Soricid Response to Canopy Gaps Created by Wind Disturbance in the Southern Appalachians

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Abstract - We used drift fences with pitfall traps to compare soricid abundance, richness, and demographic parameters among intact multiple-tree windthrow gaps, salvaged gaps, and mature forest in a xeric southern Appalachian forest type during 1997–1999. We also tested whether capture rates were correlated with rainfall, and whether similar-sized species did not co-occur as predicted by multi-species assemblage rules. We captured six species: *Blarina brevicauda* (Say) (northern short-tailed shrew), *Cryptotis parva* (Say) (least shrew), *Sorex cinereus* Kerr (masked shrew), *S. fumeus* G.M. Miller (smoky shrew), *S. hoyi* Baird (pygmy shrew), and *S. longirostris* Bachman (southeastern shrew). Tree basal area, forest structural features, and arthropod abundance differed among treatments, but species richness and abundance of most shrews did not. Captures during June–October were higher in 1998 than in 1997, although 1998 summer rainfall was low. Rainfall was correlated with shrew activity, but explained little of the variability in capture rates ($r^2 = 0.05$). The sex ratio within each species was similar among gap treatments and controls, but differed from 1:1 for *S. hoyi*, *S. longirostris,* and *S. fumeus*. The soricid assemblage did not conform to multi-species assemblage rules; three small-bodied species co-occurred in similar numbers at all study sites. Our results suggest that forest management that mimics conditions created by multiple windthrows in xeric forest of the southern Appalachians is unlikely to affect shrew communities adversely, at least in the short-term.

Introduction

Species richness of shrews in the southern Appalachians is among the highest in temperate North America (Laerm et al. 1999), and several species are abundant in temperate forest ecosystems (Kirkland and Sheppard 1994). However, because of the labor-intensive methods required to capture shrews and lack of standardized sampling techniques, their perceived importance, distribution, relative abundance, natural history, habitat relationships, and response to forest management practices remain poorly understood (Ford and Rodrigue 2001, Kirkland and Snoddy 1999).

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Moisture is thought to be a "principal factor in determining regional diversity, and by extension, local diversity of shrews" (Kirkland 1991). Ford et al. (in press) reported that in the southern Appalachians, species richness of shrews increases with elevation and in mesic forest types. However, the relationship between moisture and shrew richness and abundance is based primarily on observation and correlation; it has not been tested experimentally. If shrews require high moisture levels (Getz 1961, Kirkland 1991), they presumably would be sensitive to disturbances that cause partial or complete forest canopy removal, such as timber harvesting or multiple-tree windthrows that reduce shade and forest floor moisture (Ford et al. 1997). Yet, results of studies that address soricid response to silvicultural disturbance are equivocal. Some indicate that shrew abundance increases shortly after timber harvests (Ford et al. 2000, Healy and Brooks 1988, Kirkland 1990), whereas others report no short-term changes (Ford and Rodrigue 2001, Klein and Michael 1984).

Several studies suggest that abundance of invertebrate prey may affect shrew species richness and numbers (Healey and Brooks 1988; Kirkland 1990, 1991). Both moisture (Kirkland 1991) and coarse woody debris (CWD) (Maser et al. 1979) may play an indirect role in shrew diversity or abundance by affecting their invertebrate prey populations (Kirkland 1991). However, we have found no studies that test directly whether the abundance of invertebrate prey affects shrew abundance.

Shrews use CWD for feeding substrate and cover (Lee 1995, Loeb 1996, Raphael 1988). Several studies have explored relationships between shrew abundance and CWD or other microhabitat features, but results are also equivocal. For example, some studies report a positive relationship between CWD and shrew captures (Kitchings and Levy 1981, Loeb 1999, McComb and Rumsey 1982, Seagle 1985), whereas others have found little or no relationship (Ford and Rodrigue 2001, Getz 1961, McCay et al. 1998). Associations between shrews and specific forest structural features, such as CWD, do not necessarily indicate that the presence of such features enhances reproduction or survival (Van Horne 1983). Other variables, such as sex ratios and evidence of reproduction also provide clues as to whether an area is functioning as a "source" or "sink" (Pulliam 1988).

Few studies have linked shrew abundance to CWD using controlled experimental designs. Lee (1995) reported that some Pacific Northwest shrew species were more abundant and had higher reproductive rates in sites with high CWD levels; one species was more abundant in sites with low CWD levels. Loeb (1999) found a greater abundance of *B.*

carolinensis (Bachman 1837) (southern short-tailed shrew) in South Carolina pine plantations with relatively higher CWD levels.

Factors other than moisture and forest structure might affect the distribution of shrew species at the landscape level. Fox and Kirkland (1992) predicted that similar-sized shrews are less likely to co-occur than shrews of different sizes because of competitive exclusion. Ford et al. (in press) found that these "multi-species assemblage" rules are most likely to deviate from predicted assemblages in xeric forests.

