The Journal of Wildlife Management; DOI: 10.1002/jwmg.395

Research Article

Habitat and Landscape Correlates of Southern Flying Squirrel Use of Red-Cockaded Woodpecker Clusters

SUSAN C. LOEB,[1] *USDA Forest Service, Southern Research Station, 233 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA*
SHAWNA L. REID, *USDA Forest Service, Southern Research Station, 233 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA*
DONALD J. LIPSCOMB, *Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA*

ABSTRACT Southern flying squirrels (*Glaucomys volans*) can have significant negative impacts on red-cockaded woodpecker (*Picoides borealis*) reproductive success and group size. Although direct control of southern flying squirrels may be necessary in small red-cockaded woodpecker populations (<30 groups), creation of high quality habitat through landscape management is the preferred method for managing larger woodpecker populations. Thus, we determined the habitat and landscape factors within 100 m, 400 m, and 800 m of cluster centers that were related to southern flying squirrel use of red-cockaded woodpecker cavities at the Carolina Sandhills National Wildlife Refuge, South Carolina. At all spatial scales, the number of cavities in the cluster was the most influential variable determining use by southern flying squirrels. At the 400-m and 800-m scales, the amount of stream length was also positively associated with the presence of flying squirrels. The proximity and amount of hardwoods surrounding clusters were not related to southern flying squirrel use at any spatial scale; thus, removal or conversion of hardwood stands surrounding red-cockaded woodpeckers may not be necessary for reducing cavity kleptoparasitism by flying squirrels. However, when establishing recruitment clusters, areas with streams should be avoided and addition of artificial cavities to existing clusters should be done judiciously to minimize the number of excess cavities. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS forest composition, *Glaucomys volans*, kleptoparasitism, landscape, *Picoides borealis*, red-cockaded woodpecker, South Carolina, southern flying squirrel.

The endangered red-cockaded woodpecker (*Picoides borealis*) inhabits mature, open longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pine stands across the southeastern United States (U.S. Fish and Wildlife Service 2003) where it is dependent on the cavities it excavates in living pines for reproduction and survival (Conner et al. 2001). Red-cockaded woodpeckers are cooperative breeders and form family groups that typically consist of a pair, with or without helpers (Walters 1990). Each bird roosts in its own cavity and a cavity cluster consists of the collection of cavity trees used by a group (Walters 1990).

Although still endangered, red-cockaded woodpeckers have exhibited considerable population growth and recovery over the past few decades due to a variety of management and recovery strategies including translocation, creation of artificial cavities, habitat management, and private lands initiatives (Costa 2004). Managers have used artificial cavities and translocation techniques to establish new populations of red-cockaded woodpeckers in sites where they were not known to exist previously (Hagan et al. 2004), or recover populations that were on the brink of extirpation or had been extirpated (e.g., Gaines et al. 1995, Brown and Simpkins 2004, Hedman et al. 2004, Stober and Jack 2004). However, cavity usurpation or kleptoparasitism often occurs (e.g., Dennis 1971, Harlow and Lennartz 1983) and can impede establishment or recovery of small populations (e.g., Gaines et al. 1995).

Several species are kleptoparasites of red-cockaded woodpecker cavities, but the most common species are southern flying squirrels (*Glaucomys volans*) and red-bellied woodpeckers (*Melanerpes carolinus*; Dennis 1971, Harlow and Lennartz 1983, Rudolph et al. 1990*a*, Loeb 1993, Kappes 2008). Southern flying squirrels use red-cockaded woodpecker cavities year-round as day-time refuges and for rearing young, but cavity use is greatest during the red-cockaded woodpecker breeding season (Loeb and Ruth 2004). Although southern flying squirrel impacts on red-cockaded woodpeckers may be minimal or vary among years in some populations (Conner et al. 1996, Mitchell et al. 1999, Johnston 2006), they have been shown to have significant negative impacts on red-cockaded woodpeckers in other populations (Laves and Loeb 1999, Kappes 2008). In South Carolina, removal of southern flying squirrels from red-cockaded woodpecker cavities resulted in an increase of

Received: 15 August 2011; Accepted: 10 February 2012

[1] *E-mail: sloeb@fs.fed.us*

0.7 fledglings per group per year (Laves and Loeb 1999). Flying squirrels decrease fledging success by usurping red-cockaded woodpeckers from their cavities (Kappes 1997, Ridley et al. 1997) and crushing or eating their eggs or nestlings (Stabb et al. 1989, LaBranche and Walters 1994, Ortego et al. 1995, Richardson and Stockie 1995, Miller 2002). Flying squirrel use of red-cockaded woodpecker clusters also results in partial nest loss. Although the mechanism by which partial nest loss occurs is not known, flying squirrel attempts to enter cavities may disrupt incubation of the eggs by males at night (Laves and Loeb 1999). Flying squirrel use of red-cockaded woodpecker cavities also reduces group size (Laves and Loeb 1999, Kappes 2008), which is positively correlated with reproductive success (Walters 1990, Conner et al. 2004) and breeder survival (Khan and Walters 2002).

Because southern flying squirrels have the potential to significantly affect red-cockaded woodpecker cavity availability, reproductive success, and survival, several techniques have been tested or implemented to reduce their impacts including removal (Gaines et al. 1995, Hedman et al. 2004, Stober and Jack 2004), exclusion devices (Montague et al. 1995, Loeb 1996), nest boxes (Loeb and Hooper 1997, Borgo et al. 2006*b*), snag retention (Kappes and Harris 1995), and deterrents such as predator scents (Borgo et al. 2006*a*, Stober and Conner 2007). The United States Fish and Wildlife Service (2003) suggests that control methods only be used in critically small populations of red-cockaded woodpeckers (<30 potential breeding groups). In larger populations, an ecosystem management approach that considers the habitat needs of all native species in the region should be taken, and management should be conducted at the landscape scale rather than focusing on individual clusters.

