# SEASONAL HABITAT DISTRIBUTION OF SWAMP RABBITS, WHITE-TAILED DEER, AND SMALL MAMMALS IN OLD GROWTH AND MANAGED BOTTOMLAND HARDWOOD FORESTS

**Winston P. Smith and Patrick A. Zollner[1]**

**Abstract**—We studied swamp rabbits, white-tailed deer, and small mammals in an old-growth and adjacent second-growth and young-growth bottomland hardwood forest stands in southern Arkansas, August 1991–February 1993. Based on average home range size and degree of overlap, minimum and maximum density estimates of swamp rabbits were 31 per km$^2$ (no overlap) and 52 per km$^2$ (overlap), respectively. Pellet group estimates of white-tailed deer suggested that density varied from virtually zero in spring to 22 per km$^2$ during autumn. With 29,436 trap nights of total effort during winter, spring, and summer seasons, we captured 939 small mammals that were distributed among 14 species. There were more individuals (n = 445) of more species (S = 11) in old-growth forest than other habitats; more new animals were captured during spring (n = 378). *Peromyscus gossypinus* was clearly the most abundant species in all habitats during all seasons; but it was always more abundant in old growth than other habitats. *Ochrotomys nuttalli* was the only species that was notably more abundant in habitat other than old growth.

## INTRODUCTION

European settlement and associated development during the last three centuries were responsible for dramatic alteration of forested landscapes. Some of the greatest losses occurred in forested wetlands, presumably because of an early dependence on waterways and the readily available rich and productive soils of associated floodplains. Within the Mississippi River floodplain alone, 80 percent of the historical forested acreage (8.5 million ha, Creasman and others 1992) was converted to agriculture or cleared for urban development (MacDonald and others 1979, Rudis and Birdsey 1986). So extensive has been the transformation that southern bottomland forests are viewed as an “endangered ecosystem” (Ernst and Brown 1989). Remaining forests occur as fragments (Rudis 1993) that have experienced a variety of timber harvests. Thus, all but an estimated 0.1 percent of presettlement old-growth bottomland hardwood forests have experienced significant anthropogenic disturbance (Smith and others 1993).

There are attributes of old-growth forests (Thomas and others 1988) largely absent from second-growth forests (Runkle 1981, 1991). In bottomland forests, appreciable differences are apparent between old-growth stands and old (ca. 100 year-old) second-growth forests (Robertson and others 1978). These include substantial differences in forest structure such as the presence of large, decadent trees, stem density and volume, canopy height and cover, understory herb and shrub cover, and coarse woody debris (Bailey 1993). These and other differences are important to the relative success of different plant species (Runkle 1991) and ultimately the diversity of habitats available within a hardwood forest community (Sherman 1978). Continued disturbance of old-growth deciduous forests alters species composition and structure and generally reduces species richness and habitat diversity (Sherman 1978).

Biological investigations of floodplain forests of North America have been limited to game species such as white-tailed deer (*Odocoileus virginianus*; see Halls 1984), swamp rabbit (*Sylvilagus aquaticus*; see Whitaker and Abrell 1986; Zollner and others 1996), or waterfowl (see Reinecke and others 1989). Nongame wildlife received little attention from researchers or land managers until recently (Burdick and others 1989, Wigley and Roberts 1994). Invertebrates, plants, and other indigenous biota contribute significantly to local and regional biological diversity, yet have been virtually ignored (Harris 1989, Sharitz and others 1992).

To adequately assess and credibly project future, additional (and probable cumulative) adverse impacts of land management on the biological diversity of this unique resource, baseline information on species distribution, relative abundance, life history characteristics, and habitat requirements is essential. Moreover, these baseline studies should include previously unmanaged and relatively undisturbed environments to ensure that “the entire ecological arena within which our biota evolved” (Smith and Hamel 1991:4) is represented, even though all that remains are fragments of old-growth southern bottomland hardwood forests.

This paper presents a community profile of mammals in southern bottomland hardwood forests. Specifically, we describe seasonal habitat distribution and relative abundance of several mammal species along an age gradient of old growth, intermediate second growth, and young growth (i.e., recent high-grade harvest) from two successive years of intensive sampling. Although this study was an unreplicated retrospective study, it effectively represents a substantial portion of the quantitative information available on the mammal fauna of southern bottomland hardwood forests.

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## STUDY AREA

The study area was Moro Bottoms Natural Area, approximately 8 km east of Fordyce, AR (fig. 1). Moro Bottoms Natural Area is in the upper West Gulf Coastal Plain (James and Neal 1986) and contains a 40-ha old-growth bottomland hardwood forest along Moro Creek, in Section 10, T11S, R12W, Cleveland County, AR. The old-growth stand was part of a larger tract (ca. 70 ha) in Cleveland and Calhoun counties, under the joint stewardship of the Arkansas Natural Heritage Commission and the Arkansas Nature Conservancy.

The climate is typical of the Coastal Plain with hot and humid summers and a mean summer temperature of 27 °C. Mean annual rainfall is 123.4 cm with much of the rain occurring during spring. Portions of the study area adjacent to the creek are inundated periodically during spring and early summer, but water usually does not persist for more than a week at a time. Several sloughs and creeks join the main channel of the stream such that water is abundant throughout the study area. Elevation of the site ranges 48–51 m above mean sea level.

The Moro Bottoms site is an excellent example of an old-growth bottomland hardwood forest. Trees, especially sweetgum (*Liquidambar styraciflua*) and cherrybark oak (*Quercus falcata* var. *pagodifolia*), are quite large with exceptionally good form. Average density for overstory trees was 31 stems per ha, and average basal area was 35.0 $m^2$ per ha (153 $ft^2$ per acre; Smith and others 1995, Zollner 1993). Sweetgum, cherrybark oak, and willow oak (*Q. phellos*) are the three most common overstory species (Smith and others 1995, Zollner 1993).

Moro Bottoms provided an ideal opportunity to study mammals of unmanaged bottomland hardwood forest. Also, during August 1989 Moro Bottoms experienced a severe windstorm. Numerous windthrows occurred creating gaps in the overstory ranging in size from a single stem (0.01 ha) to about 0.3 ha. Because of these natural disturbances within old growth and the proximity to managed second-growth forests, the Natural Area presented an excellent setting to examine the effects of recent natural and anthropogenic disturbances on mammalian species habitat distribution and relative abundance.

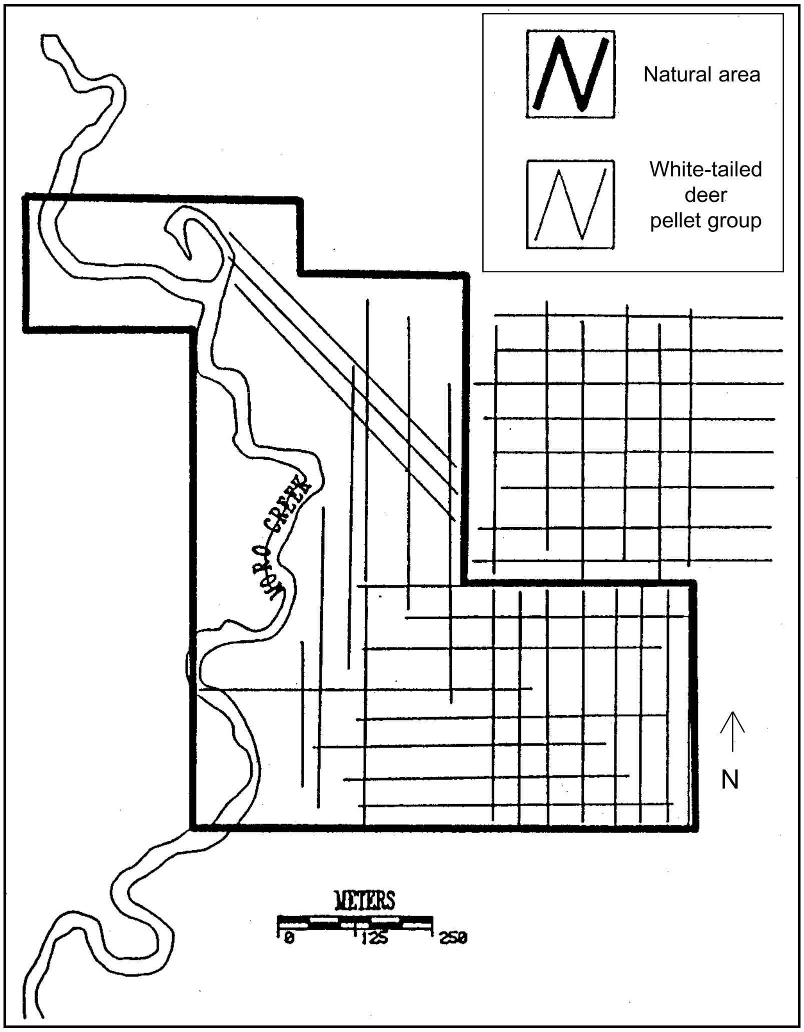

Figure 1—Distribution and orientation of deer pellet group transects, Moro Bottoms Natural Area, Cleveland County, AR.

