Fox Squirrel and Gray Squirrel Associations within Minimally Disturbed Longleaf Pine Forests

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Abstract: Fox squirrels *(Sciurus niger)* are an important species in longleaf pine *(Pinus palustris)* forests. We estimated fox squirrel density within 6 minimally disturbed longleaf pine strands, examined association between fox and gray squirrels *(S. carolinensis),* and measured habitat variables at fox and gray squirrel capture sites. Fox squirrel density estimates ranged from 12–19 squirrels/km^2 among study areas. Fox squirrel capture sites had higher pine basal area, higher total basal area, higher herbaceous groundcover, and lower woody groundcover than other sites. Gray squirrel capture sites had higher hardwood, oak, and total basal areas; lower pine basal area, higher woody groundcover, and less herbaceous groundcover than other sites. A strong negative association between fox and gray squirrel capture sites appeared related to species-specific habitat preferences. Fox squirrel capture sites had higher pine and lower hardwood basal areas than gray squirrel capture sites. Further, herbaceous groundcover, especially wiregrass *(Aristida stricta),* dominated fox squirrel capture sites, whereas woody groundcover dominated gray squirrel capture sites. Logistic regression models indicated that pine basal area and herbaceous groundcover were positively related to probability of fox squirrel capture whereas fern groundcover was negatively related to the possibility of fox squirrel capture. Oak basal area and total basal area were positively related to probability of gray squirrel capture whereas herbaceous groundcover was negatively related to possibility of gray squirrel capture. Oak basal area, total basal area, and herbaceous groundcover best discriminated between fox and gray squirrel capture sites. Prescribed fire retards hardwood enroachment, increases herbaceous groundcover, and thus may be critical to maintaining fox squirrel habitat.

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During the past 100 years, southeastern fox squirrels have declined in number and distribution. This decline was likely driven by habitat loss and fragmentation of

1. Deceased.

mature pine-hardwood forests (Loeb and Lennartz 1989, Weigl et al. 1989). Fox squirrels preferred open pine-hardwood forests and pine-hardwood ecotones (Taylor 1973, Edwards et al. 1989, Weigl et al. 1989, Kantola and Humphrey 1990). Weigl et al. (1989) emphasized the importance of longleaf pine-turkey oak *(Quercus laevis)* forests as fox squirrel habitat. Unfortunately, <3% of the former longleaf pine range is currently occupied by longleaf forests (Ware et al. 1993).

Fox squirrels are an important component of longleaf pine forests, and continued longleaf pine reduction and fragmentation make fox squirrels of particular management concern (Simberloff 1993). Because longleaf pine forests are rare and highly fragmented, baseline data from unexploited fox squirrel populations are needed from minimally disturbed longleaf pine stands. Such data are valuable for quantifying natural variability in abundance and identifying habitat needs of fox squirrels. Therefore, our objectives were to use capture-recapture methodologies to estimate densities of unexploited fox squirrels in minimally impacted, fire-maintained longleaf pine stands. We also evaluated interspecific association between fox and gray squirrels and related captures of each species to habitat variables at the capture site.

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Methods

Study Area

The study took place on Ichauway, the former quail-hunting plantation of Robert W. Woodruff and current research site of the Joseph W. Jones Ecological Research Center. Ichauway is located in Baker County, Georgia, approximately 20 km south of Newton, Georgia. Ichauway relies heavily on prescribed fire to maintain a 2-layered forest dominated by longleaf pine in the overstory and herbaceous vegetation on the understory. Scattered individual hardwoods and hardwood clumps exist within the longleaf matrix, and these hardwoods provide valuable mast for wildlife.

Within Ichauway, we chose 6 1.21-km^2 sites for study. To ensure independence among research sites, we maintained >1 km between sampled areas. We specifically selected areas that were dominated by mature (i.e., approximately 70-year-old) longleaf pines and that had minimal disturbance from timber harvest and agricultural activities. All study areas were prescribe-burned during the previous winter or early spring.