Habitat management for red-cockaded woodpeckers often focuses on removing the hardwood midstory from cluster sites (U.S. Fish and Wildlife Service 2003) because hardwood encroachment in clusters leads to cluster abandonment (Conner and Rudolph 1989, Loeb et al. 1992). The cause of abandonment in response to hardwood midstory encroachment is not known, but some have speculated that a dense hardwood midstory may attract southern flying squirrels and other cavity kleptoparasites (Conner and Rudolph 1989, Loeb et al. 1992). Flying squirrels in southern forests are dependent on oak and hickory mast (Harlow and Doyle 1990) and select nest trees in pine-hardwood habitats (Taulman 1999). During winter, flying squirrels are more abundant in pine stands with dense hardwood midstories than in those with sparse hardwood midstories (Heiterer 1994). This suggests that reducing hardwoods in red-cockaded woodpecker clusters could reduce cavity usurpation by southern flying squirrels. However, hardwood midstory removal within red-cockaded woodpecker clusters did not result in a reduction of southern flying squirrel use of red-cockaded woodpecker cavities in Texas (Conner et al. 1996) and Mitchell et al. (2005) did not find a correlation between hardwood density within a cluster and the number of squirrels using red-cockaded woodpecker cavities in Georgia.

The lack of a correlation between the presence or amount of hardwoods within a cluster and southern flying squirrel cavity use may be due to several factors. Flying squirrels can move up to 1 km between nest sites and foraging areas (Taulman and Smith 2004), and home range sizes range from 2 ha to >16 ha (Bendel and Gates 1987, Fridell and Litvaitis 1991, Taulman and Smith 2004, Holloway and Malcolm 2007*a*). Thus, flying squirrels may not require hardwoods within a cluster if sufficient hardwoods exist within their foraging range. Furthermore, the greater abundance of southern flying squirrels in pine stands with a hardwood midstory during winter is due primarily to a greater number of juveniles in these stands (Heiterer 1994). Areas with hardwoods may act as source habitats for southern flying squirrels with subsequent dispersal of juveniles into areas without hardwoods during the spring and summer. Thus, red-cockaded woodpecker clusters that are surrounded by pine-hardwood and hardwood stands may be more likely to contain southern flying squirrels than those surrounded by pine forests.

Our objective was to test whether the habitat surrounding red-cockaded woodpecker clusters was a significant determinant of southern flying squirrel use of clusters. We predicted that the amount and proximity of hardwood and pine-hardwood forest surrounding red-cockaded woodpecker clusters would be positively related to southern flying squirrel use of red-cockaded woodpecker clusters. Because southern flying squirrels select riparian zones for nightly foraging (Taulman and Smith 2004) and roads can be an impediment to small mammal movements (Oxley et al. 1974, Hughes 2006, Ford and Fahrig 2008), we predicted that southern flying squirrel use of clusters would be positively associated with streams and negatively associated with roads. Habitat use and flying squirrel density are positively associated with the number of snags or declining trees, presumably because they contain abundant cavities (Fridell and Litvaitis 1991, Holloway and Malcolm 2006). Thus, we included cavity availability in our models and predicted that southern flying squirrel use of red-cockaded woodpecker clusters would be positively related to cavity availability. We also tested whether cavity size, cavity type, and the status of the resin wells surrounding the cavities affected use. Previous studies have examined cavity size and the status of resin wells as factors affecting cavity selection by southern flying squirrels (Rudolph et al. 1990*a*, Loeb 1993, Laves and Loeb 1999) but only Lotter (1997) examined selection of southern flying squirrel use of artificial versus natural cavities. Because the response of southern flying squirrels to habitat variables may vary with scale (Holloway and Malcolm 2006), we examined the relationship of southern flying squirrel use of red-cockaded woodpecker clusters to forest composition at 3 spatial scales: 100 m, 400 m, and 800 m from the cluster center.

STUDY AREA

We conducted our study on the Carolina Sandhills National Wildlife Refuge (CSNWR) in Chesterfield County, South Carolina (Fig. 1). The refuge was approximately 18,300 ha

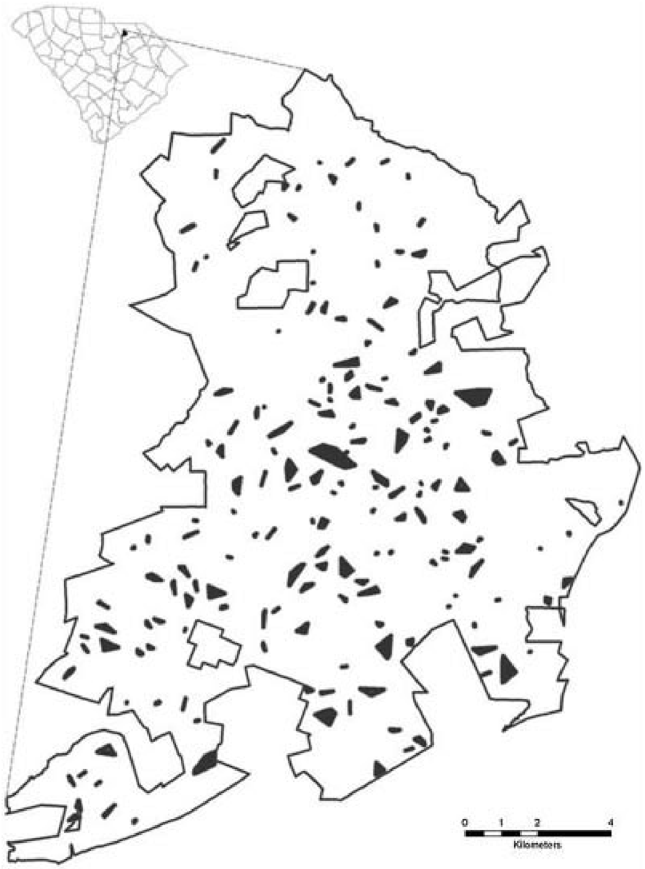

Figure 1. Location of Carolina Sandhills National Wildlife Refuge within South Carolina and a depiction of red-cockaded woodpecker clusters included in this study (solid polygons). Open polygons within the refuge boundary represent private land that was not included in this study.

and was located in the Sandhills Physiographic Region. Thirty-year (1971–2000) average maximum temperatures at the nearest weather reporting station (Cheraw, SC) during April, May, and June ranged from 23.3° C to 30.7° C and average minimum temperatures ranged from 8.2° C to 18.2° C (Southeast Regional Climate Center, www.sercc.com/cgi-bin/sercc/cliMAIN.pl?sc1588, accessed 1 Aug 2011). Average rainfall during April through June ranged from 83 mm to 122 mm.

