HABITAT USE OF FOX SQUIRRELS IN SOUTHWESTERN GEORGIA

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Abstract: Fox squirrel (*Sciurus niger*) populations are declining in the southeastern United States, presumably as a function of habitat loss. Because the ecology of southeastern subspecies of fox squirrels differs greatly from their well-studied midwestern relatives, habitat studies of midwestern fox squirrels are of limited use for managing southeastern subspecies. Therefore, we initiated a radiotelemetry study to evaluate habitat use of fox squirrels ($n = 101$) in southwestern Georgia, USA. Our results indicated that sex of fox squirrels and season did not affect habitat use and that fox squirrels did not display habitat selection within the home range. However, when selecting a home range, fox squirrels preferred mature pine (*Pinus* spp.) and mixed pine–hardwood forests and avoided hardwood forests. To provide fox squirrel habitat in southeastern pine landscapes, management strategies should maintain mixtures of mature longleaf pine (*P. palustris*) and mature mixed pine–hardwood forests.

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Key words: Euclidean distance, fox squirrel, Georgia, habitat selection, hardwood, longleaf pine, *Pinus palustris*, *Sciurus niger*.

Fox squirrel populations in the midwestern United States have received much research attention (Weigl et al. 1989, Loeb and Moncrief 1993), and midwestern populations appear to be increasing in number and distribution (Swihart and Nupp 1998). However, southeastern populations have received considerably less research interest (Weigl et al. 1989, Loeb and Moncrief 1993) and experienced significant declines in number and geographic distribution (Loeb and Lennartz 1989, Weigl et al. 1989, Loeb and Moncrief 1993). Special conservation concern has been allotted to 3 subspecies (Delmarva fox squirrel [*S. n. cinereus*], big cypress fox squirrel [*S. n. avicennia*], and Sherman's fox squirrel [*S. n. shermani*]) of the 8 recognized subspecies of fox squirrels (Loeb and Moncrief 1993, Whitaker and Hamilton 1998). Big cypress and Sherman's fox squirrels are found only in the southeastern United States.

The decrease in southeastern fox squirrel populations has been attributed to the loss of mature pine–oak (*Quercus* spp.) forests and fragmentation of remaining patches (Loeb and Lennartz 1989, Weigl et al. 1989, Loeb and Moncrief 1993). One such forest important for fox squirrels is the longleaf pine forest of the southeastern coastal plain (Kantola and Humphrey 1990, Whitaker and Hamilton 1998), which now occupies <3% of its historical range (Ware et al. 1993). The continued decrease and fragmentation of longleaf pine forests may negatively affect fox squirrels (Simberloff 1993).

Despite the decline of southeastern fox squirrel populations, habitat-selection data are rare in these populations (Edwards et al. 1989, Weigl et al. 1989). Therefore, our objectives were to (1) assess fox squirrel habitat selection at 2 spatial scales within a longleaf pine-dominated forest, and (2) test for season- and sex-specific effects on habitat selection.

STUDY AREA

We conducted our study about 20 km south of Newton, Georgia, USA, at Ichauway, the research site of the Joseph W. Jones Ecological Research Center. The 12,000-ha research site relied heavily on prescribed fire to maintain a 2-layered forest dominated by longleaf pine in the overstory, herbaceous vegetation in the understory, and an open midstory. Scattered individual hardwoods and hardwood patches existed within the longleaf matrix comprised mostly of oak species. Additionally, management for the northern bobwhite (*Colinus virginianus*) resulted in a diverse habitat mosaic of interspersed food plots and small weedy openings within the forested matrix. Rainfall averaged 132 cm/year, and average daily temperature was 11 °C during winter and 27 °C during summer. We delineated a 4,200-ha section of Ichauway for our study area.