Squirrel Capture and Processing

We captured squirrels in wooden box traps, baited with shelled corn (Baumgartner 1940). We placed traps in a 12-by-12 grid with 100 m between traps, thus each grid occupied 1.21 km^2. Following a 2-week pre-baiting period, we trapped squirrels in each grid for 4 7-day periods. The first through third periods were each separated by a 7-day non-trapping period to allow squirrels to "mix" within each site. The last period was not temporally separated from the third trapping period. Therefore, the third and fourth trapping period could be considered as 1 14-day trapping interval.

Captured squirrels were measured and uniquely marked using ear-tags, hair dye, and toe clipping. Sex and relative age (i. e, juvenile or adult) were recorded for each captured animal.

Density Estimation

We used a Z-test within CAPTURE (Otis et al. 1978) to evaluate closure of each grid following 7, 14, 21, and 28 days of trapping. After we determined the maximum number of trapping intervals that maintained statistical closure, we separated the number of trapping occasions into 2 periods—an initial capture period and a recapture period—and estimated population size using Chapman's modification of the Lincoln-Peterson estimator (Menkens and Anderson 1988). Ongoing radio telemetry studies of Ichauway fox squirrels indicated that male fox squirrel home ranges averaged 20 ha (L. M. Conner, unpubl.). Therefore, we placed a 250-m buffer, approximately the radius of a 20-ha circular home range, around each sample grid to represent the population of fox squirrel residing in a 2.56-km^2 area. We also calculated naive density estimates by assuming the total sample area was equal to the area of the trapping rid (i. e., 1.21 km^2).

Species Association

Upon cessation of trapping, each trap station was classified as having captured no squirrels, fox squirrels only, gray squirrels only, or both fox and gray squirrels. We used a 2×2 contingency table and a chi-square test to determine if species co-occurrence differed from expectation. We evaluated species association between gray squirrels and fox squirrels using Jaccard's index (Ludwig and Reynolds 1988).

Habitat Assessment

We measured habitat variables at each trap station (144 traps/grid, 864 total plots). We estimated percent groundcover using a 1 m^2 grid with 25 grid-line intersections. We placed grids at plot center (approximately 1 m from the trap) and 10 m from plot center in each cardinal direction. We recorded plant species that were located immediately underneath each grid-line intersection. We calculated percent groundcover, by species, at each trap site. We measured species-specific basal area at each trap site with a 10-factor prism.

To simplify analyses and to focus analyses on habitat structure, we pooled habitat measurements into structural groups. We calculated basal area for 4 classes: pine, hardwood, oak, and total basal area. We also calculated percentage groundcover for 9 vegetation classes: wiregrass, other grasses, forbs, vines, ferns, course woody debris, woody plants, total herbaceous cover (i. e., forbs, grasses, and ferns), and total live vegetation (i. e., all cover other than debris) (Table 1).

Table 1. Habitat variables measured within 6 trapping grids (864 sample sites) placed in minimally impacted longleaf pine stands, Joseph W. Jones Ecological Research Center, southwest Georgia, 1993.

Variables	Description
PBA	Pine basal area (m^2/ha)
HWDBA	Hardwood basal area (m^2/ha)
OBA	Oak basal area (m^2/ha)
TOTBA	Total basal area (m^2/ha)
WGGC	Wire grass groundcover (%)
GGC	*Grass groundcover, excluding wire grass (%)*
FOGC	Forb groundcover (%)
VGC	Vine groundcover (%)
FEGC	fern groundcover (%)
WGC	Woody groundcover (%)
HGC	Herbaceous groundcover (%),WGGC + GGC + FOGC + FEGC
CWGC	Coarse woody debris groundcover (%)
TOTGC	Total vegetation groundcover (%)

