Ecological Applications, 8(4), 1998, pp. 1144–1155
© 1998 by the Ecological Society of America

DEMOGRAPHIC AND BEHAVIORAL RESPONSES OF SOUTHERN FLYING SQUIRRELS TO EXPERIMENTAL LOGGING IN ARKANSAS

JAMES F. TAULMAN,[1,3] KIMBERLY G. SMITH,[1] AND RONALD E. THILL[2]

[1]*Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701 USA*
[2]*Wildlife Habitat and Silviculture Laboratory, USDA Forest Service, Southern Research Station, P.O. Box 7600 SFA Station, Nacogdoches, Texas 75961 USA*

Abstract. This study investigated responses of populations of southern flying squirrels to a range of experimental even-aged and uneven-aged timber-harvest practices along a gradient of increasing disturbance intensity. The goals were to determine whether measurable demographic parameters of squirrels in experimental forests would change after logging; whether a disturbance threshold existed within the range of harvest practices implemented beyond which squirrels would not nest on a stand; and whether squirrels would show selection in the use of nest boxes in logged and unlogged habitats.

Winter nest-box surveys were conducted in the Ouachita National Forest, Arkansas, USA, in 21 15-ha stands representing three replicated groups of six silvicultural treatments (pine–hardwood single-tree selection, pine single-tree selection, pine–hardwood shelterwood, pine shelterwood, pine–hardwood seed tree, and pine seed tree), plus an unaltered control during 1993, prior to harvest, and after harvest in 1994–1996. Neither densities of nesting squirrels nor use of boxes for nests or feeding stations differed among treatment groups prior to harvests. Densities declined on all harvested stands after treatment in 1994; during the same period population growth was observed on control stands. A partial rebound in squirrels' use of nest boxes in some harvested stands occurred in 1995 and 1996. Prior to harvest, squirrels used boxes in all habitats in similar proportions. After logging, frequency of box use in greenbelt habitat (unharvested buffer strips along intermittent streams) was significantly greater than in harvested areas. On control stands the ratio of boxes used to those available did not change throughout the study. The ratio of boxes used per squirrel increased on harvested stands, even as squirrel densities declined, indicating a reduction in natural nesting resources after logging. The presence of mature forests adjacent to harvested stands, as well as retention of greenbelt habitat, overstory hardwoods, and snags within harvested areas, reduced the severity of logging impacts on flying squirrels. The seed-tree harvest regime, particularly without retained overstory hardwoods, appears to produce a level of disturbance and resource depletion that is too severe for flying squirrel persistence.

Key words: experimental logging in Arkansas (USA); flying squirrels and forest disturbance; forest corridors through harvested areas; forest fragmentation; Glaucomys volans; *greenbelts; habitat selection; nest-box usage by flying squirrels; Ouachita National Forest (Arkansas, USA); silviculture, even-aged and uneven-aged; southern flying squirrel densities.*

INTRODUCTION

In forests held by private industry in the United States, clear-cutting of large tracts continues the diminution of native forest habitat, replacing it with monoculture pine plantations harvested in short rotations (Melchiors 1983). In publicly owned forests, managers are attempting to reduce the impact of silvicultural practices long geared primarily to timber production (Curran 1994). While clear-cut harvesting offers economic benefits over less intensive silvicultural techniques (Busby and Kluender 1994, Kluender et al. 1994), the U.S. Forest Service has recently shifted the emphasis of its management activities to better serve the other four values it is mandated to provide on public lands: wildlife, water, range, and recreation (Curran 1994).

To effectively consider needs of wildlife in forest-management planning, information on responses of native species to various disturbance regimes is required (Hurley 1986, Daily et al. 1996). Effects of clear-cut silviculture on vertebrates, primarily birds, have been documented (see review by Harlow and Van Lear [1987], Smith and Petit 1988). However, few studies have dealt with the autecological responses of mammals to the intermediate disturbances caused by management regimes such as seed-tree and shelterwood (even-aged), or single-tree-selection (uneven-aged) harvests (Muul and Lim 1978, Nixon et al. 1980, Wilson and Johns 1982, Pattanavibool and Edge 1996).

Manuscript received 21 July 1997; revised 5 February 1998; accepted 18 February 1998; final version received 16 March 1998.

[3] Present address: 1683 Tall Grass Drive, Fayetteville, Arkansas 72703 USA.

The dearth of information on the effects of anthropogenic and natural disturbances on wildlife has led many ecologists to stress the need for autecological information that could allow landscape managers to effectively protect quality wildlife habitat (Simberloff and Abele 1976, 1982, McCoy 1982, 1983, Simberloff 1982, Verner 1986, Wilcove et al. 1986, Zimmerman and Bierregaard 1986). It has been suggested that clearcut harvesting may mimic natural disturbance events and that even-aged forest management can be incorporated on a landscape without major ecosystem reorganization (Urban et al. 1987, but see Taulman 1998). Healy and Brooks (1988) concluded that even-aged silviculture did not adversely affect southern flying squirrel (*Glaucomys volans*) populations in West Virginia.

The purpose of this study was to provide additional information on the responses of populations of southern flying squirrels to a range of experimental even-aged and uneven-aged timber harvest practices along a gradient of increasing disturbance intensity and to observe whether squirrels showed habitat selectivity in the use of artificial nest boxes within fragmented forests. Known habitat requirements, such as forest structure for gliding travel (Bendel and Gates 1987), snags and other natural cavities for nesting (Muul 1974, Weigl 1978, Doby 1984, Gilmore and Gates 1985, Sawyer and Rose 1985), and hard mast as primary foods (Harlow and Doyle 1990), together with the common belief that the flying squirrel is a forest-habitat generalist (Muul 1968), suggest that flying squirrel abundance and distribution may be responsive to varying degrees of forest disturbance.

Population dynamics of flying squirrels were investigated through winter nest-box surveys on 21 stands under six different experimental silvicultural, harvest regimes, plus a control (three replicates of seven forest conditions), prior to harvest in 1993 and after harvest in 1994–1996. Data were collected on density, fecundity, reproduction, persistence, and robustness. Working hypotheses were that none of the demographic parameters investigated would be different either among treatments prior to harvest or among control and harvested areas during postharvest years. It was expected that squirrel density would decline after treatment on all harvested study areas in proportion to disturbance intensity. Control stands were expected to show no significant changes over the course of the study.

METHODS

Study areas

The Ouachita National Forest (ONF; west-central Arkansas, USA), the setting for this study, is characterized by a series of east–west ridges. South-facing forests have an overstory composition of ~80% shortleaf pine (*Pinus echinata*) and 20% hardwoods, including white oak (*Quercus alba*), post oak (*Q. stellata*), northern red oak (*Q. rubra*), mockernut hickory (*Carya tomentosa*), bitternut hickory (*C. cordiformis*), and sweetgum (*Liquidambar styraciflua*). Midstory and understory strata vary in vegetative density and include such additional species as eastern hophornbeam (*Ostrya virginiana*), flowering dogwood (*Cornus florida*), black cherry (*Prunus serotina*), winged elm (*Ulmus alata*), and red maple (*Acer rubrum*). North-slope forests are dominated by an oak–hickory association. At its boundaries with private land, the ONF lies adjacent to various altered habitats, such as grazed pasture and mixed hardwood–pine forest remnants, extensive tracts of private timber-industry pine plantations, and residential areas.