## METHODS

### Swamp Rabbits

**Capture and handling**—Beginning on 12 January 1991, and continuing through 2 June 1991, from 60 to 145 traps were maintained and checked daily. These included 20 wire-mesh traps covered in shade cloth and 125 wooden box traps (20 X 20 X 60 cm). Eight drift fences were constructed and installed near clusters of box traps to enhance trapping success (Smith and others 1993, Zollner 1993).

Following capture, rabbits were weighed, identified to age (i.e., juvenile or adult) and sex, fitted with a 350-g radio-collar, and released. Each rabbit was allowed 1 week to adjust to its collar and recover from the stress of capture. Thus, observations of movements and habitat use began during the second week post-capture (Smith and others 1993, Zollner 1993).

**Animal movements**—It is important to monitor movements during all activity periods to accurately reflect habitat selection. However, it is difficult to determine the particular time when activity begins during different times of the year. Using the results of a detailed behavioral study as our basis (Marsden and Holler 1964), we selected 1830 as a conservative estimate of when evening activity should commence during any month of the year. Likewise, 0630 was selected as a time when rabbits continued to be active during all times of the year. Accordingly, the period between 0800 and 1700 was designated as the period during which rabbits would most likely be resting during all times of the year (Smith and others 1993, Zollner 1993).

Each rabbit was monitored daily between 0630 and 1830. Because the initial response of swamp rabbits to perceived threat is to remain motionless (Hamilton, 1955), we were often able to approach within a few meters of individuals and locate specific brush piles or thickets where the animal was resting. This procedure facilitated our locating rabbits consistently within an area defined by a 5–m radius. The difficulty of moving through the study area in the dark limited our ability to monitor rabbits at night. Twice each week, rabbits were located between 1830 and 0630.

**Microhabitat use**—During June and October of 1991, 36 quadrats in each of three study grids (fig. 2) were randomly selected and searched for signs of swamp rabbit browse. This sample size was calculated based upon variance (Stein 1945) in the density of browseable stems found during a pilot study (Zollner 1993). Quadrats were searched for browse by dividing them into quarters that correspond to the corners of the quadrat. Inside each quarter 15 0.5 X 0.5-m plots were placed systematically at 2-m intervals along three rows, 5 m apart. Inside each plot, number of browseable (available) stems and browsed (used) stems of each plant species were recorded. Browseable stems were defined as

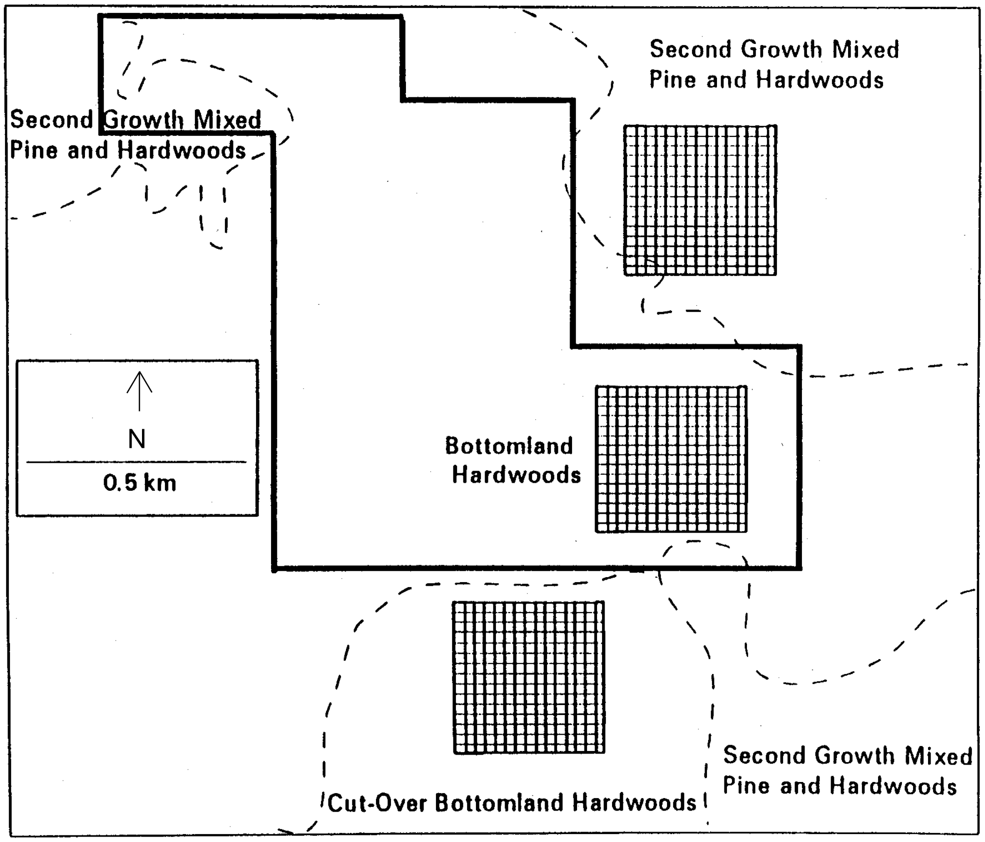

Figure 2—Location of old growth, second growth, and recently harvested (cut-over) bottomland hardwood small mammal trapping grids, Moro Bottoms Natural Area, Cleveland County, AR.

all vegetation less than 0.8 m above the ground and <1 cm in diameter. Stems were considered browsed by rabbits if they were cut off cleanly and not torn as is typical of white-tailed deer (Strole and Anderson 1990). All quarter sections where browse was observed in any plot were considered browsed for that survey and their locations were noted. During July and November of 1991, microhabitat characteristics were measured in each quadrat quarter where evidence of browsing was observed. Six characteristics were measured at each site where swamp rabbit browsing was observed and at randomly selected points in each habitat type. A 10-m north-south line transect intercepted the center of each habitat point, and was used to estimate the percent composition of herbaceous vegetation, shrub coverage, down treetops, and fallen logs at each site. The average value of spherical densiometer measurements (Vora 1988) at the center of each plot and 5 m from the center of each plot at 0, 90, 180, 270 degrees was used to estimate percent canopy closure at each site. A point-center-quarter method of habitat evaluation was used to approximate overstory basal area (Gysel and Lyon 1980). Trees >5 cm diameter at breast height (d.b.h.) with no branches from other trees over their crowns were considered in the overstory.

**Density—**Because of the small number of new captures and recaptures, we were not able to use a ratio-estimator to estimate population size and density. Instead, we present minimum population estimates that were derived from the average core area (i.e., maximum area where observed utilization distribution exceeds a uniform utilization distribution, Dixon and Chapman 1980) occupied by each adult female, adult male, and juvenile. In addition, we estimated density under the following assumptions: an average home range overlap of 25 percent among females and 50 percent between females and juveniles; and the entire study area was suitable swamp rabbit habitat.

### White-Tailed Deer

**Habitat use—**We estimated seasonal use of gaps and forested habitats by white-tailed deer from counts of fecal pellet groups (Eberhardt and Van Etten 1956). This technique requires that observers remove or mark (e.g., spray paint) all pellets encountered along a predefined transect. The observer then returns to the transect after a predetermined period of time has elapsed and records the number of pellet groups that are encountered. Typically, the sequence of transects traversed during the marking or clearing phase is maintained during the enumeration phase so that the "elapsed time," i.e., time period between clearing and counting, is approximately the same for all transects (Neff 1968). Total number of pellet groups recorded among all transects provides an estimate of deer density according to the premise that white-tailed deer on the average defecate at a predictable rate. We used the summer (24 groups per day) and autumn-winter (31 groups per day) estimates for southern white-tailed deer (Sawyer and others 1990).

In this study, we conducted bimonthly censuses; months were alternated between years so that a 2–year period provided seasonal estimates that included every month. Also, transects were established in such a fashion as to incorporate forested habitats and gaps in proportion to their occurrence across the study area. We initially (December 1990) established 17 transects: four transects were 4 m X 0.25 km; the remaining transects were 4 m X 0.5 km (fig. 1). In July 1992, we added one 4 m X 325 m transect and eight 4 m X 350 m transects. Figure 1 illustrates the spatial distribution and orientation of transects across the study area. Chi-square was used to test the null hypothesis that occurrence of deer within habitats was according to availability (i.e., proportion of study area) of gaps and forested habitats (Byers and others 1984). We used an experiment-wide error rate of 0.05; comparison-wide error rate varied according to the number of comparisons and followed the procedures of Bonferroni adjustments (Byers and others 1984).

