Habitat Use by Southern Fox Squirrel in Coastal South Carolina

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Abstract: We monitored 18 southern fox squirrels (*Sciurus niger niger*) by telemetry in coastal South Carolina to determine habitat use in relation to availability of habitat types within observed home-range areas. Fox squirrels used leaf nests primarily, although females preferred to nest in cavities during winter. Nests were concentrated in hardwoods with a preference for oak (*Quercus* spp.) and gum (*Nyssa* spp.) species with >20 cm DBH (diameter breast height). Fox squirrels preferred ($P < 0.01$) hardwood, mixed pine-hardwood, and pine with a hardwood midstory habitat types, and ecotone areas.

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The fox squirrel may be the least studied game species in the southeastern United States. Three subspecies of eastern fox squirrel are currently given special legal protection because of their perceived rarity, which is possibly related to habitat modification (Taylor 1976, Williams and Humphrey 1979, Wood 1983).

Habitat requirements of southern fox squirrel populations are currently undefined. Habitat use studies present fragmented and often inconclusive results. Weigl et al. (1989) described the primary habitat of fox squirrels as open, mature pine-oak forests, especially longleaf pine (*P. palustris*) turkey oak (*Q. laevis*) types, along with some adjacent hardwood and bottomland types and emphasized the importance of old-growth pine as a component in these types. Hilliard (1979) determined that mixed pine-hardwood types were most important to southern fox squirrel, and concluded that "mature" stands were optimal. Use of descriptive terms rather than quantitative measures in assessing fox squirrel habitat has limited the comparability of these findings.

The objective of our study was to describe habitat selection, nest characteristics,

and nesting habitat of a southern fox squirrel population in coastal South Carolina. Funding for this study was provided by the U.S. Forest Service, the South Carolina Wildlife and Marine Resources Department, and the Department of Forestry, Clemson University.

Study Area

We conducted the study on the 1,430-ha Friendfield Plantation, located 2 km west of Georgetown, South Carolina. The area is characterized by flat terrain (maximum elevation 6 m) and stands of longleaf and loblolly pine (*P. taeda*) subdivided by narrow hardwood drains or "runners" and cypress (*Taxodium* spp.) gum swamps. Canaan Creek and its associated drainages (some ephemeral) bisect the area and ultimately flow into the Sampit River. Soil associates are Yemassee-Bladen-Yauhannah (Stuckey et al. 1982).

Methods

Fox squirrels were trapped intermittently between 10 January and 10 December 1984, using Mosby-type box traps baited with shelled corn (Day et al. 1981). Captured animals were anesthetized with Ketamine Hydrochloride (about 25 mg/kg of body weight), fitted with a radio transmitter weighing 38–40 g, marked with 2 numbered ear tags, weighed, sexed, and released the following morning.

Telemetry locations were determined for 18 fox squirrels (10 male, 8 female) for the duration of transmitter battery life (4–7 months). We obtained locations on each animal every 2 hours between sunrise and sunset during 2 days of each week for 1 year. Radio locations were determined by recording 3 or more compass azimuths from permanent reference stations. To reduce the size of our error polygons, we minimized the distance between the animal and the receiver, and used angles between reading sites within 45 and 135 degrees when possible (Springer 1979).

Habitat Types

Habitat types were delineated visually by species composition and structure using aerial photographs (black and white 1:9,600 or high altitude color 1:14,800) and ground reconnaissance. Ten types were identified: pine-dominated, carolina bay, cypress, hardwood runner, mixed runner, medium-density pine, low-density pine, agricultural, old field, and marsh. We defined the overstory component as dominant and co-dominant stems and the midstory as non-dominant stems >2.5 cm DBH; each component was characterized by species, basal area, density, age, DBH, and pine-hardwood composition for each habitat type. We determined the number of sample plots needed in each habitat type from a preliminary sample using an acceptable error of 20% and the variance associated with DBH (Wenger 1984). Characteristics of the overstory and midstory in the more open and uniform pine-dominated, cypress, medium-density pine, and low-density pine types were measured with point sampling (multiple prisms 10F, 5F). Fixed radius or area plots of

0.08 ha or 0.04 ha were used in the hardwood runner and mixed runner types because they often were only 5–10 m wide. Such plots would provide representative samples within the boundaries of these types. A total tally of the overstory and a 6-m fixed width transect (oriented east to west from the type boundary to the center) in the midstory was used to measure the attributes of the carolina bay type (each carolina bay was considered to be 1 plot). No vegetative sampling was conducted in the agricultural and old field types.