Treefall gaps generate large volumes of CWD and simultaneously increase light levels reaching the forest floor. Microhabitat features that potentially affect shrews, such as cover and depth of the leaf litter and humic mat, could result from gap-induced changes in light and forest floor temperature. Salvage-logging, or tree removal from gaps further increases light levels reaching the forest floor, and heavy equipment alters leaf litter and soil properties. Slash left onsite after logging operations increases woody debris. In intact and salvage-logged gaps, changes in primary productivity due to greater light penetration and forest floor features such as leaf litter or CWD also could lead to changes in arthropod prey abundance. Currently, many forest managers use an ecosystem management approach by attempting to mimic natural disturbance. Treefall gaps are a common disturbance type in the southern Appalachians (Greenberg and McNab 1998), yet we are unaware of studies that examine soricid communities in treefall gaps or other naturally disturbed sites.

On 5 October 1995, Asheville, NC, was hit by the remnants of Hurricane Opal. Downbursts of wind created at least thirty 0.1 to 1.5-ha gaps within the Bent Creek Experimental Forest (BCEF) study area, primarily by uprooting large trees. Gaps were irregularly shaped, and retained partial canopy cover. Tree density decreased by 19–39%, and basal area (BA) by 30–52% in measured gaps (Greenberg and McNab 1998). Several gaps were salvage-logged during 1996–1997; others were left intact with fallen trees remaining in place. This allowed us to test experimentally hypotheses regarding the relationships between shrew abundance and forest structure, invertebrate prey, and moisture. Specifically, we tested whether the relative abundance, species richness, and sex ratios of shrews differed among intact (unsalvaged) gaps, salvaged gaps, and mature closed-canopy forest with different amounts of invertebrate prey and structural features such as CWD, light, and leaf litter. We also tested whether similar-sized shrews do not co-occurr, as predicted by multi-species assemblage rules, and if rainfall has a direct, positive effect on shrew capture rates.

Methods

Study area

The Bent Creek Experimental Forest encompasses a 2500-ha watershed in the Blue Ridge physiographic portion of the southern Appalachian mountains in Buncombe County, NC. Annual precipitation averages 120 cm and is evenly distributed year-round. Elevation within the watershed ranges from about 610–1070 m, and study sites range from 670–730 m. Winters are short and mild, and summers are long and warm. Common tree species on xeric sites, such as those used in this study, include *Quercus coccinea* (Meunchh.) (scarlet oak), *Q. alba* L.(white oak), *Q. prinus* L. (chestnut oak), *Q. velutina* Lam. (black oak), *Acer rubrum* L.(red maple), *Cornus florida* L.(flowering dogwood), *Nyssa sylvatica* Marshall (blackgum), *Oxydendrum arboreum* (L.) DC (sourwood), and occasional *Pinus echinata* Miller (shortleaf pine) (McNab 1996).

Study design

Treatments included intact gaps (those created by wind disturbance in 1995 and not salvage-logged), and salvage-logged gaps. Controls were mature (80–100 years old), closed canopy forest. Controls were adjacent to, but > 25 m from, intact gaps; salvaged gaps were ≤ 0.48 km from control-intact gap pairs. Salvaged gap sizes ranged from 0.52–1.50 ha, and intact gap sizes ranged from 0.15–1.09 ha. Salvage-logging during winter 1996–spring 1997 removed standing and fallen trees that were killed or heavily damaged by hurricane-related winds. One gap intended for inclusion within the salvaged treatment was not salvage-logged (hence, was "intact") until winter 1997. Therefore, in 1997 there were 5 intact gaps, 2 salvaged gaps, and 4 controls, but in 1998 and 1999 there were 4 intact gaps, 3 salvaged gaps, and 4 controls.

Pitfall trapping

Six 7.6-m long, 0.5-m high drift fences buried 5–12 cm into the ground were established at random locations and orientations within each site. Two 19-liter plastic paint buckets with 2-mm holes drilled into the bottom for drainage were sunk flush to the ground at both ends of each fence (n = 12 pitfalls per site). A sponge was placed in each bucket and dampened as necessary to reduce animal desiccation. All traps were shaded by squares of Masonite pegboard. Drift fences were more dispersed in larger gaps and controls than in small gaps, but all were within an area ≤ 0.5 ha; both gap treatments contained large and small gaps.