The Ecosystem Management Research Program of the U.S. Department of Agriculture Forest Service includes a research venture in which alternative silvicultural practices are being evaluated under rigorous scientific scrutiny. In Arkansas, researchers with the USDA Forest Service, Southern Research Station, and the Ouachita and Ozark National Forests are cooperating to meet the ecosystem management goals through a three-phase approach. Under Phase II of this project, an array of 12 cutting treatments ranging from pine–hardwood single-tree selection to clearcut, plus an uncut control, were replicated in four forest zones (Baker 1994). Fifty-two stands were selected for the study from a pool that conformed to a range of criteria (see below). Seven research teams are monitoring various economic and ecological parameters before and after treatment at the 15-ha-stand level to provide data on the relative merits and ecological effects of each cutting method. Pretreatment data were collected on all stands during 1992 and spring of 1993. All experimental stands were harvested during summer 1993, and postharvest habitat data were collected beginning in the spring of 1994. Our study of effects of a range of silvicultural harvest regimes on the ecology of southern flying squirrels was undertaken on a subset of 21 of the 52 stands.

Prior to harvests, all stands met the following selection criteria: total area was between 14.2 and 16.2 ha; pine basal area (BA) at breast height (1.5 m) ranged from 13.8 to 25.3 m^2/ha; hardwood BA was 4.6–11.5 m^2/ha; age of overstory trees was >70 yr; and stand aspect was generally south facing. Twenty-one stands consisting of three replications of seven future treatments (control, pine–hardwood single-tree selection [P-H STS], pine single-tree selection [P STS], pine–hardwood shelterwood [P-H SW], pine shelterwood [P SW], pine–hardwood seed tree [P-H ST], and pine seed tree [P ST]) were selected for this study (Fig. 1). The control stands were not altered during the study. A detailed description of harvest specifications is provided by Baker (1994). Briefly, the P-H STS treatment produced a stand with 10.3–14.9 m^2/ha remaining BA in pines and hardwoods, with the hardwood component comprising 1.1–4.6 m^2/ha. All pine-only treatments resulted in stands with total BA similar to the pine–hard-

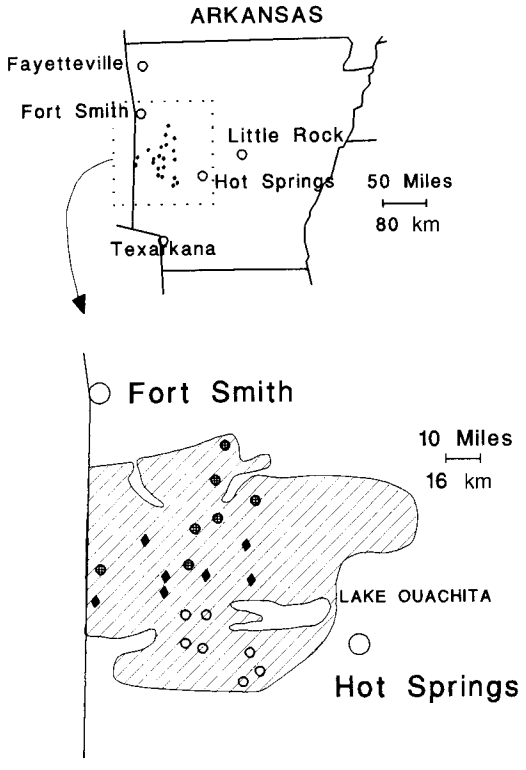

FIG. 1. Approximate location of 21 15-ha study areas in three replicated groups in the Ouachita National Forest of west-central Arkansas. Filled circles, open circles, and diamonds denote group membership. Hatched area represents the extent of the national forest.

wood treatment, but comprising only 0.5–1.1 m^2/ha of hardwoods. The P-H SW treatment retained 49–99 overstory pines and hardwoods per hectare (BA: 6.9–9.2 m^2/ha, of which 1.1–3.4 m^2/ha were hardwoods). The P-H ST treatment left 25–37 overstory trees per hectare (BA: 2.3–4.6 m^2/ha, of which 1.1–2.3 m^2/ha were hardwoods). Mature forest habitat along ephemeral drainages within harvested stands was preserved as greenbelt habitat; the width was determined by the shape and number of channels within a drainage. Greenbelts normally extended 10–15 m out of the channel on each side.

Nest-box survey

During September 1992, 630 nest boxes (30 boxes per stand on 21 stands) were installed at a height of 3–4 m on trees scheduled to be retained after cutting. Interior dimensions of next boxes were 15 × 17 × 22 cm. Box trees were selected to form a grid with 60-m spacing between trees and rows. Wilson and Anderson (1985) found that adding a buffer zone around a trapping grid equal to one half the mean maximum distance moved (MMDM) by individuals between subsequent trap captures improved the estimation of the trapped area used in animal-density estimates. In this study, a 60-m buffer zone was retained around the perimeter of the nest-box grid in initial study-area layout to approximate one half the MMDM by squirrels between nest boxes.

Boxes were opened on all 21 stands the first week of November each year, 1992–1995. Boxes were then surveyed on each stand once per month during January–March, 1993–1996. Nests were collected and boxes closed during the March survey. Females with young <8 wk old in March were returned to boxes and those boxes were closed and nests collected in April when nestlings were beyond weaning age (Sollberger 1943). Boxes remained closed during summer and early fall to reduce the effect of artificial nesting habitat on squirrel use of experimental stands. Nest boxes left open year-round would bias any harvest effect by providing enhanced nesting resources and possibly allowing squirrels to occupy a disturbed area that would otherwise be abandoned. During each survey an occupied box was removed from the tree and squirrels were processed on the ground. All squirrels large enough to receive ear tags were marked with two numbered metal ear tags (Number 1, National Band and Tag Company, Newport, Kentucky, USA) and released on the ground. Young nestlings that were too small to ear-tag were toe-clipped. Those young too small to toe-clip (without detached toes) were not marked; some were recaptured in subsequent surveys and ear-tagged, others were moved by their mothers and were not seen again. Captives were weighed, and sex and reproductive condition were noted. Males with scrotal testes were considered reproductively active; females with enlarged, perforated vaginas were considered sexually receptive.

Population demographics

The total number of squirrels captured during each winter nest-box survey was used as an estimation of the local population of flying squirrels nesting on a study area during the winter season. The population was assumed to be closed during this period and young of the year were considered separately from adults. Standard population models based on live-trapping regimes assume procedures that produce an instantaneous sample of foraging animals (Pollock et al. 1990). Nest-box surveys of flying squirrels do not yield such data. Closed-population models, such as CAPTURE (Otis et al. 1978), also do not perform well when capture probabilities are low and population sizes are small (Pollock et al. 1990), as in this study. To compare our method of population estimation with a known procedure, the Chapman (1951) modification of the Lincoln-Petersen (L-P) method (Pollock et al. 1990) was used with a sample of capture data from six study areas over a total of 14 total survey seasons in which the numbers of marked squirrels and recaptures were largest. That formula is:

$$N_c = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \qquad (1)$$

where N_c = Chapman-modified Lincoln-Peterson population estimator, n_1 = number of marked squirrels in the population, n_2 = number of squirrels in sample captured at a later time, and m_2 = number of animals in n_2 that are marked from population n_1.

