HOME RANGE, HABITAT SELECTION, AND POPULATION DYNAMICS OF SOUTHERN FLYING SQUIRRELS IN MANAGED FORESTS IN ARKANSAS

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Abstract—After experimental harvests on 18 mature pine-hardwood stands in 6 replicated groups, flying squirrels changed from uniform pre-harvest patterns of nest box use to concentrating on protected greenbelt (GB) areas on harvested stands. Squirrel densities declined on all harvested stands as densities increased on three control stands. Fifty squirrels tracked by radiotelemetry on three control and two harvested stands over three years selected mature pine-hardwood, GB, and hardwood forest habitats for foraging around control study areas; they foraged in GB and adjacent hardwood forests around harvested stands. With boxes closed, squirrels nested in mature pine-hardwood forest on control study areas and GB habitat on harvested stands. Males showed vagility around control areas where mast production was low; female and male ranges were similar, and smaller, around harvested areas where hard mast resources were more abundant.

INTRODUCTION

To effectively consider the needs of wildlife in forest management planning, information on the responses of native species to various disturbance regimes is required (Daily and others 1996, Hurley 1986). Effects of even-aged 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 alternative even-aged and selection harvests (Healy and Brooks 1988, Muul and Lim 1978, Nixon and others 1980, Pattanavibool and Edge 1996, Wilson and Johns 1982), and more information is needed (McCoy 1982, 1983; Simberloff and Abele 1976, 1982; Verner 1986; Zimmerman and Bierregaard 1986).

Flying squirrels (*Glaucomys volans*) are common inhabitants of pine-hardwood forests in the southern United States (Goertz and others 1975). Because *G. volans* glides as a primary means of escape and travel, habitat needs include trees of considerable height and a relatively open midstory (Bendel and Gates 1987). Since flying squirrels do not excavate their own tree cavities, den trees and snags are also critical habitat components (Bendel and Gates 1987, Doby 1984, Gilmore and Gates 1985, Muul 1974, Sawyer and Rose 1985, Weigl 1978). Flying squirrels have rather omnivorous food habits but rely heavily on hard mast throughout the year (Harlow and Doyle 1990), e.g. seeds, hickory nuts, and acorns (Braun 1988, Sawyer and Rose 1985, Sealander and Heidt 1990, Sollberger 1943). The life history requirements of flying squirrels suggest the species' utility as a healthy forest indicator for forest-dependent small mammals.

This study was carried out within a larger interdisciplinary research effort in which a range of experimental harvest techniques were evaluated. First, in order to examine the effect of forest alterations on flying squirrel population dynamics, winter nest box surveys were completed on 21 stands (three replicates of each forest condition), providing data on density, fecundity, reproduction, persistence, and overall robustness. Working hypotheses were that none of the demographic parameters investigated would be different either among pretreatment study area groups prior to harvest or among control and harvested study areas during postharvest years.

Second, in order to examine flying squirrel home range and habitat selection behaviors within a fragmented forest landscape, squirrels were tracked by radiotelemetry during late spring and summer on five study areas. Null hypotheses were that male and female home ranges would be similar in size and shape among the five telemetry study areas and that all habitats would be used for nightly foraging in proportion to availability, without selection. It was also assumed that nesting habitats and tree types would be used as available, without selection.

MATERIALS AND METHODS

Population Dynamics

Study areas consisted of 21 15-ha mature pine-hardwood forest stands in the Ouachita National Forest of Arkansas. In summer 1993, 18 of these stands in six replicated groups of three each were harvested to the following specifications: pine-hardwood single-tree selection (STS), pine STS, pine-hardwood shelterwood (SW), pine SW, pine-hardwood seedtree (ST), and pine ST. Detailed descriptions of these habitat characteristics are provided by Baker (1994). During fall 1992, 30 nest boxes were installed on each of the 21 experimental stands in a grid with 60-meter spacing. Boxes were opened in November and nest box surveys were completed once each month during January - March. Boxes were closed for the summer after the last survey. The total number of squirrels found nesting on a study area during the winter survey was used as the population estimate for that stand. Weight, gender, and reproductive condition were recorded for all squirrels.

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Habitat macroplots were installed on the 21 stands in a stratified random array and data were collected by the Silviculture research group in the larger Ecosystem Management research project (see Taulman 1997). Those data are used in this report.