### Small Mammals

**Habitat distribution—**We estimated seasonal species distribution and abundance across three bottomland hardwood habitats by live trapping for 2 years during spring, summer, and winter. Trapping began August 1991 and continued through February 1993. We established three 300 m X 300 m (9 ha) trapping grids, one each in old-growth, second-growth, and recently logged (cutover) bottomland hardwood forest habitats (fig. 2). A 15 X 15 array (i.e., 20–m spacing between traps) of Sherman (H.B. Sherman Traps Inc., P.O. Box 20267, Tallahassee, FL 32316) live traps (7.6 X 8.9 X 22.9 cm) was established on the forest floor of each grid. Superimposed on the existing grid in each habitat, we established a 3 X 3 array (100–m spacing) of elevated platforms (1.8 m) and a 5 X 5 array (60–m spacing) of wooden box traps on the forest floor. On each elevated platform, we placed a Sherman live trap and a wooden box trap (20 X 20 X 60 cm). All wooden box traps were equipped with a predator guard (Zollner, 1993)

Also, four "triad" arrays of 10 pitfall traps were installed, one midway on each of three sides (north, south, east), and one in the approximate center of each grid. Each triad array included a center pitfall trap and three drift fence "arms" radiating at about 120° angles from the center. Each triad arm was comprised of a center pitfall trap and a trap on each end, between which were two 10–m X 60–cm aluminum drift fences. Each pitfall trap was made of two No. 10 aluminum cans taped end-to-end; concrete "anchors" were bolted to the bottom of each pitfall trap to prevent water table pressure from expelling the cans.

Thus, each habitat grid contained 408 traps: 234 Sherman live traps, 34 wooden box traps, and 40 pitfall traps. General sampling protocol included the operation of all grids simultaneously during each season. On each grid, traps were checked once in the morning; Sherman and box live traps were baited with a mixture of rolled oats and vanilla extract. Each trapping session began during the approximate middle of each calendar season and continued continuously until we approached 100 percent recapture, or for a period not exceeding 10 days. Individuals were identified to species and sex, weighed, measured, uniquely marked, and released at the trap site. Small mammals (e.g. *Peromyscus* sp.) were toe-clipped using a standard procedure (Blair 1941); larger mammals (e.g., *Didelphis virginiana*) were marked with a numbered, self-piercing ear tag (National Band and Tag Company, Newport, KY) in both ears.

Species abundance was estimated seasonally as the number of individuals of each species captured on a habitat grid. Although total area contained within each grid was similar, number of captures was not an estimate of density because of movements of individuals from and to the grid during the sampling period (Van Horne 1982). For the purpose of estimating relative abundance, however, we assumed that the effective sampling area, i.e., total area supporting animals captured on a grid, did not vary across habitats.

## RESULTS

An initial survey of the study area revealed that at the beginning of the study, about 25 percent of the old-growth tract was in windthrow gaps. Canopy openings ranged in size from 500 m$^2$ to 5000 m$^2$ with most of the gaps being less than 1500 m$^2$; about a third of the gaps were larger than 2500 m$^2$ (Smith and others 1995).

### Swamp Rabbits

**Density**—From 12 January through 26 June 1991, 13,520 trap nights of effort were used to capture 13 swamp rabbits. Seven individuals, four adult females, one adult male, and two juveniles were large enough to carry a radio-transmitter for monitoring. A total of 107 nocturnal, 809 diurnal, and 308 crepuscular locations were recorded; 862 locations were recorded during spring-summer (summer) and 362 locations were recorded during fall-winter (winter).

Mean home range for adult females during the growing season (spring-summer) was 11.9 ha (29.3 acres), whereas the adult male had a summer home range of 19.9 ha (49.2 acres) and a juvenile home range was 5.6 ha (13.8 acres). Assuming no home range overlap among females or among males, nor between juveniles and males or females, with complete overlap of male and female home ranges, our minimum density estimate during the growing season was 8.4 adult females per km$^2$ (21.8 per mi$^2$), 5.0 adult males per km$^2$ (13 per mi$^2$), and 17.9 juveniles per km$^2$ (46.4 per mi$^2$).

With 25 percent overlap, the average exclusive area occupied by females becomes 8.9 ha (22.0 acres); for juveniles averaging 50 percent overlap, their exclusive core area is 2.8 ha (6.9 acres). Corresponding density estimates become 11.2 adult females per km$^2$ (29.1 per mi$^2$) and 35.7 juveniles per km$^2$ (92.8 per mi$^2$); adult male density estimates remain unchanged. Thus, minimum population size on the study area (40 ha) during the growing season was 13 swamp rabbits with perhaps as many as 21, if our estimates of home range overlap were reasonable.

**Habitat use and microhabitat characteristics**—The initial survey of the study area classified 27 percent of the quadrats as gaps with the remaining portion categorized as closed-canopy forest. All but five of 1,117 diurnal and crepuscular locations occurred in gaps. When compared to that expected according to the relative abundance of gaps (i.e., 27 percent of 1,117, or 302 locations) with a goodness-of-fit test (Zar 1984), we found that the probability of this occurring by random chance was very small ($\chi^2 = 2,978$, $P < 0.0001$). In some circumstances, mostly during crepuscular time periods, rabbits were first encountered in open, grassy areas; the vast majority of diurnal and crepuscular locations, however, were within resting/hiding places such as in large brushpiles or woody debris from windthrown trees, or inside a cavity in the bole of a down tree. Unfortunately, we were unable to classify nocturnal locations because of having to use triangulation rather than direct observations.

Microhabitat features of browsing sites used by rabbits during summer and winter are summarized in table 1 along with features measured at random sites. During the summer, stand density of the overstory at sites used by rabbits for browsing (42.0 stems per ha) was greater ($\chi^2 = 7.51$, d.f. = 1, $P < 0.01$) than at random sites (23.0 stems per ha). Understory basal area at browse sites (0.13 m$^2$ per ha) was less ($\chi^2 = 6.21$, d.f. = 1, $P < 0.025$) than that available across the study area (0.22 m$^2$ per ha). Also, midstory basal area at browse sites (2.35 m$^2$ per ha) was less ($\chi^2 = 4.28$, d.f. = 1, $P < 0.05$) than that recorded at random sites (2.78 m$^2$ per ha).

### White-Tailed Deer

During the period December 1990—April 1992, 17 transects were sampled in the old-growth stand (48.4 ha) bimonthly; 14 transects were sampled in adjacent second-growth stands (26.4 ha). Beginning July 1992 and continuing through November, an additional nine transects were surveyed in the old-growth stand. The elapsed time (i.e., period between cleaning a transect and enumerating pellet groups) varied from 3 to 8 days across bimonthly sampling periods according to number of investigators and amount of flooding, but was similar among transects within a sampling period (fig. 3).

Density of white-tailed deer across the old-growth and second-growth stands varied considerably among bimonthly sampling periods (fig. 3). Throughout the study period, the study area (i.e., old-growth stand) received much more use during autumn-winter (x = 13.5 deer per km$^2$ [35.0 deer per mi$^2$]) than during spring-summer (x = 1.1 deer per km$^2$ [2.8 deer per mi$^2$]). Unfortunately, estimates were not available from March or April 1991 because >90 percent of the transects were flooded. Deer densities in the adjacent second-growth stand (fig. 2) showed the same seasonal patterns as that recorded in the old-growth stand (fig. 3). Deer densities recorded during March and April in the second-growth stand (of which <25 percent was inundated) were typical of spring-summer values in the old-growth habitat (fig. 3).

Frequency of occurrence of white-tailed deer in gaps or closed-canopy forest in the old-growth stand or in an adjacent second-growth stand is summarized in table 2. In table 3, frequency of occurrence of white-tailed deer in canopy gaps or closed-canopy forest across old-growth and adjacent second-growth stands is presented. The latter provides insight into how deer used the old-growth stand relative to surrounding available forest habitat.

