

USE OF WOODY DEBRIS BY COTTON MICE
(*PEROMYSCUS GOSSYPINUS*) IN A
SOUTHEASTERN PINE FOREST

TIMOTHY S. MCCAY*

University of Georgia Museum of Natural History and Institute of Ecology, University of Georgia,
Athens, GA 30602

Present address: Biology Department, Colgate University, 13 Oak Drive, Hamilton, NY 13346

Coarse woody debris, which includes fallen logs, snags, and stumps, may be an important habitat component for many mammals. I examined use of woody debris by the cotton mouse (*Peromyscus gossypinus*) with radiotelemetry and fluorescent-powder tracking in a managed loblolly pine (*Pinus taeda*) forest. Most day refuges of cotton mice were associated with woody debris, including refuges in rotting stumps (69%), under upturned root boles (14%), and under fallen logs and brush (9%). Stumps used by cotton mice were larger in diameter ($P < 0.05$) and more highly decomposed ($P < 0.001$) than stumps randomly selected at the study area. Nighttime telemetry locations of 4 of 8 cotton mice were closer to large (10 cm diameter) fallen logs than expected by chance ($P < 0.05$), whereas locations of no mice were farther from logs than expected. Pathways of cotton mice crossed woody debris (including logs of all sizes) for a greater distance than random transects at the study area ($P < 0.05$). Logs used by powder-tracked mice were longer than randomly selected logs ($P < 0.01$). Extensive and selective use suggests that woody debris, particularly in the form of large logs and stumps, is an important habitat component for the cotton mouse in southeastern pine forests.

Key words: coarse woody debris, cotton mouse, habitat use, loblolly pine forest, *Peromyscus gossypinus*

Many investigators have studied use of woody debris, including fallen logs, snags, and stumps, by small mammals (Graves et al. 1988; Hayes and Cross 1987; McMillan and Kaufman 1995; Planz and Kirkland 1992; Tallmon and Mills 1994). These studies generally have focused on environments characterized by high structural diversity, which provides cover for animals moving on the forest floor (e.g., eastern deciduous forests—McMillan and Kaufman 1995; old-growth coniferous forests of the Pacific Northwest—Tallmon and Mills 1994). In contrast, typical managed pine forests of the southeastern United States have low structural diversity and sparse understory vege-

tation (Workman and McLeod 1990). Woody debris may be the most abundant forest-floor structure available to small mammals in these forests.

Woody debris benefits small mammals in several ways. Fallen logs serve as habitat for invertebrates and fungi eaten by insectivorous and fungivorous mammals (Fogel and Trappe 1978; Hanula 1996; Maser and Maser 1987). Logs and stumps retain moisture (Harmon et al. 1986), and many mammals, including most shrews (*Blarina*, *Sorex*), depend on burrow environments with a high relative humidity (Pruitt 1959). Snags, stumps, and logs also may be important cues used by visually navigating species (Barry and Franq 1980, 1982;

* Correspondent: tmccay@mail.colgate.edu

Drickamer and Stuart 1984). Despite the potential importance of woody debris, the extent to which mammals of the Southeast use woody debris is poorly known (Loeb 1996).

Woody debris is a habitat component amenable to management (McMinn and Crossley 1996), but effective management relies on knowledge of the attributes of woody debris used by mammals. For example, large logs are selectively used by the western red-backed vole (*Clethrionomys californicus*) but not the deer mouse (*Peromyscus maniculatus*) in northwestern forests (Hayes and Cross 1987). Data are not available on the characteristics of woody debris that may affect its use by small mammals in southeastern pine forests (Loeb 1996).

Microhabitat preferences of the cotton mouse (*P. gossypinus*), a common small mammal of southeastern pine forests (Golley 1966; Loeb 1999), have been less well studied than preferences of other members of the genus *Peromyscus* (Wolfe and Linzey 1977). Although I am aware of no systematic studies of nighttime habitat use, use of fallen logs and standing trees has been observed (Ivey 1949).

The cotton mouse has been observed to use several types of daytime refuge sites (King 1963). In a Tennessee swamp, refuges were located under fallen logs and under moss (Goodpaster and Hoffmeister 1952). In a Florida hammock, refuges were found in hollow palm logs, under palmetto litter, and in a standing pine stump (Ivey 1949). Other cotton mice in Florida selected refuges in gopher tortoise burrows, decomposing root systems, and tree cavities in a slash pine–turkey oak (*Pinus elliottii*–*Quercus laevis*) forest (Frank and Layne 1992). Other *Peromyscus* have demonstrated similar plasticity in use of daytime refuges (King 1963; Wolff and Hurlbutt 1982).

