ENHANCING BACHMAN'S SPARROW HABITAT VIA MANAGEMENT OF RED-COCKADED WOODPECKERS

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Abstract: Bachman's sparrows (Aimophila aestivalis) and red-cockaded woodpeckers (Picoides borealis) use mature pine woodlands characterized by well-spaced pines, an open midstory, and a dense understory of grasses and forbs. Populations of the Bachman's sparrow began declining in the 1930s, with both a dramatic retraction in geographic distribution and the extinction of many local populations. Current land management practices in the southeastern United States often focus on the habitat requirements of the red-cockaded woodpecker without considering other species with similar habitat requirements (i.e., Bachman's sparrow). We examined habitat requirements of the Bachman's sparrow on Eglin Air Force Base, Florida, to determine if management practices directed at recovery of red-cockaded woodpeckers are providing Bachman's sparrows with suitable habitat. Comparisons between active red-cockaded woodpecker clusters occupied (n = 8) and unoccupied (n = 8)= 13) by Bachman's sparrows showed that Bachman's sparrows selected areas with a dense understory of grasses and sparse midstory vegetation. Areas suitable for red-cockaded woodpeckers were not always suitable for Bachman's sparrows. Red-cockaded woodpeckers appear more tolerant of a hardwood midstory and do not require a dense cover of grasses and forbs. Prescribed burning is key for development and maintenance of the dense herbaceous understory preferred by Bachman's sparrow. In areas managed for red-cockaded woodpeckers, frequent (3-5 yr) burning early in the growing season appears the best way to increase habitat suitability for Bachman's sparrows.

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formerly classified as a Category 2 species by

the U.S. Fish and Wildlife Service (USFWS)

under the Endangered Species Act of 1973, is

now maintained on the list of species considered vulnerable by the USFWS, and is included

on the National Audubon Society's Blue List of

species of concern (Tate 1986). Although pop-

ulations of Bachman's sparrow are disappearing

at the periphery and within the center of their

range, too little is known about the species to

evaluate its status or to identify management

strategies for its conservation. Dunning and

Watts (1990) suggested that habitat require-

ments for Bachman's sparrows are relatively

strict, and that habitat loss may be an important

Key words: Aimophila aestivalis, Bachman's sparrow, coastal plain, longleaf pine ecosystem, *Picoides borealis*, prescribed fire, red-cockaded woodpecker.

Before colonization of North America by Europeans, the Bachman's sparrow was probably found almost exclusively in open pine forests of the southeastern United States (Jackson 1988). Conversion of deciduous forests to pasture and farmlands in the 18th and 19th centuries allowed this species to expand its geographic distribution northward as far as Pennsylvania and Indiana (Brooks 1938, Hardin and Probasco 1983). Populations of Bachman's sparrows began declining in the 1930s, with both a dramatic retraction of its range and the extinction of many local populations. The range of the Bachman's sparrow is now approximately the same as in precolonial times, but this species has become rare and locally distributed (Dunning and Watts 1990).

The Bachman's sparrow is considered potentially threatened throughout its range. It was

cause for the species' decline.

Available data show that Bachman's sparrow prefers mature pine woodlands characterized by well-spaced pines, an open midstory, and a dense understory of grasses and forbs in the first meter aboveground (Dunning and Watts

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1990). This fire-maintained, subclimax community is often referred to as the longleaf pine (Pinus palustris) ecosystem and once stretched from Virginia to Texas, covering much of the Southeastern Coastal Plain (Myers 1990, Outcalt and Sheffield 1996). This community is an upland savanna-like ecosystem with an open overstory of longleaf pine and a ground cover of perennial grasses and forbs interspersed with deciduous oaks (Quercus spp.; Platt et al. 1988b, Myers 1990). A high frequency of lightning strikes along with the dry, sandy soils characteristic of the Southeastern Coastal Plain are conducive to frequent, low-intensity natural fires (Jackson et al. 1986, Robbins and Myers 1992). Historically, fires occurred in the pine forests of the southeastern United States at intervals of approximately 3-5 years (Chapman 1932, Krusac et al. 1995). Longleaf pines resist fire and they dominate these areas (Chapman 1932, Myers 1990). Platt et al. (1988b) maintained that longleaf pine is a keystone species and, by influencing a fire regime conducive to its reproduction, it influences the composition and abundance of other species within the hab-

Bachman's sparrows seem to prefer mature pine forests but, in at least some parts of their range, they also occur in other habitat types such as young pine woodlands and early successional clearcuts with adequate ground cover (Hardin and Probasco 1983, Dunning and Watts 1990, Gobris 1992, Dunning et al. 1995). In all of these habitats, prevention of midstory hardwood development is critical to the maintenance of populations of Bachman's sparrows. Liu et al. (1995) suggested that incorporation of thinning and prescribed burning into forest management of young pine stands would create suitable habitat for Bachman's Sparrows.