A criterion was developed to help identify immature individuals (those born during late summer or fall, prior to winter surveys). The masses of squirrels (excluding maternal females) recaptured in January at least one season after first being marked were taken as a sample of squirrels known to be adults (mass = 72.47 ± 1.02 [mean ± 1 SE], range: 57–83 g, n = 30). To be conservative, squirrels weighing 40–55 g at first capture in January or February were categorized as "immature." In several instances two or more small squirrels of similar mass (but >55 g, $\bar{X}$ = 59.27 g, range: 56–64 g, n = 11) were captured in a nest with a single lactating female. These were assumed to be late-term nestlings still with their mother. Squirrels <40 g were categorized as "young" or "nestlings." Based on the growth tables of Linzey and Linzey (1979), these categories correspond to ages of about ≤4 wk for young, 4–11 wk for immature, and >11 wk for adult. All study areas were within the range of *Glaucomys volans saturatus* (Braun 1988), and squirrels in this study are assumed to belong to that race.

To compare growth rates of wild-raised young from this study with those raised in captivity by Linzey and Linzey (1979), we plotted masses of all young in litters found within 2 wk of birth (estimated using the growth table of Linzey and Linzey [1979]) that were subsequently recaptured during the same season, along with data from Linzey and Linzey. It was assumed that actual parturition date could accurately be estimated for young squirrels ≤14 d old.

Habitat description

Habitat data used in correlation analyses with squirrel density were collected by the Silviculture and Biodiversity Research Groups on permanent macroplots on each study area (Guldin et al. 1994). Circular plots with radius = 11.3 m (0.04 ha, 12 plots in nongreenbelt habitat and 2 in greenbelt habitat on each stand) were positioned in a stratified random array (Grieg-Smith 1983, Guldin et al. 1994). The Silviculture Group recorded tree counts and BA by species of trees >8.9 cm diameter at breast height (dbh, 1.5 m) on all stands in 1992 prior to harvests and in 1994 during the 1st yr after harvest. The Biodiversity Group collected data on small, woody vegetation <8.9 cm dbh on macroplots, as well as herbaceous cover on nested microplots, prior to harvest (Foti and Guldin 1994). Because the herbaceous and small, woody survey data were never made available on a stand-level basis, only data for trees >8.9 cm dbh were used in correlation analyses. Due to the high correlation of tree counts and basal area for similar categories, only tree counts, converted to density per hectare, were used (see Appendix).

We created a correlation matrix of squirrel density and six tree variables representing three diameter categories of pines and hardwoods on all pretreatment study areas in 1993. These variables describe the number of overstory trees per hectare (>24.1 cm dbh), upper-midstory (16.6–24.1 cm dbh), and lower-midstory density per hectare (8.9–16.5 cm dbh). After harvest two additional categories were added: number per hectare of overstory oak and hickory trees and total number of oak and hickory trees per hectare >8.9 cm dbh (Taulman 1997).

The Wildlife Research Group surveyed visible fruits on overstory hardwoods on nine stands representing three treatment groups (Control, P-H STS, and P-H SW) in this study during fall 1994 and 1995, producing hard-mast production indices for those stands (Perry 1995). On the two treatment groups that underwent harvests, data were collected on mast production in greenbelt and nongreenbelt habitat. In addition, snag density per hectare was estimated on the same stands during 1993, prior to harvests. Mast abundance was estimated using an ocular technique modified from Whitehead (1980). Fifteen meter-wide transects were traversed along ~1400 linear meters through each stand. Mast production was estimated for oaks >20 cm dbh and for hickories >15 cm dbh. Trees were rated based on (1) percentage of crown producing mast, (2) percentage of twigs bearing mast within the producing portion of the crown, and (3) average number of nuts per twig on bearing twigs. The mean production index consists of the mean index for all trees sampled. An estimate of total mast production per hectare was derived by dividing total production indices of all trees by the area sampled, yielding an index of overall mast production and stocking density. The nongreenbelt habitat per stand sampled in 1994 was 0.96 ± 0.11 ha (mean ± 1 SE), and in 1995, 1.19 ± 0.10 ha. The greenbelt habitat sampled per stand in 1994 was 0.30 ± 0.06 ha, and in 1995, 0.44 ± 0.08 ha.

RESULTS

Population demographics

Neither the sex ratio among newly captured adults and immatures combined nor among young differed from 1:1 in any year (Table 1). However, among recaptured squirrels more females than males were found in years after first capture among all stands and years combined (Yates χ^2 = 5.12, df = 1, P = 0.023). The number of adults and immature squirrels captured in nests on a sample of six stands of similar size (with the largest squirrel densities) over 14 cumulative winter survey periods (three controls, a pine STS, a pine SW, and a pine ST) was 15.43 ± 1.94 squirrels per stand (mean ± 1 SE); the Chapman (1951) modified L-P (Lincoln-Petersen) method produced an estimate of 14.70 ± 1.15 squirrels per stand. The similarity of those results (Mann-Whitney U = 221.5, P = 0.83, n_1 = 14

TABLE 1. Numbers of squirrels captured, by three-stand treatment group, together with estimated squirrel densities, in the Ouachita National Forest, Arkansas, USA. Data are means with 1 SE in parentheses for control stands, averaged over 1993–1996; data for treatment stands involving harvests are shown as totals for the preharvest year 1993 and as means (1 SE) for the postharvest years 1994–1996. Note the general decline in densities after harvest (with some exceptions), especially the virtual eradication of squirrels from the most intensive seed-tree harvest type (one male and one female captured in boxes during 3 yr on three stands).

Treatment†	Sex	No. of years	No. of squirrels captured‡					Total three-stand area sampled (ha)§	Density (no. squirrels/ ha)‖
			Adult	Recaptures	Immature	Young	Total		
Control									
1993–1996	M	4	11.0 (3.9)	3.0 (0.6)	0.5 (0.5)	6.0 (3.5)	79	186.8	0.423
	F	4	9.5 (4.3)	6.7 (2.2)	1.0 (0.7)	7.5 (3.1)	92	186.8	0.493
P-H STS									
1993	M	1	11	···	0	2	13	46.0	0.283
	F	1	9	···	0	5	14	46.0	0.304
1994–1996	M	3	1.0 (0.6)	0	0.7 (0.7)	3.0 (0.6)	14	138	0.101
	F	3	3.0 (0.6)	0.3 (0.3)	0	2.3 (0.3)	17	138	0.123
P STS									
1993	M	1	8	···	0	2	10	44.9	0.223
	F	1	5	···	0	3	8	44.9	0.178
1994–1996	M	3	4.3 (2.0)	0.7 (0.3)	0.3 (0.3)	1.0 (1.0)	19	134.7	0.141
	F	3	3.3 (1.9)	0.7 (0.3)	0	2.7 (1.8)	20	134.7	0.148
P-H SW									
1993	M	1	3	···	0	2	5	48.4	0.103
	F	1	3	···	0	2	5	48.4	0.103
1994–1996	M	3	4.3 (1.9)	1.3 (0.9)	2.7 (1.5)	5.0 (3.2)	40	145.2	0.275
	F	3	4.7 (1.8)	2.7 (1.5)	2.0 (1.2)	3.0 (1.7)	37	145.2	0.255
P SW									
1993	M	1	2	···	0	3	5	46.6	0.107
	F	1	4	···	0	3	7	46.6	0.150
1994–1996	M	3	3.3 (2.4)	1.0 (0.6)	0.3 (0.3)	2.0 (1.5)	20	139.8	0.143
	F	3	3.0 (1.7)	2.7 (1.2)	0	3.7 (3.2)	28	139.8	0.200
P-H ST									
1993	M	1	6	···	2	6	14	46.0	0.304
	F	1	10	···	2	0	12	46.0	0.261
1994–1996	M	3	4.7 (1.8)	1.3 (0.3)	0.3 (0.3)	1.7 (0.9)	24	138.0	0.174
	F	3	3.3 (0.9)	1.7 (1.2)	0	0.7 (0.7)	17	138.0	0.123
P ST									
1993	M	1	1	···	0	2	3	46.1	0.065
	F	1	7	···	0	0	7	46.1	0.152
1994–1996	M	3	0	0	0	0.3 (0.3)	1	138.3	0.007
	F	3	0	0.3 (0.3)	0	0	1	138.3	0.007

† Treatment codes: P-H STS = pine–hardwood single-tree selection harvest, P STS = pine single-tree selection, P-H SW = pine–hardwood shelterwood, P SW = pine shelterwood, P-H ST = pine–hardwood seed tree, P ST = pine seed tree.