Traps were open and checked 3 times weekly from 28 May–23 October 1997, and from 2 June 1998–29 May 1999. Most shrews

(65%) were bagged, labeled by date and location, and frozen for later identification. Exceptions were live shrews (19% of total captures) that were recorded and released, and some dead shrews (16% of total captures) that were discarded in the field without positive identification. However, we believe that unidentified live and dead shrews likely represented a random subsample of species, and therefore did not bias our data. All shrews collected (65% of total captures) were measured (mass; total, tail, hind foot, and ear lengths), dried, de-fleshed in *Dermestes lardarius* L. (larder beetle) colonies and identified using keys to body measurement, dental, and cranial characters (Hall 1981, Junge and Hoffman 1981) in the laboratory. Graphs of total body length versus tail length, and of condylobasal length versus maxillary breadth, showed that 98% and 99% (respectively) of *S. longirostris* and *S. cinereus* specimens, the 2 species which could be most easily confused, fell into distinct clusters. We did not include the few specimens not falling into distinct clusters as known identifications. Sex and reproductive status (e.g., lactating; swollen testes) were determined by dissection if body condition was adequate. All shrew specimens were assigned a unique catalogue number and deposited in the Bob & Betsy Campbell Museum of Natural History at Clemson University (Accession # 868) after identification.

Habitat measurements

Percent cover of bare ground, leaf litter, humic mat, shrubs, herbaceous plants, CWD (≥ 12.5 cm diameter at contact point with line transect), and fine woody debris (FWD) (< 12.5 cm diameter) was measured in summer 1998 using five randomly located 15-m line transects in each site. Depth of the leaf litter and humic mat was measured at 0, 7.5, and 15 m along each line transect. We measured the length and diameter (at contact point with line transect) of each piece of CWD encountered along transects. We subjectively categorized wood decay as follows: 1 = no visible decay; 2 = slight decay; 3 = moderate decay; 4 = slight fragmentation evident; 5 = heavy fragmentation; 6 = completely disintegrated but still distinguishable as CWD (modified from Maser et al. 1979). We did not measure the size or abundance of rocks and boulders, but neither was a prominent feature of the study sites.

We determined percent light (the inverse of canopy cover) at 6–8 points ≥ 10 m apart, using a spherical densiometer held at breast height. We calculated the BA of live trees and snags using diameter at breast height (dbh) measurements of all trees ≥ 12.5 cm dbh within a single fixed, rectangular plot that was 0.1 ha in gaps (due to the size and shape restraints of gaps) and 0.2 ha in controls. For a detailed characterization of five intact gaps, including the four used in this study, see Greenberg and McNab (1998).

As part of a different study (Greenberg and Forrest 2003), ground-dwelling arthropods were collected from the same pitfall traps at 2-week intervals from June 1998–May 1999. Arthropods were identified to family, counted, ovendried, and weighed. Precipitation was measured daily at the Bent Creek Experimental Station campus, about 8 km from the most distant study site.

Statistical analysis

We used data of June–October 1997 and 1998 (equivalent trapping periods) in a repeated measures two-way analysis of variance (ANOVA) (SAS 1990) to test for differences in the relative abundance of each shrew species and all species combined among treatments, among years, and using a treatment x year interaction. However, we used only the 1998–1999 data for subsequent analyses because they encompassed a full year of trapping, and therefore, a longer trapping period. Data from 1997 were not comparable to 1998–1999 data because the trapping period was shorter and treatment sample sizes differed between those periods. We tested for differences in species richness and the proportion of males and females among treatments using one-way ANOVA.

We used Pearson Product-Moment Correlations (Zar 1984) to examine the relationship between cumulative rainfall during each 2–3 day period between trap-checks (trap-check interval) and the number of shrews captured per trap-check interval. We used only data during June–October 1997 and 1998 because some species appeared to exhibit lower activity levels in winter (see results). Correlations were performed on each species and for all shrews (species combined).

We used one-way ANOVA (SAS 1990) to test for differences in structural habitat features among treatments. Percentage data were square-root arcsine transformed prior to statistical testing. Because replication was unequal, we used least squares means tests for pairwise comparisons among treatments and years for all ANOVAs (SAS 1990).

Because there were no differences in the abundance of most species among gap treatments and controls, we combined all study sites (using species as the "treatment;" $n = 11$ sites) for a 1-way ANOVA with Tukey's test to determine whether some species were captured more often than others. We used a log-likelihood ratio G-test (Zar 1984) to determine whether the male:female ratio differed from 1:1 for species having an adequate sample size (all captures; $n > 25$). Significance is reported at $P < 0.05$ level unless otherwise specified.