METHODS

Animal Capture and Radiotelemetry

We used wooden box traps (63 cm × 17.5 cm × 22.2 cm; Baumgartner 1940) baited with dried corn to trap squirrels periodically during January 1998–November 1999 (i.e., we had no defined

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trapping seasons). We transferred captured squirrels into a nylon mesh bag, where we sedated them using either inhalation of methoxyflorane or intramuscular injection of ketamine hydrocloride (10 mg/kg). While squirrels were sedated, we determined sex, collected standard measurements, affixed ear tags (Monel 1005-3, National Band and Tag Company, Newport, Kentucky, USA), and determined whether squirrels were juveniles or adults (i.e., sexually mature) following Weigl et al. (1989). Finally, we attached a 25-g radiotransmitter collar (Telemetry Solutions, Walnut Creek, California, USA) to all captured adults that weighed >850 g (transmitter weight ≤3% of squirrel body mass). We maintained sample sizes of radiomarked squirrels at ≥30 animals throughout the study. All squirrels were released at the capture site after they completely recovered from anesthesia. We located radiomarked squirrels ≥2 times/week using triangulation (White and Garrott 1990) from fixed reference points.

Data Analysis

We partitioned squirrel radio locations into composite and seasonal datasets. Composite data included all locations for each squirrel. We based season partitioning on availability of fox squirrel food items (Weigl et al. 1989). We defined March through June as a period of new plant growth and tree bud availability. We defined July through October as the late growing season and period of longleaf pine seed availability because longleaf pine seed is an important food item to fox squirrels (Weigl et al. 1989, Loeb and Moncrief 1993); longleaf pine seed production is at its peak from August through September (Wahlenberg 1946). Finally, we defined November through February as the period of oak mast availability because hard mast crops are important food items during fall and winter (Weigl et al. 1989).

We used a Geographic Information System (GIS) with 8 habitat types: agriculture/food plot, shrub/scrub (i.e., overstory dominated by shrubs), hardwood, pine regeneration (≤10-cm dbh), mature pine (>10-cm dbh), mixed pine–hardwood (30–70% hardwood), wetlands (forested and herbaceous), and barren land/urban. The habitat types were originally delineated from 1992, 1:12000 aerial photography, but were annually updated in ARC/INFO (Environmental Systems Research Institute 1997). Our habitat map was intersected with location-point files and home-range polygons using ARC/INFO (Environmental Systems Research Institute 1997).

To test for habitat selection, we used a Euclidean distance-based approach, which compares distances between animal locations and each habitat to expected distances (Conner and Plowman 2001, Conner et al. 2003). We included sex and seasonal effects on habitat selection.

For the following analyses, we used Johnson's (1980) second (selection of home range) and third (selection within home range) orders of habitat selection. We performed all statistical analyses using SAS software (SAS Institute 2000), and we considered statistical significance at $\alpha = 0.05$.

Selection of Home Range.—We analyzed composite and seasonal data separately for each order of selection. We created individual fox squirrel home ranges for the composite data and each of the 5 seasons (Mar–Jun 1998, Jul–Oct 1998, Nov 1998–Feb 1999, Mar–Jun 1999, Jul–Oct 1999). We calculated seasonal home ranges for squirrels with ≥30 locations/season and composite home ranges for animals with ≥40 locations that were tracked ≥6 months (Weigl et al. 1989, Schmid et al. 2003). We used CALHOME (Kie et al. 1994) to estimate home ranges using the 100% minimum convex polygon method (Mohr 1947).

We generated random locations ($\bar{x}$ = 614.23, SE = 6.72) for composite data within each home range and determined an average distance (m) from random locations to each habitat type using the ARC/INFO DISTANCE command (Environmental Systems Research Institute 1997). We then generated random locations (n = 29,358) throughout the study area and determined an average distance from random locations to each habitat type. For each fox squirrel, we created 8 distance ratios (1 ratio for each habitat type), which were the average distances from random locations within home range divided by the average distances from random locations throughout the study area (Conner and Plowman 2001, Conner et al. 2003).

Using a multivariate analysis of variance (MANOVA), we tested the hypothesis that overall habitat selection did not differ from random with sex as a main effect and animal as the experimental unit. If the mean of the 8 ratios differed from a vector of 1 (MANOVA was significant), we used univariate t-tests on each habitat type to determine which types were used disproportionately. Habitat types with a mean ratio significantly <1 were preferred, whereas a mean significantly >1 indicated avoidance (Conner and Plowman 2001, Conner et al. 2003). To rank habitat types, we performed pairwise mean comparisons using univariate t-tests.

Table 1. Habitat type distance ratios for second-order selection using composite home ranges for fox squirrels at Ichauway, Georgia, USA, 1998–1999.

