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Habitat Associated with Daytime Refugia of Fox Squirrels in a Longleaf Pine Forest

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ABSTRACT.—Fox squirrel (*Sciurus niger*) populations are declining in many areas of the eastern United States, and habitat loss may be partly responsible for these declines. We measured habitat variables at fox squirrel refuge sites and random sites and used an information theoretic approach to determine the influence of these variables on probability of a site being used for refuge. There was compelling evidence to support tree and stand level habitat variables as important predictors of refuge sites, but little evidence in support of understory variables. Fox squirrels were more likely to use hardwoods than pines (*Pinus* spp.) for refuge. Tree size (height and diameter) was positively associated with probability of use as was tree density around the refuge site. Percent debris groundcover, the only understory variable of importance, was positively related to probability of use as a refuge site, but the parameter estimate did not convincingly differ from zero. We conclude that large hardwoods within an open-canopy pine matrix are important as fox squirrel refuge sites.

INTRODUCTION

Fox squirrel populations in the Midwest appear to be expanding in number and geographic range (Swihart and Nupp, 1998) and, relative to eastern populations, more research has been conducted on fox squirrels in this region (Weigl *et al.*, 1989; Loeb and Moncrief, 1993). In contrast, many eastern fox squirrel populations are declining in number, presumably as a function of habitat loss (Taylor, 1973; Weigl *et al.*, 1989). Three [Delmarva fox squirrel (*Sciurus n. cinereus*), big cypress fox squirrel (*S. n. avicennia*) and Sherman's fox squirrel (*S. n. shermani*)] of the eight recognized subspecies of fox squirrels are afforded special conservation status (Loeb and Moncrief, 1993; Whitaker and Hamilton, 1998); and all three are found only in the eastern United States.

There are limited data on fox squirrel habitat use (Taylor, 1973; Edwards *et al.*, 1989; Weigl *et al.*, 1989; Kantola and Humphrey, 1990) and nest site selection (Weigl *et al.*, 1989; Edwards and Guynn, 1995) for fox squirrels residing in the eastern United States. However, daytime refugia (*i.e.*, resting sites) may also be important to fox squirrels, and there have been no studies that explicitly examined daytime refugia. Therefore, our objective was to identify habitat characteristics that predicted fox squirrel use of trees as refuge sites.

METHODS

Study area.—The study took place on the Joseph W. Jones Ecological Research Center, about 20 km south of Newton, Georgia, United States. The 12,000-ha research site relied heavily on prescribed fire to maintain a two-layered forest dominated by longleaf pine (*Pinus palustris*) in the overstory, herbaceous vegetation in the understory, and an open midstory. Scattered individual hardwoods and hardwood patches existed within the longleaf pine matrix. In general, forested areas were between 70 and 90 y old, but individual longleaf pines >300 y old were scattered throughout the site. Additionally, management for northern bobwhite (*Colinus virginianus*) resulted in a diverse habitat mosaic of interspersed

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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. Although fox squirrels and gray squirrels (*Sciurus carolinensis*) were sympatric on the study site, gray squirrels were generally restricted to hardwood-dominated sites, and the two species were seldom seen together (Conner *et al.*, 1999).

Animal capture and monitoring.—Fox squirrels were captured in wooden box traps (Baumgartner, 1940) baited with dried corn. We placed traps in areas known to have fox squirrels and trapped periodically during January 1998–November 1999.

Once captured, we transferred the squirrel into a nylon mesh bag where it was sedated using either inhalation of Methoxyflorane or intramuscular injection of Ketamine hydrochloride (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 if 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 (*i.e.*, transmitter weight ≤3% of squirrel body weight). All squirrels were released at the capture site after they completely recovered from anesthesia. Trapping and handling followed Animal Care and Use Committee (1998) recommendations.

Each week we used homing (Kenward, 2001) to locate daytime refuge sites of ≥2 radiotagged squirrels while they were inactive (*i.e.*, radio signal indicated the squirrel was not moving; Chamberlain *et al.*, 1998). If a squirrel moved before we positively identified the location of the refuge tree we abandoned the stalk. Initially, we chose squirrels at random and subsequent squirrels were selected until all monitored squirrels had been sampled and the sampling repeated. As new animals were captured and radiotagged they were added to the sampling regime opportunistically. We conducted our sampling to ensure that number of sites sampled/month was kept relatively uniform.

