

Small Mammal Communities In Riparian And Upland Habitats on The Upper Coastal Plain Of Virginia

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ABSTRACT

We compared small mammal communities between riparian (stream corridor) and nearby upland habitats in a hardwood forest ecosystem on Fort A.P. Hill, Caroline County, Virginia. We used a combination of small-scale drift fence/pitfall trap arrays and snap traps to capture small mammals during April - October 1998, with an additional winter sample in January 1999. We captured seven small mammal species at 14 sites (7 pairs). Numbers of species were not significantly different between habitat types. Bray-Curtis polar ordinations showed that plant and small mammal community compositions were similar in upland sites and that these communities were most varied in riparian sites. Riparian sites supported wetland and moist soil obligate plants that made this habitat type distinct from upland sites. Small mammal communities were dominated by *Peromyscus leucopus* and *Blarina brevicauda*. Numbers of individual small mammals captured were higher in riparian sites than in upland sites. Mean number of captures per trap night averaged 2.6 in riparian sites and 1.4 in upland sites but the difference was not statistically significant. Numbers of rodent captures were significantly higher in both habitat types than captures for insectivores. Hardwood habitats in riparian and upland systems support diverse small mammal communities in the upper Coastal Plain of Virginia. Because small mammals use both habitat types extensively, composition of contiguous upland habitats should be considered in studies of these animals in riparian ecosystems.

INTRODUCTION

Focus on riparian ecology and management has intensified recently because of local, state, and federal mandates to protect water quality and biodiversity (see reviews in Verry et al., 2000). For example, species and their habitats are required to be protected (or at least managed for their protection) under such federal mandates as the National Forest Management Act and Section 404 of the Clean Water Act. Most of the research that has been conducted on the ecology of small mammals in riparian ecosystems has occurred in the Midwest (Geier and Best, 1980) and the Pacific Northwest (e.g., Doyle, 1990; McComb et al., 1993). Comparatively little research has been conducted in eastern North America. Two studies in southeastern North America

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compared small mammal communities in varying widths of riparian habitats (Dickson and Williamson, 1988; Thurmond and Miller 1994). DeGraaf and Yamasaki (2000) listed no studies based in deciduous forests of northeastern North America that compared small mammal communities in these habitat types.

The purpose of our study was to compare small mammal communities between stream corridor (riparian) and adjacent upland habitats in a forested ecosystem in the Upper Coastal Plain of Virginia. Because riparian habitats are used extensively by terrestrial vertebrates in North America (Thomas et al., 1979; Brinson et al., 1981) and because riparian systems act as dispersal corridors for some species (Harris, 1984), we hypothesized that small mammal species richness and species relative abundance this habitat type would be higher than in upland habitats. Fort A.P. Hill offers a diverse array of forested habitats, a network of streams, and sufficient topographic relief to make this kind of study feasible in the Coastal Plain Physiographic Province.

MATERIALS AND METHODS

Study Location and Site Descriptions

This study was conducted at Fort A.P. Hill, Caroline County, Virginia. Fort A. P. Hill is a 30,329 ha military training installation that is located within the Coastal Plain Physiographic Province. Descriptions of the environment and habitats of the base are in Mitchell and Roble (1998), Bellows (1999), and Bellows et al. (1999).

We selected fourteen sites for study—seven in riparian forests and seven in upland forests. All study sites were located in non-impact areas of the base. Riparian sites were located on floodplains of seven different creeks. The seven upland sites were 150-250 m from the adjacent riparian site. Average elevation for riparian sites was 37 m (20-60 \pm 17 m) and average elevation for upland sites was 56 m (40-70 \pm 10 m). Two of the pairs of sites were located in the Mattaponi River watershed (RF-UF, RG-UG) and the remainder occurred in the Rappahannock River watershed. The latter drainage offered greater topographic relief than the former.

Sampling and Collection Methods

A sampling area approximately 30 m in diameter was established within each study site. Pitfall traps with drift fences and snap traps were used to collect animals. These two trapping techniques have been shown to be complementary when assessing small mammal assemblages (Kalko and Handley, 1993, Bury and Corn, 1987). Pitfall traps are effective for capturing long-tailed shrews (genus *Sorex*) and jumping mice. Snap traps are effective for capturing mice and voles and are generally as effective as pitfall traps for capturing short-tailed shrews (genus *Blarina*) (Kalko & Handley, 1993; Mitchell et al., 1993). We constructed three pitfall arrays approximately 120° apart and 15 m (\pm 2 m) from the center of each study site. Pitfall arrays followed the design in Handley & Varn (1994). We made drift fences with plastic silt fencing 61 cm high and one m in length. We used plastic 3.8-L buckets (18 cm in diameter x 19 cm in height) for the center pitfalls. We used plastic 2-L soda bottles with the tops cut off (11 cm in diameter x 20 cm in height) for the peripheral pitfalls; one 2-L bottle was placed on each side of the distal end of all three drift fences. There were a total of seven pitfalls per array. We set nine Museum Special snap traps, three per 120° sector, in each site at the beginning of each trapping session. Each was baited daily during each trapping

session with a mixture of peanut butter and oatmeal. A schematic of the combined trapping system is provided in Bellows et al. (1999).