**Table 1—Mean ($x$) and standard error ($x_s$) of microhabitat features of random sites and sites where rabbits were observed browsing, Moro Bottoms Natural Area, AR, February 1991–March 1992 ($\chi^2$ statistic is from a non-parametric analysis of variance.)**

| Variable | Random site | | Browse site | | | |
|---|---|---|---|---|---|---|
| | $x$ | $x_s$ | $x$ | $x_s$ | $\chi^2$ | $P > \chi^2$ |
| | | | **Summer** | | | |
| | (n = 46) | | (n = 30) | | | |
| Percent cover dead | | | | | | |
| Wood <5 cm | 3.13 | 1.21 | 8.37 | 2.55 | 2.13 | 0.250 |
| Wood >5 cm | 3.01 | 1.79 | 3.36 | 1.88 | 0.09 | .750 |
| Shrub cover % | 9.83 | 2.91 | 8.19 | 1.68 | .01 | .900 |
| Bare ground % | 68.23 | 5.74 | 73.85 | 3.13 | .01 | .900 |
| Herbaceous cover % | 28.77 | 5.29 | 26.11 | 3.13 | .23 | .750 |
| Basal area ($m^2$ per ha) | | | | | | |
| Overstory | 34.66 | 2.36 | 37.16 | 2.17 | .36 | .750 |
| Midstory | 2.78 | 0.45 | 2.35 | 0.31 | 4.28 | .050 |
| Understory | 0.22 | .40 | 0.13 | .03 | 6.21 | .025 |
| Density (stems per ha) | | | | | | |
| Overstory | 23.0 | 2.03 | 42.0 | 5.74 | 7.51 | .010 |
| Midstory | 137.0 | 38.65 | 118.0 | 13.31 | .26 | .750 |
| Understory | 397.0 | 67.21 | 483.0 | 131.07 | .61 | .750 |
| Canopy closure | 75.9 | 2.63 | 80.8 | 1.94 | 3.45 | .100 |
| Herbaceous density (stems per $m^2$ | 9.2 | 1.36 | 10.9 | 1.09 | .87 | .750 |
| | | | **Winter** | | | |
| | (n = 53) | | (n = 48) | | | |
| Percent cover dead | | | | | | |
| Wood <5 cm | 5.31 | 1.75 | 3.78 | 2.06 | .41 | .500 |
| Wood >5 cm | 1.77 | .62 | 1.59 | .66 | .03 | .750 |
| Shrub cover % | 4.86 | 1.65 | 9.50 | 4.63 | .09 | .750 |
| Bare ground % | 80.96 | 3.83 | 79.73 | 5.24 | 1.19 | .250 |
| Herbaceous cover % | 11.83 | 2.14 | 13.82 | 3.48 | .06 | .750 |
| Basal area ($m^2$ per ha) | | | | | | |
| Overstory | 35.34 | 1.82 | 36.00 | 2.58 | .11 | .500 |
| Midstory | 1.86 | .23 | 1.40 | .22 | .74 | .250 |
| Understory | .09 | .02 | .10 | .03 | .04 | .750 |
| Density (stems per ha) | | | | | | |
| Overstory | 31.0 | 6.70 | 23.0 | 3.23 | .03 | .750 |
| Midstory | 234.0 | 49.22 | 147.0 | 20.32 | .73 | .250 |
| Understory | 418.0 | 143.03 | 240.0 | 42.59 | .71 | .250 |
| Canopy closure | 28.5 | 1.84 | 32.7 | 3.72 | 1.08 | .250 |
| Herbaceous density (stems per $m^2$) | 5.3 | .77 | 8.3 | 1.78 | 1.36 | .750 |

Generally, white-tailed deer used gaps and closed-canopy forest in proportion to availability ($\chi^2 < 3.84$, d.f. = 1 $P > 0.05$) across the old-growth study area and in an adjacent second-growth stand Notable exceptions occurred in the old-growth stand during April 1992 ($\chi^2 = 6.4$, $P < 0.025$) and June 1992 ($\chi^2 = 4.3$, $P < 0.05$) when deer used gaps more frequently and closed-canopy forest habitat less frequently than expected from availability. Also, percent use of canopy-gaps in the second-growth stand during February 1992 was greater ($\chi^2 = 6.9$, $P < 0.01$) than expected. Although a similar pattern occurred in the old-growth stand, it was not quite significant ($\chi^2 = 2.9$, $0.05 < P < 0.10$), probably because of the effect that inundation had on area sampled (table 2) and the sample size of pellet groups.

When examined from the perspective of bimonthly distributions in habitats across both stands, deer appeared to depart (i.e., $\chi^2 > 7.82$ $P < 0.05$) more from the expected

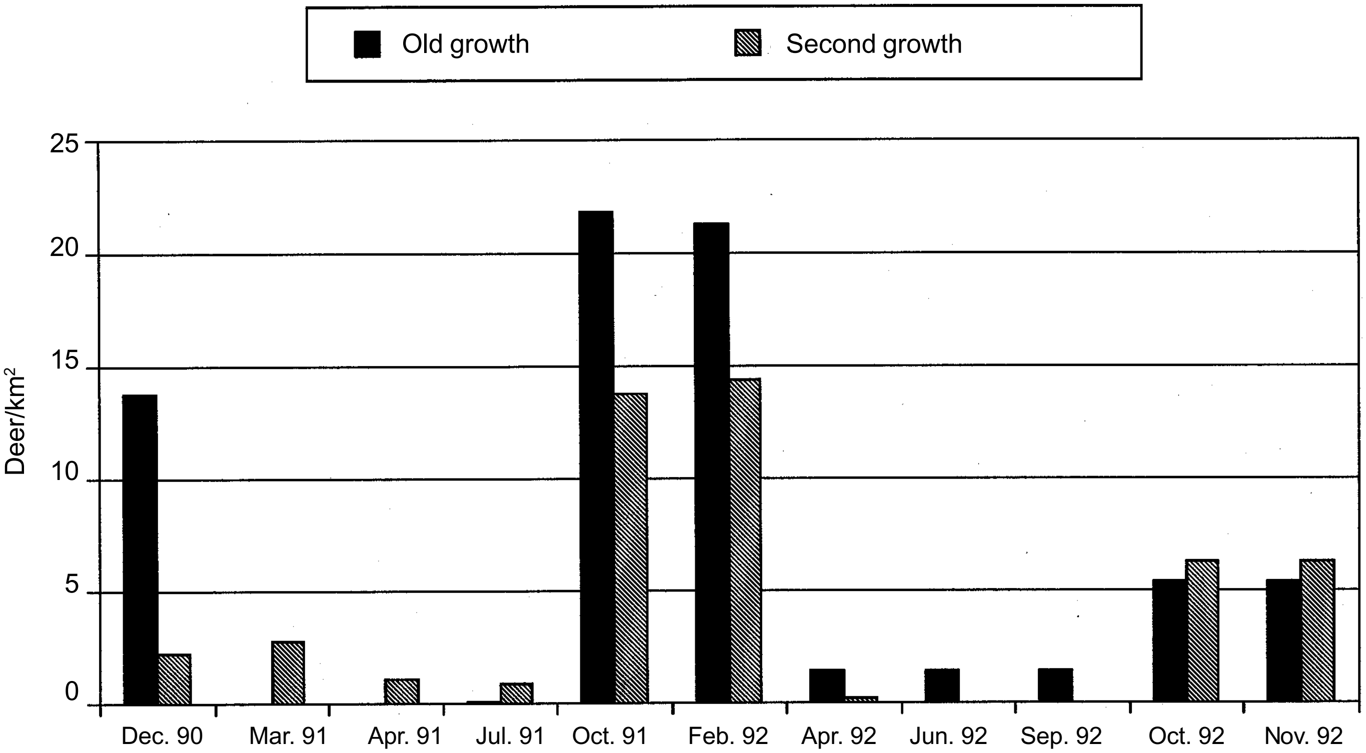

Figure 3—White-tailed deer density from bimonthly pellet group counts in bottomland hardwood forest, Moro Bottom Natural Area, AR, December 1990–November 1992.