‡ Adult, >11 wk old; immature, 4–11 wk old; young, ≤4 wk old. In 1993 all captures were new animals, so recaptures represent the 3-yr period 1994–1996; "recaptures" refers to squirrels captures during a subsequent season after initial marking.

§ Total area of all three stands in the treatment group multiplied by the no. of years during which squirrels were monitored. (Experimental stands were 14.2–16.2 ha each.)

‖ Density = total no. of individual squirrels captured divided by total stand area sampled. Squirrel densities were not different among three-stand control and postharvest treatment groups (Kruskal-Wallis ANOVA H [df = 6, N = 22] = 10.51, P = 0.10).

winter survey periods, n_2 = 33 recapture occasions) suggests that an estimate of nesting-squirrel population size based on total animals captured in a winter survey is as useful an estimator as the L-P method.

The numbers of adults and immature squirrels captured on all harvested stands declined in 1994, the first year after harvest (Table 1), but increased in control stands during the same period. The immediate impact of harvesting is further indicated by the significantly lower relative frequency of squirrels on harvested stands than on control stands in 1994, compared with all other years (Table 2). Squirrel numbers generally increased in harvested stands in 1995 and 1996, sometimes exceeding densities observed on the stands prior to harvest. An exception was the pine seed-tree group, where squirrels virtually disappeared after harvest and did not return during the three following years (Table 1).

TABLE 2. Cross tabulation of squirrel frequencies by age and stand-treatment type across years 1993 (before harvest) and post harvest, 1994–1996. Data are actual numbers of individual squirrels captured in nest boxes on all stands in each group of stands.

Stand-treatment type	Squirrel age†		
	Adult	Young	Total¶
		1993	
Control‡	19	13	32
Pre-harvest§	73	32	105
Total‖	92	45	137
		1994	
Control‡	46	10	56
Harvest§	30	8	38
Total‖	76	18	94
		1995	
Control‡	44	31	75
Harvest§	53	54	107
Total‖	97	85	182
		1996	
Control‡	8	0	8
Harvest§	79	14	93
Total‖	87	14	101

Notes: Unless otherwise noted, differences in proportions of young to adults between categories were not significant ($P > 0.05$). Yates-corrected Chi-square was used when at least one cell value was <10.

† Adult, >11 wk old; young, ≤4 wk old.

‡ Proportion of young to adults was greater on control stands in 1993 compared with 1994 ($\chi^2 = 5.47$, $P = 0.019$) and 1996 ($\chi^2 = 4.81$, $P = 0.028$); proportion of young to adults was also greater on control stands in 1995 compared with 1994 ($\chi^2 = 8.22$, $P = 0.004$) and 1996 ($\chi^2 = 14.62$, $P = 0.0001$).

§ Proportion of young to adults was greater on pre-harvested stands in 1993 than on post-harvest stands in 1996 ($\chi^2 = 8.19$, $P = 0.0014$); the young-to-adult proportion on harvested stands was also greater in 1995 compared with 1993 ($\chi^2 = 8.78$, $P = 0.003$), 1994 ($\chi^2 = 9.91$, $P = 0.0016$), and 1996 ($\chi^2 = 31.64$, $P < 0.0001$).

‖ Proportion of young to adults on control and harvested stands combined was greater in 1993 compared with 1994 ($\chi^2 = 5.27$, 1 df, $P = 0.022$) and 1996 ($\chi^2 = 11.24$, $P = 0.0008$). Proportion of young to adults was also greater in 1995 than in 1993 ($\chi^2 = 6.22$, $P = 0.013$), 1994 ($\chi^2 = 20.12$, $P < 0.0001$), or 1996 ($\chi^2 = 30.80$, $P < 0.0001$).

¶ Proportion of all squirrels on control compared with pre-harvested stands was greater in 1993 compared with the control-to-post-harvest ratio in 1996 ($\chi^2 = 20.64$, $P < 0.0001$), but less in 1993 compared with 1995 ($\chi^2 = 11.17$, $P = 0.0008$). The proportion of squirrels on control compared with harvested stands was greater in 1994 than in 1993 ($\chi^2 = 31.01$, $P < 0.0001$), 1995 ($\chi^2 = 8.38$, $P = 0.0038$), or 1996 ($\chi^2 = 56.60$, $P < 0.0001$).

The ratio of squirrels recaptured from previous years to new adult and immature squirrels was not different on harvested stands compared with control stands (harvest: recaptures = 38, new = 127; control: recaptures = 29, new = 69; $\chi^2 = 1.39$, $P = 0.24$). The same situation applied to recaptures in subsequent years of squirrels first marked as nestlings (harvest: recaptures = 4, young in litters = 60; control: recaptures = 7, young in litters = 47; $\chi^2 = 1.56$, $P = 0.21$).

The means of monthly masses of reproductively active and inactive male and female adult squirrels in four categories combined among all stands showed no among-month differences during any year. However, masses of squirrels in 1996 in all categories were significantly lighter than squirrels in the same categories during at least one previous year.

Reproduction

After a decrease in the number of young produced in nest boxes during the first year after harvest, an increase was seen in 1995. The fewest litters of any year of the study were produced in 1996. For the pine shelterwood treatment, significantly fewer young were produced in 1994 than in both 1993 and 1995 (Kruskal-Wallace ANOVA: $H = 16.03$, $P = 0.001$, multiple comparisons test [Siegel and Castellan 1988]). The ratio of young to adults was significantly greater on control stands in 1995 compared with 1994 ($\chi^2 = 8.22$, $P = 0.004$) and 1996 ($\chi^2 = 14.62$, $P = 0.0001$), and a higher young-to-adult ratio was seen on harvested stands in 1995 compared with all other years (1993: $\chi^2 = 8.78$, $P = 0.003$; 1994: $\chi^2 = 9.91$, $P = 0.002$; 1996: $\chi^2 = 31.46$, $P = 0.0001$).

Based on estimated birth dates of 35 immature squirrels from all study areas combined over the course of the study, an early fall breeding period in 1994 and 1995 resulted in several fall litters among these study areas. Fecundity of females declined after harvest in 1994, but was higher in 1995 than either 1994 or 1996. No differences were observed in female fecundity on control stands compared with groups of treatment stands before or after harvests. Results indicated no differences in growth trends between wild and captive-reared flying squirrels (Linzey and Linzey 1979). Among squirrels born on study areas (first captured as young or immature), no differences were observed in numbers of males and females recaptured in subsequent years (Yates $\chi^2 = 1.62$, $P = 0.20$; Table 2).