Data collection.—After locating a squirrel we marked the location on a map and recorded species, height and diameter (at approximately 1.25 m from the ground) of the tree used for refuge. Tree species were identified as either hardwood or pine for analysis.

We estimated percent groundcover for nine classes of understory vegetation (bare ground, wire grass, other grasses, forb, woody, vine, debris, fungi and fern) using a 0.5 m × 0.5 m quadrat. Sample sites were randomly placed in each of four quadrants and within 10 m of the refuge tree. We averaged the four samples as an estimate of groundcover for the site. Total ground cover was calculated as the sum of all classes except bare ground. We also calculated a total herbaceous groundcover by summing percent wire grass, other grass, forb and fern.

We measured tree density and basal area around the refuge tree using the point-center-quarter method (Cottam and Curtis, 1956). We also partitioned our basal area estimates into pine and hardwood categories. Canopy closure was estimated using a spherical densitometer (Lemmon, 1957).

We used ARC/INFO (ESRI, 1997) to locate random points throughout the study area. We visited random points and selected the nearest tree (diameter ≥10 cm) for sampling. We measured habitat variables associated with this random tree using identical methods as used to measure refuge sites.

Data analysis.—We considered all variables as belonging to at least one of four categories. Tree variables described the refuge tree. Stand variables described the forest structure surrounding the refuge tree. Understory variables described the understory vegetation within the stand and understory summary variables were calculated from understory variables (Table 1).

TABLE 1.—Variable categories and definitions for variables measured at fox squirrel refugia sites and random sites in southwestern Georgia, 1998–1999

Category	Variable	Definition
Tree	Height	Height (m) of refuge tree
	DBH	Diameter (cm) of refuge tree
	Type	Tree type (hardwood or pine)
Stand	Density	Tree density (trees/ha)
	BA	Total basal area (m^2/ha)
	Pine BA	Pine basal area (m^2/ha)
	Hardwood BA	Hardwood basal area (m^2/ha)
	Canopy closure	Canopy closure (%)
Understory	% wiregrass	Wiregrass ground cover (%)
	% other grass	Grass ground cover − % wiregrass
	% forb	Forb groundcover (%)
	% vine	Vine groundcover (%)
	% woody	Woody vegetation groundcover (%)
	% fern	Fern groundcover (%)
	% fungi	Fungi groundcover (%)
	% debris	Debris groundcover (%)
	% bare	Bare ground (%)
Understory summary	Total ground cover	Total live groundcover (%)
	Total herbaceous	Total herbaceous groundcover (%)
	% debris	Debris groundcover (%)

We used an information theoretic approach to data analysis (Anderson *et al.*, 2000; Burnham and Anderson, 2000). Our analysis began with 12 *a priori* models (Table 2). These models represented all possible additive combinations (*i.e.*, we did not include interaction terms) of the four variable categories. However, we did not develop models containing both understory and understory summary variables to avoid problems with collinearity. We used logistic regression (Allison, 2000) to develop models predicting the probability of a tree being used as a refuge site by fox squirrels.

We used the second order Akaike's Information Criteria (AIC_c) and Akaike weights (w_i), to identify the most parsimonious model and to predict variable importance (Anderson *et al.*, 2000; Burnham and Anderson, 2000). We calculated the Akaike weight (w_i) for each model and interpreted w_i as the probability of the ith model being the best model of the *a priori* set. We considered the model with the highest w_i as the best approximating model (Burnham and Anderson, 2000).

We calculated Σw_i for each variable to determine variable importance and used model averaging to estimate parameters and unconditional standard errors (Burnham and Anderson, 2000) for important variables (*i.e.*, variables with $\Sigma w_i \geqslant 0.20$). We also calculated odds ratios from the averaged parameter estimates for important variables. The odds ratio represents the increase in probability of a site being used for refuge by a fox squirrel for every unit increase in the predictor variable (Allison, 2000).

RESULTS

We located 217 refugia used by 76 squirrels (27 males and 49 females) between 13 April 1998 and 22 December 1999. We measured habitat variables associated with 149 random locations during this same time interval.