Home Range and Habitat Selection

Telemetry—From 8 - 15 squirrels were radiocollared on each of a subset of five study areas from the total of 21: three control, a pine-hardwood SW, and a pine-hardwood ST. Squirrels were tracked by researchers on foot at night during May - July, 1994 - 1996. One to three independent locations were obtained on each animal on a study area during a 6 - 8 hour tour. Bi-weekly diurnal telemetry led to the discovery of natural nesting locations. After arriving at a squirrel's location, that site was documented by measuring distance and direction to a tree that had been previously monumented using differentially corrected global positioning system (GPS) fixes. Universal Transverse Mercator (UTM) coordinates for each squirrel location were later computed trigonometrically.

Home range computation—Telemetry data sets were examined through location/area curves; those not showing a leveling of area with increasing number of locations were rejected as insufficient to describe an animal's home range. Those data sets showing a range shift during the data collection period were divided and only one segment was used to create a home range estimate. Home ranges were computed using the kernel method, as described by Silverman (1986), Worton (1995), and Seaman and Powell (1996); employing the computer program KERNELHR (Seaman and Powell 1995). The home range used in this report is "the smallest area containing 95 percent of the utilization distribution" (Seaman and Powell 1996). Core activity areas are areas within a contour that contain locations that are closer than would be expected given uniform use of the home range.

Habitat description—For habitat selection analyses of free-ranging squirrels at the five telemetry study areas, additional macroplots were installed and surveyed in habitats frequented by squirrels adjacent to experimental stands. Habitat variables provided a description of woody forest vegetation that was useful in comparisons within and among study areas (Taulman 1997).

Habitat selection analysis—We followed the methods of Manly and others (1993) in describing habitat selection using the resource selection function, or selection ratio, which represents the proportion of a used resource compared to the proportion of that resource available to the animal. Ninety-five percent Bonferroni confidence intervals were constructed for the mean selection ratio for each habitat type on a study area. Where an interval fell completely below 1.00, significant selection against a habitat was indicated; an interval completely above 1.00 indicated significant selection for that habitat type. Available areas were defined individually for each animal and consisted of 99 percent kernel home ranges computed with the so-called "reference" smoothing parameter. This method used with nonnormal data produces contours with inflated areas. This "buffer zone" around the home range provides a useful estimate of habitats available to an individual based on known patterns of habitat use (fig. 1).

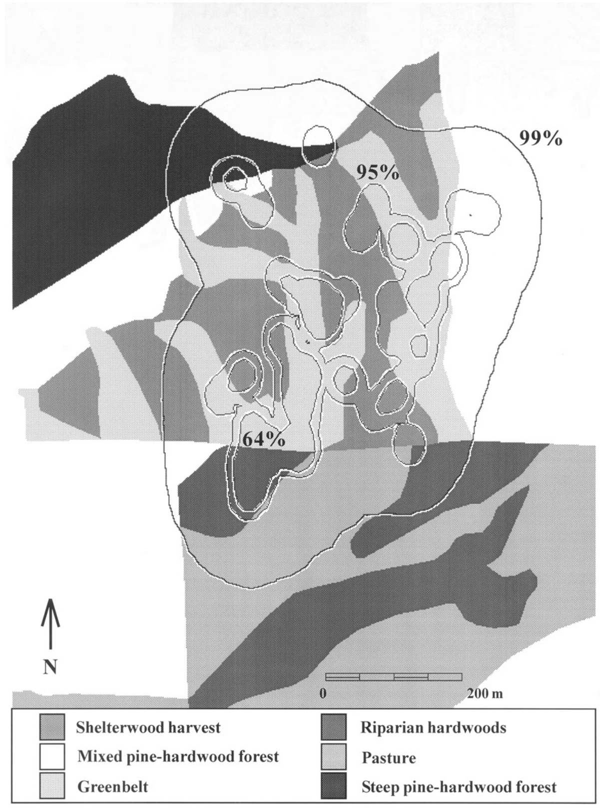

Figure 1—Habitat types around study area 27, pine-hardwood shelterwood harvest. This map shows the three contours computed from a telemetry location data set for one individual on which habitat selection analyses were based. Similar contours were created for each of the 50 squirrels in this study for which telemetry location data sets met criteria described in the text. For habitat selection analyses, the outer contour represents available areas for placement of the home range, and is the 99 percent kernel contour computed with the "reference" smoothing parameter. The 95 percent kernel home range estimate computed with least squares cross validation selection of smoothing parameter and the core activity area contours are also shown. Areas of habitats within the 95 percent contour were considered available for the analysis of habitat use within the home range. The core boundary defines an area within which locations were closer together than would be expected based on uniform use of the home range.