I hypothesized that small mammals would depend more heavily on woody debris for daytime refuge and nighttime movement in managed southeastern pine

forests than in other environments that are structurally more diverse because southeastern pine forests have less vegetative structure and fewer exposed rocks. My purpose was to measure use of woody debris by cotton mice in managed pine forests of the southeastern Coastal Plain. I quantified use of fallen logs and decomposing root systems during periods of activity and inactivity and examined attributes of logs and stumps used by cotton mice.

MATERIALS AND METHODS

Study area.—This research was conducted at the Savannah River Site, a 78,000-ha National Environmental Research Park. The Savannah River Site is located in Aiken, Barnwell, and Allendale counties, South Carolina, about 32 km south of Aiken, South Carolina (33°0–25'N, 81°25–50'W). The Savannah River Site lies in the upper portion of the Coastal Plain Physiographic Province (Fenneman 1938) and is bounded on the west by the Savannah River.

Three 45-year-old planted upland loblolly pine (*Pinus taeda*) stands were selected. Stands were selected based on similarities in vegetational structure, burn histories, and distance from roads and wetlands. Canopies of those forests consisted exclusively of loblolly pine. Common species of the forest midstory were wax myrtle (*Myrica cerifera*), sweetgum (*Liquidambar styraciflua*), blackjack oak (*Q. marilandica*), mockernut hickory (*Carya tomentosa*), and red maple (*Acer rubrum*). Plants infrequently encountered at the forest floor included poison oak (*Rhus toxicodendron*) and dog-fennel (*Eupatorium*)—Workman and McLeod 1990).

I selected the location of a 1-ha plot in each stand to typify vegetational and edaphic characteristics of the stands. Plots were >700 m apart. At each plot, I established a grid of reference markers (polyvinyl chloride stakes) at 10-m intervals, thus dividing each plot into 100 10-by-10-m cells. Universal Transverse Mercator coordinates of reference markers were determined with a global positioning system. A trap station was positioned at the center of each cell.

Trapping.—At each trap station, I placed 1 small (5.0 by 6.4 by 16.5 cm) nonfolding Sherman trap and one large (7.6 by 8.9 by 22.9 cm) folding Sherman trap (H. B. Sherman Traps, Tallahassee, Florida). Traps were set on all plots for

20 days between 1 and 27 October 1996 and for 20 days between 11 September and 4 November 1997. Cotton and sunflower seeds were placed within traps to prevent trap-related mortality. Traps were checked between 0600 and 1000 h. Mammals were identified, weighed, marked with ear tags (Size 1 Monel tags, National Band and Tag Co., Newport, Kentucky), and released.

Radiotelemetry.—Adult cotton mice captured twice within a 10-day period were considered residents of the plot (Andrzejewski and Wierzbowska 1961) and were used in radiotelemetry studies. Mice were anesthetized with methoxyflurane and fitted with radiotransmitters (SM-1 Mouse-style transmitters, AVM Instrument Co., Livermore, California) on the day of recapture. Average mass of a transmitter with collar and potting was 2.1 g. Transmitters averaged 7.3% of the mass of cotton mice ($\bar{X} = 28.6$ g). After instrumentation, animals were held for ≥ 24 h to allow recovery from anesthetic and to ensure that the collar was properly secured. Animals were released at the original capture site after sunset. I located radio-tagged animals from 5 October to 5 December 1996 and 21 September to 12 December 1997 using Challenger Model R2000 receivers and 3-element folding Yagi antennae (Advanced Telemetry Systems Inc., Isanti, Minnesota). Radiotagged animals were located once per day and about twice each night. Animals were relocated about 5 days/week until transmitters failed. Telemetry locations were not obtained on nights during which mice were trapped.