TABLE 2.—Variable combinations used in logistic regression models to predict probability of a site being used by fox squirrels as a refuge site

Model[a]	K[b]	AIC$_c$	Δ_i[c]	w_i[d]
Tree + stand	8	399.91	0	0.610
Tree + stand + understory summary	11	402.62	2.71	0.157
Tree + stand + understory	16	402.75	2.84	0.147
Tree + understory	12	405.13	5.22	0.045
Tree + understory summary	7	405.78	5.87	0.032
Tree	4	408.74	8.83	0.007
Stand	5	479.65	79.09	<0.001
Stand + understory summary	8	481.81	81.90	<0.001
Stand + understory	13	483.79	83.88	<0.001
Understory	9	490.76	90.85	<0.001
Understory summary	4	490.91	91.00	<0.001
Intercept only	1	496.26	96.35	<0.001

[a] Variable categories (Table 1) are given to variables used in the model. All models were additive combinations of variables

[b] Number of variables in the model

[c] Distance of the model from the best model ($\Delta_i = \text{AIC}_c - \min \text{AIC}_c$)

[d] The estimated probability of being the best model (Akaike weight)

The model with the lowest AIC$_c$ was obtained using tree type (pine or hardwood), tree height (m), tree diameter (cm), tree density (stems/ha), total basal area (m^2/ha), hardwood basal area (m^2/ha) and percent canopy closure (Tree + stand model; Table 2). The w_i for this model ($w_i = 0.610$) was approximately four times greater than the next closest approximating model ($w_i = 0.157$). The sum of the w_i for the best three approximating models exceeded 0.90, indicating that there was $\geq$90% chance that one of these models was the best approximating model of the 12.

The sums of the w_i for tree and stand variables were $\geq$0.914, whereas weights for understory and understory summary variables were $\leq$0.192 with exception of percent debris groundcover ($\Sigma w_i = 0.381$; Table 3). Although tree and stand variables as well as percent debris groundcover had nontrivial Σw_i values, only four of these variables (tree type, tree height, tree diameter and tree density) had confidence intervals (*i.e.*, 1.96 × SE) that did not contain zero (Table 3). Thus, of all variables measured, these four variables provided the most information about fox squirrel refugia, and we restricted further analysis and interpretation to these four variables.

Odds ratios indicated that hardwood trees had a 55.8% greater chance of being used as a refuge tree than pines. For every meter increase in tree height and for every cm increase in diameter the probability of a tree being used as a refuge site increased 3% and 7%, respectively. An increase in tree density of one tree/ha resulted in a 0.2% increase in the probability of use as a refuge site.

DISCUSSION

The model containing tree and stand variables was four times more likely to be the best approximating model than the second best model. However, this model was not convincingly the best approximating model because there was a 39% chance (*i.e.*, 1.0 − 0.610 = 0.39) that one of the other 12 models would be selected as best if new data were available (Burnham and Anderson, 2000). There was, however, overwhelming support

TABLE 3.—Average parameter estimates, unconditional standard errors, odds ratios and sum of Akaike weights of predictor variables found in approximating models of fox squirrel refugia

Variable[a]	Estimate	SE	Odds ratio[b]	Σw_i[c]
Tree type (hardwood)	0.4436	0.1706	1.558[d]	1.0
Height (m)	0.0280	0.0103	1.071	1.0
DBH (cm)	0.0655	0.0151	1.067	1.0
Density (trees/ha)	0.0018	0.0009	1.002	0.914
BA (m^2/ha)	0.0053	0.0167	1.005	0.914
Hardwood BA (m^2/ha)	0.0138	0.1352	1.014	0.914
Canopy closure (%)	0.0093	0.0074	1.009	0.914
% debris	0.0019	0.0121	1.002	0.381

[a] Only those variables with $\Sigma w_i^a \geqslant 0.381$ are included because remaining variables provided little information ($\Sigma w_i \leqslant 0.192$)

[b] Increase in probability of use as fox squirrel refugia per variable unit (*e.g.*, if tree A is 20 m tall and tree B is 21 m tall, tree B has 1.071 times greater probability of being a refuge tree)

[c] Sum of Akaike weights indicating variable importance with higher values having more support

[d] Hardwoods are 1.558 times more likely to be used as a refuge tree

for a hypothesis that fox squirrel refuge sites were related to characteristics of the refuge tree itself and the surrounding forest structure. This was evident because the Σw_i was $\geqslant$0.914 for all tree and stand variables (*e.g.*, there was >90% chance that these variables would occur in the best approximating model). In contrast, there was little support for a hypothesis concerning the importance of understory structure as a determinant of refugia for fox squirrels.