The red-cockaded woodpecker also is endemic to the open pine forests of the south-eastern United States, where destruction and alteration of the longleaf pine ecosystem has drastically reduced populations of this woodpecker (James 1995). Like Bachman's sparrows, red-cockaded woodpeckers use mature, open pine forests with an open midstory (Liu et al. 1995). Red-cockaded woodpeckers require living, old-growth trees in which to construct cavities for nesting and roosting (Jackson et al. 1979). Furthermore, cavity trees are located in low-density stands with sparse midstory vegetation (Hovis and Labisky 1985, Conner and O'Halloran

1987). A significant midstory causes woodpeckers to abandon cavity trees (Jackson 1986, Conner and Rudolph 1989, Hooper et al. 1991).

Fire is the primary management tool for maintaining red-cockaded woodpecker habitat. Unless areas are burned regularly, hardwoods eventually out-compete both shade-intolerant pines and the diverse understory of forbs and grasses (Lewis and Harshbarger 1976). Aside from prescribed burning, other management strategies for red-cockaded woodpeckers have included manual removal of hardwoods from around cavity trees, manual removal of hardwoods over extensive areas, and herbicide application to control hardwoods (Jackson 1986, Krusac et al. 1995).

Since being listed as an endangered species in 1970, the red-cockaded woodpecker has continued to decline throughout its range (James 1995). Concern for the species has prompted the development of management strategies to increase red-cockaded woodpecker populations. These management strategies are generally enacted without adequate consideration of potential effects on other organisms, such as Bachman's sparrows, that share the same habitat (but see Brennan et al. 1995).

Dunning and Watts (1990) observed that habitat management practices for red-cockaded woodpeckers likely produced habitat for Bachman's sparrows, but management practices for red-cockaded woodpeckers vary (Krusac et al. 1995). Other studies (Brennan et al. 1995, Wilson et al. 1995) found Bachman's sparrows were more abundant in areas managed for red-cockaded woodpeckers than in areas not managed for the woodpeckers. However, the habitat requirements of the 2 species are not identical. Although Bachman's sparrows inhabit mature pine woodlands, they do not always benefit from management practices directed at producing suitable habitat for red-cockaded woodpeckers (Liu et al. 1995).

In mature pine woodlands, land management practices have a strong effect on understory vegetation, and therefore habitat suitability for the Bachman's sparrow and red-cockaded woodpecker (Dunning and Watts 1990). We examined habitat requirements of breeding Bachman's sparrows in longleaf pine communities of the Southeastern Coastal Plain to determine if management techniques directed at red-cockaded woodpeckers were compatible with maintaining populations of Bachman's sparrows.

METHODS

Our study site, Eglin Air Force Base (Eglin), is a 188,000-ha reserve in northwestern Florida. Longleaf pine sandhills cover approximately 78% of Eglin (Hardesty et al. 1995). Like most pine forests in the Southeast, Eglin was used as a source of timber and turpentine between 1900 and 1979 (U.S. Department of Defense 1993). All but about 1,000 ha of Eglin were logged, but old-growth trees remained interspersed throughout most stands (Hardesty et al. 1995). Much of the second growth is now ≥80 years old. Eglin has focused its management on the restoration and maintenance of the longleaf pine community (U.S. Department of Defense 1993). During the last decade, recovery of the red-cockaded woodpecker population on Eglin , has been the primary concern in most management decisions. Because of a long history of fire suppression, much of the longleaf woodland on Eglin has a substantial hardwood midstory (Hardesty et al. 1995). Fire is the primary management tool used to remove this midstory, but many years are required before the area will resemble its condition prior to fire suppression. Our study plots were in mature second-growth forests of longleaf pine located in the sandhill and flatwood areas throughout Eglin.