Nesting Sites

We located individual nests at dawn and dusk of each telemetry day. Nests were classified as either leaf nests or den trees, and were marked with a numbered metal tag. Tree species, DBH, height, age, and height of nest were recorded for each individual nest and its location was plotted on a cover-type map. Nest type was calculated by sex of squirrel and season. Tree species utilization was examined by habitat type. We used goodness of fit tests (Sokal and Rohlf 1973) to test for preference or avoidance of a habitat type by determining if nest tree species and DBH availability by habitat type differed from expected use. Confidence intervals (90%, Neu et al. 1974) were then calculated for use by DBH class and species group where appropriate (Roscoe and Byars 1971). We determined ecotone use for nesting habitat by measuring the distance from each nest to its nearest habitat boundary.

Home Range and Habitat Use

Locations were determined by reducing the multiple compass azimuths (3 to 5 per location) to 2-bearing locations by hand-plotting all azimuths, determining their geometric center as the animal's location and then recording 2 bearings intersecting at that point. Home-range size was determined using the computer program TELEM (Koeln 1980). Independence of locations was assumed based on 2 hours between locations (Lindstedt and Calder 1981). We used the 95% minimum convex polygon (Michener 1979) to illustrate home-range boundary and area. Annual home range for each squirrel was defined by pooling data among seasons and not necessarily a 12-month monitoring period.

Total home-range area, area within each habitat type, and locations within habitat types were pooled across individual squirrels for analyses. Habitat use was based on the number of locations (active and nesting) within each type present in an individual home-range area. Availability and expected habitat use were determined from the proportion of each type found within an individual home-range area. Comparisons of preference or avoidance were made by season and among all habitat types. The Neu et al. (1974) procedure was modified slightly in that utilization-availability of habitat types was determined for each animal and then pooled across animals to form the representative test statistic. This eliminated the assumption of equal availability of habitat types for all individuals. Alldredge and Ratti (1986) found the Neu et al. (1974) procedure accurate in habitat use analysis when the number of habitats was small and sample size was adequate (>19 animals and 50 locations/animal).

We determined ecotone use by circumscribing a 30-m and 60-m boundary around each habitat type within the annual home range of each squirrel, and measured the total encompassed area using a planimeter. The total home-range area, area within each distance class, and frequency of locations (active and nesting) within each distance class were pooled and the preference/avoidance procedure employed to determine ecotone use by fox squirrel.

Results

Habitat Characteristics and Structure

Low and medium-density pine types were dominated (>98%) by longleaf pine in the overstory and contained few midstory hardwoods (Table 1). In contrast, the pine-dominated type contained a well developed midstory of mast-producing hardwood species (for a comprehensive vegetation analysis of all strata see Edwards 1986).

Nest Site Selection and Habitat Use

Telemetered fox squirrels used leaf nests more often (80%) than den trees (20%). Females occupied den trees more often during the year than males (Table 2). Den trees received relatively little use by males throughout the year with fall and winter being the seasons of greatest use; females exhibited a similar pattern during the summer and fall. In contrast, females used dens primarily during winter and in the initial part of spring. Use of den trees decreased with the approach of spring and subsequently leaf nest use increased.

Radio-collared fox squirrels (male and female) used 75 individual leaf nests; use varied by tree species as follows: oaks - 43% (N = 32), gums - 36% (N = 27),

Table 1. Species composition (%) based on stem density of 7 habitat types found on Friendfield Plantation, Georgetown, South Carolina, 1984.

Habitat[a] type	Species composition			
	Pine	Oak	Gum	Other
CBAY	48[b]/8[c]	13/22	37/65	2/5
CYPRESS	0/0	0/5	7/51	93/44
HRUN	10/0	34/43	40/22	16/35
MRUN	57/0	17/17	23/61	3/22
LDP	99/78	1/20	0/2	0/0
MDP	100/100	0/0	0/0	0/0
PH	82/25	18/63	0/0	0/12

[a]CBAY = carolina bay; LDP = low-density pine; HRUN = hardwood runner; MDP = medium-density pine; MRUN = mixed runner; PH = pine-dominated.
[b]Overstory species composition.
[c]Midstory species composition.

Table 2. Nest locations (%) by type, sex, and season used by fox squirrels on Friendfield Plantation, Georgetown, South Carolina, 1984.

