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Resource selection by southeastern fox squirrels in a fire-maintained forest system

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Fire is essential to maintain the open forest structure required by the southeastern fox squirrel (*Sciurus niger niger*). In recent decades, managers of the longleaf pine (*Pinus palustris*) ecosystem have transitioned from dormant-season to growing-season burns, which more effectively limit midstory hardwood encroachment. Similarly, aggressive hardwood removal programs have been employed to further reduce hardwood midstory. However, fox squirrels are dependent on oaks (*Quercus* spp.) for food and cover; thus, it is unclear how growing-season burns and hardwood removal may affect habitat quality for fox squirrels. We used compositional analysis to investigate selection of home ranges within the study area by 48 radiocollared fox squirrels on the Fort Bragg Military Installation, North Carolina. We used resource utilization functions with growing-season fire history and other habitat covariates as explanatory variables to test whether growing-season fires influenced the selection of habitat components within home ranges. Lastly, using a sample of fox squirrel relocations and paired random points, we performed binomial logistic regression to test whether habitat selection by fox squirrels was influenced by the availability of oaks and longleaf pines and select forest stand structural characteristics. When establishing home ranges, fox squirrels selected southern yellow pine over other cover types. Within home ranges, fox squirrel use increased with decreasing distance to a riparian area but was not affected by the application of growing-season fires. At the population level, fox squirrels selected for greater densities of reproductively mature oak stems. Fox squirrels likely benefit from growing-season fires that maintain expansive upland pine stands but are negatively affected by homogeneous fire application and mechanical hardwood removal that reduce the occurrence of reproductively mature oaks across the landscape. Managers should strive to maintain oaks in riparian areas, fire shadows, and naturally occurring patches within pine stands when managing for fox squirrels.

Key words: growing-season fire, hardwood, longleaf pine, oak, prescribed fire, *Quercus*, *Sciurus niger*

Anthropogenic fire has a long history in the southern United States (Hudson 1982; Pyne 1982). Since their arrival over 10,000 years ago, Native Americans burned southern pine forests and grasslands to drive game and clear agricultural lands (Hudson 1982; Pyne 1982; Buckner 1989; MacCleery 1993). This practice was continued by European immigrants who burned the land for many of the same reasons (Stoddard 1962; Pyne 1982). Before the arrival of European immigrants, it is thought that most of the longleaf pine (*Pinus palustris*) forests of the Southeast burned every 2–10 years (Christensen 1981; Frost 1998), and after their arrival possibly every 1–3 years (Landers et al. 1990). Globally, longleaf pine communities have one of the most frequent fire return intervals (Christensen 1981). Because of the influence fire had on the plant communities of the Southeast, fire also played a central role in shaping the animal communities of the region. Indeed, many wildlife species are dependent on the vegetative structure and resources maintained by frequent fires (Brennan et al. 1998). However, fire protection policies implemented in the early 20th century, coupled with land use changes, facilitated the decline of fire-dependent plant communities and many of the animal species they supported (Brennan 1991; Engstrom et al. 1996; Brockway and Lewis 1997).

Fire-dependent longleaf pine forests are important for southeastern fox squirrels (*Sciurus niger niger*; hereafter, fox squirrel), a species of high conservation priority in the region (Weigl et al. 1989; Perkins et al. 2008). The fox squirrel's large body size is thought to be an adaptation for living in fire-maintained pine forests, affording them increased mobility, access to widely spaced food resources, and the ability to manipulate large longleaf pine cones (Steele 1988; Weigl et al. 1989; Steele and Weigl 1993). Declines in fox squirrel populations have coincided with the degradation and loss of mature longleaf pine forests, which now occupy less than 3% of their original extent (Weigl et al. 1989; Kantola and Humphrey 1990; Loeb and Moncrief 1993; Landers et al. 1995; Perkins and Conner 2004). The drastic reduction of longleaf pine forests is credited to widespread timber harvest occurring at the turn of the 20th century, rapid urbanization of the eastern United States, conversion to slash (*P. elliottii*) or loblolly (*P. taeda*) pine plantations, and fire suppression (Frost 1993; Landers et al. 1995; Outcalt and Sheffield 1996).

