

# Initial Gray Squirrel Population Responses to Nest Boxes in Two Forest Types in Southern Alabama

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*Abstract:* We studied short-term response of gray squirrel (*Sciurus carolinensis*) populations to nest boxes in mixed-pine (*Pinus spp*) hardwood and even-aged pine forests in Alabama from December 1988 to September 1990. Nest boxes (5/ha) were installed in 3 mixed pine-hardwood and 3 even-aged pine stands. We used a split-plot design to determine if populations differed between treatment (with nest boxes) and control (without nest boxes) halves of mixed pine-hardwood areas. In even-aged pine area, post-treatment population indices of squirrels (minimum number known to be alive [MNA]) were compared to pre-treatment indices collected by Fisher and Holler (1991). We captured 260 squirrels 1,102 times in 33,480 trap-days. Number of individual squirrels captured after nest box installation was double in treatment (125) versus control halves (63) of mixed pine-hardwood areas. Population estimates did not differ between treatment and control. However, there was a significant time and treatment interaction, indicating that both treatment and control areas exhibited population changes over time due to addition of nest boxes. Population indices (MNA) of squirrels in even-aged pine areas remained low throughout the study and did not differ from pre-treatment levels. Addition of nest boxes to mixed pine-hardwood forests may increase gray squirrel numbers, but this response may be due to immigration from surrounding areas and may be influenced by age of the forest stand, basal area of mast producing trees, presence of hardwood riparian corridors, and number of existing tree cavities. Even-aged pine areas continue to be poor gray squirrel habitat even after addition of nest boxes.

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Over the past 2 centuries gray squirrel habitat has been reduced by agricultural practices (Nixon et al. 1978) and forestry practices, such as even-aged pine management (Stransky and Halls 1967, Speake 1970, Nixon et al. 1980). The latter may be the greatest threat to gray squirrel habitat in the Southeast (Davis 1978). In Alabama and across the southeastern United States, conversion of hardwood areas to pine monocultures may result in a severe reduction in gray squirrel habitat (Speake 1970,

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Davis 1978) Addition of nest boxes has been suggested as a method of ameliorating negative consequences of commercial timber production on squirrel populations (Barkalow and Soots 1965*a*, McComb and Nobel 1981, Ivey and Frampton 1987).

Maintaining tree cavities for nest sites and hard mast production for food has been considered paramount in gray squirrel management (Madson 1964, Allen 1987). The relative importance of each of these variables may vary with latitude (Baker 1944) and land use patterns. However, few studies have been conducted in southern portions of gray squirrel range. For Illinois forests, Nixon and Hanson (1987) showed that both age and species compositions of forests were determinants of mast production and number of tree cavities. Goodrum et al. (1971) measured acorn yields for several southern oak species and Sanderson et al. (1975) provided insight into important cavity tree species. However, little is known about overall habitat suitability of mixed pine-hardwood and even-aged pine forests common in the southeastern United States. The possibility exists that tree cavities are limited in these forest types because some hardwoods take as long as 60 years to develop cavities (Baumgartner 1939), whereas pines rarely develop cavities.

In Alabama, Fischer and Holler (1991) found that population densities of gray squirrels were similar in hardwood and mixed pine-hardwood forests, but much lower in even-aged pine forests. The similarity in densities between hardwood and mixed pine-hardwood forests was a somewhat surprising finding given that many researchers have emphasized the hardwood component as determining habitat suitability to gray squirrels (Allen 1987, Nixon and Hansen 1987). Young mixed pine-hardwood forests common in the Southeastern United States potentially lack natural tree cavities, and addition of nesting sites and escape cover in the form of wooden nest boxes may be a viable means to increase squirrel populations in these areas. In addition, since many southern industrial forests of these types are in short rotations (i.e., 40–60 years), the immediacy and magnitude of short-term population changes may be important to determine the efficacy of a nest box supplementation management plan. For these reasons, our objectives were to: determine the short-term behavioral response of gray squirrels to nest boxes in mixed pine-hardwood and even-aged pine stands and document short-term population changes within and surrounding nest box treated areas.