We compared habitat variables between fox squirrel capture sites and other trap sites, between gray squirrel capture sites and other trap sites, and between fox and gray squirrel sites using Wilcoxon rank sum tests (Zar 1996). We also used stepwise logistic regression (Tabachnick and Fidell 1996) to determine relationships of habitat variables in multivariate space. The first model predicted fox squirrel capture probability as a function of habitat variables at trap sites. The binary response variable for this model was fox squirrel capture or no fox squirrel capture. The second model was similar to the first, but this model predicted gray squirrel capture probability as a function of habitat variables. The last model was used to predict fox or gray squirrel capture as a function of habitat at capture sites. The binary response variable for this analysis was fox squirrel or gray squirrel capture. We evaluated all logistic regression models using a jackknife procedure with adjusted prior probabilities (i. e., before validation, we adjusted prior probabilities to reflect capture probabilities based solely on observed capture rates) (SAS Inst. 1989).

Results

Captures

We trapped squirrels from 13 May–28 June 1993. During 28 trapping occasions (24,192 trap nights), we captured 241 (90 adult and 26 juvenile M; 87 adult and 38 juvenile F) fox squirrels 464 times and 44 (15 adult and 2 juvenile M; 16 adult and 11 juvenile F) gray squirrels 82 times. We captured too few gray squirrels to warrant population estimates.

Fox Squirrel Density Estimates

None of the sampled fox squirrel populations were closed after 28 days of trapping ($P<0.05$), and the closure assumption was violated ($P<0.05$) on 3 study sites

Table 2. Fox squirrel density estimates and capture probabilities in longleaf pine forest sites, Joseph W. Jones Ecological Research Center, southwest Georgia, 1993.

Site No.	Density[a]		Naive Density[b]		P (Capture)[c]
1	18	(17–20)[d]	33	(30–35)	0.78
2	16	(14–18)	29	(26–33)	0.80
3	17	(14–20)	30	(24–35)	0.71
4	16	(11–21)	28	(19–37)	0.47
5	12	(9–15)	22	(17–26)	0.43
6	19	(12–26)	34	(22–46)	0.50

a. Fox squirrels / km^2 assuming a 2.56 km^2 area of effect.

b. Fox squirrels / km^2 assuming area of effect = trapping grid size (i.e., 1.21 km^2).

c. Proportion of marked animals in the second capture interval.

d. Values in parentheses represent 95% confidence intervals.

after 21 days of trapping. However, all sampled populations appeared closed (P>0.72, all cases) during the first 14 days of trapping.

We divided the first 14 trapping occasions into 2 7-day periods and pooled capture information to increase within period capture probabilities. Thus, we created 1 capture period and 1 period in which marked animals were available for recapture.

Fox squirrel density ranged from 12 squirrels/km^2 (95% CI=9–15 squirrels/km^2 to 19 squirrels/km2 (95% CI=12–26 squirrels/km^2). Naive density estimates, assuming all captured animals resided entirely within the 1.21 km^2 trapping grid, ranged from 21 squirrels/km^2 (95% CI=17–26 squirrels/km^2) to 34 squirrels/km^2 (95% CI=22–46 squirrels/km^2). Capture probabilities (i. e., recaptures/number animals captured during second capture interval) ranged from 0.43–0.8 (Table 2).

Species Association

We seldom captured fox and gray squirrels at the same trap station. Only 12 of 864 trapping stations captured both fox and gray squirrels, whereas we captured fox or gray squirrels only at 331 and 32 stations, respectively. Fox and gray squirrel cooccurrence was less than expected (X^2 =7.39, P<0.001). Jaccard's index was 0.03, indicating a strong negative association between species. We eliminated trap sites where both species were captured from further analysis.

Habitat

Few habitat variables differed between fox squirrel capture sites (N=331) and other sites (N=521). Pine basal area and total basal area were higher (P<0.001 and P=0.007, respectively) at fox squirrel capture sites than at other sites. Percent woody groundcover was lower (P=0.031) and herbaceous groundcover higher (P< 0.040) at fox squirrel capture sites than at other sites (Table 3). The logistic regression model indicated pine basal area and herbaceous groundcover were positively related to probability of fox squirrel capture, whereas fern groundcover was negatively related to probability of fox squirrel capture (Table 4). However, jackknife validation

Table 3. Means and standard errors, in parentheses, of habitat variables measured at fox squirrel capture sites (N = 331) and at sites where fox squirrels were not captured (N = 521) in longleaf pine stands, Joseph W. Jones Ecological Research Center, southwest Georgia, 1993.