Results

Pitfall trapping

We captured a total of 548 individuals of six shrew species during 67,056 trapnights (186 in 18,876 trapnights in 1997 and 362 in 48,180 trapnights in 1998–1999); 356 were identified to species (272 in 1998–1999). Shrew species captured were *Blarina brevicauda* (Say) (northern short-tailed shrew), *Cryptotis parva* (Say) (least shrew), *Sorex cinereus* Kerr (masked shrew), *S. fumeus* G.M. Miller (smoky shrew), *S. hoyi* Baird (pygmy shrew), and *S. longirostris* Bachman (southeastern shrew). Three talpid species also were captured, including *Condylura cristata* (L.) (starnose mole), *Scalopus aquaticus* (L.) (eastern mole), and *Parascalops breweri* Bachman (hairytail mole). Murids captured in pitfalls included *Microtus pennsylvanicus* (Ord) (meadow vole), *M. pinetorum* (Le Conte) (pine vole), *Peromyscus leucopus* (Rafinesque) (white-footed mouse), and *Ochrotomys nuttalli* (Harlan) (golden mouse). *Cryptotis parva* composed only 2.5% of the identified shrews; other species composed 15%–26% of identified captures.

Table 1. Mean number (± SE) of shrews captured from June–October, 1997 and 1998 using drift fences and pitfall traps in intact (n = 4) and salvage-logged gaps (n = 3), and forested controls (n = 4) at the Bent Creek Experimental Forest, Asheville, NC. Statistical results are for a repeated measures 2-way ANOVA using treatment (df = 2), year (df = 1), and treatment X year (df = 2) as factors. Different letters within rows (reported in top row only) indicate differences in relative abundance among treatments. Asterisks indicate the year in which more shrews were captured when differences between years were significant.

		Treatment						
Species	Year	Intact gap	Salvaged gap	Forested control	P_{trt}	P_{repeat}	P_{yr}	P_{trtXyr}
Blarina	1997	1.4 ± 0.9	2.5 ± 0.5	2.0 ± 0.6	0.2813	0.1620	0.4914	0.1813
brevicauda	1998	3.3 ± 0.9	2.3 ± 0.9	1.0 ± 0.7				
Cryptotis	1997	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1930	0.2221	0.0176	0.7978
parva	1998*	0.5 ± 0.3	1.0 ± 0.6	0.8 ± 0.3				
Sorex	1997	1.2 ± 0.4	0.5 ± 0.5	1.3 ± 0.6	0.1885	0.0610	0.0935	0.7947
cinereus	1998	4.0 ± 1.9	6.0 ± 4.6	4.3 ± 2.0				
S. fumeus	1997	2.8 ± 1.4	0.5 ± 0.5	4.0 ± 2.5	0.0747	0.0009	0.6960	0.4167
	1998	2.8 ± 2.1	1.7 ± 0.9	2.8 ± 2.4				
S. hoyi	1997	0.8 ± 0.4	1.5 ± 1.5	0.8 ± 0.5	0.7296	0.4805	0.3689	0.5487
	1998	1.8 ± 0.9	1.7 ± 0.9	2.0 ± 0.6				
S. longirostris	1997	1.2 ± 0.6^{a}	1.5 ± 0.5^{b}	0.5 ± 0.3^{a}	0.0176	0.0033	0.0002	0.0002
	1998*	1.0 ± 0.4	6.3 ± 2.7	1.3 ± 0.5				
Unidentified	1997	11.4 ± 4.3	5.5 ± 0.5	8.5 ± 3.9	0.8274	0.1582	0.3061	0.6216
	1998	5.3 ± 1.1	7.0 ± 2.0	6.5 ± 1.6				
Total	1997	18.8 ± 5.9	12.0 ± 0.0	17.0 ± 7.4	0.8479	0.0431	0.4358	0.7263
	1998	18.5 ± 3.9	26.0 ± 5.2	18.5 ± 4.9				

June–October captures of *C. parva*, *S. longirostris*, and (marginally) *S. cinereus* were greater in 1998 than in 1997 (Table 1). There was no treatment effect on total shrew captures ($P = 0.8479$) or for any species ($P > 0.05$) except *S. longirostris,* which was more abundant in salvaged than intact gaps or controls ($P = 0.0176$; Table 1). *Sorex fumeus* was marginally ($P = 0.0747$) less abundant in salvaged gaps than in intact gaps. A repeated measures effect was detected for total shrews, and for

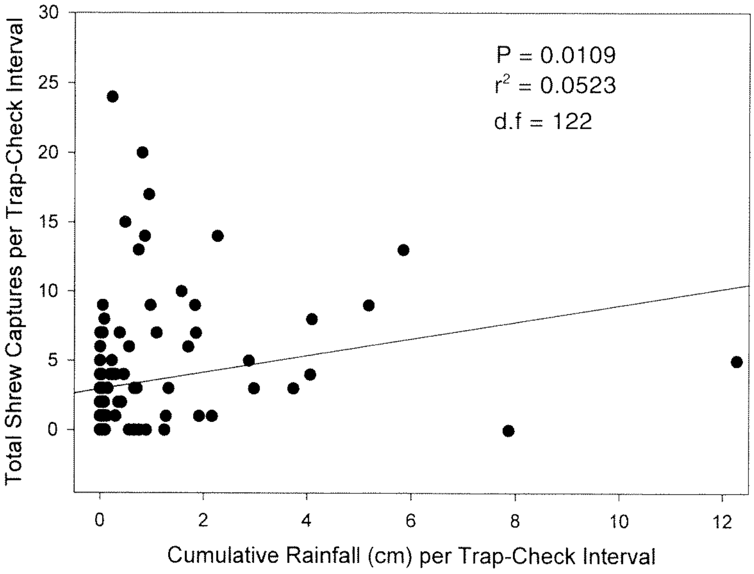

Figure 1. Relationship between cumulative rainfall per trap-check interval and total number of shrews captured per trap-check interval during June–October 1997 and June–October 1998 at the Bent Creek Experimental Forest, Asheville, NC.