The historical longleaf pine ecosystem was characterized by widely spaced longleaf pine trees, scattered hardwood patches, and diverse understory vegetation (Frost 2006). Large, mature pine and hardwood trees provide important seasonal food resources for fox squirrels (Moore 1957; Ha 1983; Kantola 1986; Weigl et al. 1989). Additionally, large hardwood trees serve as refugia and provide cavities for rearing young (Moore 1957; Weigl et al. 1989, Kantola 1992; Conner and Godbois 2003). However, compared to longleaf pine, hardwood species are generally less tolerant of fire (though tolerance varies considerably among hardwood species). Consequently, the extent of hardwoods within longleaf pine forests is limited by frequent and homogeneous prescribed fires (Lashley et al. 2014), and hardwoods often naturally occur on fire-maintained properties only as individual canopy trees or in small isolated patches within the pine matrix (Greenberg and Simons 1999).

Within the historical range of the longleaf pine ecosystem, the focus of contemporary restoration and management practices is reduction of hardwood species that have invaded pine uplands as a result of fire suppression (Provencher et al. 2001; Kush et al. 2004; Varner et al. 2005). In many cases, land managers use machinery, herbicides, and growing-season fire to achieve and maintain hardwood-free upland pine forests (Boyer 1990; Means 1996; Provencher et al. 2001; Varner et al. 2005). However, a pure pine forest is not representative of presettlement conditions (Frost 1993), and there is a growing concern about the negative ecological effects of oak (*Quercus* spp.) reduction or removal on mast-dependent wildlife species like the fox squirrel (Hiers et al. 2014; Lashley et al. 2014). Historically, variation in fire regime and intensity allowed large canopy hardwood trees and isolated patches of smaller hardwood trees to persist at 10–60 trees per hectare within pine-hardwood forests (Moore 1957; Frost 1993; Rebertus et al. 1993; Greenberg and Simons 1999).

Although resource managers currently use dormant-season and growing-season prescribed fire to restore and maintain longleaf pine forests, some prescribed fire programs within the southeastern United States are beginning to emphasize the timing of natural fires (i.e., lightning-ignited) and are shifting to the use of more early growing-season prescribed fire (Cantrell et al. 1995; Fill et al. 2012). Frequent prescribed fires during the growing season maintain the open forest conditions required by fox squirrels, but these burns can reduce the prevalence of mature hardwoods within longleaf pine forests (Robbins and Myers 1992). Because fox squirrels rely heavily on acorns and other hard mast for a large percentage of their diet, the negative effects of fire on oaks and the subsequent decreased availability of hard mast could be limiting their populations (Baumgartner 1940; Allen 1943; Weigl et al. 1989; Kantola and Humphrey 1990; Greenberg and Simons 1999). Conversely, in the absence of frequent fires, longleaf pine communities shift from open-canopy forests to closed-canopy systems dominated by shade-tolerant and fire-sensitive plant species (Heyward 1939; Garren 1943; Nowacki and Abrams 2008), a condition more suitable for the eastern gray squirrel (*S. carolinensis*—Whitaker and Hamilton 1998).

Currently, there is limited information on the effects of prescribed burning or hardwood removal on fox squirrels. Although prescribed burning is commonly recommended for managing fox squirrel habitat, these recommendations often do not specify a season or frequency for prescribed fire application (Weigl et al. 1989; Conner et al. 1999; Conner and Godbois 2003; Perkins and Conner 2004). Our objective was to investigate habitat selection by southeastern fox squirrels at multiple ecological scales in an area with a large-scale, growing-season fire regime and targeted removal of oaks and other upland hardwoods. We predicted that fox squirrels would select upland pine stands but would concentrate use in areas with remnant hardwoods, which should be more prevalent in units with lower burn frequencies and in fire shadows (e.g., moist soil depressions and drainages).