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## Methods

### Study Area

Our study was conducted at the Solon Dixon Forestry Education Center (DFC), School of Forestry, Auburn University, Alabama. This approximately 2,165-ha area lies within the lower coastal plain physiographic region of Alabama and includes parts of Covington and Escambia counties. Topography of the DFC is varied and contains upland and bottomland hardwoods (22.9%), upland mixed pine-hardwoods (39.9%), even-aged pine plantations (32.7%), and regenerating cutover areas (4.5%; Fischer and Holler 1991). Fischer and Holler (1991) sampled 3 research sites in each of the representative forest types. We sampled larger sections of the same 3 mixed pine-hardwood areas (PH 1-3) totaling 125.64 ha and the same even-aged pine sites (P 1-3) totaling 73.44 ha. Generally, mixed pine-hardwood areas were characterized by an overstory of longleaf pine (*P. palustris*), loblolly pine (*P. taeda*), southern red oak (*Quercus falcata*), laurel oak (*Q. laurifolia*), turkey oak (*Q. laevis*), and post oak (*Q. stellata*). Even-aged pine areas were composed mainly of longleaf and loblolly pines. Hardwood riparian corridors (narrow bands of hardwood trees bordering permanent or ephemeral streams) were found in both mixed pine-hardwood and even-aged pine areas and were characterized by an overstory of red bay (*Persea borbonia*), black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), water oak (*Q. nigra*), and southern magnolia (*Magnolia grandiflora*). The mixed pine-hardwood and even-aged pine areas used in this study were approximately 40–50 years old and underwent prescribed burns every 3 years. Except for removal of individual lightning-damaged trees, no timber harvest occurred on the research sites.

### Livetrapping

We livetrapped and marked gray squirrels from December 1988 to September 1990. We established sampling grids using 60-m intervals between trap stations. Mixed pine-hardwood and even-aged pine sites contained 100 and 50 trap stations, respectively. Grids in mixed pine-hardwood sites were bisected by a 120-m buffer zone separating the trapping grid of the treatment (with nest boxes) and control (without nest boxes) sides. Grids were separated by a 120-m buffer zone based on previous trapping results of Fischer (1989) which indicated that squirrels rarely moved >120m during a 7-day trapping period. Thus we could be confident that populations within treatment and control grids were independent at least during 1 trapping period. Control areas were not used in pine areas because squirrel populations in these sites were consistently low in previous years (Fischer and Holler 1991) so that any population response to nest box installation should have been readily apparent. We collected data seasonally as follows: Autumn (Oct–Dec); Winter (Jan–Mar); Spring (Apr–Jun); Summer (Jul–Sep).

We placed 2 No. 203 Tomahawk double-door livetraps (Tomahawk® Live Traps, Tomahawk, Wisc.; reference to trade names does not imply endorsement by the federal government) at each trap station and baited them with cracked and whole pecans. Three days of prebaiting were followed by 7 trapping days. We checked traps

twice daily; once approximately 2 hours after sunrise and again at dusk. Trapped squirrels were driven into a wire mesh handling cone and aged (juvenile, subadult, or adult) from tail pelage characteristics (Sharp 1958), sexed, weighed, and eartagged with a No. 1 size Monel tag. All trapped squirrels were released at the site of capture. All areas were trapped either in autumn 1988 or winter 1989 before nest box installation. Thereafter, mixed pine-hardwood PH3 and even-aged pine P3 areas were independently selected for trapping during winter, spring, and summer 1989 in order to examine short-term population responses and provide squirrels for radiocollaring. All areas were trapped in random order during autumn 1989 and winter, spring, and summer 1990.

### Population Estimation

We used program CAPTURE (Otis et al. 1978) to generate population estimates for control and treatment sites of mixed pine-hardwood areas. Program CAPTURE uses a closed population modeling procedure limited by most of the same assumptions of other closed population estimation techniques such as Lincoln-Peterson (i.e., closed population, equal catchability, marks not lost or overlooked). However, program CAPTURE contains estimation procedures designed to relax the assumption of equal capture probability among individuals and over time. In our study program CAPTURE's model selection algorithm selected the null model (Model  $M_0$  — capture probabilities are assumed constant) for 21 of 36 trapping sessions. For 15 of these trapping occasions, the null model was selected because capture data was too sparse to complete the model selection procedure (Menkens and Anderson 1988).

The raw trapping data suggested that there was heterogeneity in probability of capture, because many squirrels were captured only once and others were captured multiple times. Because the jackknife estimator is less negatively biased under cases of heterogeneity than the null estimator, only jackknife ( $M_h$ ) estimates were used in the analysis. This is consistent with the procedure used by Humphrey (1988), who noticed a similar output when using program CAPTURE to estimate Key Largo woodrat (*Neotoma floridana smalli*) and cotton mouse (*Peromyscus gossypinus allapaticola*) populations. Because there was an insufficient number of captures for CAPTURE to produce estimates for mixed pine-hardwood area PH2 for 3 seasons, a regression equation relating minimum number known to be alive indices (MNA) to program CAPTURE population estimates for other periods and areas was used to generate values for these 3 seasons (Proc REG, SAS 1987). The regression equation used to generate values was: Predicted CAPTURE estimate =  $1.30 * MNA$  ( $F_{1,31} = 71.9, P < 0.001$ ).