Mortality

Five instances of mortality due to predation were discovered through the retrieval of the radio-transmitter collars. In one case a black rat snake (*Elaphe obsoleta*) was found in the process of ingesting the carcass of a radio-collared female squirrel. Two other cases showed evidence of Screech Owl predation at forest edges. In the final two instances the digested carcass of one squirrel and the mutilated collar of another were retrieved from the seed-tree harvest portion of a study area.

Nest-box usage

Flying squirrels used boxes primarily as nests or feeding stations; another use included temporary escape refugia. The ratio of boxes used as nests to those available was not different between control and pre-harvest stands in 1993 ($\chi^2 = 0.93$, $P = 0.34$), or in comparison of control stands in 1993 with control

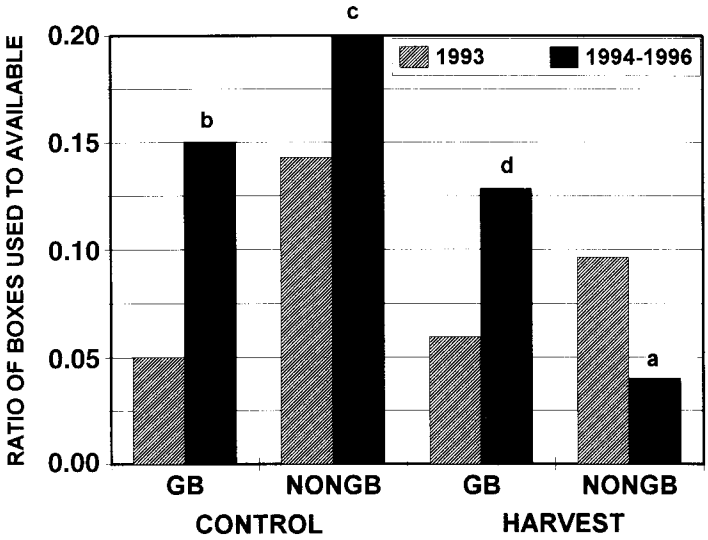

FIG. 2. Ratio of boxes used as nests compared with those available on control and harvested stands, in greenbelt and nongreenbelt habitat, before harvests in 1993 and in all postharvest years (1994–1996) combined. Box use-to-availability ratios were not different among habitats or treatment groups prior to harvest in 1993 or among habitats on control stands in 1993 compared with 1994–1996. During postharvest years the ratio of boxes used to those available was lower ($P < 0.01$) in logged (nongreenbelt) areas (a) than in control greenbelt habitat (b), control nongreenbelt habitat (c), and greenbelt habitat on harvested stands (d).

stands during 1994–1996 combined ($\chi^2 = 2.81$, $P = 0.094$) (Fig. 2). However, during the three combined postharvest years the ratio of boxes used to those available in harvested areas was significantly lower than that seen on control stands (greenbelt: Yates $\chi^2 = 11.10$, $P < 0.009$; nongreenbelt: $\chi^2 = 83.70$, $P < 0.0001$) or in greenbelt habitat on harvested stands ($\chi^2 = 34.19$, $P < 0.0001$) (Fig. 2).

Subtracting the number of boxes containing nests from those available on each stand yielded the number of boxes available for use as feeding stations. The proportion of boxes used as feeding stations to those available on harvested stands was greater in greenbelt habitat compared with logged habitat in all postharvest years (1994: $\chi^2 = 6.01$, $P < 0.014$; 1995: $\chi^2 = 10.44$, $P = 0.001$; 1996: $\chi^2 = 14.12$, $P = 0.0002$).

The ratio of boxes used for nesting and feeding stations to adult and immature squirrels increased dramatically on harvested stands in 1994 to become significantly greater than the ratio of boxes used to number of squirrels on control stands (Mann-Whitney $U = 2.00$, $P = 0.033$, $n = 3$ control stands, $n = 9$ harvested stands) (Fig. 3). The per squirrel increase in nest-box use on harvested stands occurred as squirrel densities declined on those stands. The densities of adult and immature squirrels combined were significantly correlated with the number of nests in boxes among all study areas during all years (1993: $r_s = 0.875$, $P < 0.00001$; 1994: $r_s = 0.903$, $P < 0.00001$; 1995: $r_s = 0.859$, $P < 0.00001$; 1996: $r_s = 0.800$, $P < 0.00001$).

Squirrel density–habitat correlations

Prior to harvest, lower-midstory pine density was negatively correlated with squirrel densities ($r_s = -0.56$, $P = 0.001$, $N = 21$ experimental stands [3 control, 18 harvested]); overstory pine density was positively correlated with squirrel density ($r_s = 0.44$, $P = 0.045$, $N = 21$). Lower-midstory hardwood tree density was positively correlated with squirrel density in greenbelt habitat during all postharvest years (Taulman 1997). Together, lower-midstory pine and overstory pine densities accounted for 38% (R^2) of the variability in squirrel density in 1993, but only overstory pine density made a significant contribution to the prediction of squirrel density ($P = 0.040$). For 1994, lower-midstory pine, upper-midstory hardwood, and lower-midstory hardwoods in greenbelt explained 66% (R^2) of the variability in squirrel density. The hardwood variables both made significant contributions to squirrel density, upper-midstory hardwood counts ($P = 0.001$) and lower-midstory hardwoods in greenbelt ($P = 0.019$). The resulting equation predicting squirrel density in 1994 using these three variables was $y = -0.767 + 0.000045$ MEDPINCT $+ 0.0113$ LGHDWCT $+ 0.0027$ GMEDHDWCT (see Appendix for variable code definitions). None of the variables provided significant predictive power for squirrel density in 1995 or 1996 and regression models explained <20% of the variability in squirrel density.

Mast-production indices were estimated for the nine total control, P-H STS, and P-H SW stands during 1994 and 1995. Indices decreased on two of the three control stands from 1994 to 1995, but increased on most harvested stands during the same time period (Table 3). Differences in mast-production indices were not significant between the same stands from 1994 to 1995. In nongreenbelt habitat on harvested stands total mast-production indices were significantly higher in 1995 compared with 1994 (Wilcoxon matched-pairs test $z = 1.99$, $P = 0.046$, $N = 6$ harvested stands [where the same trees were surveyed each year]). Densities of adult and immature squirrels on these nine stands prior to harvest in 1993 were positively correlated with snag density per hectare ($r_s = 0.83$, $P = 0.006$). With one exception, neither density of adult and immature squirrels combined nor density of young were correlated

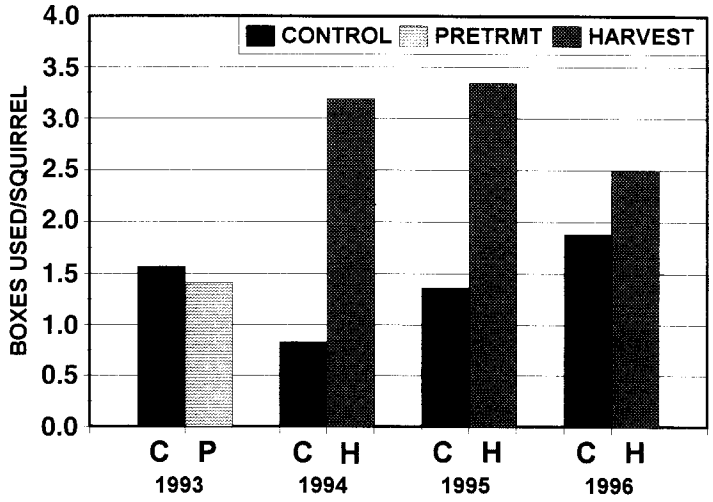

FIG. 3. The ratio of boxes used as nests and feeding stations per adult and immature squirrel on three control (C) and 18 pretreatment (P) stands in 1993 and on control and 18 harvested (H) stands during 1994–1996. (Each year the number of stands included in the ratio depended on how many of the stands actually had any squirrels on them in any nest boxes.) Differences in ratios between control and harvested stands were significant ($P < 0.05$) in 1994.

with either total hard-mast production or mean mast-production indices among all three treatment categories or among greenbelt and nongreenbelt portions of harvested stands. Adult and immature squirrel density in 1994 showed a significant negative correlation with total mast-production indices ($r_s = -0.89$, $P = 0.016$).