Selection was evaluated for placement of the home range within available habitats and for use of habitats within the home range, Johnson's (1980) second and third order selection, respectively. Habitat selection for location of diurnal nesting sites was also investigated (Taulman 1999).

RESULTS

Population Dynamics

While numbers of adult and immature squirrels captured by treatment group increased on control stands from 1993 - 1995, a sharp decline was observed on harvested stands in 1994 (Taulman and others 1998). A partial rebound was seen on some harvested stands during 1995 and 1996;

most of the recovery seen was due to population surges on a few stands that had adjacent hardwood forest habitats. Squirrels on control stands virtually disappeared in 1996 (Taulman and others 1998); most of the squirrels encountered were recaptures from previous years. The ratio of litters to adult females was variable among years and mirrored the change in numbers of litters produced (Taulman 1997), indicating yearly changes in female fecundity.

Nest box use was uniform on all pre-treatment stands, but per capita box use declined on control stands in 1994, as squirrel numbers rose, without a corresponding increase in boxes used (Taulman and others 1998). However, on harvested stands per capita box use increased to a significant level over that seen on control stands, even as squirrel numbers decreased. Comparing nest boxes used to those available, boxes were used significantly more in nonGB habitat on control stands than nonGB on harvested stands in all post-harvest years (Taulman and others 1998). Also, after harvest boxes were used significantly more in GB habitat on harvested stands than in cutover nonGB habitat. Squirrel density on the set of 21 mature pine-hardwood stands in 1993 was significantly correlated with snag density ($r_s = 0.83$, $p = 0.006$) (Taulman and others 1998).

Five mortalities showed direct or circumstantial evidence of predation. Four of those involved collars and remains retrieved either from seedtree harvest habitat (two screech owls [*Otis asio*] and two of unknown causes), and one occurred in a forest/clearing ecotone (rat snake, *Elaphe obsoletus*).

Home Range and Habitat Selection

Habitats categorized differently on each study area were significantly different for many of the measured descriptive variables (Taulman 1997). Overall, habitat types categorized similarly were not significantly different for the same set of variables. Home range areas of males were significantly different among study areas (Kruskal-Wallis ANOVA $p = 0.03$); those of females were similar (table 1). Ranges were smallest and most equal among males and females on harvested study areas; the large male ranges were associated with control study areas. Comparisons with other telemetry studies on flying squirrels show similarities to range areas on the harvested study areas (Taulman 1997).

Mature pine-hardwood forest, GB, and adjacent hardwood-rich forests were selected more than expected for foraging; the selection of GB for home range placement was signifi-

Table 1—Kernel 95 percent topographic home range areas, with 1 standard error (SE), of males and females by study area[a]

	Study areas									
	MAT P-H									
Squirrel gender	N	I	N	II	N	III	N	P-H SW	N	P-H ST
Male	2	14.3	6	19.09 (5.65)	3	44.0 (15.16)	5	4.79 (0.82)	2	2.76
Female	6	6.43 (1.57)	8	6.09 (1.87)	2	6.04	9	5.57 (0.81)	1	3.38

The Kruskal-Wallis ANOVA results indicated that female range areas did not differ among study areas. The K-W ANOVA indicated a significant difference among male range areas ($p < 0.05$), but the multiple comparisons test show no significant difference for any pair due to small sample size.

[a] Only squirrels for which number of locations was ≥ 30 are included.

Table 2—Mean selection ratios (with standard error and 95 percent confidence intervals) for young (< 15 years old) and immature (15 - 40 years old) pine plantation habitats, mature pine-hardwood forest, mature hardwood forest, and greenbelt habitats, including data from all squirrels (N) for which those habitats were available[a]

	95 percent home range			95 percent C.I.		Locations in range			95 percent C.I.	
Habitat	Mean	SE	N	Lower	Upper	Mean	SE	N	Lower	Upper
Young plantation	0.401	0.054	31	0.290	0.511[b]	0.337	0.065	28	0.203	0.471[b]
Immature plantation	0.395	0.115	14	0.147	0.643[b]	0.282	0.102	12	0.058	0.506[b]
Mature pine-hardwood	1.119	0.078	33	0.959	1.279	1.060	0.038	29	0.982	1.137
Mature hardwood	1.555	0.301	15	0.910	2.200	1.414	0.286	11	0.776	2.052
Greenbelt	1.549	0.181	19	1.168	1.930[c]	1.283	0.147	27	0.981	1.586

[a] Selection ratio means for 95 percent home range represent the percentage of habitats in 95 percent kernel home ranges (used) compared with the percentage of those habitats available in a larger area. Available areas and home ranges were computed individually for each squirrel. Means for locations in range represent the percentage of locations in a habitat type in the home range (used) compared with percent area of that habitat in the home range (available).