I recorded the type of refuge (e.g., stumps, root boles) used by each radiotagged animal each day. For refuges in stumps, I recorded diameter of the stump just above root swell, decomposition class (Maser et al. 1979; McCay 1998), diameter of conspicuous entrances, and species group (pine or hardwood). For refuges under root boles, I measured volume of the root bole, species group, diameter, and decomposition class of the stem (Maser et al. 1979; McCay 1998). Attributes of daytime refuges were compared with attributes of randomly sampled habitat features. Stumps and root boles were cluster sampled by randomly selecting 10 cells in each plot. Within each cell, all stumps and root boles were recorded. Forest-floor litter was removed from the entire cell with a steel rake to reveal highly decomposed stumps, which were included in the sample.

Nighttime locations were taken ≥ 2 h after sunset. A field assistant and I located animals by moving toward the source of the radio signal from different directions until we were an estimated 20–30 m from the mouse (Mineau and Madison 1977). Two bearings were then taken simultaneously (≤ 1 min apart) from the nearest reference markers. If an individual animal was located more than once in a night, sequential locations were >1 h apart. Precision of triangulation was estimated by finding 10 transmitters hidden by an assistant in each of the 3 plots. Bearings from 2 reference markers to each hidden transmitter were estimated using the protocol described above, and differences between estimated and true bearings were calculated.

Nighttime telemetry locations of mice were compared with locations of mapped logs. Locations of all logs ≥ 10 cm in diameter within each plot were determined by measuring the direction and distance of each end of the log from the nearest reference stake. Locations of logs were entered into an ArcInfo geographic information system and buffered in all directions by 2.5 m, which was the approximate mean euclidean error of locations. For each log, I recorded species group (pine or hardwood), midpoint diameter, length, decomposition class, portion of the log covered with bark, and portion of the log in contact with the ground. I compared attributes of logs with buffer areas including telemetry locations (used) to attributes of logs with buffer areas including no telemetry locations (unused).

Powder tracking.—Mice that were used for powder tracking were held during the day of their capture and released after sunset. Animals were shaken in a plastic bag containing 5 ml of dry fluorescent powder (Radiant Color, Richmond, California—Lemen and Freeman 1985). The following night, an ultraviolet lamp (Model ML-49 Blak Ray, UV Products, Upland, California) was used to follow trails left by mice. Metal stake flags were placed along the trail wherever a perceptible change in direction had occurred. Each span between successive stake flags was classified as on log, under log, beside log, or not associated with a log. For trail segments that were not associated with a log, I noted the proportion of the segment that incidentally crossed pieces of woody debris (≥ 1 cm).

Use of logs determined from powder trails was compared with cover of woody debris at each plot, as estimated using line-transect sam-

pling. A tape was stretched between opposing corners within each of 10 randomly chosen cells. The distance of the tape intersecting woody debris (>1 cm) divided by the total transect length provided an estimate of cover of woody debris for each plot. I also measured the midpoint diameter, decomposition class, and length of logs intersected by the tape. Attributes of logs intersected by random transects were compared with attributes of logs used by powder-tracked mice.

Statistical analysis.—Attributes of stumps and root boles used as daytime refuges were compared with attributes of sampled stumps and root boles using *t*-tests or *G*-tests (Sokal and Rohlf 1995); *t*-tests were performed using an error term modified for cluster-sampled data (Thompson 1992). Characteristics of used logs were compared with those of randomly sampled logs (powder tracking) or unused logs (telemetry) with 1-way analyses of variance (ANOVA), Wilcoxon's 2-sample tests, or *G*-tests. Mean percentage of powder trails intersecting woody debris was compared with mean percentage of random transects intersecting woody debris with a 1-way ANOVA after arcsine transformation (Sokal and Rohlf 1995). Distributions of angular telemetry errors were compared among the 3 plots using a test of homogeneity for circular samples (Fisher 1993:122). For all parametric tests, samples within each plot were considered subsamples and were averaged (i.e., $n = 3$ plots). All differences were considered significant at $P < 0.05$.

A simulation approach was used to test the hypothesis that telemetry locations of mice were no closer to or farther from logs than would be expected by chance (McCay 1998). To account for sampling error in each telemetry location, I created 100 simulated locations for each observed telemetry location by varying each of the actual bearings by a value that was drawn randomly from the empirical distribution of errors. I measured distance between each of those 100 simulated locations and the nearest log and took the average of those values. I then took an average of those distances across all locations for an individual, resulting in a mean smallest distance (MSD) statistic. The observed MSD for each mouse was compared with the distribution of MSD under the null hypothesis of random (arbitrary with respect to logs) movement. I simulated 1,000 sets of n random points, where n was the number of locations for a particular

mouse, at the plot where the individual was tracked. Observed MSD values were compared with the lower and upper 2.5% of ordered simulated values to test the hypothesis of random movement at $\alpha = 0.05$.