DISCUSSION

Squirrel demographics

Reported flying squirrel densities range from 2.82 animals/ha in oak–hickory forests (Jordan 1948) to 38.4 animals/ha in hardwood–pine forests in which the pine component accounted for 7.5% of overstory trees (Sawyer and Rose 1985). The low densities in the mature pine–hardwood forests (0.21–0.92 squirrels/ha) in this study (Table 1) suggest that these forests are marginal flying squirrel habitat. These forests may also be marginal for other small-mammal species, as well. Tappe et al. (1994) captured only three species of small mammals in densities >0.06 animals/ha (the highest was 0.41 animals/ha) in nine of these stands prior to harvest).

Harvests carried out in this study produced expected declines in squirrel density and reproduction in 1994 (Tables 1 and 2), while squirrel populations increased on all control stands during 1993–1995. It is assumed that the dearth of adult squirrels on harvested stands in 1994 represented a combination of mortality and emigration of previous residents and a lack of new immigration. Similar population declines following logging disturbances have been documented elsewhere (Burgess 1971, Wilson and Johns 1982). Dunstan and Fox (1996) found that small-mammal species richness in Australian rain forest declined with decreasing remnant patch size and with increasing disturbance level. They emphasized the importance of maintaining corridors through altered landscapes connecting remnant forest patches with larger source forests.

Squirrels returning to, or pioneering previously unoccupied, stands after harvest may do so partly because

TABLE 3. Mean hard-mast production index (per tree) and total mast-production indices (total per-tree indices per hectare) in fall 1994 and 1995 on two habitat types on three stand-treatment groups. Oaks > 20 cm dbh and hickories > 15 cm dbh were surveyed for (1) percentage of crown bearing mast, (2) percentage of twigs bearing nuts within producing portion of crown, and (3) average number of nuts per twig on bearing twigs.

			1994				1995			
			Nongreenbelt		Greenbelt		Nongreenbelt		Greenbelt	
Treatment†	Stand no.‡	1993 Snags/ha§	Total	Mean	Total	Mean	Total	Mean	Total	Mean
Control	23	6.7	30.77	1.17	...	...	14.81	0.41	...	...
	605	25.0	25.27	0.56	...	...	4.36	0.11	...	...
	284	16.1	0.00	0.00	...	...	15.15	0.28	...	...
P-H STS	609	14.8	0.00	0.00	0.00	0.00	85.80	2.87	308.03	2.50
	1649	30.4	104.61	1.93	50.53	0.47	201.44	2.93	168.35	1.39
	70	8.7	20.20	0.71	0.00	0.00	159.33	5.43	0.00	0.00
P-H SW	27	14.8	36.79	4.17	67.68	1.11	36.59	2.65	71.09	0.89
	1119N	15.1	49.84	2.47	11.06	0.16	51.02	3.07	128.34	1.61
	833	4.7	27.17	0.85	0.00	0.00	185.14	5.71	251.81	3.55

† Treatment codes: P-H STS = pine–hardwood single-tree selection harvest; P-H SW = pine–hardwood shelterwood.
‡ Numbers are stand designations (U.S. Forest Service compartment identifiers).
§ Snags were surveyed on these stands in 1993 prior to harvest.

of the high hard-mast production in residual overstory oaks and hickories. For example, on stand 27 squirrels were not present prior to harvest, but immigrated in 1994 and persisted during the three succeeding postharvest years, when mast indices were higher than on any of the control stands. Comparisons of mast-production indices on control and harvested stands during fall of 1994 and 1995 also indicated higher levels of hard mast on harvested stands after logging (Table 3). Pioneering squirrels may be able to find and exploit such new resources quickly; the greenbelt habitat offers nearby resources for nesting and auxiliary refugia. Mares and Lacher (1987) and Lacher and Mares (1996) found that eastern chipmunks (*Tamias striatus*) responded rapidly to changes in mast abundance. However, there is a potential for increased predation risk for pioneers repopulating disturbed areas (Hokkanen et al. 1982). Four of five instances of predation on squirrels observed in this study occurred along forest edges or in seed-tree harvest areas.

The higher frequency of new adults compared with recaptures on all stands during the study (with the exception of control stands in 1996 [Table 1]), indicates either a high immigration rate or the production of young on the study area in natural cavities, rather than boxes. The low recapture frequency of young produced on harvested stands during subsequent years also suggests either high juvenile mortality, emigration, or both. In at least one instance (study area 27), a propagule of four adults colonized the stand after harvest and pioneered what appeared to be (2 yr later) a sustaining local population, with stable population density, recaptures, and multiple litters produced each year following colonization.

A marked population decline was noted on control stands in 1996, including reduced density, reproduction, and robustness (as determined by significantly lower masses for all four sex and reproductive categories of squirrels in 1996 compared with at least one preceding year). Steadily increasing population densities on two control stands during 1993–1995 in the absence of strong mast production by hardwoods during fall of 1994 and 1995 may have resulted in local overpopulation and emigration from those two study areas, resulting in the lower population density observed in 1996.

Dispersal and local migrations appear to be important behavioral adaptations permitting flying squirrels to persist in these marginal, fragmented pine–hardwood forests. Roff (1974*a*, *b*) predicted that movements between local populations can increase overall persistence time by several orders of magnitude. He suggested that dispersal is a significant factor contributing to the long-term survival of small populations, in particular, and that selection will favor individuals with "dispersal-prone" genotypes (Roff 1975). Noss (1993) emphasized the importance of protected forest-habitat corridors as escape routes from disturbed areas, as refuges, and as pathways for eventual immigration and recolonization of depauperate patches.

Nest-box use and habitat factors

Analysis of ratios of boxes used to boxes available in greenbelt and nongreenbelt habitats on control and harvested stands indicates a shift in squirrel habitat use away from logged areas and into greenbelts during postharvest years (Fig. 2). Squirrels that remained on harvested stands made greater use of boxes in greenbelt areas and avoided harvested (nongreenbelt) habitats. The high correlation of squirrel density with snag density on the nine surveyed pretreatment stands in 1993 ($r_s = 0.83$, $P = 0.006$) suggests the importance of snags as cavity resources to squirrels. Nesting habitat does not appear to be in short supply in mature pine–hardwood forests, as indicated by the decrease in the ratio of nest boxes used per squirrel on control stands in 1994 and 1995, compared with 1993, even as population density rose during the same period on those study areas (Fig. 3). However, logging reduced nesting resources significantly. On harvested stands in 1994, significantly more boxes were used per squirrel compared with box use on control stands, though population density was lower on harvested stands in 1994 than it had been prior to harvest in 1993 (Fig. 3).