**Table 2—Relative abundance (percent occurrence) of white-tailed deer in closed-canopy forest and canopy openings (gaps) in bottomland forest, Moro Bottoms Natural Area, AR, December 1990–November 1992 (percentages computed for within habitat totals; Chi-square statistic [$\chi^2$] computed for goodness-of-fit test, d.f. = 1)**

| | Old growth | | | | | Second growth | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Availability | | Use | | | Availability | | Use | | |
| Month per year | Gaps | Forest | Gaps | Forest | $\chi^2$ | Gaps | Forest | Gaps | Forest | $\chi^2$ |
| December 1990 | 8.5 | 91.5 | 12.0 | 88.0 | 0.2 | 10.3 | 89.7 | 0.0 | 100.0 | 0.4 |
| March 1991 | — | — | — | — | — | 10.3 | 89.7 | 23.0 | 77.0 | .2 |
| April 1991 | — | — | — | — | — | 10.3 | 89.7 | .0 | 100.0 | .6 |
| July 1991 | 18.8 | 81.2 | 0.0 | 100.0 | .1 | 10.3 | 89.7 | .0 | 100.0 | .6 |
| October 1991 | 18.8 | 81.2 | 17.3 | 82.7 | .2 | 10.3 | 89.7 | 11.5 | 88.5 | .3 |
| February 1992 | 18.8 | 81.2 | 32.0 | 68.0 | 2.9 | 10.3 | 89.7 | 22.2 | 77.8 | 6.9 |
| April 1992 | 18.8 | 81.2 | 50.0 | 50.0 | 6.4 | 10.3 | 89.7 | .0 | 100.0 | .1 |
| June 1992 | 18.8 | 81.2 | 100.0 | 0.0 | 4.3 | 10.3 | 89.7 | .0 | 0.0 | .0 |
| September 1992 | 18.8 | 81.2 | 50.0 | 50.0 | 1.3 | 10.3 | 89.7 | 33.3 | 66.7 | 1.7 |
| October 1992 | 18.8 | 81.2 | 16.7 | 83.3 | .1 | 10.3 | 89.7 | 7.1 | 92.9 | .3 |
| November 1992 | 18.8 | 81.2 | 12.0 | 88.0 | .8 | 10.3 | 89.7 | 3.6 | 96.4 | 1.3 |

**Table 3—Relative abundance (percent occurrence) of white-tailed deer in closed-canopy forest and canopy openings (gaps) in bottomland forest, Moro Bottoms Natural Area, AR, December 1990–November 1992 (percentages computed for across habitat totals; Chi-square statistic [$\chi^2$] computed for goodness-of-fit test, d.f. = 3)**

| | Old growth | | | | Second growth | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Availability | | Use | | Availability | | Use | | |
| | Gaps | Forest | Gaps | Forest | Gaps | Forest | Gaps | Forest | $\chi^2$ |
| December 1990 | 4.6 | 49.4 | 6.0 | 78.6 | 1.4 | 44.7 | 0.0 | 15.4 | 32.0 |
| March 1991 | — | — | — | — | 10.3 | 89.7 | 23.0 | 77.0 | 4.3 |
| April 1991 | — | — | — | — | 10.3 | 89.7 | .0 | 100.0 | .6 |
| July 1991 | 12.0 | 52.0 | 0 | 20.0 | 3.7 | 32.3 | .0 | 80.0 | 4.5 |
| October 1991 | 12.0 | 52.0 | 15.1 | 71.9 | 3.7 | 32.3 | 1.5 | 11.5 | 45.6 |
| February 1992 | 12.0 | 52.0 | 11.4 | 24.3 | 3.7 | 32.3 | 14.3 | 50.0 | 38.4 |
| April 1992 | 12.0 | 52.0 | 45.5 | 45.5 | 3.7 | 32.3 | .0 | 9.0 | 12.6 |
| June 1992 | 12.0 | 52.0 | 100.0 | 0.0 | 3.7 | 32.3 | .0 | 0 | 7.3 |
| September 1992 | 12.0 | 52.0 | 20.0 | 20.0 | 3.7 | 32.3 | 20.0 | 40.0 | 6.9 |
| October 1992 | 12.0 | 52.0 | 10.0 | 2.9 | 3.7 | 32.3 | 50.0 | 37.1 | 1.0 |
| November 1992 | 12.0 | 52.0 | 5.7 | 41.5 | 3.7 | 32.3 | 1.9 | 50.9 | 9.2 |

null model (table 2). In particular, deer used closed-canopy, old-growth forest more often ($\chi^2$ = 14.5, d.f. = 1, *P* < 0.001) and closed-canopy, second-growth forest less often ($\chi^2$ = 16.0, d.f. = 1, *P* < 0.001) than expected in December 1990. This pattern occurred again during early autumn (October) 1991 (old-growth: $\chi^2$ = 15.1, d.f. = 1, *P* < 0.001; second-growth: $\chi^2$ = 26.4, d.f. - 1, *P* < 0.001). Conversely, deer used closed-canopy second-growth forest more often during autumn (November) of 1992 ($\chi^2$ = 5.8, d.f. = 1, *P* < 0.01) while showing proportional use among other habitats. During February 1992, deer mostly occurred in the second-growth stand with greater than expected use of both gaps ($\chi^2$ = 21.2, d.f. = 1, *P* < 0.001) and closed-canopy forests ($\chi^2$ = 6.8, d.f. = 1, *P* < 0.01). This pattern was reversed in the following spring (April) when deer occurred almost exclusively within the old-growth stand (table 4), with a significant preference for canopy gaps ($\chi^2$ = 10.2, d.f. = 1, *P* < 0.01).

## Small Mammals

During the study, 29,436 trap nights of effort were equally distributed across habitats as follows: summer—2,396 trap nights; winter—8,520 trap nights, and spring—8,520 trap nights. We captured a total of 871 terrestrial small mammals distributed among 9 species (table 4); we also captured 2 southern flying squirrels (*Glaucomys volans*), 6 gray squirrels (*Sciurus carolinensis*), 1 fox squirrel (*S. niger*), 51 opossum (*Didelphis virginiana*), and 8 raccoons (*Procyon lotor*). More animals were captured during spring (n = 378) than either winter (n = 330) or summer (n = 231). Old growth produced the largest number of new captures (n = 445) and species (S = 11), whereas second growth produced the fewest new captures (n = 183).

Mammal species composition of habitats varied across seasons and years. The cotton mouse (*Peromyscus gossypinus*) was clearly the predominant species during all seasons and across all habitats (table 4); it was more abundant in old-growth habitat during all seasons. The only other small mammals that were consistently captured across habitats and seasons were hispid cotton rat (*Sigmodon hispidus*) and golden mouse (*Ochrotomys nuttalli*). The golden mouse was the only small mammal species that was notably less common in old growth as compared to the other habitats (table 4).

There were limited data, but some interesting variation in platform captures of terrestrial small mammals was apparent. During spring 1992, relatively heavy rainfall occurred at the end of the trapping session. During the initial 4 days of trapping, when there was no measurable precipitation, we captured 11 *Peromyscus gossypinus* in elevated platform traps; no other species were recorded. Results from one night of trapping following and during rainfall yielded 19 *P. gossypinus* and 2 *Ochrotomys nuttalli*. Nine *P. gossypinus* were recaptures of individuals previously caught in forest floor traps; the other 10 platform captures were unmarked *P. gossypinus*. When we examined data from the 9 nearest forest floor traps (i.e., surrounding 3 X 3 array), in only one instance did we find >1 trap occupied. In that one instance, there were four occupied traps.

Another interesting anecdote was a dramatic increase in the number of gray squirrels captured during April—May 1991. While trapping swamp rabbits with wooden box traps on the forest floor, we captured squirrels at a rate that was an order of magnitude greater than previously observed during this study. Typically, efforts to capture swamp rabbits during this study averaged 1 to 2 gray squirrels per week. After 2 to 3 weeks of catching notably more gray squirrels, comparable trapping efforts again yielded about 1 to 2 gray squirrels per week. A relatively large proportion of the gray squirrels was represented by juveniles, suggesting perhaps that the sudden increase in number of captures was related to dispersal.

## DISCUSSION

### Assumptions and Limitations

The Moro Bottoms Natural Area and adjacent private lands represented a natural laboratory and unique opportunity to examine small mammal communities across a variation of unmanaged and managed bottomland hardwood forests. Unfortunately, this was not a replicated experiment and thus one should be cautious about drawing general inferences beyond our study.

Sources of error in this study included escape of captured individuals before confirming whether they were new captures. Unconfirmed small mammal captures occurred infrequently (≤1 per grid per season). We recorded them as new animals and thus may have over-estimated relative abundance of some species. Another potential source of error was misidentification of *Peromyscus gossypinus* and *P. leucopus*, which are extremely difficult to differentiate in the field (Lowery 1974, St. Romain 1976). Adult *P. gossypinus* were relatively easy to recognize in this study because their weights clearly exceeded the maximum reported for *P. leucopus* (36 g; Sealander and Heidt 1990). The primary difficulty was determining whether smaller (<35 g) individuals were juvenile *P. gossypinus* or adult *P. leucopus*. Pelage of juvenile and adult *Peromyscus* typically differ, but variation exists and opportunities for confusion are not uncommon (St. Romain 1976, Lowery 1974). Consequently, we likely misclassified some individual *Peromyscus*.