When the average parameter estimates and their unconditional standard errors were examined for each of the variables with nontrivial Σw_i, only four variables had parameter estimates that convincingly differed from 0 (*i.e.*, the 95% confidence interval for the parameter estimate did not contain zero). Three of these four variables described the the refuge tree. The other variable was tree density, a stand variable (Table 3). Therefore, we suggest that of all measured variables, the variables describing the refuge tree and the estimate of tree density around the refuge tree provided the most information regarding fox squirrel refugia.

Use of hardwood trees by fox squirrels is often linked to availability of food, but our data suggest that hardwoods are also important as refuge sites. Most studies of fox squirrel habitat have found pine-hardwood forests and pine-hardwood ecotones to be preferred habitats (Taylor, 1973; Edwards *et al.*, 1989; Weigl *et al.*, 1989; Kantola and Humphrey, 1990). Presumably, the mixture of hardwoods and pines permits fox squirrels to take advantage of seasonally available foods. Our data indicated that hardwood trees were 55.8% more likely to be used by fox squirrels for refugia than were pines, emphasizing the importance of hardwoods scattered within the pine forests.

Tree height and diameter were important predictors of fox squirrel refugia. Importance of large trees to fox squirrels has been recognized for some time (Weigl *et al.*, 1989). This importance is generally related to the greater mast production associated with larger trees (Goodrum *et al.*, 1971). However, Edwards and Guynn (1995) found that fox squirrels used nests in large trees more than expected, indicating that large trees were also important for nests. Here, we provide evidence that large trees are also important for daytime refugia. By seeking refuge in large trees, especially evergreen hardwoods with a dense foliar crown, fox squirrels may reduce the probability that they are detected and captured by predators.

Additionally, large trees with dense crowns may provide shelter from inclement weather and may reduce energy expended by squirrels for thermoregulation.

Increased tree density was associated with an increased probability of the area being used as a refuge site. However, this association may be misleading. On our study, area tree density was relatively low. We speculate that as tree density increases to the point that vegetation diversity decreases, fox squirrel use of the area for refuge will decline. Unfortunately, the rarity of densely forested stands on our study area resulted in few to none of these sites being included in our sample.

Fox squirrels are perhaps the least arboreal of the North American tree squirrels. Therefore, we originally thought that groundcover composition may have been important to fox squirrels when selecting refuge sites. Indeed, earlier work on Ichauway (Conner *et al.*, 1999) revealed that herbaceous groundcover, especially wire grass (*Aristida beyrichiana*), was strongly associated with fox squirrel capture sites. However, we found little evidence to support understory variables as being important to fox squirrels when selecting daytime refugia.

Conclusions and recommendations.—Within the southeastern portion of their range, fox squirrels may be a keystone species of the longleaf pine forest (Simberloff, 1993) and an indicator of quality oak-pine habitat (Weigl *et al.*, 1989). Importance of hardwoods within the pine matrix should be stressed when managing for fox squirrels. Moreover, forest management practices that promote retention of mature hardwood trees within a mature pine matrix should be encouraged. Uneven-aged management and single-tree selection may be an especially beneficial silviculture model to achieve desired overstory structure.

Although understory variables seemed to be relatively unimportant predictors of fox squirrel refugia, we emphasize that all upland forests on our study site were managed using prescribed fire, and a successful prescribed fire program relies on sufficient fine fuels to carry fire across the landscape. Thus, presence of a dense herbaceous layer in the understory permitted appropriate overstory structure and composition to be maintained using prescribed fire. In the absence of prescribed fires, hardwood encroachment would gradually replace pines in the overstory, eventually rendering the habitat unsuitable for fox squirrels (Conner *et al.*, 1999).

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