RESULTS

Twenty-three adult cotton mice were captured during 1996, and 15 were captured during 1997. Twelve mice were captured more than once during each of 1996 and 1997, for a total of 24 mice available for tracking. Other small mammals captured included the old-field mouse (*P. polionotus*, 15 captures), golden mouse (*Ochrotomys nuttalli*, 10 captures), harvest mouse (*Reithrodontomys humulis*, 6 captures), and southern short-tailed shrew (*Blarina carolinensis*, 11 captures).

Daytime refuges.—Repeated location of mice during the day indicated that cotton mice were not active on the surface during daylight hours (cf. Frank and Layne 1992, for similar results). Twenty mice were located 349 times during the day at 108 refuges. Seventy-five (69.4%) refuges were in rotted stumps, 15 (13.9%) were under upturned root boles, 8 (7.4%) were in shallow burrows not associated with woody debris (e.g., mole tunnels), 6 (5.6%) occurred in brush piles, and 4 (3.7%) occurred under fallen logs. Thus, 100 of 108 refuge sites were associated with some form of woody debris.

Stumps used as refuges were in a later stage of decomposition ($G^2 = 72.64$, $d.f. = 4$, $P < 0.001$) than were stumps sampled randomly. Mean diameter of used stumps (36.2 cm) was greater ($t = 2.86$, $d.f. = 4$, $P < 0.05$) than that of sampled stumps (24.7 cm). There were no differences in entrance diameter ($t = 0.35$, $d.f. = 4$, $P > 0.05$) or species group ($G^2 = 0.19$, $d.f. = 1$, $P > 0.50$) between stumps used as refuges and randomly sampled stumps. Cotton mice selected a greater number of root boles of pine than expected given the ratio of root boles of pine to those of hardwood available in plots ($G^2 = 5.80$, $d.f. = 1$, $P <$

TABLE 1.—Mean smallest distance (MSD) of telemetry locations to the nearest log (≥ 10 cm diameter) for 8 cotton mice (*Peromyscus gossypinus*) in three 1-ha plots in a mature loblolly pine (*Pinus taeda*) forest in the Upper Coastal Plain Province of South Carolina, autumn 1996 and 1997. Distributions of MSD values given random movement were determined by simulation.

| Mouse no. | Sex | Telemetry locations | MSD (m) | MSD for random movement (m) | |
|-----------|-----|---------------------|-------------------|-----------------------------|------------|
| | | | | \bar{X} | 95% CI |
| 0086 | F | 5 | 7.15 | 6.65 | 3.51–10.40 |
| 1908 | M | 9 | 4.32 ^a | 7.10 | 4.45–9.85 |
| 1955 | F | 5 | 6.13 ^a | 12.07 | 6.37–18.69 |
| 1971 | M | 22 | 5.28 | 6.50 | 4.96–8.18 |
| 1987 | M | 10 | 2.97 ^a | 11.75 | 7.57–16.30 |
| 1990 | F | 28 | 4.31 ^a | 6.91 | 5.44–8.50 |
| 4002 | M | 14 | 5.79 | 6.52 | 4.72–8.70 |
| 4077 | F | 18 | 5.72 | 6.52 | 4.78–8.46 |

^a Locations were closer to mapped logs than expected by chance ($P < 0.05$).

0.05). Mice also selected root boles associated with logs that were in a more advanced stage of decomposition than root boles sampled randomly ($G^2 = 16.54$, $d.f. = 5$, $P < 0.01$). There were no differences in size of the stem ($t = 0.88$, $d.f. = 4$, $P > 0.05$) or volume of the root bole ($t = 0.74$, $d.f. = 4$, $P > 0.05$).

Nighttime locations.—There were no differences among distributions of angular errors in the 3 plots ($W = 5.65$, $d.f. = 4$, $P > 0.15$). The mean euclidean distance between estimated and true telemetry locations also did not differ among plots ($F = 0.04$; $d.f. = 2, 26$; $P > 0.50$). Thus, precision of locations estimated using triangulation was relatively homogeneous throughout the study area.