Table 2. Mean (± SE) number of shrews captured per study site ($n = 11$), and male:female (M:F) sex ratio (N), June 1998–May 1999, Bent Creek Experimental Forest, Asheville, NC. Different letters among rows indicate that capture rates differed significantly ($P < 0.05$) among the species (using 1-way ANOVA). Asterisks beside sex ratios indicate that the sex ratio differs significantly from 1:1 using log-likelihood ratio for contingency tables, or G-test (* indicates $P < 0.025$; ** indicates $P < 0.0001$).

Species	Mean (± SE) captures/site	M:F
Blarina brevicauda	$3.1 \pm 0.6^{a,b}$	1.23 (29)
Cryptotis parva	0.8 ± 0.2^{b}	–
Sorex cinereus	7.2 ± 1.9^{a}	0.97 (67)
S. fumeus	$4.3 \pm 1.4^{a,b}$	0.45 (42)*
S. hoyi	$5.4 \pm 0.9^{a,b}$	3.08 (49)**
S. longirostris	$4.0 \pm 1.2^{a,b}$	3.63 (37)**

some species, suggesting that repeated trapping within sites affected capture rates between years (Table 1).

No treatment effect was detected for total shrew captures or for any species, including *S. longirostris* (P = 0.1066) and *S. fumeus* (P = 0.9725), using only data for the full year capture period (June 1998–May 1999; one-way ANOVA). Species richness of shrews did not differ among treatments (P = 0.9140) (mean range ± SE was 5.5 ± 0.3 to 5.7 ± 0.3).

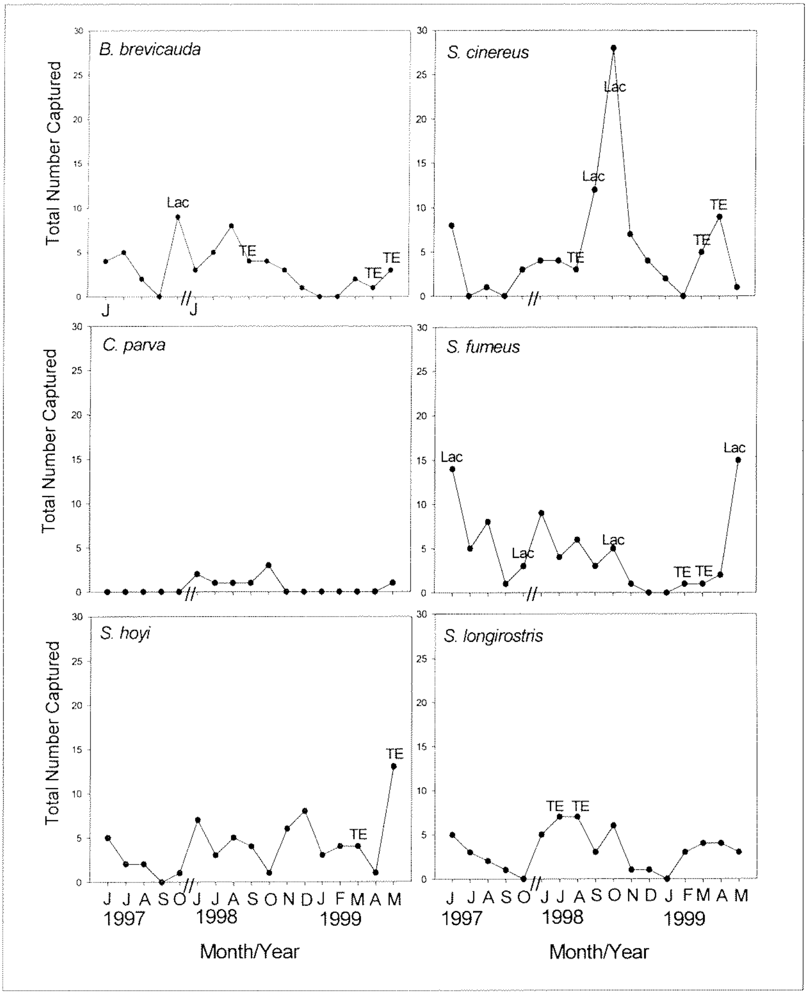

Figure 2. Total monthly capture rates of six soricid species using drift fences and pitfall traps (67,056 total trapnights at 11 sites including intact gaps, salvaged gaps, and forested controls) during June–October 1997 and June 1998–May 1999 at the Bent Creek Experimental Forest, Asheville, NC. Lac = lactating female; TE = testes enlarged.