The refuge was predominately (87%) pine forest. Longleaf pine was the dominant species, but loblolly pine, slash pine (*P. elliotii*), and pond pine (*P. serotina*) were also present. Approximately 35% of the pine acreage was in plantations and approximately 13% was pine-scrub. Pine-hardwood stands made up 3.0% of the forest area, upland hardwood stands made up 1.2%, and bottomland hardwood stands made up 4.7%. Hardwoods were dominated by oaks (*Quercus* spp.) and were common along streams, on lower slopes, and as part of the midstory of many pine stands. Several creeks and ponds were distributed across the refuge. The majority of the forest area (86%) was sawtimber- or pulpwood-sized trees. The remainder of CSNWR was made up of seedling or sapling stage forests, open fields, ponds, and lakes. CSNWR was actively managed for red-cockaded woodpeckers including dormant and growing season burns, roller-chopping to reduce the midstory within clusters, placement of restrictor plates on enlarged cavities, and installation of artificial cavities. At the time of the study, approximately 90 active red-cockaded woodpecker groups resided in the area with additional inactive trees and clusters (Fig. 1).

METHODS

We conducted our study during the red-cockaded woodpecker breeding seasons (Apr–Jun) of 1998 and 1999. We inspected all known red-cockaded woodpecker cavities on the refuge ≤ 10 m high with a camera (MDP type 2R Microcam 25; Furhman Diversified, Inc., Seabrook, TX) mounted on a 10-m extension pole. We climbed trees with cavities >10 m high with Swedish ladders and inspected cavities with a droplight and mirror. We inspected cavities once per year unless they were newly created between 1998 and 1999, had not been located in 1998, could not be re-located by the observer in 1999, or broke or fell between 1998 and 1999. We recorded cavity height, relative entrance size (normal or enlarged), the status of the resin wells (active or inactive), cavity type (natural or artificial), and the cavity contents. Two types of artificial cavities were used on CSNWR, drilled cavities, and artificial inserts. Drilled cavities are made by drilling 2 tunnels into a mature (≥ 80 yr) pine with ≥ 15.5 cm of heartwood (Copeyon 1990). Artificial cavity inserts are pre-fabricated boxes with pre-drilled cavities that are inserted into an opening made in the tree with a chainsaw (Allen 1991). Cavities classified as active had well-maintained resin wells surrounding the cavity entrance whereas little or no resin surrounded inactive cavities, or the resin that was present had hardened and was no longer sticky (Hooper et al. 1980). We recorded the location of each cavity tree with a Trimble PRO-XR or a Trimble GeoExplorer (Trimble Navigation Limited, Sunnyvale, CA).

At the time of this study, cavity trees at the refuge were not assigned to specific red-cockaded woodpecker clusters. Therefore, we defined clusters using methods developed by Lipscomb and Williams (1996) that were based on United States Fish and Wildlife guidelines (Henry 1989, U.S. Fish and Wildlife Service 2003). We assigned all trees within 122 m of each other to a cluster and created a 61-m buffer around the polygon (convex hull plus 61 m) containing these trees (Lipscomb and Williams 1995). We included outlying single trees that were not assigned to the cluster, but were <402 m from it, in the cluster and expanded the buffer to include these trees. This method has an 86–95% accuracy rate of assignment (Lipscomb and Williams 2004). We determined the geographic center of the cluster using the Arcscript centroid.dll (ESRI, Redlands, CA), which calculates the center of the weighted area.

We created a Geographic Information System (GIS) database using ArcGIS 8.3 (ESRI). We scanned stand and compartment maps created by the CSNWR forestry staff, which included stand boundaries, forest types, and size class (e.g., sawtimber, pole timber), digitally converted them to vectored line features, and georeferenced the maps using

ERDAS Imagine software (ERDAS, Inc., Norcross, GA). Because we were primarily interested in whether flying squirrel use of clusters was related to pine versus hardwood forest types and riparian zones, we combined forest types into pine (natural pine stands and pine plantations), pine-hardwood (pine-hardwood and pine-scrub stands), upland hardwood (scrub oak and upland hardwood stands), and bottomland (pine bottomland and bottomland hardwood). The GIS database also included road and stream layers. We obtained the road layer from CSNWR and the stream layer from the South Carolina Department of Natural Resources and the National Wetlands Inventory Database. For each cluster, we determined the amount of each forest type (ha), the total length of roads (km), and the total length of streams (km) within 100 m, 400 m, and 800 m of each cluster center; the distance to the closest road, stream, cluster edge, and cluster center; and the cluster area. We based the 3 spatial scales on distances moved by southern flying squirrels on a nightly and seasonal basis (Bendel and Gates 1987, Fridell and Litvaitis 1991, Taulman and Smith 2004, Holloway and Malcolm 2007*a*).

Data Analysis

We used chi-squared tests of independence to test whether southern flying squirrels selected cavities based on relative cavity size, resin activity, and cavity type. Because of the low number of drilled cavities (9), we combined drilled and insert cavities for analysis.

We used logistic regression and an information–theoretic approach to determine the most influential variables related to southern flying squirrel use of red-cockaded woodpecker clusters at each spatial scale. We considered each inspection of a cavity an observation and we classified a cluster as used if $\geq$1 southern flying squirrel was observed in a cluster during 1998 or 1999; we excluded clusters that had $<$4 observations from subsequent analyses. The 400-m and 800-m radius circles of some clusters, particularly those on the refuge edge, included areas for which we had no data on forest type. We excluded these clusters from the analyses at spatial scales for which we were missing data. Thus, sample size varied among spatial scales (169 clusters at the 100-m scale, 148 clusters at the 400-m scale, and 119 clusters at the 800-m scale) and we ran models for each scale separately. We developed 4 a priori models (Table 1) for each spatial scale, and tested each of these models separately and in all possible combinations with the other models. Thus, we tested 16 models including the null and global models at each spatial scale. Prior to developing models we tested for collinearity among variables and deleted 1 variable of each pair that was highly correlated ($r > 0.70$). Pine and pine-hardwood area were highly correlated at the 100-m and 400-m scale, road length and distance to roads were highly correlated at the 400-m scale, and number of cavity trees and cluster area, and distance to closest cluster center and distance to closest cluster edge were highly correlated at all scales. Thus, we did not include pine area, distance to roads, cluster area, or distance to closest cluster edge in our models. Further, because only 2 clusters had streams within 100 m, models including stream length at the 100-m scale did not converge because of quasi-separation of data points. Thus, stream length was not included in bottomland models at the 100-m scale (Table 1).