Habitat type	Mean[a,b]	SE	t_{65}[c]	P
Mature pine	0.620	0.086	–4.41	≤0.001
Mixed pine–hardwood	0.627	0.111	–3.37	0.001
Shrub/scrub	1.254	0.078	3.24	0.002
Forested and herbaceous wetlands	1.356	0.075	4.76	≤0.001
Hardwood	1.366	0.180	2.03	0.046
Agriculture/food plot	1.430	0.159	2.70	0.009
Pine regeneration	1.447	0.098	4.54	≤0.001
Barren land/urban	1.667	0.054	12.41	≤0.001

[a] Average distance from random locations within home ranges divided by average distance from random locations throughout study area.
[b] Significant mean ratios <1 indicate habitat preference, >1 habitat avoidance.
[c] Univariate *t*-tests testing ratio difference from a value of 1.

For the seasonal analysis, we used the same methods but used seasonal home ranges and treated season as a repeated measure. We tested the hypothesis that season and season × sex interaction did not affect Johnson's (1980) second order of habitat selection.

Selection within Home Range.—For composite data, we used all squirrel locations within a home range to calculate an average distance from animal location to each habitat type. We again used an average distance from random locations to each habitat type within a home range. Then for each fox squirrel, we calculated 8 distance ratios (1 ratio for each habitat type), which were the average distances from animal locations divided by the average random distances within the home range (Conner and Plowman 2001, Conner et al. 2003).

We then used a MANOVA to test the hypothesis that overall habitat selection did not differ from random with sex as a main effect and animal as the experimental unit. We again used univariate *t*-tests to determine which habitat types were used disproportionately and pairwise mean comparisons to rank habitats if the MANOVA was significant.

For the seasonal analysis, we used the same methods but used seasonal home ranges and treated season as a repeated measure. We tested the hypothesis that season and season × sex interaction did not affect Johnson's (1980) third order of habitat selection.

RESULTS

We trapped 128 individual fox squirrels during 26,867 trap-nights. Of these, we monitored 101 fox squirrels and used 66 (41 F, 25 M) individuals for composite analyses and 62 (41 F, 21 M) for seasonal analyses. Within the study area, season ($F_{4,52}$ = 1.09, P = 0.373) and the season × sex interaction ($F_{4,52}$ = 0.50, P = 0.739) did not affect habitat selection for the home range. Using composite analysis, fox squirrels selected ($F_{8,57}$ = 51.22, $P \leq$ 0.001) habitats when choosing the home range, but sex ($F_{8,57}$ = 0.70, P = 0.687) did not affect habitat selection. Fox squirrels preferred mature pine forests and mixed pine–hardwood forests but avoided shrub/scrub, wetlands, hardwood forest, agriculture, pine regeneration, and barren land/urban (Table 1). We found no difference between the 2 preferred habitat types (mature pine and mixed pine–hardwood), but these were more preferred than remaining habitat types (Table 2).

Within the home range, season ($F_{4,52}$ = 0.45, P = 0.773) and the season × sex interaction ($F_{4,52}$ =

Table 2. A ranking matrix composed of *P*-values from pairwise univariate *t*-tests (df = 65) between habitat type distance ratios for second-order selection[a] using composite home ranges for fox squirrels at Ichauway, Georgia, USA, 1998–1999.[b]

	Mixed[c]	Shrub	Wetland	Hardwood	Agr[d]	Pine Regen[e]	Barren
Mature pine	0.964	≤0.001	≤0.001	0.001	≤0.001	≤0.001	≤0.001
Mixed[c]		≤0.001	≤0.001	0.002	≤0.001	≤0.001	≤0.001
Shrub			0.280	0.595	0.298	0.118	≤0.001
Wetland				0.961	0.605	0.298	0.002
Hardwood					0.821	0.710	0.099
Agr[d]						0.876	0.171
Pine Regen[e]							0.075

[a] Average distances from random locations within home range divided by the average distances from random locations throughout the study area.
[b] *P*-values are from *t*-tests of the null hypothesis that the distance to the column habitat minus the distance to the row habitat equals zero. All cells with significant *P*-values indicate row habitat preferred over column habitat.
[c] Mixed pine–hardwood.
[d] Agriculture/food plot.
[e] Pine regeneration.

0.62, P = 0.650) did not affect seasonal habitat selection. Also within home range, fox squirrels did not select ($F_{8,57}$ = 1.32, P = 0.252) habitats, and we found no sex ($F_{8,57}$ = 1.30, P = 0.262) effect on habitat selection within composite home ranges.