We selected 20 study plots at random from known locations of active red-cockaded woodpecker clusters on Eglin between May and June 1994. Each plot had relatively uniform heterogeneity of vegetation and was at least 200 m in diameter. The locations of red-cockaded woodpecker clusters were provided by the red-cockaded woodpecker research team from the University of Florida. One plot was burned between the 1994 and 1995 surveys and was replaced in spring 1995.

We conducted point counts 4 times each on 20 plots in both 1994 and 1995. Counts were conducted in June and July 1994, and in April, May, and June 1995. We considered a site occupied by Bachman's sparrows if sparrows were present during any of the 8 point counts. However, Bachman's sparrows were present ≥3 times in all but 2 of the occupied sites. We placed points at the estimated midpoint of the cluster of cavity trees, and we flagged and marked each point with wooden stakes. We conducted counts for 10 min each within 4 hr after sunrise. During the first 5 min, we recorded all birds seen or heard within 100 m of the

point. During the second 5 min, we played a tape-recorded song of the Bachman's sparrow (Dunning and Watts 1991) 4 times (90 sec), and we recorded new birds seen or heard within 100 m of the point. Preliminary observations indicated that Bachman's sparrows could be heard singing ≥200 m away, but we limited our observations to within 100 m to achieve accuracy and remain within uniform habitat.

We quantified vegetation characteristics by determining relative vegetation densities at 30 points within each 100-m radius plot. We selected the 30 sampling points randomly within a grid of 200×200 m centered at the counting point. Because previous studies of habitat use by the Bachman's sparrow emphasized the importance of understory vegetation (Dunning and Watts 1990, Gobris 1992), we used the pole method to measure vegetation in the first 4 m aboveground (Mills et al. 1989). We identified all plants within a series of 0.1 m radius cylinders around a pole separated into 0.1-m sections. We used species occurrence records to calculate relative densities of 5 vegetation categories (grass [including sedges], forb, shrub [including trees], vine, dead vegetation) for each plot by summing the number of 0.1-m height intervals within the 30 sample points that contained vegetation of that category. We calculated total relative density of vegetation by summing relative densities for all vegetation categories present within the plot. We chose not to convert the relative densities to volume as described in Mills et al. (1989) because this conversion alters the data by a constant, but no new information is gained. Visual inspection of vegetation density by height revealed that most of the vegetation on our plots was within the first 0.5 m of the ground. Therefore, we calculated vegetation density at or below 0.5 m for analysis of the herbaceous layer. To examine differences in the midstory of occupied and unoccupied sites, we calculated the density of shrubs between 1.0 and 4.0 m. We measured canopy cover with a spherical densiometer.

We measured vegetation on the original 20 plots in July 1994 and the replacement plot in June 1995. We could not sample vegetation at all sites in both years; however, significant changes in vegetative composition or structure were not expected between years because vegetation measurements in 1994 were made near the end of the growing season.

We calculated the mean number (no./count)

Table 1. Mean (± SE) relative density^a of ground cover (vegetation ≤ 0.5 m aboveground) by categories, and total relative density of vegetation at a random sample of active red-cockaded woodpecker clusters with (present) and without (absent) Bachman's sparrows at Eglin Air Force Base, Florida, during spring and summer 1994 and 1995.

| Vegetation category | Present $(n = 8)$ | | Absent $(n = 13)$ | | | |
|---------------------|-------------------|------|-------------------|-----|---------|--------|
| | x | SE | x | SE | Z_{P} | P |
| Grass | 73.75 | 6.0 | 44.61 | 5.5 | 2.864 | 0.004° |
| \mathbf{Forb} | 37.62 | 5.7 | 20.77 | 2.3 | 2.320 | 0.020 |
| Vine | 11.63 | 3.2 | 11.08 | 3.2 | 0.689 | 0.491 |
| Dead vegetation | 64.25 | 5.0 | 49.85 | 3.2 | 2.138 | 0.033 |
| Shrub | 57.13 | 6.0 | 48.85 | 4.4 | 1.123 | 0.261 |
| Total | 244.38 | 18.6 | 175.15 | 8.2 | 2.717 | 0.0079 |

³ Relative density = sum of the number of 0.1-m height intervals within the 30 sample points/plot that contained vegetation of that category. Total relative density = number of vegetation categories present within each 0.1 m radius cylinder at 0.1-m height intervals, summed for 30 sample points/plot.

of Bachman's sparrows and red-cockaded woodpeckers detected at a site as indices of relative abundance. We used the normal approximation to the Mann-Whitney *U*-test to compare relative densities of the vegetation variables in the herbaceous layer (≤0.5 m) and shrub density in the midstory (1.0-4.0 m) between sites occupied and unoccupied by Bachman's sparrows. We used Spearman's correlation (r) to examine the influence of vegetation density on relative abundance of Bachman's sparrows and redcockaded woodpeckers. To control the experimentwise error rate, we used a Bonferroni adjustment of the alpha level when we examined vegetation variables below 0.5 m (Howell 1982). Null hypotheses were rejected at P < 0.05 (adjusted P < 0.008).