Variable[a]	Capture site	Noncapture site	P[b]
PBA	8.7 (0.3)	7.3 (0.2)	<0.001
HWDBA	1.8 (0.2)	2.2 (0.2)	0.664
OBA	1.7 (0.2)	2.1 (0.2)	0.693
TOTBA	10.5 (0.3)	9.5 (0.2	0.007
WGGC	12.3 (0.8)	11.0 (0.6)	0.328
GGC	18.5 (0.6)	17.5 (0.6)	0.059
FOGC	19.9 (0.5)	18.5 (0.4)	0.075
VGC	1.8 (0.2)	2.4 (0.2)	0.073
FEGC	1.3 (0.1)	1.2 (0.2)	0.654
WGC	6.4 (0.4)	7.6 (0.3)	0.031
HGC	51.9 (0.9)	48.7 (0.9)	0.040
CWGC	0.1 (0.0)	0.1 (0.0)	0.611
TOTGC	60.2 (0.8)	58.8 (0.8)	0.309

a. See Table 1 for variable description.
b. P-values based on Wilcoxon test.

indicated the resulting model only performed slightly better, 56.2% correct classification, than random expectation.

Gray squirrel capture locations (N=32) differed markedly from other sites (N =820). Hardwood and total basal area were higher (P<0.001 and P=0.026, respectively) and pine basal area was lower (P<0.001) at gray squirrel capture sites than at

Table 4. Logistic regression coefficients for predicting squirrel captures at live traps placed in longleaf pine stands, Joseph W. Jones Ecological Research Center, south west Georgia, 1993.

Response Variable	Independent Variable[a]	Coefficient	P[b]
Fox squirrel capture[c]	Intercept	−1.308	<0.001
	PBA	0.012	<0.001
	FEGC	-0.064	0.009
	HGC	0.010	0.007
Gray squirrel capture[d]	Intercept	0.404	0.542
	OBA	0.068	<0.001
	TOTBA	-0.059	<0.001
	HGC	-0.072	<0.001
Squirrel capture[e]	Intercept	-1.956	0.028
	OBA	-0.073	<0.001
	TOTBA	0.063	<0.001
	HGC	0.080	<0.001

a. See Table 1 for explanation of variables.
b. Probability the coefficient = 0, Chi-square test.
c. *Predicts fox squirrel capture site or not fox squirrel capture site.*
d. Predicts gray squirrel capture site or not gray squirrel capture site.
e. Predicts fox squirrel capture site or gray squirrel capture site.

Table 5. Means and standard errors, in parentheses, of habitat variables measured at gray squirrel capture sites (N = 32) and at sites where gray squirrels were not captured (N = 820) in longleaf pine stands, Joseph W. Jones Ecological Research Center, southwest Georgia, 1993.

Variable[a]	Capture Site	Noncapture Site	P[b]
PBA	2.5 (0.5)	8.1 (0.2)	<0.001
HWDBA	9.4 (1.2)	1.7 (0.1)	<0.001
OBA	9.1 (1.1)	1.6 (0.1)	<0.001
TOTBA	12.0 (1.0)	9.8 (0.1)	0.026
WGGC	2.0 (1.2)	11.9 (0.5)	<0.001
GGC	6.6 (1.5)	18.3 (0.4)	<0.001
FOGC	9.2 (1.5)	19.4 (0.3)	<0.001
VGC	2.7 (0.8)	2.1 (0.1)	0.789
FEGC	0.3 (0.2)	1.6 (0.1)	0.005
WGC	14.4 (1.4)	6.8 (0.2)	<0.001
HGC	18.2 (2.9)	51.2 (0.6)	<0.001
CWGC	0.2 (0.1)	0.1 (0.0)	0.441
TOTGC	35.5 (2.8)	60.3 (0.6)	<0.001

a. See Table 1 for variable description.
b. P-values based on Wilcoxon test.