Too few squirrels were captured in even-aged pine areas to generate estimates using program CAPTURE, so MNA population indices were compared to those given by Fischer and Holler (1991). We used repeated measures analysis of variance (Proc GLM, SAS 1987) to determine if population size differed between treatment and control halves of mixed pine-hardwood areas, and to determine if population size differed between pre- and post-treatment even-aged pine areas.

### Nest boxes

We constructed 360 wooden nest boxes from 2.5 x 25.4 cm pressure treated pine boards following the design of Barkalow and Soots (1965*b*) and erected them between December 1988 and January 1989 in even-aged pine areas and treatment sides of mixed pine-hardwood areas. We installed nest boxes at grid intersection points on the nearest live tree >30 cm dbh and at randomly chosen grid interior points to achieve a density of approximately 5/ha. Since Barkalow and Soots (1965*b*) and Stone et al. (1996) found squirrels did not select nest boxes for use based on height, we chose to install boxes approximately 6.5 m from the ground to facilitate ease of nest box checks using 2 sections of 3-m Swedish tree ladders and/or a 7.25-m extension ladder. Boxes were faced in a random direction. We attached pesticide strips (Propoxur, active ingredient, Rainbow Mfg., Birmingham, Ala.) to the inside roof of each nest box in spring 1989 to reduce wasp use. Nest boxes were checked for use at midday, once each season from spring 1989 to summer 1990. The top of each box was removed and its contents were examined briefly to detect the presence of adult squirrels, nestlings, or nesting material.

### Radiotelemetry

We obtained additional information about nest box acceptance and use by using radiotelemetry (Beal 1967). We radio-marked 34 adult squirrels (18 females, 16 males) representing the 6 PH study sites. Radio-collars (Wildl. Materials, Inc., Carbondale, Ill.) were maneuvered through the wire mesh of a handling cone and affixed to the squirrels. We located radio-collared squirrels during midday (900 to 1600 hours) to determine their shelter use. Locations were taken twice monthly during spring and summer 1989 and twice weekly from autumn 1989 through summer 1990. Exact locations were recorded as direction and distance from a trapping grid intersection point and shelter use of non-active squirrels was classified as a nest box, leaf nest, tree cavity, or none. Additionally, we recorded tree species in which the squirrel was found. A Chi-square analysis (Proc FREQ, SAS 1987) was used to determine if squirrel shelter use differed among seasons.

## Results

### Squirrel Populations

We captured 260 individual squirrels 1,102 times in 33,480 trap days in all areas combined. Only 20 squirrels were captured in even-aged pine areas. Of 201 squirrels captured post-treatment in mixed pine-hardwood area, 125 were captured in the treatment halves, whereas 63 were captured in the control halves. Thirteen squirrels were considered transients and were captured in both treatment and control halves. Thirty-nine squirrels captured during the pre-treatment trapping of the 3 mixed pine-hardwood areas were never recaptured. Of squirrels livetrapped in both pre- and post-treatment trapping, 12 (32%) moved from control to treatment halves after nest boxes were installed, whereas 3 squirrels (8%) moved from treatment to control halves.

**Table 1.** Densities and associated 95% confidence intervals of gray squirrels (Jackknife CAPTURE estimate/ha) in treatment and control halves of mixed pine-hardwood study sites during pre- and post-treatment trapping at the Solon Dixon Forestry Education Center, Covington and Escambia counties, Alabama (Jan 1987–Sep 1990).