We conducted trapping sessions every 12-16 days during 9 April through 12 October 1998. Exceptions included one trapping session scheduled for late June 1998 that was cancelled and one session in mid-July postponed one week; both alterations were due to intense training activity and limited access. We also conducted a mid-winter trapping session 21-24 January 1999. There were a total of 12 four-day (three-night) trapping sessions that amassed a total of 8,468 trap nights—5,854 associated with pitfalls and 2,614 associated with snap traps. One trap night equals one functional trap open for one 24-hour period. At the beginning of each trapping session, we uncovered the pitfall traps and filled them with water to a depth of 6 to 9 cm. Pitfall traps, when uncovered and not flooded, were considered functional. Flooded pitfall traps were subtracted from the total effort. Snap traps found sprung and empty were also considered nonfunctional, and one trap night was subtracted from the total effort for each sprung trap (after Nelson & Clark, 1973).

We collected specimens on days 2-4 of each trapping session. On the final day of each trapping session, pitfall traps were covered and snap traps were removed from the site. All mammals collected will be deposited in the Virginia Commonwealth University Mammal Collection.

Habitat Analysis

We identified to species all trees ≥ 4.5 m in height within each study site. Trees were placed into three size classes based on diameter at breast height (dbh): saplings (< 2.5 cm), understory trees (2.5-9.9 cm), and overstory trees (≥ 10 cm).

We assessed habitat variables for each study site by a line intercept method (after Canfield, 1941) using eight equally-spaced 25-m transects that radiated from the center of each study site. Variables were recorded at one-meter intervals (total = 200) and included presence or absence of downed woody debris (DWD), stumps, snags, herbs, shrubs, and a subcanopy. We also recorded litter type (i.e., evergreen, deciduous, both) and the species of all forbs and shrubs. These data and the aforementioned tree data allowed us to calculate frequencies for individual plant species. Percent canopy closure was estimated visually over each point by viewing the canopy through a cardboard tube (4.5 cm diameter x 11.5 cm in length). Habitat Descriptions

Riparian sites - The overstory tree community of all riparian study sites consisted primarily of hardwood species. Loblolly pine (*Pinus taeda*) was the only pine species observed and only in low numbers. Several commonly observed hardwood species, including river birch (*Betula nigra*), red maple (*Acer rubrum*), sycamore (*Platanus occidentalis*), and black gum (*Nyssa sylvatica*) are considered facultative wetland species in this region (Reed, 1988). Others, including white oak (*Quercus alba*), chestnut oak (*Q. prinus*), and American beech (*Fagus grandifolia*), are considered facultative upland species within this region. One frequently observed species, sweetgum (*Liquidambar styraciflua*), is common to both riparian and upland habitats. Understory tree communities were represented by sapling overstory species and understory species such as American holly (*Ilex opaca*), flowering dogwood (*Cornus florida*), ironwood (*Carpinus caroliniana*), and sweetbay (*Magnolia virginiana*). Shrub species were dominated by blueberries (*Vaccinium* spp.), coast pepperbush (*Clethra alnifolia*), and spicebush (*Lindera benzoin*), all of which are common in

wetland habitats. Ground level forbs were represented by obligatory wetland species, including royal fern (*Osmunda regalis*), lizard's tail (*Saururus cernuus*), skunk cabbage (*Symplocarpus foetidus*), golden club (*Orontium aquaticum*), and broad-leaved arrowhead (*Sagittaria latifolia*), as well as facultative wetland species, including cinnamon fern (*Osmunda cinnamomea*), netted chain fern (*Woodwradia areolata*), sensitive fern (*Onoclea sensibilis*), and false nettle (*Boehmeria cylindrica*). Partridgeberry (*Mitchella repens*) was the only facultative upland forb observed in our riparian study sites.

Upland sites - The overstory tree community of all upland study sites consisted primarily of hardwood species. Both *P. taeda* and Virginia pine (*P. virginiana*) were observed, and in one study site (UF) these were the dominant species. Most hardwood species, including *Q. alba*, southern red oak (*Q. falcata*), pignut hickory (*Carya glabra*), tuliptree (*Liriodendron tulipifera*), and *F. grandifolia*, are facultative upland species in this region (Reed, 1988). Other common tree species were either facultatively upland, such as *A. rubrum* and *N. sylvatica*, or common in riparian and upland habitats, such as *L. styraciflua*. Understory tree communities were represented by sapling overstory species and understory species and similar in composition to riparian sites. Commonly observed shrub species were blueberries (*Vaccinium* spp.) and mountain laurel (*Kalmia latifolia*). Ground level forbs were relatively sparse and represented primarily by facultative upland species, including Christmas fern (*Polystichum acrostichoides*), *M. repens*, spotted wintergreen (*Chimophila maculata*), and hog-peanut (*Amphicarpa bracteata*).