We tested model fit of the global model at each spatial scale using the Hosmer–Lemshow test. We used Akaike's Information Criteria corrected for small sample sizes (AIC_c), the difference between the lowest AIC_c and the AIC_c for the ith model (Δ_i), and Akaike weights (w_i) to identify the most parsimonious model or model set (Burnham and Anderson 2002). We calculated model-averaged parameter estimates and unconditional standard errors for the model set that made up $\geq$90% of the model weights (Burnham and Anderson 2002) and calculated 85% confidence intervals for each variable as suggested by Arnold (2010).

RESULTS

We examined 883 cavities in 793 trees in 1998 and 923 cavities in 808 trees in 1999; we examined 707 trees in both years, 86 in 1998 only and 101 in 1999 only. Red-cockaded woodpeckers or evidence of their nests (e.g., a layer of fresh wood chips, eggs, or nestlings) were the most common occupant of cavities and were found in 24.6% and 28.4% of the cavities in 1998 and 1999, respectively. Southern flying squirrels were the most common species other than red-cockaded woodpeckers and were found in 18.7% and 19.0% of cavities in 1998 and 1999. Birds other than red-cockaded woodpeckers or their nests were found in 6.0% and 7.2% of cavities in 1998 and 1999, respectively. Bird species

Table 1. Variables in each of 4 logistic regression models to predict the presence of southern flying squirrels in red-cockaded woodpecker clusters in the Carolina Sandhills National Wildlife Refuge, April through June, 1998–1999.

Model	Variables	Definition
Cavity	Cavity trees	Number of cavity trees in the cluster
	Distance to cluster center	Distance (km) to the closest cluster center
Hardwood	Pine-hardwood	Total amount of pine-hardwood forest (ha) within 100 m, 400 m, or 800 m of the cluster center
	Upland hardwood	Total amount of upland hardwood forest (ha) within 100 m, 400 m, or 800 m of the cluster center
	Bottomland	Total amount of bottomland forest (ha) within 100 m, 400 m, or 800 m of the cluster center
	Distance to hardwood	Distance to the closest hardwood stand (km)
Bottomland	Bottomland	Total amount of bottomland forest (ha) within 100 m, 400 m, or 800 m of the cluster center
	Distance to stream	Distance to the closest stream (km)
	Streams[a]	Total length (km) of streams within 400 m or 800 m of the cluster center
Roads	Roads	Total length (km) of roads within 100 m, 400 m, or 800 m of the cluster center

[a] This variable was not included in the 100-m scale models.

Table 2. Number (*n*) and percent of available (% avail) red-cockaded woodpecker cavities that were artificial or natural, enlarged or non-enlarged, and active or inactive, and the percent usage by southern flying squirrels at the Carolina Sandhills National Wildlife Refuge, South Carolina, USA, April through June, 1998–1999.

	1998			**1999**		
Cavity characteristic	***n***	**% Avail**	**% Use**	***n***	**% Avail**	**% Use**
Artificial	161	18.3	26.1	186	20.2	23.4
Natural	717	81.7	73.9	736	79.8	76.6
Non-enlarged	712	80.6	95.8	643	69.7	80.0
Enlarged	171	19.4	4.2	279	30.3	20.0
Active	308	34.9	34.6	230	24.9	10.9
Inactive	575	65.1	65.4	693	75.1	89.1

we encountered included eastern screech owl (*Otus asio*), northern flicker (*Colaptes auratus*), eastern bluebird (*Sialia sialis*), great crested flycatcher (*Myiarchus crinitus*), American kestrel (*Falco sparverius*), wood duck (*Aix sponsa*), tufted titmouse (*Baeolophus bicolor*), and red-bellied woodpecker. We found unidentified nest material or debris in 28.5% and 24.6% of the cavities in 1998 and 1999, respectively. Other species found in small numbers were fox squirrel (*Sciurus niger*), unidentified snakes, an unidentified bat, and bees.

In 1998, southern flying squirrels used artificial cavities in greater proportion than their availability ($\chi^2_1 = 8.09$, $P = 0.004$; Table 2). However, in 1999 flying squirrels used cavity types in proportion to their availability ($\chi^2_1 = 1.42$, $P = 0.23$). In both years, southern flying squirrels selected non-enlarged cavities over enlarged cavities ($\chi^2_1 = 29.72$, $P \leq 0.001$ in 1998 and $\chi^2_1 = 10.78$, $P = 0.001$ in 1999; Table 2). Flying squirrels used active and inactive cavities in proportion to their availability in 1998 ($\chi^2_1 = 0.01$, $P = 0.92$), but in 1999, they selected cavities with inactive resin wells over those with active resin wells ($\chi^2_1 = 22.82$, $P \leq 0.001$; Table 2).

Based on the Hosmer–Lemeshow test, the global models at all scales adequately fit the logistic model (100 m: $\chi^2_8 = 2.98$, $P = 0.935$; 400 m: $\chi^2_8 = 6.21$, $P = 0.642$; 800 m: $\chi^2_8 = 6.75$, $P = 0.56$). The null model was not included in any of the 90% model sets except at the 800-m scale and it had little support at that scale (Table 3). At the 100-m scale, all of the top models included variables associated with cavity availability and the top model included cavity variables only (Table 3). The presence of flying squirrels was positively associated with the number of cavity trees within a cluster (Table 4). Clusters with flying squirrels were farther from other clusters (Table 5), but the parameter estimate for this variable included zero, suggesting that it did not have a strong influence on cluster use (Table 4). The second most likely model at the 100-m scale included cavity availability and bottomland variables. Flying squirrel presence was positively related to the amount of bottomland forest and negatively related to the distance to the closest stream although the confidence intervals on parameter estimates for both variables included zero (Table 4). Hardwood availability and road length were also included in some of the top models (Table 3), but distance to hardwoods was the only

Table 3. Models predicting use of red-cockaded woodpecker clusters by southern flying squirrels at Carolina Sandhills National Wildlife Refuge, South Carolina, April through June, 1998–1999 included in the model sets ($\Sigma w_i \geq 0.90$), number of clusters included in each model (*n*), number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), the difference between the model with lowest AIC_c and the model's AIC_c (ΔAIC_c), and Akaike model weights (w_i), at each spatial scale (100 m, 400 m, and 800 m from the cluster center).