Materials and Methods

Study area.—Fort Bragg Military Installation (hereafter, Fort Bragg) is a 64,280-ha active military base in the Sandhills physiographic region of North Carolina, United States. Dominated by an overstory of longleaf pine and an understory of wiregrass (*Aristida* spp.), Fort Bragg and other adjacent areas form the largest contiguous tract of longleaf pine-wiregrass ecosystem remaining in North Carolina (Sorrie et al. 2006). Large hardwood trees, including turkey oak (*Quercus laevis*), sand post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), southern red oak (*Q. falcata*), and hickory (*Carya* spp.), are scattered throughout the base and are present in small patches in the uplands, along riparian areas and firebreaks (Lashley et al. 2014), and bordering parachute drop zones. Fort Bragg's land managers use prescribed fire extensively to maintain an open forest midstory for the federally endangered red-cockaded woodpecker (*Picoides borealis*—Lashley et al. 2014). Beginning in 1989, prescribed fires were conducted primarily during the growing season (April–June) every 3 years to prevent hardwood encroachment in the uplands (Lashley et al. 2014); however, dormant-season burns were conducted yearly in the parachute drop zones and in areas not burned due to weather or lack of personnel the previous year. Hunters at Fort Bragg were allowed to harvest 1 fox squirrel per day with a season limit of 10 from October to December. According to Fort Bragg harvest records, squirrel hunter effort decreased since 1982, but fox squirrel harvest remained relatively constant with an increasing trend since 2008; on average, hunters harvested 78 fox squirrels annually from 2001 to 2011.

Animal capture and monitoring.—We trapped fox squirrels using wooden box traps (Baumgartner 1940) and wire cage traps (Model 103, Tomahawk Live Trap Company, Hazelhurst, Wisconsin) baited with dried whole kernel corn. Trap locations were chosen based on captures of fox squirrels in traps placed randomly by Scott (2011). Once captured, we transferred fox squirrels into a modified capture cone (Koprowski 2002). Fox squirrels were weighed, sexed, aged (juvenile or adult—Weigl et al. 1989), assessed for reproductive condition, and individually ear-tagged (Monel 1005-1/1005-3, National Band and Tag Company, Newport, Kentucky). Adult fox squirrels weighing > 750 g (collar weight [19 g] was ≤ 3% body weight; Model SI-2C, Holohil Systems Ltd., Ontario, Canada) were radiocollared and released at the capture location. We had 33 radiocollars available for deployment, and we trapped periodically from February 2011 to May 2012 to maintain 33 radiocollared fox squirrels throughout the study period. When a fox squirrel died, the collar was retrieved and redeployed on another fox squirrel. All capture and processing methods met the specifications set forth by the Institutional Animal Care and Use Committee at North Carolina State University (IACUC # 10-153-O) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

We relocated radiocollared fox squirrels once per day and at least 3 times per week using the homing technique at random times between 0.5 h after sunrise and 0.5 h before sunset (White and Garrott 1990). If a squirrel was actively moving away from us as we were approaching it, we stopped tracking and estimated its original location using signal strength and direction. In addition, we recorded whether a radiosignal was active or inactive before homing to each squirrel. The majority (> 75%) of squirrels were inactive before we tracked to them, meaning they were not actively moving away or had already frozen in place before we started tracking. Radiocollared fox squirrels were monitored continually until death, radio failure, or they could no longer be tracked because they had moved into an artillery impact area. All fox squirrel relocations were recorded using a handheld GPS (Rino120, Garmin International, Inc., Olathe, Kansas).