RESULTS

We detected Bachman's sparrows during point counts at 8 of 21 randomly selected red-cockaded woodpecker clusters. At occupied sites, the number of Bachman's sparrows detected during a count ranged from 0 to 3 (mean relative abundance = 0.73, SE = 0.2, n = 8). Red-cockaded woodpeckers were detected during point counts at all 21 clusters, and numbers detected during a count ranged from 0 to 2 (mean relative abundance = 0.73, SE = 0.1, n = 21).

Across plots, the most frequently encountered grasses (mean percentage of points within plots that contained the species) were bluestem (Andropogon sp., Schizachyrium sp.; $\bar{x}=43.2$, SE = 4.2), panic grass (Panicum spp.; $\bar{x}=18.4$, SE = 1.9), and wiregrass (Aristida stricta; $\bar{x}=15.7$, SE = 7.1). The most frequently encountered species (Aristida stricta) and stricta (Aristida stricta) and stri

tered forbs were golden aster (*Pityopsis graminifolia*; $\bar{x}=11.8$, SE = 3.7), silver croton (*Croton argyranthemus*; $\bar{x}=6.5$, SE = 1.1), and goldenrod (*Solidago* spp.; $\bar{x}=6.4$, SE = 1.9). Blueberry (*Vaccinium* spp.; $\bar{x}=25.6$, SE = 3.8), gopher apple (*Licania michauxii*; $\bar{x}=21.6$, SE = 3.2), and turkey oak (*Quercus laevis*; $\bar{x}=17.6$, SE = 2.1), were the most frequently encountered shrubs. Greenbrier (*Smilax auriculata*; $\bar{x}=11.4$, SE = 2.8) was the most frequently encountered vine, and bracken ferm (*Pteridium aquilinum*; $\bar{x}=30.0$, SE = 6.2) was, by far, the most abundant fern.

Randomly selected clusters occupied by Bachman's sparrows had higher total vegetation densities at and below 0.5 m than did unoccupied plots (P = 0.007; Table 1). We analyzed the major vegetation components individually and found higher densities of grasses at and below 0.5 m in occupied compared to unoccupied plots (P = 0.004; Table 1). Midstory density (shrubs ≥ 1.0 m) was marginally greater (Z = 1.922, P = 0.055) at sites not occupied ($\bar{x} =$ 20.7, SE = 4.3) than at sites occupied ($\bar{x} = 7.4$, SE = 2.2) by Bachman's sparrows, and relative abundance of Bachman's sparrows was negatively correlated with midstory density (r =-0.446, P = 0.043, n = 21). Canopy cover did not differ (Z = 1.505, P = 0.133) between occupied ($\bar{x} = 30.2$, SE = 3.5) and unoccupied (\bar{x} = 35.1, SE = 2.1) sites, and relative abundance of Bachman's sparrows was not correlated with canopy cover (r = -0.371, P = 0.107, n = 21). We did not find any correlations between relative abundance of red-cockaded woodpeckers and our measures of vegetation density ($r \leq$ $0.345, P \ge 0.125, n = 21$).

 $^{^{\}mathrm{b}}$ Normal approximation to Mann-Whitney U-test.

c Significant (P < 0.008) after Bonferroni adjustment to maintain experimentwise error rate at P < 0.05.

DISCUSSION

Our results indicate that Bachman's sparrows have specific habitat requirements on Eglin. We found Bachman's sparrows in areas with high densities of grasses in the first 0.5 m above-ground. While we did not find a difference in canopy cover between occupied and unoccupied sites, all sites had relatively open canopies (range = 19–50%), which is characteristic of locations used as red-cockaded woodpecker clusters. There also were nonsignificant higher densities of forbs, shrubs, vines, and dead vegetation in occupied sites (Table 1).