Model	***n***	***K***	**AIC_c**	**ΔAIC_c**	**w_i**
100 m					
Cavity	169	3	185.864	0	0.264
Cavity + Bottomland	169	5	186.305	0.442	0.211
Cavity + Roads	169	4	186.977	1.113	0.151
Cavity + Bottomland + Roads	169	6	187.750	1.887	0.102
Cavity + Hardwood	169	7	188.094	2.230	0.086
Cavity + Hardwood + Bottomland	169	8	188.242	2.378	0.080
Cavity + Hardwood + Roads	169	8	188.827	2.964	0.060
400 m					
Cavity + Bottomland	148	6	156.167	0	0.456
Cavity	148	3	157.505	1.338	0.234
Cavity + Bottomland + Roads	148	7	158.264	2.097	0.160
Cavity + Roads	148	4	159.376	3.209	0.092
800 m					
Cavity + Bottomland	119	6	130.442	0	0.262
Cavity	119	3	131.120	0.678	0.187
Cavity + Bottomland + Road	119	7	131.652	1.210	0.143
Cavity + Roads	119	4	132.026	1.584	0.119
Bottomland	119	4	132.498	2.056	0.094
Bottomland + Roads	119	5	133.277	2.835	0.064
Null	119	1	134.196	3.754	0.040

Table 4. Average parameter estimates, unconditional standard errors, and 85% confidence intervals for the parameter estimates for variables included in supported models ($\Sigma w_i \geq 0.90$) predicting use of red-cockaded woodpecker clusters by southern flying squirrels at Carolina Sandhills National Wildlife Refuge, South Carolina April through June 1998–1999.

Scale	Variable	Estimate	SE	85% CI
100 m	Number of cavity trees	0.4870	0.1286	0.3018, 0.6722
	Distance cluster center (km)	0.6076	0.9436	−0.7512, 1.9664
	Pine-hardwood area (ha)	0.0883	0.2512	−0.2734, 0.4500
	Upland hardwood area (ha)	−0.8440	1.1225	−2.4604, 0.7724
	Distance to hardwood stand (km)	2.8998	1.9100	0.1494, 5.6502
	Bottomland area (ha)	1.4191	1.2847	−0.4309, 3.2691
	Distance to stream (km)	−0.9017	0.7196	−1.9379, 0.1345
	Road length (km)	1.9509	2.0417	−0.9891, 4.8909
400 m	Number of cavity trees	0.4216	0.1383	0.2224, 0.6208
	Distance cluster center (km)	0.5123	1.1918	−1.2039, 2.2285
	Bottomland area (ha)	−0.1000	0.0624	−0.1899, −0.0101
	Distance to nearest stream (km)	−0.3778	1.2101	−2.1203, 1.3647
	Stream length (km)	1.8322	0.9666	0.4403, 3.2241
	Road length (km)	−0.1490	0.3827	−0.7001, 0.4021
800 m	Number of cavity trees	0.3036	0.1390	0.1034, 0.5038
	Distance cluster center (km)	−0.5133	1.2900	−2.3709, 1.3443
	Bottomland area (ha)	−0.0341	0.0175	−0.0593, −0.0089
	Distance to nearest stream (km)	−0.1081	1.2900	−1.9657, 1.7495
	Stream length (km)	0.6910	0.3610	0.1712, 1.2108
	Road length (km)	0.2009	0.1861	−0.0671, 0.4689

variable that had a parameter estimate with confidence intervals that did not include zero (Table 4). Surprisingly, clusters with flying squirrels were farther from hardwood stands than those without flying squirrels (Table 5).

At the 400-m scale, the model that included cavity availability and bottomland variables had the strongest support and was almost twice as likely to be the best-approximating model than the next model which included cavity variables only (Table 3). None of the top models included hardwood variables. Only the parameter estimates for number of cavity trees, bottomland area, and stream length had confidence intervals that did not include zero (Table 4). Clusters with southern flying squirrels had more cavity trees and more stream length compared to those that did not have southern

Table 5. Number of clusters, means, and standard errors of landscape variables within 100 m, 400 m, and 800 m surrounding red-cockaded woodpecker clusters used and not used by southern flying squirrels at Carolina Sandhills National Wildlife Refuge, South Carolina April through June 1998–1999.

	Used			Not used		
Variable	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
100 m						
Number of cavity trees	121	5.231	0.294	48	3.458	0.197
Distance cluster center (km)	121	0.527	0.019	48	0.497	0.024
Pine-hardwood area (ha)	121	0.580	0.086	48	0.680	0.142
Upland hardwood area (ha)	121	0.018	0.009	48	0.062	0.038
Bottomland area (ha)	121	0.071	0.028	48	0.026	0.022
Distance to hardwood stand (km)	121	0.130	0.013	48	0.100	0.016
Distance to stream (km)	121	0.402	0.023	48	0.468	0.036
Road length (km)	121	0.068	0.008	48	0.054	0.012
400 m						
Number of cavity trees	111	5.180	0.302	37	3.568	0.231
Distance cluster center (km)	111	0.512	0.017	37	0.479	0.024
Pine-hardwood area (ha)	111	8.208	0.758	37	8.753	1.210
Upland hardwood area (ha)	111	0.580	0.112	37	0.553	0.175
Bottomland area (ha)	111	3.243	0.375	37	3.645	0.734
Distance to hardwood stand (km)	111	0.120	0.013	37	0.110	0.019
Distance to stream (km)	111	0.390	0.022	37	0.462	0.035
Stream length (km)	111	0.353	0.037	37	0.207	0.056
Road length (km)	111	0.919	0.524	37	0.956	0.092
800 m						
Number of cavity trees	90	5.067	0.351	29	3.724	0.276
Distance cluster center (km)	90	0.493	0.018	29	0.505	0.029
Pine-hardwood area (ha)	90	32.095	2.116	29	35.468	4.295
Upland hardwood area (ha)	90	3.447	0.427	29	2.953	0.552
Bottomland Area (ha)	90	20.042	1.674	29	22.168	3.182
Distance to hardwood stand (km)	90	0.124	0.015	29	0.103	0.021
Distance to stream (km)	90	0.379	0.023	29	0.453	0.041
Stream length (km)	90	1.814	0.114	29	1.406	0.204
Road length (km)	90	3.483	0.126	29	3.166	0.243

flying squirrels; however, the amount of bottomland forest surrounding clusters with flying squirrels was lower than that surrounding clusters without flying squirrels (Table 5).