To assess the importance of hardwoods (especially oaks) on habitat selection by fox squirrels, we randomly selected a subset of relocations ($n = 20$) for each fox squirrel and returned to each relocation point. We set the relocation point as the plot center and used a fixed-radius plot (area = 0.04 ha—James and Shugart 1970) to measure diameter at breast height (DBH) for all trees within the plot. For each tree species, we counted all trees with DBH ≥ 10 cm. For each fox squirrel relocation, we repeated the protocol at a random point, which we established via a random bearing (0–360°) and distance (25–75 m away).

Data analysis.—We assessed habitat selection of home ranges using compositional analysis (Aebischer et al. 1993) as modified by Millspaugh et al. (2006); we compared cover types available within the study area to a utilization distribution (UD)-weighted estimate of habitat use within each home range. We only included fox squirrels with ≥ 30 relocations during our study period (March 2011–June 2012) in this analysis. Individual fox squirrels were treated as the sampling unit, and we considered all cover types simultaneously. Cover-type data were from the North Carolina Corporate Geographic Database (10-m resolution—Earth Satellite Corporation 1997). We used 7 cover types based on dominant vegetation: southern yellow pine (primarily longleaf pine), bottomland hardwood forest, managed herbaceous cover, mixed hardwood/conifers, mixed shrubland, mixed upland hardwoods, and upland herbaceous (Table 1). We estimated fixed kernel density home ranges using Geospatial Modeling Environment (GME—Beyer 2012) and output UD grids with a 10 × 10-m cell size. We used the bivariate plug-in option within GME to estimate the bandwidth for each fox squirrel's kernel density estimate (Wand and Jones 1995; Gitzen et al. 2006). Use values were assigned based on the 95% UD, where the proportion of UD volume in each cover type represented an individual's habitat use within the home range (Millspaugh et al. 2006). We tested the null hypothesis (i.e., no selection) using multivariate analysis of variance (Wilks' lambda). Rejection of the null hypothesis led to a series of paired *t*-tests that ranked cover types from most to least selected (Aebischer et al. 1993). We used the adehabitatHS package within program R (R Development Core Team 2012) to implement compositional analysis and to rank cover types within the study area (Calenge 2006).

We investigated habitat selection within each fox squirrel's home range using resource utilization functions (RUFs—Marzluff et al. 2004). We related UDs to habitat covariates believed to influence habitat selection by fox squirrels

Table 1.—Descriptions of the 7 cover types used in analyses of resource selection by southeastern fox squirrels on Fort Bragg, North Carolina, 2011–2012.

Cover type	Description
Bottomland hardwoods	Lowland areas with deciduous dominant woody vegetation ≥ 3 m in height and crown density ≥ 25%.
Managed herbaceous cover	Actively managed areas of herbaceous cover, including drop zones and artillery firing points.
Mixed hardwoods/conifers	Areas with ≥ 25% intermixture of deciduous and evergreen species. Hardwoods constitute a plurality of stocking, but pines account for 25–50% of the stocking.
Mixed shrubland	Areas with vegetation (evergreen and/or deciduous) dominated by shrubs and/or woody plants < 3 m in height.
Mixed hardwoods	Upland areas with deciduous dominant woody vegetation > 3 m in height and crown density ≥ 25%.
Southern yellow pine	Forested areas with 75% pine, including longleaf pine, loblolly slash pine, and/or pond pine.
Upland herbaceous	Unmanaged upland areas covered by herbaceous vegetation.

using multiple regression adjusted for spatial autocorrelation (Marzluff et al. 2004). Habitat covariates included number of large hardwood trees (≥ 26 cm DBH) per hectare, number of large pine trees (≥ 37 cm DBH) per hectare, number of growing-season burns in the previous 20 years, distance to nearest riparian area (m), and distance to nearest road (m). Roads included paved surfaces, unpaved surfaces, and firebreaks, and riparian areas were defined by the presence of permanent wetland vegetation (Fort Bragg GIS Database). We only included fox squirrels with ≥ 30 relocations in the RUF analysis. Using the isopleth command in GME, we converted each UD to 99% volume contour polygons, where contours represented 1–99 percentiles of use probabilities. We overlaid 30 × 30-m sampling grids centered on the habitat raster layers on each percent volume polygon within ArcGIS10 (ESRI 2012). The sample tool was used within ArcGIS10 to extract relative use values and covariates associated with each point in the sampling grid. We acquired GIS layers from Fort Bragg personnel that contained all habitat covariates used in the analyses.