Statistical Analyses

Most analyses of small mammal data were based on captures per unit effort because effort varied among study sites and because some traps were found nonfunctional. We assumed that riparian sites and their adjacent upland sites were not ecologically independent. For this reason we used paired t-tests to compare mean total captures/100 trap nights (TN) and captures per 100TN for individual species between riparian and upland habitats (Zar, 1996). We also used paired t-tests to compare insectivore and rodent captures per 100TN for all sites, among riparian and upland sites, and between riparian and upland sites for both insectivores and rodents. Wilcoxon rank sum test was used to compare species richness between riparian and upland habitats because of non-normal distribution of small mammal species richness values within these data sets (Zar, 1996). We used Kruskal-Wallis one-way ANOVA on ranks followed by Kruskal-Wallis multiple comparison Z-value test compare captures per 100TN among small mammal species (Hintze, 1998).

We used Bray-Curtis polar ordinations (Euclidean distance measure) to examine similarities of the 14 study sites based on (1) the frequencies of forb, vine, shrub and overstory tree species and (2) small mammal community compositions. Bray-Curtis was selected because it is relatively insensitive to nonlinear relationships present in most ecological data sets (Gauch and Whitaker 1972). Polar ordination positions sites within a coordinate system (along axes), such that a site position in relation to each axis and other sites indicates general similarity among sites (Ludwig and Reynolds 1988). These positions should reflect site relations with environmental gradients, in this case (1) plant community and (2) small mammal community composition. In addition, we used Kendall's rank correlation to determine if there were relationships

between each small mammal species and the position of study sites along the three polar ordination axes (Zar, 1996).

RESULTS

Habitat Analysis

The first three Bray-Curtis polar ordination axes explained 60% of the variation in plant communities among the 14 study sites (Figure 1a and 1b). All but one of the upland sites (UF) were grouped together along axis I (32% of explained variance) reflecting the general similarity among their plant communities. Site UF was isolated from the other upland sites primarily because of the relatively high frequencies of *Pinus taeda* and *P. virginiana*. Riparian sites were arranged into three general groups (RA; RB, RD, and RE; RC, RF, and RG) along axis I. Site RA was isolated due to high frequency of grasses, high diversity of vine species relative to all other sites, and low diversity of overstory tree species. Sites RB, RD, and RE were grouped together based primarily on the mutual absence or low abundance of several plant species. Sites RC, RF, and RG were grouped together due to similar shrub communities. All upland sites were grouped together along axis II (16%) and III (12%) based primarily on similar plant communities. Sites RF and RB were isolated from the other five riparian sites along axis II. Site RF was the only riparian site with a substantial number of overstory pines. Shrub frequency of site RB was represented by only one species, spicebush (*Lindera benzoin*). Sites RE and RG were isolated from the other five riparian sites along axis III. Site RE had high fern frequency relative to all other sites and low forb diversity relative to the other riparian sites. Site RG was the only riparian site with substantial numbers of the normally upland white oak (*Quercus alba*).

Small Mammals

A total of 162 small mammals representing four insectivore and three rodent species were collected (Table 1). Two species, star-nosed mole (*Condylura cristata*) and eastern chipmunk (*Tamias striatus*), were represented by single individuals. Our protocol was not designed to accurately assess the abundance of either of these species and data for these two species were excluded from most analyses.

Median number of small mammal species recorded for riparian sites was 4 (25% quartile=3, 75% quartile=4) and for upland sites averaged 2 (25%=2, 75%=3) (see Table 2). Three species of insectivores were caught in the riparian sites and four were caught in upland sites (Table 1). Two species of rodents were caught in riparian sites and two in upland sites. Total number of species was similar between habitat types (5 riparian, 6 upland). There was no significant difference ($P=0.16$, $T=-18.0$) in small mammal species richness between riparian and upland sites.

Mean small mammal captures per 100TN in riparian study sites (2.6 ± 1.5) ranged from 1.0 (site RF) to 5.3 (RA) (Table 2). Mean small mammal captures per 100TN in upland study sites (1.4 ± 0.5) ranged from 0.9 (UE) to 2.1 (UF) (Table 2). There was no significant difference between mean numbers of small mammals captured in riparian and upland habitats ($P=0.12$, $t=1.82$). Median captures per 100TN for *Peromyscus leucopus* (1.1, 25% quartile=0.8, 75% quartile=1.5) were significantly higher ($P<0.05$) than *Sorex longirostris* (0.2, 0.0, 0.3) ($Z=3.83$, critical value = 1.96), *S. hoyi* (0.0, 0.0, 0.2) ($Z=5.62$), *Blarina brevicauda* (0.2, 0.2, 0.4) ($Z=3.03$), and *Zapus*