Several strongly competing models explained southern flying squirrel use of red-cockaded woodpecker clusters at the 800-m scale (Table 3). The top 4 models included cavity variables, and bottomland variables were in 4 of the top 7 models, including the top model. Again, none of the top models included hardwood variables. Number of cavities, bottomland forest area, and stream length had parameter estimates with confidence intervals that did not include zero (Table 4). Similar to the 400-m scale, flying squirrels used clusters with more cavities, had lower amount of bottomland forest area, but had greater amounts of stream length (Table 5).

DISCUSSION

Southern flying squirrels were common inhabitants of red-cockaded woodpecker clusters on CSNWR during our study and the number of cavity trees within clusters was influential in explaining use of red-cockaded woodpecker clusters across the 3 scales we examined. At the 400-m and 800-m scales, flying squirrel use of red-cockaded woodpecker clusters was also positively associated with stream length, but negatively associated with the amount of bottomland forest. Contrary to our predictions, the amount of hardwood forest and the distance to hardwood stands were not influential variables at any spatial scale except 100 m. However, at the 100-m scale, flying squirrels were more likely to use clusters that were farther from hardwood stands, not closer as we expected. This suggests that removal or conversion of hardwood stands in the areas surrounding red-cockaded woodpecker clusters will not decrease the use of clusters by southern flying squirrels, although it may increase red-cockaded woodpecker foraging habitat suitability (Conner et al. 2001, U.S. Fish and Wildlife Service 2003).

As in previous studies, flying squirrels selected normal (non-enlarged) cavities over enlarged cavities (Rudolph et al. 1990*a*, Loeb 1993, Laves and Loeb 1999). Use of non-enlarged cavities may reduce competition with larger species such as gray squirrels (*Sciurus carolinensis*) and fox squirrels (Muul 1968, Bendel and Gates 1987), and non-enlarged cavities are less likely to contain water (Loeb 1993). Similar to another site in the Sandhills-Upper Coastal Plain of South Carolina (Lotter 1997), flying squirrels at CSNWR used artificial cavities in greater proportion than their availability in both years of the study although the difference in use of artificial and natural cavities was only statistically significant in 1998. Artificial cavity inserts have a metal restrictor plate to prevent enlargement by pileated woodpeckers (*Dryocopus pileatus*) and other species (Allen 1991) and thus, flying squirrels may select them because of their small openings. Further, only a small number of artificial inserts in our study were used by red-cockaded woodpeckers (13 in 1998 and 10 in 1999), and the lack of competition with red-cockaded woodpeckers may have made them more suitable for use by southern flying squirrels (Borgo et al. 2006*b*).

Red-cockaded woodpeckers excavate small holes in the cambium surrounding the cavity resulting in a layer of sticky resin around the entire cavity entrance area (Conner et al. 2001). The active maintenance of these resin wells suggests that this behavior evolved to deter rat snakes (*Elaphe obsoleta*), a major predator of red-cockaded woodpeckers, from entering the cavities (Rudolph et al. 1990*b*, Conner et al. 2001). The presence of fresh resin did not deter flying squirrels from using red-cockaded woodpecker cavities in 1998 although they avoided cavities with fresh resin in 1999. Rat snakes are effective predators on southern flying squirrels (Rudolph et al. 2009), and the resin barrier deters rat snakes from entering red-cockaded woodpecker cavities (Rudolph et al. 1990*b*). However, the lack of consistent selection or avoidance of cavities with fresh resin across years and studies (Rudolph et al. 1990*a*, Loeb 1993, this study) suggests that there has not been sufficient selective pressure on southern flying squirrels to select cavities with fresh resin, perhaps because red-cockaded woodpecker cavities represent a small proportion of nest sites used by flying squirrels.

The number of cavity trees within clusters was an influential variable explaining southern flying squirrel use of red-cockaded woodpecker clusters across all spatial scales. The number of cavity trees also explains southern flying squirrel use of red-cockaded woodpecker clusters at the Savannah River Site in South Carolina (Lotter 1997). In contrast, the number of southern flying squirrels using red-cockaded woodpecker cavities is not influenced by the number of red-cockaded woodpecker cavities in clusters at Fort Stewart, Georgia (Mitchell et al. 2005). Even though southern flying squirrel populations in the Upper Coastal Plain of South Carolina are not limited by nest sites (Brady et al. 2000), they appear to be attracted to areas with numerous cavities for nesting. Artificial cavities and nest boxes are readily used by flying squirrels in a variety of pine forests throughout the southeastern United States (Loeb and Hooper 1997, Lotter 1997, Taulman et al. 1998, Brady et al. 2000, Borgo et al. 2006*b*) and our data suggest that addition of artificial cavities may result in greater use of clusters by southern flying squirrels. Interactions among cavity nesters in southeastern pine forests are often complex, and removal or addition of cavity nesters through cavity exclusion, species removal, or addition of nest sites may have unintended consequences (Blanc and Walters 2008, Kappes and Davis 2008). Because flying squirrels may also select artificial cavities over natural cavities (Lotter 1997, this study), addition of a large number of artificial cavities may result in increased cavity competition between southern flying squirrels and red-cockaded woodpeckers, not less. Thus, artificial cavity provisioning in existing clusters should be done judiciously and with a clear plan as suggested by the United States Fish and Wildlife Service (U.S. Fish and Wildlife Service 2003).

Southern flying squirrel use of red-cockaded woodpecker cavities was also associated with stream length at the 400-m and 800-m scales. Many studies have examined microhabitat features related to southern flying squirrel nest and foraging habitats (e.g., Sonenshine and Levy 1981; Bendel and Gates 1987; Fridell and Litvaitis 1991; Taulman and Smith 2004; Holloway and Malcolm 2007*a*, *b*). However, only Nupp and Swihart (2000) examined landscape factors affecting habitat use, and their study concentrated on characteristics such as patch area and connectivity in a highly fragmented agricultural landscape. To our knowledge, no data are available on whether southern flying squirrels select nest sites in close proximity to streams or other water bodies, although Taulman and Smith (2004) found that southern flying squirrels selected riparian areas for foraging. However, during summer, fox squirrels in the Sandhills and Coastal Plain of North Carolina shift their activity away from longleaf pine stands to moister lowland habitats perhaps because of cooler temperatures, more abundant food, and better access to water (Weigl et al. 1989). The amount of bottomland forest was not more abundant in the areas surrounding used clusters even though stream length was, suggesting that southern flying squirrels in the xeric Sandhills landscape may require easy access to water (Wharton 1978). Future studies of southern flying habitat use should examine the influence of riparian areas on habitat selection, particularly in drier habitat types.