Similarly, Dunning and Watts (1990) found that Bachman's sparrows selected areas with low densities of trees and high densities of grasses and forbs in the first meter aboveground. Dunning and Watts (1990) found sparrows occupied sites in areas with low densities of shrubs, while we found sparrows in areas with fairly high densities of shrubs below 0.5 m (Table 1), but lower densities of shrubs from 1.0 to 4.0 m. Higher shrub densities below 0.5 m at Eglin probably reflect recent management practices rather than a preference by Bachman's sparrows. The reintroduction of fire into many areas where fire was suppressed for decades has resulted in profuse sprouting of shrubs. Waldrop et al. (1992) reported an increase in the number of hardwood sprouts following periodic (3-7 yr) winter and summer burns. Additional fires, especially during the growing season (Waldrop et at. 1992, Glitzenstein et. al. 1995), may be required to reduce shrub vegetation to densities originally found in longleaf pine woodlands in this region.

In contrast to Dunning and Watts (1990), we found that habitat suitable for red-cockaded woodpeckers at Eglin was not always suitable for Bachman's sparrows. Only 8 of 21 randomly selected red-cockaded woodpecker clusters were occupied by Bachman's sparrows. Although some of our unoccupied sites possibly were suitable for Bachman's sparrows, randomly selected sites with and without Bachman's sparrows differed in total vegetation density and specific vegetation variables in the herbaceous layer and the midstory. Although we did not measure vegetation variables specifically to examine their influences on red-cockaded woodpeckers, none of our vegetation variables were correlated with relative abundance of red-cockaded woodpeckers ($r \le 0.345$, $P \ge 0.125$, n =21). Hence, our results suggest that although

both species occupy the same habitat, they respond to different habitat features. Red-cockaded woodpeckers both nest and forage in trees, and Bachman's sparrows both nest and forage on the ground. Thus, the habitat niches occupied by these 2 species are easily discriminated. This difference in habitat use may explain why Bachman's sparrows benefit more from an open midstory and a denser ground cover than do red-cockaded woodpeckers.

Our results, however, do not necessarily mean that management practices for red-cockaded woodpeckers do not produce suitable habitat for Bachman's sparrows. On Eglin, some areas may not have been managed for woodpeckers long enough to reestablish the dense ground cover preferred by Bachman's sparrows (see Waldrop et al. 1992). Because of their intolerance of a dense hardwood midstory, Bachman's sparrows disappear from areas within a few years following fire suppression. Conversely, red-cockaded woodpeckers, although negatively affected by a dense midstory, apparently persist until hardwoods reach cavity height (Jackson 1986, Conner and Rudolph 1989). Thus, areas currently occupied by red-cockaded woodpeckers may have lost breeding populations of Bachman's sparrows decades earlier. Although these areas are not currently suitable for Bachman's sparrows, they may become so after several years of regular burning.

At Eglin, 4 primary management strategies are used to maintain suitable habitat for red-cockaded woodpeckers: (1) prescribed burning, (2) large-scale midstory removal, (3) manual midstory removal around cavity trees, and (4) the use of herbicides (U.S. Department of Defense 1993). In most cases, a combination of these strategies is used at each cluster, so we only are able to provide circumstantial evidence as to the specific effects of each.

Prescribed burning appears most beneficial for both Bachman's sparrows and red-cockaded woodpeckers. Burns during the growing season are particularly advantageous because they are lethal to young hardwoods (Glitzenstein et al. 1995) and increase growth of grass-stage long-leaf pines and various grasses and forbs in the understory (Robbins and Myers 1992). Large-scale midstory removal creates an open midstory and prevents hardwoods from encroaching on red-cockaded woodpecker cavities, but midstory removal does not have the same effects on the understory as fire (see Platt et al. 1988a).

In areas where fire has been suppressed for many years, prescribed burns of low intensity may not kill the large hardwoods (Waldrop et al. 1992). Additionally, the development of a dense midstory may reduce the herbaceous ground cover to an extent that fires will not burn with enough intensity to kill oaks (Platt et al. 1991). In this situation, large-scale midstory removal is necessary before fire becomes an effective management tool (Krusac et al. 1995).