Season of trapping	Mixed pine-hardwood site					
	PH1		PH2		PH3	
	Treatment	Control	Treatment	Control	Treatment	Control
<i>Pre-treatment trapping</i> <sup>a</sup>						
Autumn/winter 1988/1989	1.44±0.31	1.75±0.02	0.16± <sup>b</sup> 0.50	±0.15	0.88±0.09	2.55±0.56
<i>Post-treatment trapping</i>						
Spring 1989		c		c	1.71±0.32	1.53±0.20
Summer 1989		c		c	1.11±0.14	1.71±0.32
Autumn 1989	2.21±0.30	0.78±0.08	0.49±0.08	0.12±0.05	1.39±0.24	0.74±0.09
Winter 1990	1.90±0.22	1.12±0.17	0.98±0.29	0.21±0.07	1.65±0.14	0.97±0.23
Spring 1990	3.04±0.26	0.97±0.08	0.27±0.03	0.62±0.23	1.44±0.16	1.20±0.16
Summer 1990	2.06±0.42	0.73±0.11	0.11± <sup>b</sup> 0.08	± <sup>b</sup>	1.48±0.15	0.42±0.05

a. From Fischer and Holler 1991.

b. Population density estimate derived from regression equation relating MNA to CAPTURE estimate.

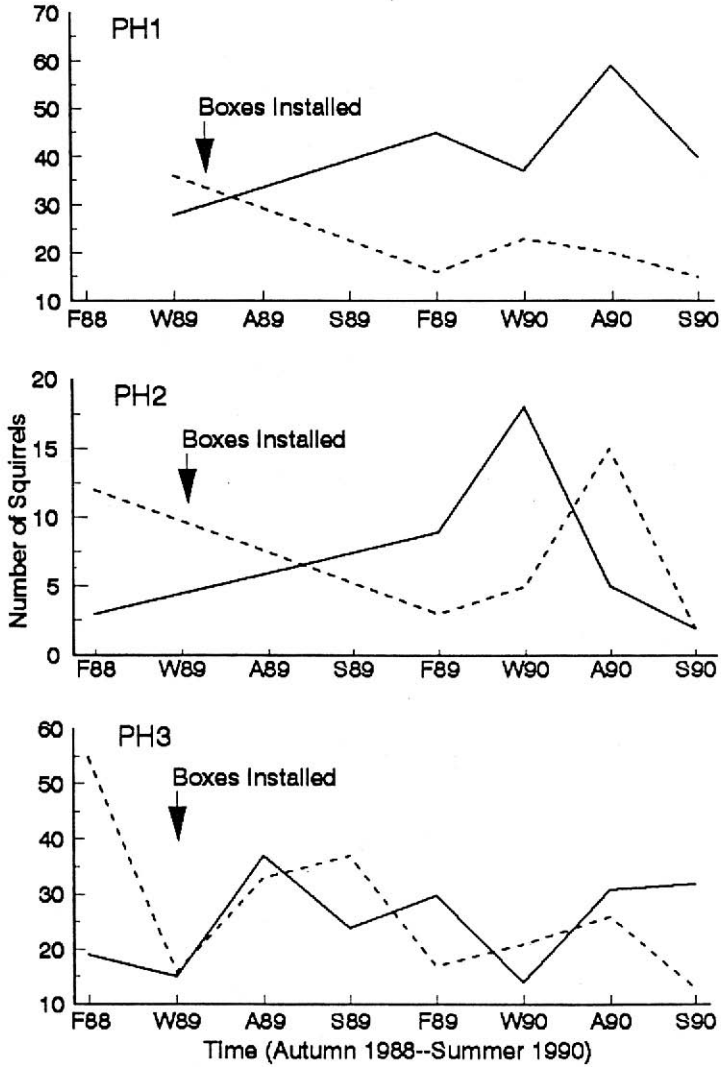
c. Sites not trapped during this season.

Population estimates of treatment and control halves of mixed pine-hardwood areas did not differ ( $F_{1,4} = 0.29, P = 0.62$ ; Table 1). However, there was a time and treatment interaction ( $F_{4,16} = 4.61, P = 0.01$ ), indicating squirrel populations changed in both treatment and control halves following addition of nest boxes. Namely, treatment halves showed increased population estimates, whereas population estimates for control halves decreased over time (Fig. 1). Also, comparisons of post-treatment with pre-treatment population estimates for control and treatment sides of each study site showed increases in the treatment sides and decreases in control sides ( $F_{1,4} = 13.90, P = 0.02$ ). The greatest difference occurred in spring 1990 in mixed pine-hardwood area PH1, with population estimates of 59 for the treatment half and 20 for the control half. PH1 had population estimates averaging 26.8 more squirrels each season in the treatment than the control. PH3 and PH2 had population estimates in treatment halves that averaged 7.5 and 2.3 more squirrels each seasons, respectively.

Population indices (MNA) of squirrels in pine areas remained low throughout the study ( $P_1 = 1-18, P_2 = 0-3, P_3 = 0-3$ ) and did not differ ( $F_{1,4} = 0.34, P = 0.52$ ) from pre-treatment levels (Table 2).