Contrary to our predictions, the presence or proximity of hardwood stands were not associated with southern flying squirrel use of red-cockaded woodpecker clusters at larger spatial scales, and at the scale of the cluster (100 m), southern flying squirrels were more likely to use clusters that were farther from hardwood stands. Two factors may have contributed to the lack of a relationship between hardwoods and southern flying squirrel use of red-cockaded woodpecker clusters on CSNWR. Hardwoods represent a small percentage of the forested area of CSNWR and southern flying squirrels may not select for hardwoods during summer when hardwood mast is less available (Edwards et al. 1993). Further, although hardwood stands on the refuge were sparse, all clusters were relatively close (mean distance 100–130 m) to at least 1 hardwood, pine-hardwood, or pine-scrub stand, and some clusters were contained in pine-hardwood or pine-scrub habitats.

Our data, along with those of Conner et al. (1996) and Mitchell et al. (2005) suggest a small amount of hardwood acreage distributed across the landscape may be sufficient to support flying squirrels during the summer. Thus, reducing the amount of hardwood stands in the vicinity of red-cockaded woodpecker clusters is not necessary as this is not likely to reduce use of the clusters by southern flying squirrels. Maintaining some hardwoods across the landscape will provide resources for other species associated with longleaf pine habitats, such as fox squirrel (Perkins et al. 2008), wild turkey (*Meleagris gallopavo*), and white-tailed deer (*Odocoileus virginianus*; Yarrow and Yarrow 1999).

MANAGEMENT IMPLICATIONS

Reduction of hardwoods within cluster sites and foraging habitat is a hallmark of current red-cockaded woodpecker management (U.S. Fish and Wildlife Service 2003). Our data and that of Conner et al. (1996) and Mitchell et al. (2005) suggest that reduction of hardwoods either within clusters or the surrounding areas will not reduce potential interactions between red-cockaded woodpeckers and southern flying squirrels. Thus, hardwood reductions beyond those in the guidelines to maintain quality red-cockaded woodpecker nesting and foraging habitat are not warranted.

Red-cockaded woodpeckers are less likely to initiate a nest or fledge young when ≥ 1 cavity is occupied by another species (Loeb and Hooper 1997). We found that southern flying squirrels sometimes select artificial cavities and also found a strong positive relationship between southern flying squirrel cluster use and the number of red-cockaded woodpecker cavity trees; therefore, we suggest that installation of artificial cavities should be done cautiously and only where needed to maintain at least 4–6 suitable cavities in active and recruitment clusters as suggested by the United States Fish and Wildlife Service (2003). Further, recruitment clusters should be established to minimize the amount of stream length within them as these clusters may be more likely to experience interference from southern flying squirrels.

ACKNOWLEDGMENTS

We thank the staff of the Carolina Sandhills National Wildlife Refuge for their logistical support and assistance throughout this study. We especially thank C. Ware for assistance with development of the GIS database. We also thank P. D. Brose, C. A. Dachelet, and D. Fox for assistance in the field and P. G. R. Jodice, P. A. Johnston, D. Saenz, and S. J. Zarnoch for providing helpful comments on previous drafts of this study.

LITERATURE CITED

Allen, D. H. 1991. An insert technique for constructing artificial red-cockaded woodpecker cavities. U.S. Forest Service, Southeastern Forest Experiment Station, General Technical, Report SE-73, Asheville, North Carolina, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178.

Bendel, P. R., and J. E. Gates. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). Journal of Mammalogy 68:243–255.

Blanc, L. A., and J. R. Walters. 2008. Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. Ecology 89:506–514.

Borgo, J. S., L. M. Conner, and M. R. Conover. 2006*a*. Role of predator odor in roost site selection of southern flying squirrels. Wildlife Society Bulletin 34:144–149.

Borgo, J. S., M. R. Conover, and L. M. Conner. 2006*b*. Nest boxes reduce flying squirrel use of red-cockaded woodpecker cavities. Wildlife Society Bulletin 34:171–176.

Brady, M. J., T. S. Risch, and F. S. Dobson. 2000. Availability of nest sites does not limit population size of southern flying squirrels. Canadian Journal of Zoology 78:1144–1149.

Brown, C. V., and S. Simpkins. 2004. The Chickasawhay story: saving a small population from certain extinction. Pages 361–367 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Second edition. Spring-Verlag, Inc, New York, New York, USA.

Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett and Sabine National Forests. U.S. Forest Service, Southern Forest Experiment Station, Report SO-250, New Orleans, Louisiana, USA.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1996. Red-cockaded woodpecker nesting success, forest structure, and southern flying squirrels in Texas. Wilson Bulletin 108:697–711.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, USA.

Conner, R. N., D. Saenz, R. R. Schaefer, J. R. McCormick, D. C. Rudolph, and D. B. Burt. 2004. Group size and nest success in red-cockaded woodpeckers in the West Gulf Coastal Plain: helpers make a difference. Journal of Field Ornithology 75:74–78.

Copeyon, C. K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. Wildlife Society Bulletin 18:303–311.

Costa, R. 2004. State of the red-cockaded woodpecker world: highlights of the previous decade (1992–2002). Pages 39–46 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Dennis, J. V. 1971. Species using red-cockaded woodpecker holes in north-eastern South Carolina. Bird-Banding 42:79–87.

Edwards, J. W., D. C. Guynn, and S. C. Loeb. 1993. Seasonal mast availability for wildlife in the Piedmont Region of Georgia. U.S. Forest Service, Southeastern Forest Experiment Station, Research Paper SE-287, Asheville, North Carolina, USA.

Ford, A. T., and L. Fahrig. 2008. Movement patterns of eastern chipmunks (*Tamias striatus*) near roads. Journal of Mammalogy 89:895–903.

Fridell, R. A., and J. A. Litvaitis. 1991. Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. Canadian Journal of Zoology 69:2589–2593.

Gaines, G. D., K. E. Franzreb, D. H. Allen, K. S. Laves, and W. L. Jarvis. 1995. Red-cockaded woodpecker management on the Savannah River Site: a management/research success story. Pages 81–88 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Hagan, G. T., R. Costa, and M. K. Phillips. 2004. Reintroduction of the first red-cockaded woodpeckers into unoccupied habitat: a private land and conservation success story. Pages 341–346 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Harlow, R. F., and A. T. Doyle. 1990. Food habits of southern flying squirrels (*Glaucomys volans*) collected from red-cockaded woodpecker (*Picoides borealis*) colonies in South Carolina. American Midland Naturalist 124:187–191.