### Swamp Rabbit

**Density**—The swamp rabbit is confined to southern bottomland forests of the Southeastern United States (Chapman and others 1982). Historically, its range extended from east Texas to extreme northeast South Carolina, and from southern Illinois and extreme southwestern Indiana, to the coast of the Gulf of Mexico. The lower Mississippi Alluvial Valley (MAV) likely was a center of abundance for

**Table 4—Seasonal abundance of small mammals in old-growth (OG), second-growth (SG), and young-growth (YG) bottomland hardwood forest, Moro Bottoms Natural Area, AR, during the period August 1991–February 1993**

| | Summer | | | Winter | | | Spring | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | OG | SG | YG | OG | SG | YG | OG | SG | YG |
| | | | | | **1991–92** | | | | |
| *Peromyscus gossypinus*<br>cotton mouse | 42 | 21 | 24 | 56 | 24 | 28 | 48 | 23 | 25 |
| *Peromyscus leucopus*<br>white-footed mouse | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 2 | 0 |
| *Sigmodon hispidus*<br>hispid cotton rat | 3 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 3 |
| *Ochrotomys nuttalli*<br>golden mouse | 0 | 8 | 0 | 0 | 2 | 2 | 0 | 10 | 0 |
| *Reithrodontomys fulvescens*<br>fulvous harvest mouse | 1 | 1 | 3 | 0 | 1 | 4 | 0 | 0 | 0 |
| *Microtus pinetorum*<br>woodland vole | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cryptotis parva*<br>least shrew | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Blarina carolinensis*<br>southern short-tailed shrew | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciurus carolinensis*<br>gray squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciurus niger*<br>fox squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Glaucomys volans*<br>southern flying squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Didelphis virginiana*<br>opossum | 4 | 9 | 1 | 1 | 1 | 0 | 2 | 1 | 0 |
| *Procyon lotor*<br>raccoon | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rattus rattus*<br>black rat | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 55 | 40 | 31 | 57 | 28 | 34 | 55 | 38 | 28 |

*continued*

**Table 4—Seasonal abundance of small mammals in old-growth (OG), second-growth (SG), and young-growth (YG) bottomland hardwood forest, Moro Bottoms Natural Area, AR, during the period August 1991–February 1993 (continued)**

| | Summer | | | Winter | | | Spring | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | OG | SG | YG | OG | SG | YG | OG | SG | YG |
| | | | | | **1992–93** | | | | |
| *Peromyscus gossypinus*<br>cotton mouse | 33 | 17 | 16 | 74 | 15 | 71 | 118 | 14 | 79 |
| *Peromyscus leucopus*<br>white-footed mouse | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 3 |
| *Sigmodon hispidus*<br>hispid cotton rat | 4 | 0 | 7 | 8 | 4 | 6 | 10 | 0 | 10 |
| *Ochrotomys nuttalli*<br>golden mouse | 1 | 0 | 0 | 2 | 6 | 9 | 0 | 4 | 2 |
| *Reithrodontomys fulvescens*<br>fulvous harvest mouse | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Microtus pinetorum*<br>woodland vole | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Cryptotis parva*<br>least shrew | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Blarina carolinensis*<br>southern short-tailed shrew | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sciurus carolinensis*<br>grey squirrel | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 0 |
| *Sciurus niger*<br>fox squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Glaucomys volans*<br>southern flying squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Didelphis virginiana*<br>opossum | 3 | 6 | 5 | 7 | 4 | 2 | 3 | 1 | 1 |
| *Procyon lotor*<br>raccoon | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Rattus rattus*<br>black rat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 47 | 26 | 32 | 92 | 30 | 89 | 139 | 21 | 97 |

this species; indeed, the MAV historically included 65 percent of all southern bottomland forests (Smith and others 1993) and perhaps as much as 80 percent of the bottomland forests in the range of Sylvilagus aquaticus.

In recent years, the distribution of the swamp rabbit has diminished southward (Chapman and others 1982) and population levels have decreased (Korte and Fredrickson 1977), presumably because of habitat loss and fragmentation. In Missouri, Korte and Fredrickson (1977) reported a decrease in distribution and abundance of this species that coincided with the reduction of potential habitat from 850,000 ha in 1870 to fewer than 40,000 ha in 1973. Conversion of bottomland forests to row crops and urbanization continued on into the mid–1980's (Rudis and Birdsey 1986); recall, 80 percent of the bottomland forests in the lower MAV has been lost since European settlement. Comparable loss of potential habitat was reported for other portions of the range of this species (Whitaker and Abrell 1986). Consequently, the swamp rabbit is listed as a species of special concern in Illinois, Indiana, Kentucky, and Missouri.

In Indiana, Whitaker and Abrell (1986) attributed the decline of swamp rabbits to four factors: (1) loss of available habitat, (2) hunting pressure, (3) flooding, and (4) predator pressure. Also, landscape context was listed as an important factor determining long-term viability of swamp rabbit populations. Apparently, populations occupying prime habitat nearby are important as sources for marginal, less suitable habitat, which may support swamp rabbits in good years.

Little information exists regarding historical or current densities of swamp rabbit populations across its geographical range. Terrel (1972) reported an autumn density of 0.4 per ha (40 per km$^2$) in Indiana, with individuals typically requiring a home range of 4.4 ha. More recently, Whitaker and Abrell (1986) reported that an estimated 80 rabbits were distributed across 10 sites totaling 700 acres (283.4 ha), which represents an average density of 0.28

rabbits per ha (28.2 per km$^2$). In this study, the minimum density estimate during the growing season was 31.3 per km$^2$ (0.31 per ha); average home range (100 percent) during this period was 19.8 ha (Smith and others 1993, Zollner 1993). Our less conservative estimate (i.e., assuming 25 percent overlap in home range among females and 50 percent overlap between females and juveniles) of swamp rabbit density approached 52 rabbits per km$^2$ (0.52 per ha). Given the observed overlap in home ranges among females, and between females and juveniles (Smith and others 1993, Zollner 1993), we suspect that swamp rabbit density during our study was greater than the minimum 0.31 per ha; and perhaps was not very different from that reported for Indiana (Terrel 1972).

Nevertheless, it is difficult to ascertain whether densities observed in this study (or reported in the literature) represented low, intermediate, or high population levels. If frequency of encountering pellet groups or incidental direct observations are indicative of population levels, Moro Bottoms Natural Area supported a conspicuously lower density of swamp rabbits than Delta Experimental Forest, an essentially contiguous 1050–ha tract of secondary bottomland forests within the Mississippi River floodplain, near Stoneville, Washington County, MS (W.P. Smith, personal observation). Behavioral experiments and other observations conducted during this study support the hypothesis that swamp rabbit latrines (i.e., pellet groups) represent territorial markers (Zollner and others, in press) and thus, are probably a fair indication of relative abundance.

**Habitat use—**One of the earliest investigations of this species (Harrison and Hickie 1931) concluded that *S. aquaticus* was associated with canebrakes, hence the common name “cane cutter.” Whitaker and Abrell (1986) later reported that good swamp rabbit habitat included cane (*Arundinaria gigantea*), or elderberry (*Sambucus canadensis*) on elevated areas with sufficient cover and protected from most flooding. They noted that several tree species were common among these sites: sugarberry (*Celtis laevigata*), hackberry (*C. occidentalis*), silver maple (*Acer saccharinum*), hickories and pecan (*Carya laciniosa*, *C. cordiformis*, *C. p*ecan [*illinoensis*]) elms (*Ulmus* spp.), ashes, (*Fraxinus* spp.), sweetgum, cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), oaks, and boxelder (*Acer negundo*).

Although it varied considerably, giant cane was common in portions of Moro Bottoms, especially where the canopy previously had been interrupted. Generally, swamp rabbits were observed more often where cane occurred than expected; but it is unclear as to whether this was a causal relationship, or if the co-occurrence of swamp rabbits and cane are ecological correlates of some other phenomenon, i.e., response to an interruption of the forest canopy. Clearly, swamp rabbits occurred in canopy gaps much more frequently than would be predicted from availability; but many gaps did not have cane. The close association of swamp rabbits with cane in Indiana (Harrison and Hickie 1931, Whitaker and Abrell 1986) was also likely a circumstance where two bottomland hardwood endemics with similar ecological requirements occupied the same habitat rather than an obligate, or even facultative, relationship.

Similar to Whitaker and Abrell (1986), we observed greater than expected occurrence of certain tree species at sites used by swamp rabbits, especially at browsing sites (Zollner 1993). Many of the species were similar to those reported by Whitaker and Abrell (1986), notably elms, hickories, and oaks. Since swamp rabbits typically do not use soft or hard fruit, nor do they have any known needs affiliated with certain tree species, we suspect that these associations are reflecting common favorable environmental circumstances rather than any life history need. One notable exception is the predisposition that certain tree species have for forming bole or buttress cavities, which may offer ideal refuge against predation or inclement weather. Red maple was identified in lowland sites as a cavity-prone species (W.P. Smith, unpublished data).