### Nest Box Use

On average, 10.9% of nest boxes were used by squirrels seasonally. Reproduction in nest boxes was documented by presence of 51 litters (average litter size = 2.92) found in 7 seasonal checks. Counting litters and adults, live squirrels were found in boxes 78 times and evidence of gray squirrel use (nest material) was found 153 times. All even-aged pine areas had lower average use (4.3%) compared to



**Figure 1.** Program CAPTURE (Otis et al. 1978) population estimates for treatment (solid lines) and control (dashed lines) halves of mixed pine-hardwood study areas at the Solon Dixon Forestry Education Center, Covington and Escambia counties, Alabama.

**Table 2.** Densities of gray squirrels (MNA/ha) in even-aged pine study sites at the Solon Dixon Forestry Education Center, Covington and Escambia counties, Alabama (Sep 1987–Sep 1990).

Season of trapping	Even-aged pine site		
	P1	P2	P3
<i>Pre-treatment trapping<sup>a</sup></i>			
Autumn 1987	0.20	0	0
Winter 1988	0.32	0.04	0.12
Spring 1988	0.72	0.09	0.08
Summer 1988	0.32	0	0
Autumn 1988	0.28	b	b
<i>Post-treatment trapping</i>			
Winter 1989	b	b	0
Spring 1989	b	b	0
Summer 1989	b	b	0.08
Autumn 1989	0.28	0.04	0
Winter 1990	0.16	0.04	0.08
Spring 1990	0.04	0.12	0
Summer 1990	0.08	0.04	0

a. From Fischer and Holler 1991.

b. Area not trapped during this season.

mixed pine-hardwood areas (14.2%). Coincident with its high population estimates, PH1 also had greatest average use per season (22.9%).

### Radiotelemetry

Midday shelter use from 1,272 radiotelemetry locations was as follows: leaf nests (35.5%), no shelter (33.6%), nest boxes (20.8%), and tree cavities (10.1%). Squirrels differed ( $\chi^2_9 = 213.45$ ,  $P = 0.001$ ) in shelter use among seasons with nest boxes being used most frequently during winter and spring. Tree cavities also were used most frequently in the winter and spring, whereas leaf nests showed consistent use throughout the year. Fewer instances of no shelter use were recorded in winter and spring, than in summer or autumn. Most leaf nests were constructed in hardwood trees (83.9%) with laurel oak being selected most often (217 nests). Other important leaf nest trees were water oak (86 nests), black gum (31 nests), and southern red oak (31 nests). Most cavities used by radiocollared squirrels were in black gums (43.4%) or water oaks (27.9%).

Nest boxes used by squirrels (as evidenced by nest box checks and radiotelemetry locations) were not associated with tree species upon which the nest box was installed ( $\chi^2_3 = 2.59$ ,  $P = 0.46$ ) or the direction the box was faced ( $\chi^2_7 = 6.14$ ,  $P = 0.42$ ). However, all nest boxes used by squirrels were within 120 m of a hardwood riparian corridor.



## Discussion

Mixed pine-hardwood areas showed a short-term population response to added nest boxes as evidenced by the significant time and treatment interaction of the repeated measures ANOVA. A treatment effect alone would have been detected as increased population densities in treatment halves of mixed pine-hardwood sites and little or no change in control halves. However, population densities of control halves decreased over time, while population densities of treatment halves increased, leading to the observed time and treatment interaction. We suggest that a likely cause of this response was immigration from control (without nest boxes) to treatment (with nest boxes) sides of mixed pine-hardwood areas and subsequent reproduction there. We documented movement of 12 squirrels from control to treatment sites following nest box installation. We also documented reproduction in nest boxes by visual checks and verified their use by radiocollared squirrels. However, there was considerable variation in response among mixed pine-hardwood areas with the strongest effect shown by PH1 (see Table 1 and Fig. 1). The other 2 mixed pine-hardwood sites had greater post-treatment populations in treatment sides than control sides but the difference was not large. The disparity in magnitudes of population increases in the 3 areas suggests that more detailed information on specific limiting factors influencing squirrel populations is needed.