For the RUF analysis, we used the ruf package within program R (Handcock 2012). We used each fox squirrel's bandwidth estimate from the bivariate plug-in as the starting point for estimating the range of spatial dependence and used 1.5 for the smoothing estimate within the ruf.fit function. We evaluated the need for transformations by examining the residual plots from univariate RUFs for 5 randomly selected fox squirrels. The response variable for all fox squirrels was log-transformed, which normalized the response variable and residuals from the univariate RUFs. All covariates were used to create RUFs for each fox squirrel and we averaged the standardized coefficients to create a population-level RUF. We used the relative use value as the dependent variable and habitat covariates as the independent values in the multiple regression analysis. The magnitude and sign of the standardized coefficients indicated the importance of resources and the direction of use, respectively.

We also investigated the relative importance of pine and hardwood trees in explaining fox squirrel relocations. We used logistic regression with fox squirrel relocations (set to 1) and random points (set to 0) as the binary response. We tested pine DBH, hardwood DBH, largest pine DBH, count of trees, and count of oak trees as independent variables. Originally, we included oak DBH and largest oak DBH, but both were highly correlated with count of oaks ($r > 0.75$), so we removed them from the analysis. We used the sign of parameter estimates to indicate directionality of effect for independent variables. Results were considered to be statistically significant at $\alpha = 0.05$. We performed the analysis in JMP Pro 10 (SAS Institute Inc. 2012, Cary, North Carolina).

Results

From January 2011 to May 2012, we captured 76 (28 F, 47 M, 1 Unk) fox squirrels on Fort Bragg and equipped 52 (20 F, 31 M, 1 Unk) with radiocollars. One squirrel (unknown sex) was released before recording sex on the data form. Forty-eight fox squirrels (22 F, 25 M, 1 Unk) had sufficient relocations to include in the analysis of habitat selection. For fox squirrels included in our analyses, the number of relocations ranged from 30 to 208 ($\bar{X} = 116 \pm 62$), and tracking times varied from 54 to 452 ($\bar{X} = 243 \pm 137$) days.

Fox squirrels used cover types at Fort Bragg in a nonrandom manner ($\Lambda = 0.02$, $d.f. = 2$, $P = 0.001$) when establishing home ranges. We detected the following order of selection: southern yellow pine > mixed hardwood/conifer > bottomland hardwood > upland herbaceous > mixed shrubland > mixed hardwood > managed herbaceous (Table 2). However, the differences between mixed hardwood/conifer and bottomland hardwood, and upland herbaceous, mixed shrubland, mixed hardwood, and managed herbaceous were not significant.

Distance to riparian area was the only significant predictor of fox squirrel habitat use in the population-level RUF; use increased with decreasing distance to a riparian area (Table 3). Predictor variables were not consistently correlated with use among individual fox squirrels, and predictor variables varied in degree of importance among squirrels (Table 3). The logistic regression model ($X^2 = 41.58$, $d.f. = 5$, $P \leq 0.0001$) indicated that hardwood DBH and largest pine DBH were negatively associated with fox squirrel locations, whereas the count of oak trees was positively associated with fox squirrel locations (Table 4).

Discussion

Fox squirrels selected home ranges composed of upland yellow pine, a cover type that dominated the fire-maintained systems

Table 2.—Cover-type selection rankings for selection of home ranges by southeastern fox squirrels on Fort Bragg, North Carolina, 2011–2012. The sign of the *t* statistic is indicated with + or − signs; +++ and −−− represent significant deviation from zero.