	Nest Locations			
	Male (N = 118)		Female (N = 168)	
Season	Leaf nest	Den	Leaf nest	Den
Spring	93.3	6.7	77.8	22.2
Summer	100.0	0.0	100.0	0.0
Fall	90.9	9.1	91.7	8.3
Winter	90.7	9.3	31.4	68.6
Annual	93.0	7.0	71.0	29.0

pine - 15% (N = 11), and cypress - 7% (N = 5). In contrast, 12 of 13 dens were found in gum and oak species. Structural characteristics of den and leaf nest trees selected by telemetered fox squirrels were similar (Table 3).

Avoidance-preference analysis on DBH showed a preference for larger (>20 cm) trees and an avoidance of smaller (<20 cm) trees in the low-density pine, pine-dominated, and runner types. Similar analysis on tree species indicated a preference for oaks in the pine-dominated and runner types and a preference for both oaks and gums in the low-density pine type.

Spring, fall, and winter nests were used most often in pine-dominated and hardwood runner types (Table 4). Summer nests were most often (>50%) in pine types. Of 87 nest trees examined, 90% (N = 78) were within 60 m of a habitat boundary. The most common types associated with nesting habitat were low-density pine (49%) and medium-density pine (17%).

Fox squirrels preferred ($P < 0.10$) (based on annual home range locations) carolina bay, mixed runner, hardwood runner, and pine-dominated types, and avoided marsh and low-density pine habitat types (Table 4). Seasonal variation in use was found in all types except marsh, agricultural, and old field where avoidance

Table 3. Nest tree characteristics of nests examined on Friendfield Plantation, Georgetown, South Carolina, 1984.

	Nest Type			
	Leaf (N = 75)		Den (N = 12)	
Characteristic	$\bar{x}$	SE	$\bar{x}$	SE
Tree height (m)	20.2	0.55	19.9	1.46
Nest height (m)	12.3	0.46	10.3	1.03
DBH (cm)[a]	40.4	1.31	45.6	3.39
Tree age (years)	60.3	4.47	59.0	8.00

[a]Diameter measured at breast height.

Table 4. Habitat use and percent nest locations by habitat type and season of fox squirrels on Friendfield Plantation, Georgetown, South Carolina, 1984.

	Season									
	Spring		Summer		Fall		Winter		Annual	
Habitat type[a]	Use[b]	%	Use[b]	%	Use[b]	%	Use[b]	%	Use[b]	%
CBAY	P	4.3	P	15.8	N	1.7	N	0.9	P	7.2
MRUN	P	6.9	N	5.8	N	7.3	N	9.7	P	4.9
CYPRESS	N	6.0	A	1.9	C	0.0	N	7.6	A	3.8
HRUN	P	30.6	N	13.5	P	43.1	P	43.7	P	33.0
PH	P	35.7	N	0.9	P	38.5	P	26.3	P	24.2
LDP	A	16.5	A	36.7	A	1.7	A	1.4	A	14.6
MDP	A	0.0	P	25.4	C	7.7	P	10.4	N	12.3
MARSH	A	0.0	A	0.0	C	0.0	A	0.0	A	0.0
AG	A	0.0	A	0.0	A	0.0	A	0.0	A	0.0
OLDFLD	A	0.0	A	0.0	A	0.0	A	0.0	A	0.0

[a]CBAY = carolina bay; MRUN = mixed runner; HRUN = hardwood runner; PH = pine dominated; LDP = low-density pine; MDP = medium-density pine; AG = agricultural; OLDFLD = old field.
[b] = preference; A = avoidance; N = proportional use; C = insufficient locations to perform test.

was indicated over all seasons (Table 4). Fox squirrel habitat use showed a preference ($P < 0.10$) for ecotone (30-m and 60-m) boundaries based on locations (both nesting and active) within annual home range.

Discussion

Sanderson (1966) stressed that the size and shape of a home range area in itself may be of little or no ecological consequence; more important is why an area is selected and how it is used by an animal. Considering our limited knowledge of southern fox squirrel ecology, an appropriate initial approach for assessing their habitat requirements is to examine use of habitat types present within home ranges, termed third-order selection by Johnson (1980). Fox squirrels preferred carolina bay, mixed runner, pine-dominated, and hardwood runner habitat types. These types contained both pine and hardwoods, especially oaks and gums, with either dominating or in a mixed composition. Non-pine types (including pine-dominated) generally were preferred during all seasons but the use of the carolina bay and mixed runner types, which contained the fewest oaks of the preferred types, declined from preferred to proportional in fall and winter. Fox squirrels preferred ecotones, especially along border areas in pine-dominated, medium-density pine, and low-density pine types; fox squirrels only minimally used the central portion of large blocks. This concentrated use of "edge" in the pine types suggests the importance of pine-hardwood associations.