Annual precipitation at the study area was 124.1 cm in 1997, 129.6 cm in 1998, and 112.3 cm in 1999. Precipitation during June–October, the study period that was compared between years, was 61.1 cm in 1997, but only 29.1 cm in 1998. This was extremely low compared to the average 1971–2000 rainfall of 49.4 cm for that period (National Climatic Data Center, ncdc.info@noaa.gov). Total June–October shrew captures per trap-check interval was correlated with cumulative rainfall per trap-check interval ($P = 0.0109$; $r^2 = 0.0523$; $d.f._{total} = 122$) (Fig. 1). No correlations were significant when performed separately by species ($P \geq 0.3156$).

The relative abundance of all soricid species (all study sites combined) was similar, except *C. parva* was significantly less abundant than *S. cinereus* (Table 2). All 6 species were captured at each of the 11 study areas, except for *C. parva* which was absent from 3 sites (one control, one intact gap, and one salvaged gap). Hence, all 3 small-bodied shrew species, *S. cinereus*, *S. hoyi*, and *S. longirostris*, co-occurred at all study sites.

Most species were captured year-round, although capture rates of *S. fumeus*, *S. longirostris*, and *B. brevicauda* were low in late fall and winter (Fig. 2). Most *C. parva* were captured during summer and fall of 1998 (Fig. 2).

Captures of both male and female *S. cinereus* peaked in October 1998. Lactating females of some species (11 individuals) were captured in late spring (*S. fumeus*) and fall (*B. brevicauda*, *S. cinereus*, and *S. fumeus*) in both gap treatments and controls. Males with swollen testes (14 individuals) were noted in late summer (*B. brevicauda*, *S. cinereus*, and *S. longirostris*) and late winter-spring (*B. brevicauda*, *S. cinereus*, *S. fumeus*, and *S. hoyi*) in both gap treat-

Table 3. Percent cover (± SE) of habitat features in intact (n = 4) and salvage-logged (n = 3) gaps created in 1995 by hurricane Opal, and closed canopy, mature forest (controls) (n = 4). Different letters within rows denote significant differences among treatments.

	Treatment (mean ± SE)			
Feature	Intact	Salvaged	Control	P
Bare ground (%)	$1.5 \pm 0.6^{a,b}$	5.6 ± 2.4^{b}	0.5 ± 0.3^{a}	0.0230
Shrub (%)	55.6 ± 7.3^{a}	29.3 ± 8.0^{b}	26.6 ± 6.6^{b}	0.0450
Herbaceous (%)	3.5 ± 2.4	27.8 ± 15.3	1.2 ± 1.0	0.1376
Leaf litter (%)	89.5 ± 2.5^{a}	76.4 ± 2.7^{b}	99.1 ± 0.2^{c}	0.0001
Leaf litter depth (cm)	$3.4 \pm 0.6^{a,b}$	1.6 ± 0.1^{a}	2.8 ± 0.1^{b}	0.0411
Coarse woody debris (%)	2.5 ± 0.4^{a}	0.7 ± 0.4^{b}	0.4 ± 0.1^{b}	0.0070
Fine woody debris (%)	1.1 ± 0.3	2.8 ± 0.4	1.7 ± 0.9	0.2178
Humic mat (%)	80.2 ± 9.4^{a}	19.7 ± 19.7^{b}	98.8 ± 0.7^{a}	0.0030
Humic mat depth (cm)	1.8 ± 0.4	0.3 ± 0.3	2.0 ± 0.6	0.0905
Light (%)	29.1 ± 2.3^{a}	50.4 ± 3.3^{b}	3.3 ± 0.5^{c}	0.0001
Live tree BA (m^2/ha)	9.8 ± 1.6^{a}	9.0 ± 1.0^{a}	27.8 ± 1.9^{b}	0.0001
Snag BA (m^2/ha)	3.2 ± 0.3^{a}	0.6 ± 0.5^{b}	2.6 ± 0.8^{a}	0.0423

ments and controls (Fig. 2). The proportion of males to females did not differ among gap treatments or controls for any tested species (P range 0.2433–0.8035) (*C. parva* was omitted due to low sample size). However, more male than female (all study sites combined) *S. hoyi* and *S. longirostris* were captured, and more female than male *S. fumeus* were captured (Table 2).