	Cover type							
Cover type	Bottomland hardwood	Managed herbaceous	Mixed hardwood/ conifer	Mixed shrubland	Mixed hardwood	Southern yellow pine	Upland herbaceous	Rank
Bottomland hardwood	•	+++	−	+++	+++	−−−	+++	3
Managed herbaceous	−−−	•	−−−	+	+++	−−−	−	7
Mixed hardwood/ conifer	+	+++	•	+++	+++	−−−	+++	2
Mixed shrubland	−−−	−	−−−	•	+	−−−	−	5
Mixed hardwood	−−−	−−−	−−−	−	•	−−−	−−−	6
Southern yellow pine	+++	+++	+++	+++	+++	•	+++	1
Upland herbaceous	−−−	+	−−−	+	+++	−−−	•	4

Table 3.—Standardized resource utilization function coefficients for 48 radiocollared southeastern fox squirrels and the number of individual squirrels with significant positive (+) and negative (−) use associated with each habitat variable on Fort Bragg, North Carolina, 2011–2012.

Variable	Standardized $\bar{\beta}$	95% *CI*	$P(\bar{\beta} = 0)$	Number of individuals	
				+	−
Distance to riparian area (m)	−0.057	−0.108, −0.006	0.035	4	13
Distance to road (m)	0.032	−0.009, 0.073	0.135	9	6
Growing-season fires[a]	−0.010	−0.028, 0.008	0.277	3	4
Large pine trees/ha	0.011	−0.014, 0.035	0.415	3	2
Large hardwood trees/ha	0.003	−0.025, 0.030	0.860	2	0

[a]Number of fires in the last 20 years.

Table 4.—Parameters of the logistic regression model of habitat selection by southeastern fox squirrels on Fort Bragg, North Carolina, 2011–2012.

	β	*SE*	X^2	*P* value
Intercept	1.0646	0.2421	19.34	< 0.0001
Pine DBH	0.0001	0.0010	0.01	0.9072
Hardwood DBH	−0.0052	0.0013	16.51	< 0.0001
Largest pine DBH	−0.0514	0.0118	18.72	< 0.0001
Count of trees	−0.0112	0.0084	1.78	0.1823
Count of oaks	0.0488	0.0158	9.59	0.0020

in which fox squirrels evolved (Weigl et al. 1989; Perkins and Conner 2004; Perkins et al. 2008). During summer months, fox squirrels feed heavily on seeds obtained from longleaf pine cones, commonly consuming 20–30 cones per day (Steele 1988; Weigl et al. 1989; Steele and Weigl 1993). Fox squirrels are influenced by understory vegetation height and have been observed to feed on the ground close to 70% of the time (Ditgen et al. 2007; Eisenberg et al. 2011). However, at finer scales of habitat selection, fox squirrels consistently selected areas with a hardwood component, likely because of the food and cover resources they provided. Within longleaf pine stands, fox squirrels concentrated their activities near riparian areas, which likely supported less fire-tolerant hardwood species that produce seasonally important cover and food resources (Hoctor et al. 2006). During our study, fox squirrels selected areas with more oak trees during all seasons of the year, highlighting the importance of oaks for food, cover, and nesting sites, which is similar to other studies (Hilliard 1979; Kantola 1986; Weigl et al. 1989; Powers 1993). Perkins et al. (2008) suggested that optimal fox squirrel habitat contains 88.2% mature pine cover and 11.8% hardwood cover; they speculated that the upland hardwood component could be lower if pine stands were adjacent to streams where hardwoods were more prevalent. At Fort Bragg, hardwoods were removed mechanically in upland stands, potentially restricting mature mast-producing oaks to riparian areas that did not burn or along firebreaks that provided a fire shadow (Lashley et al. 2014).