Several plots without Bachman's sparrows in our study had been managed by manual removal of midstory hardwoods only from around cavity trees. This treatment does not appear to produce sufficient open areas for Bachman's sparrows. Several studies of red-cockaded woodpeckers (e.g., Conner et al. 1995) suggest that treatments should be conducted at the level of the stand rather than the immediate area surrounding cavity trees. Lastly, herbicides kill hardwoods and may benefit red-cockaded woodpeckers, but effects on other plants and animals are unknown. Our observations suggest that any treatment for midstory control should include frequent burning to enhance habitat quality for Bachman's sparrows. In addition, the beneficial effects (i.e., midstory reduction) gained by more intensive treatments are at risk of being lost if the area is not burned frequently enough to prevent reestablishment of hardwoods (Escano 1995).

In conclusion, our results generally concur with other studies in that Bachman's sparrows select open pine forests with a dense cover of herbaceous vegetation (Dunning and Watts 1990). Evidence also suggests that use of this habitat is relatively consistent across the geographic range of this species (Brooks 1938, Hardin and Probasco 1983, Dunning and Watts 1990, Gobris 1992).

However, whereas Dunning and Watts (1990) found management practices that produce suitable habitat for red-cockaded woodpeckers also provide habitat for Bachman's sparrows, we found that management practices may not benefit Bachman's sparrow unless these practices include prescribed burning to promote development of herbaceous ground cover. Indeed, although both red-cockaded woodpeckers and Bachman's sparrows are found in mature, open pine woodlands, the presence of 1 species does not guarantee presence of the other. Frequent (3–5 yr) burning during the growing season is the preferred management treatment for red-

cockaded woodpeckers and is especially beneficial for Bachman's sparrows because it stimulates development of a dense cover of herbaceous vegetation (Platt et al. 1991, Waldrop et al. 1992). However, prescribed burning may be insufficient to control hardwoods if the midstory has become well established, and mechanical or chemical treatments may be necessary. Although mechanical or chemical treatments will benefit red-cockaded woodpeckers, these treatments will not benefit Bachman's sparrows unless followed by prescribed burning to stimulate the growth of herbaceous ground cover. In addition, the midstory will rapidly become reestablished following removal, if a frequent program of burning is not initiated.

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NICHE OVERLAP IN SYMPATRIC POPULATIONS OF FOX AND GRAY SQUIRRELS

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Abstract: Resource overlap between fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) has been reported, but quantitative measures of niche overlap in sympatric populations are unavailable. We examined niche breadth and niche overlap in habitat and nest characteristics among sympatric fox and gray squirrels in central Georgia during 1989–90. We used radiocollared squirrels to locate nests and record locations within forested stands. We classified habitat and nest characteristics into 12 niche dimensions: 2 nest and 10 habitat. On several dimensions, fox squirrels occupied narrower niches relative to gray squirrels. Gray squirrels nested in a greater variety of tree species and selected stands with broader ranges in midstory pine (*Pinus* spp.) stems per hectare and overstory species. Intraspecific niche overlap between species was greater (P < 0.05) than interspecific overlap on 9 of 12 dimensions. Intraspecific and interspecific niche overlap did not differ (P > 0.05) on overstory hardwood stems per hectare, overstory pine per hectare, and midstory tree species. These findings suggest that coexistence between fox and gray squirrels was maintained, in part, through niche partitioning on several dimensions.

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Fox and gray squirrels coexist over a large extent of their range (Flyger and Gates 1980, Gurnell 1987), despite their reported overlap in food habits (Barber 1955, Nixon et al. 1968, Smith and Follmer 1972, Webster et al. 1985), nest sites (Nixon and Hansen 1987, Weigl et al. 1989, Edwards and Guynn 1995), and habitat use (Flyger and Gates 1980, Flyger and Smith 1980). Sympatry in populations of fox and gray squirrels is believed maintained by differences in habitat preference (Taylor 1973, Flyger and

Gates 1980; Weigl et al. 1989:76) and nest selection (Edwards and Guynn 1995). Mature and open upland-pine and pine-hardwood associations are considered preferred habitats of fox squirrels (Edwards et al. 1989, Loeb and Lennartz 1989, Weigl et al. 1989). In contrast, gray squirrels inhabit extensive, mature hardwood forests with dense undergrowth (Flyger and Gates 1980). Moreover, southeastern fox squirrels (S. n. niger) are believed to differ substantially from Midwestern subspecies in their ecological requirements; they select more pinedominated habitats as compared to deciduous habitats selected by Midwestern fox squirrels (Weigl et al. 1989).

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