Hilliard (1979) concluded the preferred habitat of fox squirrel was loblolly pine-oak and reported only incidental use of bottomland hardwoods. His conclusion was based on the percent of locations within each type and not on availability

of types. Reanalysis of Hilliard's data, using availability of types, indicates: (1) a preference for loblolly pine-oak and bottomland hardwood types; (2) a proportional use of loblolly pine-pole (pole stage) type; and (3) an avoidance of the longleaf pine-oak type. Both the loblolly pine-oak and bottomland hardwood types were found in close association throughout Hilliard's study area. The loblolly pine-oak type is different from the pine types (medium-density and low-density) we described. Hilliard's pine-oak type contained a mature pine overstory with small clumps of mast producing oaks in the midstory. Hilliard made no mention of ecotone use, but did state that 7% ($N = 113$) of his telemetry locations were discarded because they fell on habitat boundaries. Weigl et al. (1989) described preferred habitat of fox squirrel, based on percent of locations, as longleaf pine-oak and, to a lesser degree, "edge" types. He also stated that during summer (June–September inclusive) and winter (14 Jan–14 Mar), use of bottomland and "edge" types was greater than expected based on availability. In contrast to the pine types found on Friendfield, the longleaf pine-oak types described by Weigl et al. (1989) contained an oak component but similarly were associated with more mesic hardwood and wetland types.

Preferred nesting habitat was characterized by hardwood runner and pine-dominated types during the spring, fall, and winter. During the summer, fox squirrels preferred medium-density and low-density pine types. Within the low-density pine type, larger stems (>20 cm DBH) and oak and gum species were preferred. Ecotone use also was indicated by nest placement, with 90% of the nests occurring within 60 m of a habitat boundary. In contrast, Moore (1957), Hilliard (1979), and Weigl et al. (1989) concluded preferred nesting habitats were pine-oak communities including mature stands of longleaf pine-turkey oak, loblolly pine-oak (oak comprising > 30% of basal area), and pine-oak with little understory and a low diversity index.

Both the higher incidence of den trees and the use of hardwood species as nesting sites further suggests the fox squirrel's preference for a mixture of hardwood-pine types. Of the nests occurring in the low-density pine type, a preference was shown for sites in oak and gum species. The higher use of den trees as compared to Moore (1957), Hilliard (1979), and Kantola (1986) may be related to increased availability of suitable natural cavities. Hilliard (1979) found the distribution of leaf nests in pine and oak to be 81% and 16%, respectively. These were used proportionately in terms of availability. Gum species, found in only 1 habitat type comprising < 7% of his study area, received no use. Kantola (1986) located 88 leaf nests distributed primarily (82%) in oaks and less often (18%) in pine. Initiation of cavities in hardwoods can be caused by fire, suppression, disease, or other forces (Carey 1983). Prescribed fire, which is conducted annually on Friendfield, and suppression may be 2 of the forces acting to produce the numerous cavity trees found along the hardwood drains.

The disparity we found between preferred use of hardwood and mixed-pine hardwood types and preferred habitat as reported by previous researchers may be explained by the fact that the study areas of Moore (1957), Hilliard (1979), and Weigl et al. (1989) were more contiguous and offered less interspersion among habitat types than on our area. The high degree of interspersion found here is

attributable to both the narrow drainages that bisect the pine types and the elongated configuration of the pine-dominated type. The "virgin" longleaf pine-oak communities in which fox squirrel are presumed to have evolved were described by Moore (1957) as containing great longleaf pines towering over sporadic clumps of 12–15 m turkey oak. Realizing that the previously mentioned study areas contain no stands of this magnitude, we suggest that the differences in use of the pine-oak types recorded by Hilliard (1979) and Weigl et al. (1989) as compared to those pine types (except pine-dominated) we found may be related to a lack of a hardwood component on our area. We believe the narrow hardwood runner and carolina bay types found on Friendfield may be analogous to the sporadic clumps of turkey oak mentioned by Moore (1957). The demonstrated preference for ecotones in the low-density pine and medium-density pine types suggests that the association of hardwood and pine habitat types and their juxtaposition are important considerations to the ecology of the southern fox squirrel.

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