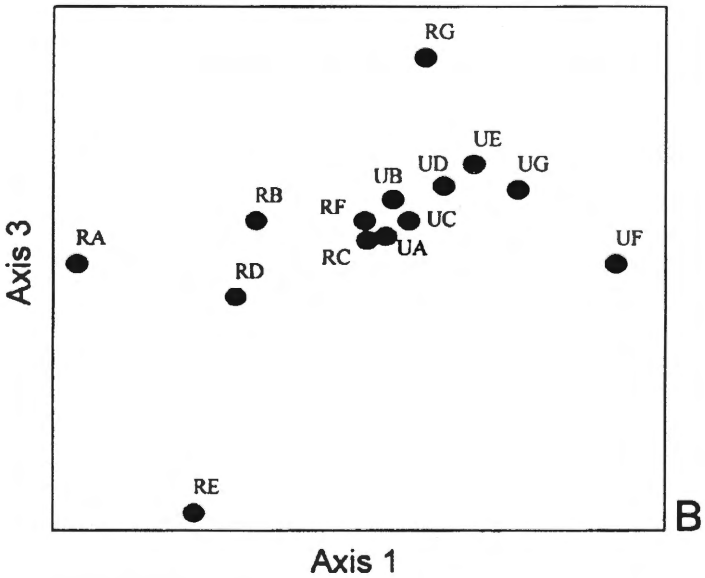
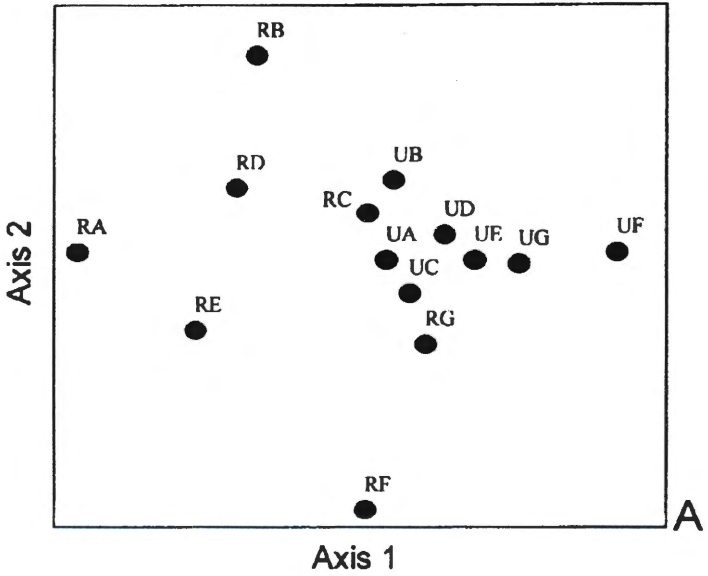


FIGURE 1. Bray-Curtis polar ordination diagram based on similarities in plant communities among the 14 trapping sites. Distance between points relative to each axis reflects similarity of plant communities for that axis. (A) Axes I and II, (B) Axes I and III.

TABLE 1. Summary of insectivore and rodent captures in riparian and upland habitats from April 1998 to January 1999 on Fort A.P. Hill, Caroline County, Virginia.

Species	Riparian	Upland	Total
Insectivora			
<i>Blarina brevicauda</i> (northern short-tailed shrew)	11	12	23
<i>Condylura cristata</i> (star-nosed mole)	0	1	1
<i>Sorex hoyi</i> (pygmy shrew)	4	1	5
<i>Sorex longirostris</i> (southeastern shrew)	9	6	15
Subtotal	24	20	44
Rodentia			
<i>Peromyscus leucopus</i> (white-footed mouse)	74	41	115
<i>Tamias striatus</i> (eastern chipmunk)	0	1	1
<i>Zapus hudsonius</i> (meadow jumping mouse)	2	0	2
Subtotal	76	43	118
Total number of captures	100	62	162
Total number of species	5	6	

hudsonius (0.0, 0.0, 0.0) ($Z=6.03$) (Table 2). Median captures for *B. brevicauda* were significantly higher ($P<0.05$) than *S. hoyi* ($Z=2.59$) and *Z. hudsonius* ($Z=3.01$). Median captures for *S. longirostris* were significantly higher ($P<0.05$) than *Z. hudsonius* ($Z=2.19$). No small mammal species was captured with significantly higher success ($P<0.05$) in either riparian or upland habitats: *S. longirostris* ($P=0.43$, $t=0.85$), *S. hoyi* ($P=0.26$, $t=1.24$), *B. brevicauda* ($P=0.97$, $t=0.04$), *P. leucopus* ($P=0.08$, $t=2.08$), and *Z. hudsonius* ($P=0.17$, $t=1.55$).