The significant positive correlation of overstory pine density, and the negative correlation of lower-midstory pine density, with squirrel density on mature-forest study areas in 1993 agree well with reported habitat requirements of flying squirrels by Bendel and Gates (1987). They suggested that high overstory tree densities and a relatively open midstory were important habitat characteristics for flying squirrels. The lack of correlation between squirrel density and overstory hardwood density may be due to the low mast production of hardwoods under mature pine canopies observed during mast surveys in 1994 and 1995. Mast production increased on hardwoods retained in harvested stands in 1994 as canopy coverage was reduced (Table 3), but squirrel avoidance of disturbed harvested areas resulted in a seemingly unusual negative correlation of squirrel density and total mast-production indices. However, the higher female fecundity observed in 1995 compared with 1994 and 1996, and the greater young-to-adult ratio on harvested stands in 1995 compared with all other years, may have been a demographic response to high food-resource levels in fall 1994, as noted for populations of *Peromyscus maniculatus, P. leucopus,* and *Tamias striatus* (Wolff 1996). The consistent significant positive correlation of squirrel nesting density and lower-midstory hardwood density (GMEDHDWCT; 1994: $P = 0.015$; 1995: $P = 0.031$; 1996: $P = 0.006$) in greenbelt habitat during postharvest years may indicate selection for areas with coverage provided by hardwoods in the diameter class 8.9–16.5 cm dbh. A similar finding was reported by Bendel and Gates (1987), in which core activity areas

were found to have high coverage values in the 10–15 m tree-canopy stratum. Alternatively, the disturbance and resource depletions in harvested areas may have caused squirrels to shift their activities to greenbelt habitats, which only coincidentally had high lower-midstory hardwood densities.

Conclusions

Results of this study indicate that flying squirrels are able to persist in fragmented pine–hardwood forests where overall mast production is relatively low by concentrating activities in mature pine–hardwood and hardwood forest areas, by using protected greenbelt habitat within harvested areas, and by avoiding logged habitats. All levels of harvest activity appear to initially force squirrels to emigrate from the stand. A similar result was reported for many bird and mammal species after selective logging operations in Indonesia (Wilson and Johns 1982). Though population densities were too low to clearly discriminate demographic responses to the entire range of treatments, the increasing gradient of disturbance in this study design did show a threshold at the pine seed-tree harvest level that squirrels were not able to tolerate during the first three postharvest years. Predation-caused mortalities also appeared to occur with greater frequency in disturbed habitats. In this study, harvest of stands surrounded by unsuitable habitat, such as pasture or young pine plantation, decimated local squirrel populations. Without protected forest corridors to other mature forests, such stands will not be accessible to recolonization until such time as surrounding habitat matures and connects with another source forest.

The shift to less intensive harvesting in public forests will require more frequent disturbance to a given site (particularly for single-tree selection), and more total hectares disturbed, if timber production quotas are held constant. To ensure the persistence of flying squirrels, and other forest-dependent mammals such as gray squirrels (Nixon et al. 1980, Brown and Batzli 1984), it is important to manage forests from a landscape perspective, preserving areas of mature, undisturbed forest, retaining hardwoods and snags within harvested areas, and providing corridors of protected, mature forest habitat through disturbed areas (Pulliam 1988, Bright 1993, Noss 1993, Dunstan and Fox 1996). Harvest regimes in which most or all hardwoods are removed should be discouraged.

Acknowledgments

The loan of an ATV by D. M. Harris greatly facilitated nest-box installation. The comments and suggestions of D. A. James, W. J. Etges, J. N. Layne, T. E. Lacher, Jr., and an anonymous reviewer on earlier drafts of this paper are greatly appreciated. This research was supported by the USDA Forest Service Southern Research Station, the Theodore Roosevelt Fund of the American Museum of Natural History, the Max McGraw Wildlife Foundation, the USDA Forest Service Ouachita National Forest, the University of Arkansas, and the estate of D. C. and V. S. Taulman.

Literature Cited

Baker, J. B. 1994. An overview of stand-level ecosystem management research in the Ouachita/Ozark National Forests. Pages 18–28 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Bendel, P. R., and J. E. Gates. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). Journal of Mammalogy **68**:243–255.

Braun, J. K. 1988. Systematics and biogeography of the southern flying squirrel, *Glaucomys volans*. Journal of Mammalogy **69**:422–426.

Bright, P. W. 1993. Habitat fragmentation—problems and predictions for British mammals. Mammal Review **23**:101–111.

Brown, B. W., and G. O. Batzli. 1984. Habitat selection by fox and gray squirrels: a multivariate analysis. Journal of Wildlife Management **48**:616–621.

Burgess, P. F. 1971. The effect of logging on hill dipterocarp forests. Malaysian Nature Journal **4**:231–237.

Busby, R. L., and R. A. Kluender. 1994. Management costs associated with various reproduction cutting methods. Pages 253–254 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics **1**: 131–160.

Curran, M. 1994. Evolution of ecosystem management and research on the Ouachita and Ozark-St. Francis National Forests. Pages 1–4 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Daily, G. C., P. R. Ehrlich, and M. Alberti. 1996. Managing Earth's life support systems: the game, the players, and getting everyone to play. Ecological Applications **6**:19–21.

Doby, W. J. 1984. Resource base as a determinant of abundance in the southern flying squirrel (*Glaucomys volans*). Dissertation. Wake Forest University, Winston-Salem, North Carolina, USA.

Dunstan, C. E., and B. J. Fox. 1996. The effects of fragmentation and disturbance of rainforest on ground-dwelling small mammals on the Robertson Plateau, New South Wales, Australia. Journal of Biogeography **23**:187–201.

Foti, T. L., and J. M. Guldin. 1994. Multivariate analysis of the ground cover layer, midstory, and overstory of the Ouachita/Ozark National Forests. Pages 61–73 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Gilmore, R. M., and J. E. Gates. 1985. Habitat use by the southern flying squirrel at a hemlock–northern hardwood ecotone. Journal of Wildlife Management **49**:703–710.

Greig-Smith, P. 1983. Quantitative plant ecology. University of California Press, Berkeley, California, USA.

Guldin, J. M., J. B. Baker, and M. G. Shelton. 1994. Pretreatment conditions in mature pine/hardwood stands on south-facing slopes of the Ouachita/Ozark National Forests: midstory and overstory plants. Pages 29–49 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains:

pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Harlow, R. F., and A. T. Doyle. 1990. Food habits of southern flying squirrels (*Glaucomys volans*) collected from Red-cockaded Woodpecker (*Picoides borealis*) colonies in South Carolina. American Midland Naturalist **124**:187–191.

Harlow, R. F., and D. H. Van Lear. 1987. Silvicultural effects on wildlife habitat in the south (an annotated bibliography)—1980–1985. Clemson University Department of Forestry Technical Paper **17**.

Healy, W. M., and R. T. Brooks. 1988. Small mammal abundance in northern hardwood stands in West Virginia. Journal of Wildlife Management **52**:491–496.

Hokkanen, H., T. Törmälä, and H Vuorinen. 1982. Decline of the flying squirrel *Pteromys volans* L. populations in Finland. Biological Conservation **23**:273–284.

Hurley, J. F. 1986. Summary: development, testing, and application of wildlife-habitat models—the manager's viewpoint. Pages 151–153 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Jordan, J. S. 1948. A midsummer study of the southern flying squirrel. Journal of Mammalogy **29**:44–48.