Some tree species were observed less often at browse sites than random sites, notably black gum, Carolina ash, shellbark hickory, and Nuttall oak (Zollner 1993). But again, this is probably a coincidence related to specific habitat needs. Microsite distribution of many bottomland tree species is often influenced greatly by smal1 (10–20 cm) variations in elevation (Castleberry and others 1996, Pauley and others 1996, Putnam and others 1960). Many of the tree species that occurred less frequently at sites where rabbits were observed foraging (as compared to random sites) typically occur at lower elevations (e.g., Nuttall oak vs. water oak, Zollner 1993) where flooding occurs more frequently and for longer periods. Conversely, loblolly pine was three times more likely to occur at sites used by rabbits for foraging as compared to random sites. Loblolly pine typically occurs on the highest sites within a floodplain, usually on a small, elevated knoll.

Thus, it may be that the seasonal schedule of inundation to a large extent dictates habitat use by swamp rabbits by limiting the availability of the more hydric habitat types, especially during winter and early spring. Strole and Anderson (1992) clearly demonstrated that use of browse resources by a mammalian herbivore is directly related to the availability of those resources. That flooding in Moro Bottoms Natural Area restricted access to portions of individual home ranges, or availability of resources, was supported by the behavioral response of swamp rabbits to inundation (Zollner 1993). During periods of prolonged flooding, swamp rabbits with home ranges near the adjacent, upland pine per hardwood forest moved into the uplands until the water receded. Individuals on the western portion of the study area restricted their movements, remaining on patches of small, elevated ridges.

If inundation frequently imposes restrictions on the use of resources within a floodplain, such as often happened in Moro Bottoms Natural Area, then the quality of swamp rabbit habitat may be as much dependent on the nature of adjacent upland sites as the species composition and structure of the more hydric forest associations. Moreover, when these ecological bottlenecks occur during periods of resource impoverishment, such as in winter and early spring, short-term carrying capacity and long-term population viability are directly linked to frequency and duration of perennial flooding and the quality of adjacent elevated habitat, respectively. Whitaker and Abrell (1986) reported that elevated areas that were protected from most flooding represented an important feature of good swamp rabbit habitat. It appears that the landscape context of bottomland forests may be an equally important feature of swamp rabbit habitat, especially where minor bottoms (i.e., bottomland forests of relatively narrow streams and floodplains) occur in an agriculture-dominated landscape or matrix of upland, even-aged pine forests.

## White-Tailed Deer

**Natural history**—The white-tailed deer has an almost ubiquitous distribution in the coterminous United States with a geographic range that extends into southern Canada and south to northern South America (Smith 1991). Among forest biomes, the density of white-tailed deer generally is directly related to the number of forest openings. In the Southeast, bottomland hardwood forests of the Coastal Plain produce some of the highest quality food for white-tailed deer, which attain densities of 25 deer per km$^2$. Bottomland forests adjacent to agricultural row crops, such as soybean, can support substantially higher densities of white-tailed deer. Where agricultural crops add significant amounts of nutrients to their diet, deer are much larger and local populations can be more than twice the density of comparable areas without row crops nearby (Smith 1991). Although early regeneration stands offer much variety and biomass of herbaceous and woody forage, the lowest quality foods in the Southeast occur in homogeneous loblolly pine and slash pine (*Pinus elliottii*) forests (Newsom 1984).

White-tailed deer allocate more time to feeding than any other activity. Significant seasonal shifts in center of activity often occur in response to local changes in food availability. Generally, grasses and forbs dominate the diet during spring and early summer; as herbs mature, deer switch to succulent, new-growth leaves and twigs. During autumn, soft and hard fruit (e.g., berries and acorns, respectively) predominate in the diet, including fruits of beech, *Smilax* spp., *Crataegus* spp., *Vaccinium* spp. *Rhus* spp., *Vitis* spp., *Rubus* spp., and *Pyrus* spp. Winter diets are determined largely by availability. Dried leaves of deciduous trees, sedges, grasses, mushrooms and other fungi, and woody browse comprise a large proportion of the diet (Smith 1991).

**Habitat distribution and density**—In this study, use of old-growth bottomland hardwoods by deer varied seasonally with the greatest use occurring during autumn (table 2). Even then, densities were about one-half the average reported for southern bottomland forests (Smith 1991). Although it is uncertain why deer density in the old-growth stand was less than expected, we suspect it was at least in part related to the landscape context of Moro Bottoms Natural Area (Castleberry and others, in press). Moro Bottoms is a segment of a relatively narrow, riparian corridor that dissects a landscape of intensively managed timberland, mostly even-aged stands of loblolly pine. This habitat represents one of the poorest quality environments for white-tailed deer, typically supporting from one-third to one-fifth the density of deer that can be sustained in bottomland forests (Newsom 1984).

The pattern of seasonal use observed in our study (table 2) is probably typical of deer inhabiting minor bottoms (Castleberry and others, in press). White-tailed deer of the Coastal Plain will often make short-distant movements (as opposed to migrations elsewhere) in response to changes in the abundance of local food resources. Because of the importance of acorns as a high-energy food item during autumn, deer in this study were probably attracted to the bottoms during October 1991 to exploit a va1uable but ephemeral resource. That deer did not concentrate in the bottoms in November 1992 (table 2) may have been related to early, prolonged periods of inundation. When prolonged flooding occurs in early autumn, acorns that otherwise would be easily accessible are either submerged or washed away. Alternatively, acorns may not have been readily available because 1992 was a poor year for acorn production.

Few deer used the old-growth or second-growth bottomland hardwood stands during spring or summer (table 2). Again, this was probably related to food availability. Although even-aged loblolly pine stands offer little in the way of palatable forage, nearby (<1 km) young regeneration stands probably provided a greater abundance of better quality forage than was available in the bottomland forests. Indeed, deer use of the bottoms was in early succession habitat of forest gaps where one would expect to find more palatable herbaceous and woody new-growth during this period.

## Small Mammals

**Species habitat distribution and abundance**—According to season, Peromyscus gossypinus comprised 50–98 percent of new captures across habitat grids (fig. 2). In 12 of 18 samples (3 habitats X 3 seasons X 2 years), $\geq$70 percent of new captures were *P. gossypinus*. Its prevalence was most apparent in old-growth habitat, especially during winter and spring (table 4). Its abundance in second-growth habitat was less than in old growth with new captures often less than 50 percent of that recorded on the old-growth grid. The cut-over site supported comparable (1991–1992) or greater numbers (winter and spring 1992–1993) of *P. gossypinus* than did second-growth habitat (Table 4).

*Peromyscus gossypinus* is primarily an inhabitant of moist forest habitats, especially common within dense underbrush along streams and throughout bottomland hardwood forest (Sealander and Heidt 1990). Where *P. gossypinus* and *P. leucopus* are sympatric, *P. gossypinus* typically diminishes in abundance along a mesic-xeric gradient (St. Romain 1976); it is absent from drier upland forest types (Sealander and Heidt 1990). *Peromyscus gossypinus* nests in hollow stumps, tree cavities, or beneath logs.

Old-growth forests possess many characteristics that are absent in second-growth forest (Runkle 1991). In bottomland forests, even older (ca. 100 year-old) second-growth stands lack many of the features typical of their old-growth counterparts (Robertson and others 1978). Abundant snags, dead or dying tree limbs, and coarse woody debris, typical of old-growth forest (Harmon and others 1986, Thomas and others 1988), contribute critical nesting microhabitat components and provide an array of substrates within which a plethora of invertebrates proliferate (Bailey 1993, Savely 1939). Moreover, natural disturbances and regeneration typical of old-growth gap dynamics (Runkle 1991) contribute significantly to habitat diversity (Sherman 1978).

Variation between old-growth and second growth bottomland hardwood forest in abundance of *P. gossypinus* can probably be explained by many of the habitat differences outlined above. However, the second-growth grid also included some drier, upland forest habitat components. Elevational differences between adjacent lowland habitats were probably important during periods of inundation as the second-growth grid rarely became flooded. Although *P. gossypinus* is arboreal and apparently can move vertically in response to heavy rainfall, many individuals may be forced to move to higher sites during periods of prolonged flooding (Andrzejewski 1963). Temporary immigrants may be more susceptible to live capture as they are presumably pressed to search for food. The lowest capture rates in second growth occurred during spring 1993 when lower elevation habitat was not flooded and old growth experienced its highest number of new captures of *P. gossypinus* (table 4). Conversely, water was common across lowland sites during spring 1992, and we captured more new *Peromyscus* spp. and more new *Ochrotomys nuttalli* than in spring 1993. But, there was not a clear inverse relationship between new captures on old-growth and second-growth grids during the entire study.