Mean captures per 100TN for insectivores for the 14 study sites (0.5 ± 0.4) ranged from 0.0 (UG) to 1.1 (RA and UC). Mean captures for rodents for the 14 sites (1.4 ± 1.0) ranged from 0.5 (UD) to 4.2 (RA) (Table 2). For all sites, mean captures for rodents was significantly higher ($P<0.01$, $t=-4.07$) than mean captures for insectivores. Mean captures for rodents was significantly higher in riparian sites ($P=0.01$, $t=-3.55$) and upland sites ($P=0.04$, $t=-2.61$) than mean captures for insectivores. There was no significant difference in mean captures of insectivores ($P=0.32$, $t=1.07$) between riparian and upland study sites. There was no significant difference in mean captures of rodents ($P=0.07$, $t=2.19$) between riparian and upland study sites.

The first three Bray-Curtis polar ordination axes explained 99% of the variation in small mammal communities among the 14 study sites. In general, upland habitats were grouped together along axis I (91% of explained variation) and riparian sites were grouped together along axis II (6% of explained variation) (Figure 2). Study site positions in relation to axis I were strongly influenced by the distribution of *P. leucopus* as shown by the positive correlation between the positions of study sites along axis I and the abundance of *P. leucopus* among study sites ($\tau = 0.966$) (Figure 3a). Site positions in relation to axis II were influenced primarily by the distribution of *B. brevicauda* as shown by the positive correlation between the positions of study sites along axis II and the abundance of *B. brevicauda* among study sites ($\tau = 0.788$).

TABLE 2. Summary of effort, captures per 100TN, and species richness for all trapping sites, and captures per 100TN for three insectivore and two rodent species collected from 10 April 1998 through 24 January 1999 on Fort A. P. Hill, Caroline County, Virginia. Mean (± 1 sd) captures per 100TN for all sites, mean (± 1 sd) captures per 100TN for insectivores and rodents, median (25% quartile and 75% quartile) small mammal species richness, and median (25%, 75%) captures per 100TN for each mammal species are provided. (-) denotes no captures

Site	TNs	<i>S. long</i>	<i>S. hoyi</i>	<i>B. brev</i>	<i>P. leuc</i>	<i>Z. huds</i>	Insectivore	Rodent	Total	Richness
RA	553	0.4	0.2	0.5	4.2	-	1.1	4.2	5.3	4
RB	512	0.6	-	0.4	2.7	-	1.0	2.7	3.7	3
RC	630	0.2	0.2	0.2	2.1	-	0.6	2.1	2.7	4
RD	552	0.2	-	0.2	0.9	0.2	0.4	1.1	1.5	4
RE	631	0.2	0.3	0.3	1.1	-	0.8	1.1	1.9	4
RF	593	-	-	0.2	0.8	-	0.2	0.8	1.0	2
RG	601	0.2	-	0.2	1.2	0.2	0.4	1.4	1.8	4
Total (riparian)	4072									
Mean (riparian)	582 \pm 44						0.6 \pm 0.3	1.9 \pm 1.2	2.6 \pm 1.5	
Median (riparian)		0.2 (0.2, 0.3)	0.0 (0.0, 0.2)	0.2 (0.2, 0.4)	1.2 (1.0, 2.6)	0.0 (0.0, 0.1)				4 (3, 4)
UA	566	0.2	-	-	1.1	-	0.2	1.1	1.3	2
UB	592	-	-	0.2	1.4	-	0.2	1.4	1.6	2
UC	613	0.3	-	0.8	0.8	-	1.1	0.8	1.9	3
UD	593	0.3	-	0.2	0.5	-	0.5	0.5	1.0	3
UE	699	-	-	0.3	0.6	-	0.3	0.6	0.9	2
UF	675	0.1	0.1	0.4	1.5	-	0.6	1.5	2.1	4
UG	658	-	-	-	0.8	-	-	0.8	0.8	1
Total (upland)	4396									
Mean (upland)	628 \pm 50						0.4 \pm 0.4	1.0 \pm 0.4	1.4 \pm 0.5	
Median (riparian)		0.2 (0.0, 0.3)	0.0 (0.0, 0.0)	0.2 (0.0, 0.4)	0.8 (0.6, 1.3)	0.0 (0.0, 0.0)				2 (2, 3)
Total Trappnights	8468									
Mean (all sites)	605 \pm 51						0.5 \pm 0.4	1.4 \pm 1.0	2.0 \pm 1.2	
Median (all sites)	605 \pm 51	0.2 (0.0, 0.3)	0.0 (0.0, 0.2)	0.2 (0.2, 0.4)	1.1 (0.8, 1.5)	0.0 (0.0, 0.0)				3 (2, 4)