[b] Indicates significant selection against a habitat type (95 percent confidence interval below 1.00).

[c] Indicates significant selection for a habitat type (95 percent confidence interval above 1.00).

cant (table 2). Mature pine-hardwood forest was significantly selected for diurnal nesting on control study areas; nests were concentrated in GB habitat on the two harvested stands (Taulman 1999). Maps of core activity areas graphically illustrate habitat use and avoidance patterns at all five study areas (Taulman 1997).

The densities of overstory oaks and hickories can provide an indication of the mast production potential in a habitat (Goodrum and others 1971, Wolff 1996). Overstory oak and hickory densities in habitats on these study areas, and fall mast surveys on experimental stands, showed that control study areas were depauperate in overstory hardwoods and mast production (Taulman 1997). The two harvested study areas had habitats containing high densities of overstory hardwoods within or adjacent to experimental stands.

DISCUSSION

Population declines following harvest have been previously documented for flying squirrels (Hokkanen and others 1982) and other vertebrates (Burgess 1971, Wilson and Johns 1982). The marked declines observed on control stands in 1996, and the significantly lower weights of squirrels in 1996, may indicate a metapopulation response to low mast production in 1994 and 1995 (Taulman 1997). Wolff (1996) found that over 14 years population densities of three rodent species varied in synchrony with hard mast production.

Male vagility in areas with limited food resources may be an evolutionary strategy, increasing survival chances of females and offspring kin in familiar nesting areas through reduced competition. Males on distant forays also increase their own likelihood of encountering new females and producing additional offspring. Female philopatry conserves energy and permits young to learn the locations of nearby feeding sites and refugia.

Contrary to the suggestion of some foresters and landscape ecologists (Urban and others 1987) that clearcut harvests mimic natural disturbance events, clearcut silviculture has produced a pattern in which undisturbed forests are now found within the matrix of a fragmented landscape (DellaSala and others 1995, Moloney and Levin 1996), the reverse of the pattern historically observed under natural disturbance regimes (Agee 1994). To ensure the persistence of native terrestrial forest-dependent wildlife, public forests should be managed from a landscape perspective, preserving areas of mature undisturbed forest, with interconnecting corridors of forest habitat (Bright 1993, Dunstan and Fox 1996).

Pickett and Thompson (1978) have suggested the "minimum dynamic area" method as an approach to managing a fragmented ecosystem for the persistence of given species. This method emphasizes landscape management at a scale that can ensure the protection of "recolonization sources" in order to prevent the isolation of small patches and to reduce the possibility of long-term local extinctions. Henderson and others (1985) found that eastern chipmunks (*Tamias striatus*) inhabiting isolated woodlots amid an "ecologically hostile" agricultural landscape were able to disperse rapidly along brushy fencerows to repopulate wooded areas which had undergone local extinctions.

Results of the present study suggest that the U.S. Forest Service compartment level (approximately 10 - 20 sq km) should be an appropriate scale at which to manage habitat for flying squirrels. Within each management compartment many 15 - 40 ha patches of mature pine-hardwood forest, as well as north-slope hardwood forests, should be maintained along with interconnecting corridors through harvested habitats to other undisturbed areas. Some overstory hardwoods and snags should be retained within harvested areas. Provided adjacent mature pine-hardwood, or hardwood, forests are available, and protected GB areas are retained along ephemeral drainages within a treated stand, harvests as severe as the shelterwood prescription should not adversely affect flying squirrel populations. The seedtree harvest regime, even with retained hardwoods, produces a reduction of forest cover which greatly enhances opportunities for such predators as screech owls. The higher predation risk, together with the diminution of mast and cavity resources created by the seedtree harvest regime, appear to render forests subjected to this prescription unsuitable for the long-term persistence of flying squirrels.

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