Cotton rats usually are found in grass-dominated habitats (Cameron and Spencer, 1981), and I am unaware of any studies that have associated presence or abundance of cotton rats with CWD. However, based on the data in my study, future studies should explore the contribution of CWD to habitat quality for those small mammals.

Abundance of CWD in unsalvaged plots probably was greater than that typically found in southeastern pine forests. Nonetheless, results of my study clearly illustrate that CWD is an important habitat component for some southeastern small mammals and should be included in future studies of habitat selection and population dynamics. Relative importance of characteristics of CWD, such as size and state of decomposition, and relative importance of logs versus snags also need further investigation.

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