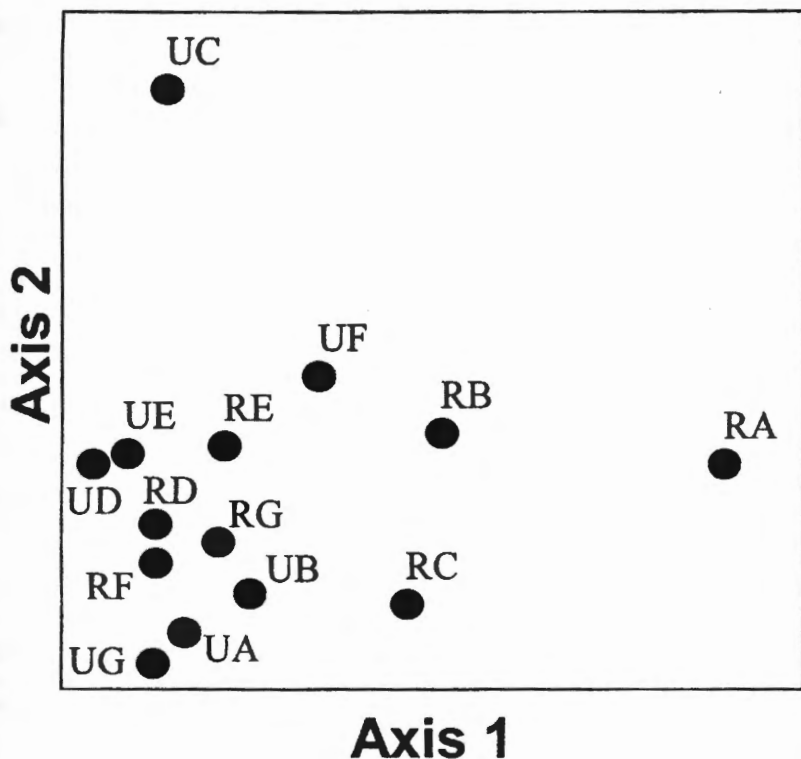


FIGURE 2. Bray-Curtis polar ordination diagram based on similarities in small mammal communities among the 14 trapping sites. Distance between points relative to each axis reflects similarity of small mammal communities for that axis.

(Figure 3b). The position of study sites along axis III (2% of explained variance) is due to the distributions of the remaining three species, *S. longirostris*, *S. hoyi*, and *Z. hudsonius*. No strong correlations, positive or negative, were shown between any of these remaining three species and the position of sites in relation to any of the three polar ordination axes.

DISCUSSION

Habitats

Results of the Bray-Curtis polar ordination indicated that the seven upland sites had similar plant communities. We attribute this similarity to two factors, (1) the contiguous nature of upland habitats across the landscape on Fort A. P. Hill, and (2) the fact that upland forests on Fort A. P. Hill are subject to perturbations as a result of forest management practices (e. g., timber harvest) more frequently than riparian forests. Overstory tree species heterogeneity was higher in upland sites and forb and shrub species heterogeneity was lower than in riparian sites. In general, plant communities among the seven riparian sites varied more than in upland sites. We attribute this