Traditionally, suitable gray squirrel habitat has been described as a combination of 2 potentially limiting factors, namely the availability of a winter-storable food supply and suitable nest cavities (Madson 1964, Allen 1987). Three experimental studies concluded that under specific circumstances, nest sites were a limiting resource for squirrels (Barkalow and Soots 1965a, Burger 1969, Nixon et al. 1984). However, the possible interplay between availability of winter-storable food and suitable nesting sites has not been well described for squirrels. Ivey and Frampton (1987) found greater nest box use by squirrels in a hardwood stand that was intensively managed with high quality timber but few cavities and less use in an unmanaged stand. The relative roles that food and nest sites play in determining gray squirrel populations may explain why even-aged pine sites in this study did not benefit from the addition of nest boxes, and why mixed pine-hardwood areas benefited to varying degrees. Nest boxes were used less frequently in our even-aged pine sites than in mixed pine-hardwood sites, which may indicate that winter storable food supply was more limiting than nest locations in pine sites.

Squirrels will use nest boxes placed in even-aged pine areas as evidenced by the squirrel litters and nests found during nest box checks; however, trapping results indicate that this represents only temporary use of even-aged pine sites. Squirrel populations in mixed pine-hardwood areas probably varied in their response to the addition of nest boxes because of inherent variability in quantity of mast and cavity trees that they contain. Fischer (1989) measured basal area of mast producing trees for portions of the mixed pine-hardwood areas used in the study, and found that PH1 had the greatest basal area of mast producing trees followed by PH2 and PH3. In this study, PH1 showed the greatest change in population size following nest box installa-

tion, suggesting a possible interaction between the availability of nest sites and food resources. However, we did not measure the number of natural cavities in the study sites.

Addition of nest boxes might lead to population increases in areas where nest sites are limiting and food is abundant through increases in squirrel fecundity, survival, or immigration from surrounding areas. Although reproduction was documented in nest boxes, we do not know if reproduction was increased in treatment areas since we did not measure reproduction in control areas. However, immigration of squirrels into treatment halves of mixed pine-hardwood areas from control halves was recorded, and may be the most likely explanation for the increased populations in treatment halves and decreased populations in control halves. We also documented considerable use of nest boxes by radiocollared squirrels and in fact, radiocollared squirrels used nest boxes approximately twice as often as tree cavities, but less often than leaf nests. McComb and Noble (1981) postulated that gray squirrels may prefer nest boxes to natural cavities or leaf nests, but since we did not estimate density of natural cavities in each study site, we can not verify this claim.

Placement of nest boxes may be an important determinant of their use, as evidenced by telemetry locations in the study. Since most squirrels centered their mid-day locations near hardwood riparian corridors, boxes placed close to these riparian corridors received greatest use. Similarly, Dickson and Huntley (1987) and Fischer and Holler (1991) found that squirrels used hardwood riparian corridor habitat to a greater degree than surrounding habitat. The importance of hardwood riparian corridors within mixed pine-hardwood and even-aged pine timber stands has been stressed by several authors (Heuer and Perry 1976, Warren and Hurst 1980, Dickson and Huntley 1987, Fischer and Holler 1991) and is further emphasized here. Hardwood riparian corridors provide not only a diversity of mast producing trees, but also cavity trees. Although radiocollared squirrels were found to use cavities in a variety of tree species, cavities in black gums and water oaks were the most frequently used. These 2 species were under-represented in the total basal areas of trees in mixed pine-hardwood areas (4.6% and 2.4% respectively; Fischer 1989). The importance of hardwood trees in upland areas of mixed pine-hardwood timber stands must not be discounted. In fact, the basal area of hardwood trees in these stands may directly affect efficacy of using nest boxes as a management tool. Radiotelemetry data collected in this study suggested that gray squirrels chose hardwood trees more often than pine trees as locations for leaf nests. In particular, squirrels most often chose laurel oak which comprised only 7.8% of the total basal area in the mixed pine-hardwood study areas (Fischer 1989).

## **Management Implications**

The destruction of hardwood areas through development and various forestry practices continues to be the greatest threat to gray squirrel populations. Addition of nest boxes to mixed pine-hardwood timber stands may increase squirrel numbers, but this response may be due to immigration from surrounding areas and also may be re-

lated to the age of the stand, the basal area of mast trees, presence of hardwood riparian corridors, and number of exiting tree cavities. Before implementing a management plan incorporating use of nest boxes, careful consideration of these factors is imperative. Indeed, this study points out the variability of responses among different mixed pine-hardwood areas. Exact conditions leading to a positive effect of added nest boxes such as existing cavity density, nest box density, and basal area of mast producing trees remain to be determined and deserve further study. Even-aged pine areas are poor gray squirrel habitat and continue to be so even after addition of nest boxes.

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