Habitat characteristics

Basal area of live trees was higher in controls than in intact or salvaged gaps (P = 0.0001), and snag BA was lower in salvaged gaps than in intact gaps or controls (P = 0.0423). Percent light (the inverse of canopy cover) differed among all treatments and controls (P = 0.0001); the highest was in salvaged gaps, followed by intact gaps and controls. Leaf litter cover was highest in controls and lowest in salvaged gaps. Litter depth was lower in salvaged gaps than in controls, and marginally lower than in intact gaps (P = 0.0641). Percent cover of the humic mat was marginally lower in salvaged gaps than in intact gaps or controls (P = 0.0905). Salvaged gaps had the most bare ground, controls had the least, and bare ground in intact gaps differed from neither. Herbaceous plant and FWD cover did not differ among the treatments. Percent cover of CWD was higher in intact gaps than in salvaged gaps or controls (Table 3). CWD pieces were longest, and their diameters were marginally greater (P = 0.0859) in intact gaps. Wood decay was greatest in controls, followed by salvaged gaps, and lowest in intact gaps (Greenberg 2001). Arthropod abundance and biomass were higher in forested controls than in intact or salvaged gaps (Greenberg and Forrest 2003).

Discussion

Despite differences in tree BA, light, CWD, and other forest floor features, shrew abundance and richness were similar among intact gaps, salvaged gaps, and forested controls. Only *S. longirostris* was more abundant in salvaged gaps, suggesting that even heavily disturbed forest (multiple windthrows followed by salvage-logging) does not adversely affect it, and possibly provides better habitat for the species than intact gaps or closed canopy forest. Alternatively, the high variability in *S. longirostris* abundance among salvaged gaps, in combination with no difference in abundance for 1997 alone or whole-year (1998–1999) data could indicate that the result was not biologically significant.

Our results are not surprising, given that correlations between forest structural features and shrew captures reported in other studies are weak, nonexistent, or inconsistent. For example, several studies show a weak, positive correlation between CWD and habitat use by *B. brevicauda* (Kitchings and Levy 1981, McCay et al. 1998, McComb and Rumsey 1982, Seagle 1985), but not by other species (McCay et al. 1998). McCay and Komoroski (2004) found that only one (*C. parva*), of three shrew species present declined in abundance after CWD removal from a Coastal Plain study area. Ford et al. (1997) found a weak relationship between leaf litter depth and capture rates of *B. brevicauda* and *S. fumeus*, but no shrew species was correlated with CWD. Although we did not sample microhabitat variables at each pitfall trap, our results indicate that shrew abundance (with the possible exception of *S. longirostris*) is not affected by differences in the availability of the structural features we measured at a habitat scale.

Several studies suggest that shrew abundance and community richness are linked to the abundance of arthropod prey (Healy and Brooks 1988, Kirkland 1990). Our results did not support this; the relative abundance of shrews was similar among treatments despite higher numbers and biomass of ground-dwelling arthropods in forested controls than in intact or salvaged gaps (Greenberg and Forrest 2003). Possibly, differences in arthropod abundance or structural features (such as CWD or leaf litter) among our treatments and controls did not exceed a theoretical threshold necessary to elicit changes in shrew abundance. However, because multiple-tree windthrows are somewhat common (Greenberg and McNab 1998), our results are likely representative of shrew response to natural disturbance in xeric upland hardwoods in the southern Appalachians.

In the southern Appalachians, *B. brevicauda*, *S. fumeus*, and *S. cinereus* are habitat generalists, but are reported as being more abundant in mesic forests with ample structural debris and leaf litter (Ford et al. 1999, Kitchings and Levy 1981, Laerm et al. 1999, Pagels et al.1994). Our study indicates that these species also are common inhabitants of xeric upland forest within the study area.

High moisture requirements (Kirkland 1991) presumably would make soricids sensitive to soil or leaf litter disturbance and desiccation following canopy removal during silvicultural or natural disturbances (Ford et al. 1997). Further, if shrews are moisture-sensitive, drought conditions might be expected to induce higher densities in sites with more CWD or shrub cover, as in intact gaps, or in forested controls with more shade, leaf litter cover, and litter depth than gaps. Yet, except for *S. longirostris*, which was more abundant in salvaged gaps (when June–October data were used), our results did not indicate any differences in shrew abundance among treatments even during drought years. Capture rates during June–October were higher in 1998 than in 1997, even though there was twice as much rainfall during the 1997 trapping period (61.1 cm in 1997 versus 29.1 cm in 1998). Possibly, higher shrew captures during the year after higher than average summer rainfall (1997) was a delayed population response to precipitation. Smith et al. (1974) reported a delay between summer precipitation and a population increase of *B. carolinensis* during the following winter. Alternatively, shrews may not be as moisture-sensitive as previously thought.