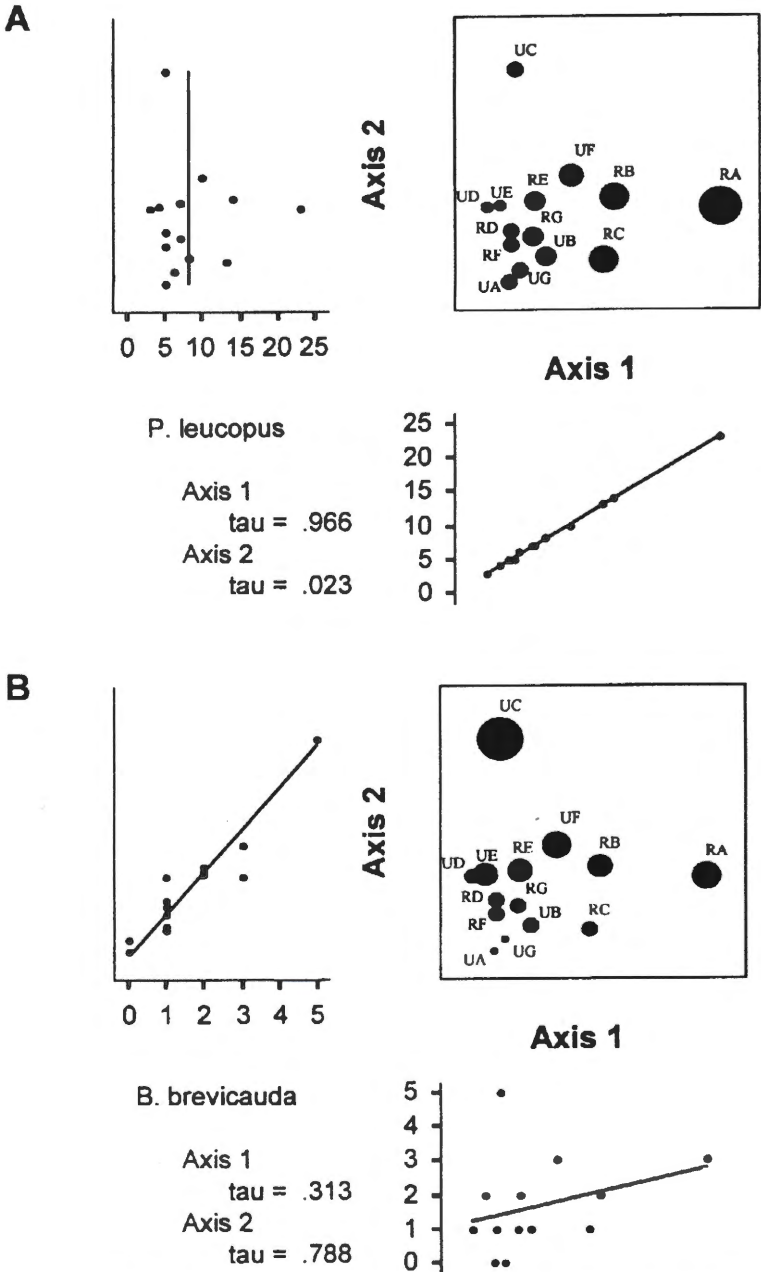


FIGURE 3. Graphic overlays of the abundances of the most frequently encountered rodent (*Peromyscus leucopus*, 3a) and insectivore (*Blarina brevicauda*, 3b) to Bray-Curtis polar ordination diagram points (see Figure 2). The sizes of study site points indicate relative abundance of that species for that site. Scatterplots depict the relationship between the small mammal species and explained variance for each axis. Kendall's rank correlation coefficients (tau) for these relationships are provided.

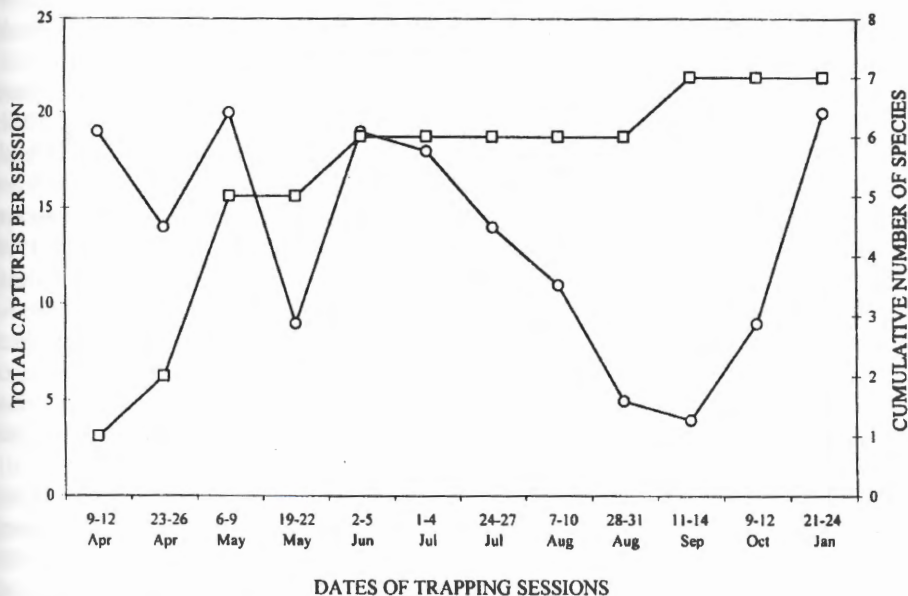


FIGURE 4. Comparison of total captures per session (circles) and cumulative number of small mammal species encountered (squares) for both riparian and upland habitats on Fort A. P. Hill from April 1998 through January 1999.

to the fact that riparian habitats on Fort A. P. Hill, while numerous and relatively isolated, occur in two different drainage systems and include different soil types and a wider variety of plant species. Williams and Moriarity (1998) found plant species composition in four streamside riparian habitats in Pennsylvania to be comprised of a mix of upland and riparian species, thus, supporting a wider variety of plant species than nearby upland habitats.

Small Mammals

Our use of small-scale pitfall/drift fence arrays and Museum Special snap traps in a combined trapping protocol ensured that the widest variety non-volant small mammal species living within our study sites would be represented. Even so, the disproportionate numbers of captures between rodents and insectivores in this study is consistent with other studies that have used snap trap and pitfalls (e.g., Snyder & Best, 1988; Kalko & Handley, 1993). All of the small mammal species captured in this study are known to occur in the mid-Atlantic region (Hall, 1981; Linzey 1998). No introduced species, such as the black rat (*Rattus rattus*), Norway rat (*R. norvegicus*), and house mouse (*Mus musculus*), were encountered.

Species accumulation curves and trapping success for this survey (Figure 4) support our conclusion from our 1997 study (Bellows et al., 1999) that assessment of small mammal species richness and the composition of small mammal assemblages within the region can be accomplished in about five months using our protocol. However, because rodent capture success was high in our mid-winter trapping session (January

1999), we maintain our original recommendation that small mammal surveys conducted within this region should include mid-winter sampling in order to provide an accurate representation of all species present.