I obtained 252 nighttime locations of 8 animals (5 males, 3 females) during 1996 and 236 locations of 9 animals (4 males, 5 females) during 1997; however, only 83 and 48 locations were within plot boundaries during 1996 and 1997, respectively. The remaining locations fell within the surrounding forest and were not used in this analysis. My analysis focused on 8 mice for which ≥ 5 locations were available in study plots. Telemetry locations of 4 mice were closer ($P < 0.05$) to the nearest log than would be expected given a random placement of telemetry locations, whereas loca-

tions of no mice were farther from the nearest logs than expected (Table 1).

The mean diameter of logs with buffer zones containing telemetry locations was not significantly larger than the mean diameter of logs without telemetry locations ($F = 2.88$; $d.f. = 1, 4$; $P > 0.15$). Similarly, length did not differ between used and unused logs ($F = 2.71$; $d.f. = 1, 4$; $P > 0.15$). Relative use of pine and hardwood stems did not differ between used and unused logs ($G^2 = 0.04$, $d.f. = 1$, $P > 0.50$) or decomposition stage ($G^2 = 3.71$, $d.f. = 1$, $P > 0.40$). The proportion of the log covered with bark and the proportion of the log lying on the ground did not differ between used and unused logs (Wilcoxon's 2-sample tests, $P > 0.05$).

Powder trails.—Thirteen mice (8 males, 5 females) were tracked using fluorescent powders, with a mean trail length (combined trail length for 3 individuals with 2 trails) of 89.2 m. The mean portion of trail associated with fallen logs (portion on, under, or beside logs) was 23.9%, with the greatest portion of trail occurring on logs (18.5%, Table 2).

Mean percentage of powder trails intersecting woody debris (portion on, under, and crossing woody debris; 24.1%) was greater ($F = 11.76$; $d.f. = 1, 4$; $P < 0.05$) than the mean portion of transects inter-

TABLE 2.—Attributes of pathways taken by cotton mice (*Peromyscus gossypinus*) in 3 plots in a managed pine forest, presented as mean percentages of total pathway length and estimated percent cover of woody debris.

| Plot | n | % associated with log | | | | | | | | | | | | | |
|------|----|-----------------------|------|-----------|------|-----------|-----|-----------|-----|---------------------|-----|------------------------------|------|---------------------------|-----|
| | | Mean length | | Above | | Under | | Beside | | Crossing debris (%) | | Total woody intersection (%) | | Estimated woody cover (%) | |
| | | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD |
| A | 3 | 71.0 | 38.9 | 13.9 | 8.5 | 0.5 | 0.8 | 3.9 | 3.8 | 4.0 | 1.5 | 18.4 | 6.1 | 3.9 | 2.3 |
| B | 5 | 64.4 | 41.2 | 9.6 | 8.6 | 0.2 | 0.3 | 2.9 | 2.9 | 6.9 | 5.5 | 16.7 | 13.8 | 2.0 | 1.3 |
| C | 5 | 124.9 | 63.2 | 30.3 | 15.9 | 0.5 | 0.4 | 7.0 | 4.0 | 4.1 | 1.1 | 34.8 | 15.1 | 4.2 | 3.2 |
| All | 13 | 89.2 | 55.0 | 18.5 | 14.8 | 0.4 | 0.5 | 4.7 | 3.8 | 5.1 | 3.6 | 24.1 | 15.0 | 3.3 | 2.5 |

secting woody debris (3.3%). Logs used by powder-tracked mice were longer on average (5.0 m) than logs selected randomly (2.1 m; $F = 22.61$; $d.f. = 1, 4$; $P < 0.01$) but not larger in diameter ($F = 1.01$; $d.f. = 1, 4$; $P > 0.30$). The pine:hardwood ratio of logs used by mice was different than the ratio of logs sampled randomly ($G^2 = 12.16$, $d.f. = 4$, $P < 0.01$), reflecting a greater use of hardwood stems than was expected given their abundance at the study plots.

DISCUSSION

Similar to Frank and Layne (1992), Goodpaster and Hoffmeister (1952), and Ivey (1949), I found that cotton mice primarily used below-ground refuge sites. There were few alternatives to the use of stumps and root boles as day refuges in the study area. Surface rock formations, which are used as day refuges by other *Peromyscus* species (Hall and Morrison 1997), are not found in the sandy soils of the region. Although *Peromyscus* sometimes use burrows of large vertebrates as refuges (Frank and Layne 1992; Madison 1977), few large burrows occurred in the study plots. Snags were uncommon at the study area, and living loblolly pines rarely contained cavities. Thus, rotting root systems and the voids left by their decomposition provided the most abundant and suitable day refuges for cotton mice.