Our results indicate that precipitation was correlated with activity levels (capture rates) of shrews during June–October, but the relationship was negligible. We were unable to detect any such relationship for individual species, likely because the capture rate per trap-check of any given species was low. In contrast, Doucet and Bider (1974) reported that *S. cinereus* activity was greater during precipitation events. If greater activity by shrews after rains does occur, it could be an indirect response to higher invertebrate availability after rains, and does not necessarily indicate that shrews are moisture-sensitive per se. Our results indicate that soricids of the southern Appalachians are active regardless of annual or daily precipitation, and appear tolerant of changes in forest conditions that occur following partial canopy removal created by wind disturbance.

Results of other studies that examine shrew response to silvicultural disturbance are equivocal. Ford and Rodrigue (2001) found similar abundance of soricids (*S. cinereus*, *B. brevicauda*, and *S. fumeus*) in recently cut (two-aged harvests and diameter-limit thinnings) and uncut northern hardwood forests of West Virginia. Ford et al. (2000) found that *S. cinereus* was more abundant in two-age than in 2-year old group-selection timber harvests in the southern Appalachians, but capture rates of other shrew species did not differ between treatments. DeGraaf et al. (1991) found similar numbers of *C. parva*, *S. hoyi*, and *S. cinereus* in poletimber and sawtimber stands in northern hardwood forests of New Hampshire. Klein and Michael (1984) report that *B. brevicauda* was equally abundant in small-patch fuelwood cuts (0.05 ha) and forest. In a review of 21 published studies conducted in the central and northern Appalachians, Kirkland (1990) reported a positive initial response by soricids to clearcutting. However, most of the studies he reviewed did not involve pitfall trapping, and species were not analyzed separately. Differences among studies in the size of study sites (ranging from fuelwood cuts to large clearcuts) also could affect results since the home ranges of some shrew species might exceed the area of the study sites.

Disturbed areas could function as shrew sources or sinks (Pulliam 1988) by affecting reproduction or survival. We did not measure these parameters. However, male:female ratios were similar among treatments within species, although some were not 1:1. Further, evidence of reproduction was seen in both treatments and in controls. These demographic indicators, in combination with a similar abundance of most shrew species among treatments, suggest that shrews are not adversely affected by multiple-tree windthrows, with or without subsequent salvage-logging, at least in the short-term.

Multi-species assemblage rules predict that similar-sized shrews are less likely to co-occur than shrews of different sizes because of competitive exclusion (Fox and Kirkland 1992). For example, Kirkland (1991) suggests that *S. cinereus* competitively excludes *S. hoyi* (both are small shrews) where they are sympatric because of similar diets (Ryan 1986); *S. longirostris* and *S. cinereus* are reportedly "contiguously allopatric" in the southern Appalachians because of competitive exclusion (Ford et al. 2001, Pagels and Handley 1989). Yet, we captured all three small-bodied soricids (*S. cinereus*, *S. hoyi,* and *S. longirostris*) in similar numbers at each of our 11 study sites. Further, similar seasonal activity patterns among the three species suggest that temporal segregation is not occurring, nor do increases in one species result in decreases by another. Clearly, interspecific competition among small-bodied shrew species is not sufficiently intense to exclude any of these species, and the soricid assemblage does not conform to multi-species assemblage rules within our study area. Ford et al. (in press) analyzed data from 303 sites in the central and southern Appalachians, and found that most sites exhibiting inequitable distributions of shrew size-class composition occur in xeric forests.

The co-occurrence of *S. cinereus* and *S. longirostris* at our study sites is of special interest, because these species have not been found together in the southern Appalachians (Ford et al. 2001, Pagels and Handley 1989). *Sorex longirostris* tends to occur in xeric or early successional forest at lower elevations, and *S. cinereus* in mesic forest at higher elevations (Laerm et al. 1999); although there is some elevational overlap, the two species never have been recorded on the same sites (Ford et al. 2001, Pagels and Handley 1989). Our results indicate that the two species coexist in at least some mid-elevation xeric forests where habitat conditions are adequate for both.

Our study indicates that shrews in the southern Appalachians tolerate a wide range of habitat characteristics that result from forest disturbance, at least in small areas and in the short-term. The abundance of most shrew species was similar despite significant differences among treatments in habitat features such as BA, canopy cover, CWD, leaf litter cover and depth, and humic thickness. This absence of among-treatment differences, even under dry conditions when shrews might be expected to use sites with more shade and leaf litter (controls) or CWD (intact gaps), is striking. The lack of a treatment effect, higher captures during a droughty than a wet summer, a negligible but significant response by shrews to rainfall, and the common occurrence of two mesic-associated species on xeric sites, indicate that shrews are not as moisture-sensitive as conventional wisdom suggests. Experimental studies that manipulate moisture and forest structure would facilitate a more precise determination of their effects on shrews. Our results suggest that in xeric southern Appalachians forest types, forest management that mimics conditions created by multiple windthrows is unlikely to adversely affect shrew communities in the short-term.

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