other sites. Woody groundcover was higher (P<0.001) whereas herbaceous and total groundcover were lower (P<0.001) at gray squirrel capture sites (Table 5). The logistic regression model indicated that oak basal and total basal area were positively related to probability of gray squirrel capture (Table 4). Jackknife validation indicated this model performed better, 86.9% correct classification, than random expectation.

Table 6. Means and standard errors, in parentheses, of habitat variables measured at fox squirrel capture sites (N = 331) and gray squirrel capture sites (N = 32) in longleaf pine stands, Joseph W. Jones Ecological Research Center, southwest Georgia, 1993.

Variable[a]	Fox Squirrel	Gray Squirrel	P[b]
PBA	8.7 (0.3)	2.5 (0.5)	<0.001
HWDBA	1.8 (0.2)	9.4 (1.2)	<0.001
OBA	1.7 (0.2)	9.1 (1.1)	<0.001
TOTBA	10.5 (0.3)	12.0 (1.0)	0.137
WGGC	12.3 (0.8)	2.0 (1.2)	<0.001
GGC	18.5 (0.6)	6.6 (1.5)	<0.001
FOGC	19.9 (0.5)	9.2 (1.5)	<0.001
VGC	1.8 (0.2)	2.7 (0.8)	0.513
FEGC	1.3 (0.1)	0.3 (0.2)	0.008
WGC	6.4 (0.4)	14.4 (1.4)	<0.001
HGC	51.9 (0.9)	18.2 (2.9)	<0.001
CWGC	0.1 (0.0)	0.2 (0.1)	0.397
TOTGC	60.2 (0.8)	35.5 (2.8)	<0.001

a. See Table 1 for variable description.
b. P-values based on Wilcoxon test.

Fox squirrel capture sites had higher *($P<0.001$)* pine basal area and lower *($P<0.001$)* hardwood basal area than gray squirrel capture sites. Total groundcover and herbaceous groundcover were higher *($P<0.001$)* and woody groundcover was lower *($P<0.001$)* at fox squirrel capture sites than at gray squirrel capture sites (Table 6). Oak basal area, total basal area, and herbaceous groundcover discriminated between fox and gray squirrel capture sites (Table 4). Jackknife validation indicated this model performed better, 87.6% correct classifications, than random expectation.

Discussion

Our fox squirrel density estimates—12–19 squirrels/km^2—were within the range of density estimates reported elsewhere. Moore (1957) and Humphrey et al. (1985) estimated density of 2 Florida fox squirrel populations at 38 squirrels/km^2 and 8.4 squirrels/km^2, respectively. Hilliard (1979) estimated density of a fox squirrel population in Georgia at 20 squirrels/km^2. In North Carolina, Weigl et al. (1989) estimated fox squirrel density between 1–17 squirrels/km^2. Tappe et al. (1993) estimated fox squirrel densities of 17.7 squirrels/km^2 in 1991 and 15.3 squirrels/km^2 in 1992 on Piedmont National Wildlife refuge, Georgia. Williams and Humphrey (1979) estimated mangrove fox squirrel *(S. n. avicennia)* densities of 0.09 squirrels/km^2 and 1.9 squirrels/km^2 on 2 study areas in south Florida. Although our density estimates fell within the reported range of density estimates, there was great variability in estimation procedures among studies; thus results may not be comparable.