Fox squirrels in our study were similar to other tree squirrel species in their dependence on habitat heterogeneity. For example, Douman (2010) showed that Mexican fox squirrels (*S. nayaritensis*) used low-severity burned forests more heavily than those that burned at higher severities, but suggested heterogeneously burned forests may help distribute resources across forest patches. In Florida, Kantola and Humphrey (1990) observed Sherman's fox squirrels using ecotones between pine stands and hardwood stands. Further, Abert's squirrel (*S. aberti*), once believed to be dependent on ponderosa pine (*P. ponderosa*) forests (that have changed in ecological structure at least in part due to fire suppression—see Allen et al. 2002), showed adaptability to other tree species and forest types, indicating selection for structural components of forests (Edelman and Koprowski 2005). Indeed, in our study, fox squirrels depended on both pine and hardwood components for dietary and cover requirements, which indicate that burn heterogeneity on the landscape may improve habitat quality for fox squirrels.

Similar to other reports of oaks being important to fox squirrel resource selection (Weigl et al. 1989; Conner and Godbois 2003), squirrel relocations in our study were positively associated with increasing numbers of reproductively mature oak stems. However, we detected a negative association between fox squirrel relocations and hardwood DBH and largest pine DBH, which seems counterintuitive. We believe this was an artifact of our sampling, as most of the largest DBH hardwoods and pines were located in riparian areas at Fort Bragg which contain low densities of reproductively mature oaks (Lashley et al. 2014). Because fox squirrel relocations were often in ecotones, paired random points commonly fell well inside the riparian area and much closer to the large non-oak hardwoods (e.g., blackgum [*Nyssa sylvatica*], tulip poplar [*Liriodendron tulipifera*]) and pines (e.g., loblolly) that are common in more mesic conditions. Thus, squirrel selection for sites with the most oak trees, but not for the largest DBH hardwoods, supports the well-established importance of oaks to fox squirrels. Chamberlain et al. (1999) found that fox squirrel abundance increased with decreasing stand basal area, but only when percentage of hardwoods increased. Though we did not measure percentage of hardwood (or oak) in the stands, fire-maintained longleaf pine forests generally have low basal area in the uplands, which may help explain why fox squirrels at Fort Bragg showed selection for patches of oaks in uplands, but also concentrated use in close proximity to riparian areas.

Because oaks and other hardwoods provide important food and cover resources, management actions (i.e., frequent high-intensity fires, chemical treatments) that limit the abundance and distribution of mature hardwoods could decrease fox squirrel survival and reproductive success (Weigl et al.

1989; Conner and Godbois 2003). Nesting sites can include natural cavities and leaf nests and are critical to fox squirrels for a variety of reasons, including protection against predators and shelter from poor weather conditions (Baumgartner 1939; Moore 1957; Nixon et al. 1984). In North Carolina, fox squirrels used artificial cavities (nest boxes) more often in rainy or cold weather and during periods of low food supply (Weigl et al. 1989). Weigl et al. (1989) hypothesized that a lack of cavities for rearing young in upland areas was limiting fox squirrel populations in North Carolina. Evaluating the effects of frequent prescribed fires during the growing season on fox squirrel reproductive success could help determine whether relegation of hardwood stems to riparian areas provides the food and cover needed to sustain fox squirrel populations.

Frequent fires in upland pine stands likely benefited fox squirrels by preventing the succession of open, pine-dominated uplands to high-density hardwood stands favored by gray squirrels. When developing a prescribed-fire program, resource managers should strive to leave burns patchy, allowing for the regeneration and maturation of oaks and other hardwoods in areas of low topography and mesic areas adjacent to streams (i.e., in fire shadows). A frequent growing-season fire regime that suppresses hardwoods completely within upland pine stands should be balanced with low-intensity fires in riparian areas that shelter less fire-tolerant hardwood species. If riparian areas with canopy-level hardwoods are not widely distributed across a site, managers striving to maintain structural conditions that benefit fox squirrels should leave mature hardwoods scattered throughout fire-maintained upland pine stands, rather than completely eliminating them through mechanical removal or frequent growing-season fires.

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