Because rainfall patterns are known to affect small mammal activity and capture success (Gentry & Odum, 1957; Sidorowicz, 1960; Mystkowska & Sidorowicz, 1961; Vickory & Bider, 1978; Kalko & Handley, 1993), low captures per unit effort for both rodents and insectivorous small mammals in late summer and early fall 1998 are presumably a function of below normal rainfall experienced in the region during our study. Rainfall averaged 17% below normal for the months we trapped in 1998 (National Oceanic and Atmospheric Administration, Climatological Data for Virginia, 1998). We attribute fluctuations in capture success throughout the survey to episodic rainfall events. Our capture success was greater in months with higher than normal rainfall. Lower than normal rainfall during this survey may be responsible for higher overall captures of rodents than insectivores for all sites. Insectivores have higher metabolic requirements than rodents and they are intolerant of low moisture situations (Getz, 1961).

Bray-Curtis polar ordination indicated that small mammal community composition varied more among riparian habitats than upland sites. We make this conclusion based on relatively large distances between riparian sites compared to upland sites with respect to axis I—the axis with the highest amount of explained variance (91%) (Figure 2). These results are similar to those we found for plant communities and were likely influenced by (1) the variation in plant communities among riparian sites, (2) a suite of physical factors responsible for the variation in plant communities among riparian habitats, and (3) the distribution of our riparian study sites in two drainages.

Captures were dominated by one rodent species, *Peromyscus leucopus* (n=115; 71% of all captures). Populations of *P. leucopus* in riparian and upland habitats in Illinois were similar in density and demographic structure but the floodplain population served as a source of recruitment for the upland population (Batzli, 1977). *Blarina brevicauda* (n=23) was the most commonly encountered insectivore, representing 14% of all individuals captured. Clearly, small mammal community composition for riparian and upland habitats was directed by the distributions of *P. leucopus* and *B. brevicauda*. Both of these species are extremely common on Fort A. P. Hill and were the predominate small mammal species in this survey and our initial survey involving a much wider range of upland habitats (n=11) (Bellows et al., 1999). These two species are well known as habitat generalists (Jameson, 1949; Wrigley et al, 1979; Kirkland, 1981; Adler and Wilson, 1987; Pagels et al., 1992) that can occupy wide variations in habitat and environmental conditions. Thus, the importance of these habitat generalists as integral components of regional ecological communities can not be understated. As modern land-use practices continue to fragment natural habitats, the preservation of those species considered common and/or habitat generalists will be essential to maintain natural levels of biodiversity.

Olson and Knopf (1988) determined that small mammal communities in riparian and upland sites in Colorado were similar at low elevations but dissimilar at high elevations. Plant community composition, and attributes that increase habitat structure correlated positively with small mammal species richness in riparian systems in Iowa (Geier and Best, 1980). We could not discriminate between two possible explanations for the differences in captures between riparian and upland habitats because of below

normal rainfall during the study. Higher captures in riparian habitats may have been due to (1) reduced moisture levels in upland sites and the subsequent movement of individuals to nearby riparian zones or (2) due to riparian zones being used as normal resident areas and dispersal corridors that year. In addition, low mean elevation of our study sites may have influenced the lack of significant differences in small mammal species richness and relative abundance. Whereas, variation in plant community composition was greater among riparian sites than upland sites, commonalities in plant species composition between the two habitat types likely influenced small mammal species distributions and may have contributed to the lack of significance for many of our analyses.

Riparian habitats are used extensively by small mammals for permanent residence and dispersal corridors (Brinson et al, 1981). Species composition of small mammal communities in Georgia was effected by width of the riparian zone (Thurmond and Miller, 1994). Wide streamside riparian zones maintained populations characteristic of mature riparian habitats whereas narrow zones did not. These results contrasted with those of Dickson and Williamson (1988) who found more small mammals, predominately the fulvous harvest mouse (*Reithrodontomys fulvescens*), in narrow riparian zones (< 25 m) compared to wider zones (>30 m) in Texas. *Peromyscus* spp. were abundant in all widths studied. Riparian zone width in the upper Coastal Plain of Virginia may determine whether small mammals reside in this habitat type or use it temporarily for residence or dispersal, but this aspect of their ecologies has not been studied in this area. Although we did not measure them, riparian habitat zones in our study were highly variable in width. How width of habitat zones correlates with small mammal home ranges and movement patterns is unknown.

Hardwood habitats in riparian and upland systems support diverse small mammal communities in the upper Coastal Plain of Virginia. Because small mammals use both habitat types extensively, composition of contiguous upland habitats should be considered in studies of these animals in riparian ecosystems. We conclude that both hardwood habitat types are essential to the long-term survival of the small mammal fauna in the upper Coastal Plain of Virginia.

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