In addition to differences in elevation and moisture, there were apparent differences between old-growth and second-growth habitat in soil and vegetation; loblolly pine, for example, was a significant component of the overstory (Zollner 1993). Some of the variation we observed in *P. gossypinus* habitat distribution was likely attributable to upland habitat features that were common across the second-growth grid. Afterall, *P. gossypinus* is reported to be less abundant or absent in drier, upland woodlands where *P. leucopus* is apparently more abundant (Sealander and Heidt 1990).

The recently harvested (cut-over) site was high graded during 1989–1990 and had some habitat features that were similar to old growth. In particular, the remaining slash was an abundant source of coarse woody debris. Also, many portions of the cutover were not different in habitat structure to windthrow gaps that occurred across the old-growth site. An obvious difference was the absence of large, old trees and associated canopy cover and standing basal area. Whether these similarities in habitat contributed to *P. gossypinus* abundance more closely resembling old-growth habitat than second-growth habitat is unclear. Indeed, it is uncertain whether variation in *P. gossypinus* abundance between second-growth and recently harvested sites (table 4) reflected real differences associated with habitat quality, or as with old-growth habitat, represented an influence of seasonal flooding.

Features of the second-growth grid probably contributed to variation in habitat distribution of other species. In particular, *Ochrotomys nuttalli* was captured more frequently than predicted from random chance; 65 percent (30 per 46) of its captures occurred in second-growth habitat (table 4). *Ochrotomys nuttalli*, like *P. gossypinus*, is common in moist, lowland forests with dense underbrush and is arboreal, often building nests in vine thickets as high as 5 m above the forest floor (Sealander and Heidt 1990). Both *O. nuttalli* and *P. gossypinus* readily move vertically in bottomland forest; in our study, they were the only species that were regularly captured in elevated platform traps. Food items of *O. nuttalli* are apparently similar, but contain less animal matter than *P. gossypinus* (Sealander and Heidt 1990).

Given its reputed preference for bottomland forests, it is unclear why we caught so few *O. nuttalli*. Overall, *P. gossypinus* was nearly 16 times more abundant than *O. nuttalli*; in old-growth habitat, the disparity in abundance between the two species was much greater (table 4). Perhaps the variation we recorded reflected differences in habitat preference. Although both species occur in moist, lowland forests, *O. nuttalli* also occurs in drier, upland forests of pine and cedar (Sealander and Heidt 1990). Thus, although both habitats may be generally suitable, each species may find microhabitat features common to one habitat more attractive; or, each may be behaviorally or physiologically predisposed to successfully responding to peculiar ecological scales.

Regular and frequent inundation, typical of the old-growth grid, may have had a greater influence on the distribution and abundance of *O. nuttalli* as compared to *P. gossypinus*. Some small mammals, notably shrews (Soricidae), are not predisposed to moving vertically in forested habitats. In circumstances where lowland forests become flooded for prolonged periods, terrestrial small mammals presumably must seek higher elevation, suitable habitat as refugia. Voles (*Clethrionomys* spp.) of European bottomland forests typically moved from lowland forest into surrounding habitat during flooding episodes (Andrzejewski 1963).

Alternatively, interspecific interactions may have contributed to the variation in distribution of *O. nuttalli. Peromyscus gossypinus* is very aggressive, whereas *O. nuttalli* is notably docile (Sealander and Heidt 1990). Perhaps the abundance and aggressive nature of *P. gossypinus* influenced the occurrence of *O. nuttalli* on the old-growth grid. It is not uncommon for competitive interactions to influence the structure of rodent communities (Brown 1975, Grant 1972). Moreover, interspecific aggression is a common mechanism mediating competitive exclusion, indeed, “the machinery of competition” (MacArthur 1972). This conclusion also is supported by the more frequent occurrence of *O. nuttalli* in second-growth habitat where abundance of *P. gossypinus* was 30 percent of that in old growth, and less than 4 times more abundant than *O. nuttalli* on the second-growth grid (table 4).

The remaining species were captured in too few numbers to detect response to habitat variation. There were many species, shrews in particular, whose scarcity or absence in our samples remains confusing. Shrews are difficult to capture and typically are under-represented with Sherman live traps (Kirkland 1977), but we totaled over 1,300 trap nights of effort with pitfall traps. Further study of bottomland forest is necessary to determine whether shrews are an insignificant component of the mammal fauna, or whether more innovative or intensive measures of sampling are needed to adequately include this guild.

*Didelphis virginiana* appeared to be more abundant on the second-growth grid with 22 of 51 captures (table 4), but we suspect that this result could have just as easily occurred because of unrelated factors. *Didelphis virginiana* prefers riparian woodlands and typically to a lesser extent, occurs in drier upland forest (Sealander and Heidt 1990). In this study, the second-growth grid had elements of both lowland deciduous woodlands and upland mixed forests. If its more frequent capture was a response to habitat condition, occurrence on the second-growth grid may have been a reflection of habitat heterogeneity rather than specific microhabitat features.

### Managed Versus Unmanaged Forest

The effect of forest management on indigenous vertebrate populations has gained prominence in recent years and is probably one of the most pressing questions of applied ecologists (Smith, in press). There are notable limitations (e.g., unreplicated study design) to what general conclusions can be drawn from direct comparisons of the three habitats studied in our experiment. Still, examining the results of this study in the context of a disturbance and forest stand age gradient may provide some useful insights regarding the impacts of logging on the mammal fauna of bottomland forest.

In a retrospective study of managed and unmanaged stands, McComb and Noble (1980) reported that densities of some small mammals typical of bottomland hardwood forests (e.g., *Peromyscus leucopus*) can decline following intensive timber harvesting. However, they reported more captures for most species in harvested stands than in unmanaged stands. In our study, there was no consistent disparity in abundance between the old-growth and cutover grids. However, we did not sample the cutover site until two growing seasons following harvest.

Studies of upland hardwood forests in the Eastern United States have produced somewhat ambiguous and inconclusive results. Healy and Brooks (1988) reported no differences in small mammal community composition across seedling, sapling, sawtimber, and mature hardwood forest habitats. These were somewhat surprising results as clearcutting Appalachian hardwood forests is usually followed by a dramatic increase in small mammal abundance (Kirkland 1977).

In northern hardwoods, Degraaf and others (1991) reported striking differences in the abundance of some mammals between poletimber and sawtimber stands. Overall, shrews occurred in somewhat higher numbers in poletimber stands, but primarily because of the response of a single species. The remaining three shrew species had comparable captures in both habitats. Other species, such as the woodland jumping mouse (*Napeozapus insignis*), showed a similar preference for poletimber stands. In contrast, *Peromyscus maniculatus* was nearly twice as abundant in sawtimber than poletimber stands.

According to Kirkland (1977), small mammal communities increase in abundance following harvest, but decrease in abundance and diversity to below preharvest levels by the time a stand reaches the pole stage. Subsequently, both abundance and diversity of small mammal communities tend to increase as northern Appalachian hardwood forests mature. This same pattern was generally observed in our study with the fewest number of individuals and species recorded in the second-growth stand (table 4). The old-growth grid typically had the greatest species richness and abundance of mammals, whereas the recently harvested stand was intermediate between old-growth and second-growth habitats (table 4).

The general pattern of small mammal distribution observed in this study and reported by Kirkland (1977) parallels changes that occur in understory vegetation structure in response to disturbance. Old-growth forests show considerable spatial heterogeneity because of the interspersion of canopy gaps. Where the canopy has been interrupted because of windthrow, a dense herbaceous and woody understory develops and existing regeneration surges into the midstory. Anthropogenic disturbance, such as diameter-limit logging, also creates considerable spatial heterogeneity within a forest with uniform canopy. In recent cutovers, understory vegetation increases dramatically and young-growth stands in many ways resemble canopy gaps found within old-growth forests. Conversely, poletimber and young sawtimber second-growth stands can have relatively homogeneous horizontal and vertical structure as compared to old-growth forests or young-growth stands, particularly cutovers with some sort of legacy. This is especially true of second-growth stands that have not undergone intermediate stand management and the canopy closes in, becomes fairly dense, and very little sunlight reaches the forest floor.

Maintaining spatial heterogeneity, especially vertical and horizontal structure, may be the single most important feature of habitat management of bottomland forests for indigenous small mammal communities. Considerations of scale of disturbance, both temporal and spatial, also may be important (Hayward and others 1999) to sustain populations of forest habitat specialists. This is especially true of species, such as *Peromyscus gossypinus*, that apparently require moist forest habitat. Single tree or group selection harvests of late seral forests will likely create the understory and midstory structure typical of gap-phase old growth without overly exposing these stands to drying and other detrimental consequences that arise when the entire forest canopy is removed through clearcutting (Hayward and others 1999).

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