Few habitat variables differed between fox squirrel capture sites and remaining trap sites, and our logistic regression model was a poor predictor of fox squirrel capture locations. The best explanation for lack of habitat preference is that our study areas lacked variability in fox squirrel habitat quality. There were habitat variables, however, that differed between fox squirrel capture sites and other sites. Pine basal area and total basal area were higher at fox squirrel capture sites than any other sites. Taylor (1973) and Weigl et al. (1989) found that fox squirrels preferred areas with sparse understories. In contrast, we found no difference in total groundcover between fox squirrel capture sites and other sites, but fox squirrel capture sites had more herbaceous groundcover and less woody groundcover than other locations. Large dominant stems and relatively dense herbaceous vegetation are characteristic of fire-maintained longleaf pine forests (Platt et al. 1988, Stout and Marion 1993). Because southeastern fox squirrels have narrow habitat preferences relative to gray squirrel densities, we believe that our study areas represented excellent habitat for fox squirrels.

Most habitat variables associated with gray squirrel capture sites differed from habitat variables at other sites. Preference for hardwood-dominated sites may be due to increased mast availability associated with higher hardwood basal areas. Additionally, because gray squirrels are more arboreal than fox squirrels (Whitaker and Hamilton 1998), the expansive canopies of hardwoods may be important for travel and protection from predators. Contrary to others (Taylor 1973, Flyger and Gates 1908), we found that gray squirrels preferred areas with relatively sparse groundcover. Further, although sparse groundcover was preferred, the percentage of woody groundcover was higher at gray squirrel sites than at other sites. Because oak basal area had a positive relationship and total basal area had a negative relationship to gray squirrel capture probability, oak patches must be of vital importance to gray squirrels in a longleaf pine matrix. Within a longleaf pine forest, hardwood-dominated sites and associated sparse, woody-dominated groundcover primarily occur in areas that do not readily burn (e.g., fire shadows, wetland edges, etc.) (Stout and Marion 1993).

Edwards et al. (1998) indicated that coexistence of fox and gray squirrels is a function of niche partitioning on several dimensions. Gray squirrels are generally found in closed-canopy hardwood forests (Whitaker and Hamilton 1998), whereas fox squirrels are generally located in mixed pine-hardwood forests (Weigl et al. 1989, Whitaker and Hamilton 1998). We believe that the negative association between fox and gray squirrels on Ichauway resulted from species-specific habitat preferences rather than behavioral interactions (e.g., aggression). Our conclusion was based on numerous habitat differences between fox and gray squirrel capture sites. For example, longleaf pines were dominant at fox squirrel capture sites, whereas hardwoods were dominant at gray squirrel capture sites. Further, fox squirrels preferred areas with dense herbaceous groundcover, especially wiregrass, whereas, gray squirrels preferred sparse groundcover dominated by woody species. Because fire disturbances strongly influences succession in the Deep South (Stout and Marion 1993), fox and gray squirrel relationships are likely an artifact of fires history in this region.

Management Implications and Future Research

Fire is a necessary component of longleaf pine management and regeneration (Wahlenberg 1946). Prescribed fire within longleaf pine forests retards hardwood encroachment and encourages herbaceous groundcover (Wahlenberg 1946, Platt et al. 1988). In the absence of fire, hardwoods will gradually replace longleaf pines, and the fox squirrel will likely be replaced by the more hardwood-adapted gray squirrel.

Although our results indicated the importance of fire-maintained longleaf pine forest, we emphasize that embedded hardwoods were a major component of these forests. Scattered hardwoods produce important mast for wildlife and should be encouraged within the longleaf pine matrix (Greenberg and Simons 1999). Moreover, ongoing work indicated that scattered hardwoods within the longleaf pine matrix may be vital to fox squirrels (L. M. Conner, unpubl.).

Future research should focus on landscape factors that may influence fox squirrel populations. There are virtually no data that address effects of habitat interspersion and connectivity on fox squirrel behavior and population dynamics. Such data are important to fox squirrel management in the Southeast. Additional research should assess habitat use by fox and gray squirrels in the absence of other species. Such work, although theoretical in nature, would allow a more quantitative picture of each species' niche breadth and provide evidence for evaluating potential competition between the species.

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