DISCUSSION

Fox squirrels selected mature pine and mixed pine–hardwood habitats when selecting a home range. Similarly, important habitats for southeastern fox squirrels are mature longleaf pine–oak forests (Weigl et al. 1989, Kantola and Humphrey 1990), mature mixed pine–oak forests (Edwards et al. 1989, Loeb and Lennartz 1989, Kantola and Humphrey 1990, Loeb and Moncrief 1993), and pine–oak ecotones (Edwards et al. 1989, Weigl et al. 1989, Kantola and Humphrey 1990, Loeb and Moncrief 1993). Hard mast (Loeb and Lennartz 1989, Weigl et al. 1989, Kantola and Humphrey 1990, Whitaker and Hamilton 1998), pine seeds, fungi, and vegetative plant parts (Loeb and Lennartz 1989, Weigl et al. 1989) are important food items for fox squirrels in the southeastern United States. These food supplies can be obtained within open mature pine forests and mixed pine–hardwood forests; thus, food availability perhaps explains the preference for these habitats (Weigl et al. 1989, Kantola and Humphrey 1990).

During our study, mature pine and mixed pine–hardwood habitats were of similar importance to fox squirrels. However, isolated pine forests without imbedded or adjacent hardwoods may not provide year-round habitat requirements. A tree-level analysis of our same study population indicated that fox squirrels preferred hardwood trees for daytime refugia (Conner and Godbois 2003). However, in our study and others (Whitaker and Hamilton 1998, Conner et al. 1999), fox squirrels avoided hardwood habitats. Hardwood encroachment with accelerated canopy closure allows gray squirrel (*Sciurus carolinensis*; fox squirrel competitor) immigration (Tappe and Guynn 1998, Whitaker and Hamilton 1998).

The arrangement and juxtaposition of mature longleaf pine and hardwood patches and pine–hardwood ecotones are important for southeastern fox squirrels (Loeb and Lennartz 1989, Tappe and Guynn 1998). During our study, fox squirrels did not select habitat patches within their home range. We suggest that the large body size and mobility of southeastern fox squirrels (Whitaker and Hamilton 1998) permitted individuals to select home ranges that contained preferred habitat components in a suitable extent and juxtaposition. Further research is needed to determine the amount of hardwoods needed in mature pine forests and the spatial arrangement and configuration of habitat patches at home-range and landscape levels to optimize habitat quality for fox squirrels.

Habitat selection by fox squirrels did not vary between sexes or among seasons. Because male fox squirrels tend to have larger home ranges than females (Weigl et al. 1989, Conner 2000), we could logically predict less-pronounced habitat selection in males. However, this was not observed in our study because both sexes selected similar habitats. A lack of sexual dimorphism between males and females likely contributed to similar habitat selection of males and females. Because mixed pine–hardwood forests and individual hardwood trees tended to exist as patches within the mature pine matrix on our study area, we suggest that juxtaposition of preferred habitats may have led to the observed similarity of habitat selection among seasons.

MANAGEMENT IMPLICATIONS

Fox squirrel populations in the southeastern United States are declining, and preferred habitats are decreasing and being replaced by industrial pine forests (Weigl et al. 1989, Whitaker and Hamilton 1998), agriculture, and fire-suppressed hardwood forests. To encourage fox squirrel habitat, our research suggests that management strategies should provide a matrix of mature longleaf pine–hardwood habitats. Such management strategies should include the use of prescribed fire, which aids in the management of mature longleaf pine forests (Ware et al. 1993). Prescribed fire will also prevent excessive hardwood encroachment and gradual conversion of fox squirrel habitat into gray squirrel habitat (Conner et al. 1999).

If timber harvest is to occur, uneven-aged forest management strategies can be supplemented with a prescribed fire program to promote pine dominance while retaining a hardwood component. Such management will permit mature pine and pine–hardwood forests to persist on the landscape without creating areas of low habitat suitability such as would result following a clearcut under even-aged forest management. Individual mature hardwood trees and small hardwood patches within the mature pine matrix should be retained to provide seasonally important foods (Weigl et al. 1989) while maintaining refuge and nesting sites (Conner and Godbois 2003).

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