Analysis of pathways chosen by cotton mice indicated that mice selected long logs for travel. However, length of logs used by radiotagged mice did not differ from length of logs for which use was not detected. Because only large logs (>10 cm diameter) were considered in the telemetry analysis, the range in log length (1.10–23.97 m) was smaller and the mean length (4.75 m) was greater than the range in length (0.02–24.50 m) and mean length (3.09 m) of logs considered in the powder-tracking study. Thus, the small range of the data and lack of very short logs may have made selection difficult to demonstrate in the telemetry analysis.

Furthermore, radiotelemetry and powder tracking yield estimates of different types of habitat use (Mullican 1988). Radiotelemetry yields an estimate of the relative amount of time spent, whereas powder tracking yields an estimate of the relative amount of travel distance. If mice ran quickly over long logs, powder tracking might reveal that they had a relatively large travel distance at long logs, but radiotelemetry would indicate that relatively little time was spent there. *Peromyscus* have often been observed rapidly traversing long logs (Barry and Franq 1980).

Use of long logs by cotton mice may reduce travel on the forest floor. Under dry conditions, travel over leaf litter at the forest floor may attract predators. White-footed mice (*P. leucopus*) strongly avoid travel over deciduous leaf litter in favor of travel over logs, unless the litter is moist, and when forced to traverse dry forest litter, mice alter their gait apparently to minimize noise (Fitzgerald and Wolff 1988). Long logs also may be easier to see from a distance and thus be more useful in navigation (Barry and Franq 1980, 1982; Drickamer and Stuart 1984).

Use of tops of logs, as estimated with powder tracking (18.5%), was lower than other reported values for *Peromyscus*. Pathways selected by white-footed mice in eastern deciduous forests have consistently included >40% travel over logs (40–60%, Barnum et al. 1992; 41%, Graves et al. 1988; 42%, McMillan and Kaufman 1995; 52%, Planz and Kirkland 1992). Similar values have been recorded for deer mice (37%, Graves et al. 1988). Perhaps the less extensive travel on logs by cotton mice in this study was due to a relative lack of woody debris. McMinin and Hardt (1996) reported that standing crop of woody debris in managed pine forests of the southeastern United States was lower than that in hardwood stands of the southern Appalachians and deciduous forests of the mid-Atlantic region. Although log abundance was low in this study and probably lower than in other

comparable studies, direct comparisons were impossible because of the lack of available data. An alternative explanation for the reduced use of logs in this study is that risk of predation while moving across pine litter may be lower than risk of predation while moving across deciduous litter because pine litter makes less noise when disrupted.

Cotton mice also selected hardwood stems for travel. Hardwood species commonly used by mice included wax myrtle and sweetgum, which have tight bark with small furrows. Movement across these logs may have caused less surface disruption, and hence less noise, than movement across loblolly pine logs, which have relatively loose bark with deep furrows. This result is consistent with the hypothesis that *Peromyscus* benefit from quiet travel routes provided by logs (Planz and Kirkland 1992).

Cotton mice did not select logs based on decomposition class or diameter. Similarly, Hayes and Cross (1987) found that capture rate of *P. maniculatus* at logs was not related to decomposition class or size of the log. In contrast, there is evidence that western red-backed voles select logs based on size (Hayes and Cross 1987) and level of decay (Tallmon and Mills 1994). The difference may be due to diet, because the western red-backed vole feeds largely on hypogeous fungi that are commonly associated with decaying wood (Ure and Maser 1982). *P. maniculatus*, like other members of this genus, has a more generalized diet (Whitaker 1966; Williams 1959).

Because of the timing of field observations, my conclusions are restricted to behaviors of the cotton mouse during autumn. However, there is no reason to believe that habitat use during autumn differs markedly from habitat use during other times of the year (Wolfe and Linzey 1977). These results provide evidence that use of woody debris by similar small mammal species may differ between southeastern pine forests and eastern deciduous forests. In southeastern pine forests, woody debris may be

used less extensively for travel because of low availability or characteristics of pine litter but may be used more extensively for daytime refuge because few other types of refuges are available.

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