Kluender, R. A., D. A. Lortz, and B. J. Stokes. 1994. Production time, total costs and residual damage at varying harvest intensities. Pages 229–240 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Lacher, T. E., Jr., and M. A. Mares. 1996. Availability of resources and use of space in eastern chipmunks, *Tamias striatus*. Journal of Mammalogy **77**:833–849.

Linzey, D. W., and A. V. Linzey. 1979. Growth and development of the southern flying squirrel (*Glaucomys volans volans*). Journal of Mammalogy **60**:615–620.

Mares, M. A., and T. E. Lacher, Jr. 1987. Social spacing in small mammals: patterns of individual variation. American Zoologist **27**:293–306.

McCoy, E. D. 1982. The application of island-biogeographic theory to forest tracts: problems in the determination of turnover rates. Biological Conservation **22**:217–227.

———. 1983. The application of island-biogeographic theory to patches of habitat: how much land is enough? Biological Conservation **25**:53–61.

Melchiors, M. A. 1983. Wildlife management on Weyerhaeuser Company lands in Oklahoma. Pages 21–36 *in* R. F. Wittwer, editor. Proceedings of a conference: creating good wildlife habitat through forest management and conservation. Oklahoma State University, Stillwater, Oklahoma, USA.

Muul, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. Miscellaneous Publications of the Museum of Zoology, University of Michigan, Ann Arbor, USA.

———. 1974. Geographic variation in the nesting habits of *Glaucomys volans*. Journal of Mammalogy **55**:840–844.

Muul, I., and B. L. Lim. 1978. Comparative morphology, food habits, and ecology of some Malaysian arboreal rodents. Pages 361–368 *in* G. G. Montgomery, editor. The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C., USA.

Nixon, C. M., M. W. McClain, and R. W. Donohoe. 1980. Effects of clear-cutting on gray squirrels. Journal of Wildlife Management **44**:403–412.

Noss, R. F. 1993. Wildlife corridors. Pages 43–68 *in* D. S. Smith and P. C. Hellmund, editors. Ecology of greenways: design and function of linear conservation areas. University of Minnesota Press, Minneapolis, Minnesota, USA.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs **62**:1–135.

Pattanavibool, A., and W. D. Edge. 1996. Single-tree selection silviculture affects cavity resources in mixed deciduous forests in Thailand. Journal of Wildlife Management **60**:67–73.

Perry, R. W. 1995. Effects of alternative harvest methods on mast and fruit production in the Ozark and Ouachita National forests. USDA Forest Service, Southern Forest Experiment Station, Progress Report **FS-SO-4251-3.4**.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs **107**:1–97.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Roff, D. A. 1974*a*. Spatial heterogeneity and the persistence of populations. Oecologia **15**:245–258.

———. 1974*b*. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia **15**:259–275.

———. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia **19**:217–237.

Sawyer, S. L., and R. K. Rose. 1985. Homing in and ecology of the southern flying squirrel *Glaucomys volans* in southeastern Virginia. American Midland Naturalist **113**:238–244.

Siegel, S., and N. J. Castellan, Jr. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.

Simberloff, D. S. 1982. Island biogeographic theory and the design of wildlife refuges. Soviet Journal of Ecology **13**: 215–225.

Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. Science **191**:285–286.

Simberloff, D. S., and L. G. Abele. 1982. Refuge design and island biogeographic theory: effects of fragmentation. American Naturalist **120**:41–50.

Smith, K. G., and D. R. Petit. 1988. Breeding birds and forestry practices in the Ozarks: past, present, and future relationships. Bird Conservation **3**:23–49.

Sollberger, D. E. 1943. Notes on the breeding habits of the eastern flying squirrel (*Glaucomys volans volans*). Journal of Mammalogy **24**:163–173.

Tappe, P. A., R. E. Thill, J. J. Krystofik, and G. A. Heidt. 1994. Small mammal communities of mature pine–hardwood stands in the Ouachita Mountains. Pages 74–81 *in* J. B. Baker, compiler. Proceedings of the symposium on ecosystem management research in the Ouachita Mountains: pretreatment conditions and preliminary findings. USDA Forest Service, Southern Forest Experiment Station, General Technical Report **SO-112**.

Taulman, J. F. 1997. Effect of forest alterations on population dynamics, home range, and habitat selection in the southern flying squirrel, *Glaucomys volans*. Dissertation, University of Arkansas, Fayetteville, Arkansas, USA.

———. 1998. Modification of a hierarchical model of forest disturbance. Environmental Conservation **25**:3–7.

Urban, D. L., R. V. O'Neill, and H. H. Shugart, Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. BioScience **37**:119–127.

Verner, J. 1986. Predicting effects of habitat patchiness and fragmentation–the researcher's viewpoint. Pages 327–329 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors.

Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Weigl, P. D. 1978. Resource overlap, interspecific interactions and the distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*. American Midland Naturalist **100**: 83–96.

Whitehead, C. J. 1980. A qualitative study of mast production in the southern Appalachian region of Georgia, North Carolina, and Tennessee (the tri-state black bear study region). Tennessee Wildlife Resources Agency Technical Report **80-2**.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy **66**:13–21.

Wilson, W. L., and A. D. Johns. 1982. Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in east Kalimantan, Indonesia. Biological Conservation **24**:205–218.

Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy **77**:850–856.

Zimmerman, B. L., and R. O. Bierregaard. 1986. Relevance of the equilibrium theory of biogeography and species–area relations to conservation with a case from Amazonia. Journal of Biogeography **13**:133–143.

APPENDIX

Tree variables used in comparisons among stand-treatment groups of three trees each, combined over 14 (11.3-m radius, 0.04-ha) macroplots per stand (12 plots in areas of the stand subject to harvest, 2 plots in unharvested greenbelts along ephemeral creeks).

Variable codes	Description
Subject to harvest	
MEDPINCT	Density (no./ha) of pine trees 8.9–16.5 cm dbh
LGPINCT	Density (no./ha) of pine trees 16.6–24.1 cm dbh
OVPINCT	Density (no./ha) of pine trees > 24.1 cm dbh
TOTOKHKCT	Density (no./ha) of all oak and hickory trees > 8.9 cm dbh
OVOKHKCT	Density (no./ha) of oak and hickory trees > 24.1 cm dbh
MEDHDWCT	Density (no./ha) of all hardwood trees 8.9–16.5 cm dbh
LGHDWCT	Density (no./ha) of all hardwood trees 16.6–24.1 cm dbh
OVHDWCT	Density (no./ha) of all hardwood trees > 24.1 cm dbh
Greenbelt	
GMEDPINCT	Density (no./ha) of pine trees 8.9–16.5 cm dbh
GLGPINCT	Density (no./ha) of pine trees 16.6–24.1 cm dbh
GOVPINCT	Density (no./ha) of pine trees > 24.1 cm dbh
GTOTOKHKCT	Density (no./ha) of all oak and hickory trees > 8.9 cm dbh
GOVOKHKCT	Density (no./ha) of oak and hickory trees > 24.1 cm dbh
GMEDHDWCT	Density (no./ha) of all hardwood trees 8.9–16.5 cm dbh
GLGHDWCT	Density (no./ha) of all hardwood trees 16.6–24.1 cm dbh
GOVHDWCT	Density (no./ha) of all hardwood trees > 24.1 cm dbh