Harlow, R. F., and M. R. Lennartz. 1983. Interspecific competition for red-cockaded woodpecker cavities during the nesting season in South Carolina. Pages 41–43 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II. Proceedings Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Hedman, C. W., J. R. Poirier, P. E. Durfield, and M. A. Register. 2004. International Papers's habitat conservation plan for the red-cockaded woodpecker: implementation and early success. Pages 355–360 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Heiterer, A. J. 1994. Effects of hardwood midstory on utilization of south-eastern pine forests by southern flying squirrels, *Glaucomys volans*. Thesis, Clemson University, Clemson, South Carolina, USA.

Henry, V. G. 1989. Guidelines for preparation of biological assessments and evaluations for the red-cockaded woodpecker. U.S. Fish and Wildlife Service Southeast Region, Atlanta, Georgia, USA.

Holloway, G. L., and J. R. Malcolm. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. Journal of Wildlife Management 70:1735–1745.

Holloway, G. L., and J. R. Malcolm. 2007*a*. Northern and southern flying squirrel use of space within home ranges in central Ontario. Forest Ecology and Management 242:747–755.

Holloway, G. L., and J. R. Malcolm. 2007*b*. Nest-tree use by northern and southern flying squirrels in central Ontario. Journal of Mammalogy 88:226–233.

Hooper, R. G., A. F. Robinson, Jr., and J. A. Jackson. 1980. The red-cockaded woodpecker: notes on life history and management. U.S. Forest Service, Southeastern Area, State and Private Forestry, Report SA-GR 9, Atlanta, Georgia, USA.

Hughes, R. S. 2006. Home ranges of the endangered Carolina northern flying squirrel in the Unicoi Mountains of North Carolina. Proceedings Annual Conference Southeastern Association of Fish and Wildlife Agencies 60:19–24.

Johnston, P. J. 2006. Reproductive success and interspecific competition of the red-cockaded woodpecker. Thesis, University of South Carolina, Columbia, USA.

Kappes, J. J. Jr. 1997. Defining cavity-associated interactions between red-cockaded woodpeckers and other cavity-dependent species: interspecific competition or cavity kleptoparasitism? Auk 114:778–780.

Kappes, J. J. Jr. 2008. Cavity number and use by other species as correlates of group size in red-cockaded woodpeckers. Wilson Journal of Ornithology 120:181–189.

Kappes, J. J. Jr., and J. M. Davis. 2008. Evidence of positive indirect effects within a community of cavity-nesting vertebrates. Condor 110:441–449.

Kappes, J. J. Jr., and L. D. Harris. 1995. Interspecific competition for red-cockaded woodpecker cavities in the Apalachicola National Forest. Pages 389–393 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Khan, M. Z., and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 51:336–344.

LaBranche, M. S., and J. R. Walters. 1994. Patterns of mortality in nests of red-cockaded woodpeckers in the Sandhills of southcentral North Carolina. Wilson Bulletin 106:258–271.

Laves, K. S., and S. C. Loeb. 1999. Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker *Picoides borealis* reproductive success. Animal Conservation 2:295–303.

Lipscomb, D. J., and T. M. Williams. 1995. Use of Geographic Information Systems for determination of red-cockaded woodpecker management areas. Pages 137–144 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Lipscomb, D. J., and T. M. Williams. 1996. A technique for using PC-ARC/INFO GIS to determine red-cockaded woodpecker foraging areas on private lands. Pages 255–264 *in* Proceedings of the southern forestry Geographic Information Systems conference. University of Georgia, Athens, USA.

Lipscomb, D. J., and T. M. Williams. 2004. Development of a Geographic Information System based model of red-cockaded woodpecker habitat. Pages 520–525 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Loeb, S. C. 1993. Use and selection of red-cockaded woodpecker cavities by southern flying squirrels. Journal of Wildlife Management 57:329–335.

Loeb, S. C. 1996. Effectiveness of flying squirrel excluder devices on red-cockaded woodpecker cavities. Proceedings of the Southeastern Association of Game and Fish Commissions 50:303–313.

Loeb, S. C., and R. G. Hooper. 1997. An experimental test of interspecific competition for red-cockaded woodpecker cavities. Journal of Wildlife Management 61:1268–1280.

Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. Southern Journal of Applied Forestry 16:120–125.

Loeb, S. C., and D. L. Ruth. 2004. Seasonal use of red-cockaded woodpecker cavities by southern flying squirrels. Pages 501–502 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Lotter, D. M. 1997. Factors influencing southern flying squirrel use of red-cockaded woodpecker cavities at Savannah River Site, S.C. Thesis, Clemson University, Clemson, South Carolina, USA.

Miller, K. E. 2002. Nesting success of the great crested flycatcher in nest boxes and in tree cavities: are nest boxes safer from nest predation? Wilson Bulletin 114:179–185.

Mitchell, L. R., L. D. Carlile, and C. R. Chandler. 1999. Effects of southern flying squirrels on nest success of red-cockaded woodpeckers. Journal of Wildlife Management 63:538–545.

Mitchell, L. R., C. R. Chandler, and L. D. Carlile. 2005. Habitat as a predictor of southern flying squirrel abundance in red-cockaded woodpecker cavity clusters. Journal of Wildlife Management 69:418–423.

Montague, W. G., J. C. Neal, J. E. Johnson, and D. A. James. 1995. Techniques for excluding southern flying squirrels from cavities of red-cockaded woodpeckers. Pages 401–409 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Muul, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. Miscellaneous Publication, Museum of Zoology, University of Michigan 131: 1–66.

Nupp, T. E., and R. K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy 81:512–526.

Ortego, B., D. Carrie, and K. Moore. 1995. Red-cockaded woodpecker nesting success in the Sam Houston National Forest in 1989. Pages 320–322 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on populations of small mammals. Journal of Applied Ecology 11:51–59.

Perkins, M. W., L. M. Conner, and M. B. Howze. 2008. The importance of hardwood trees in the longleaf pine forest ecosystem for Sherman's fox squirrels. Forest Ecology and Management 255:1618–1625.

Richardson, D. M., and J. M. Stockie. 1995. Response of a small red-cockaded woodpecker population to intensive management at Noxubee National Wildlife Refuge. Pages 98–105 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Ridley, T. R., G. L. Chapman, and S. C. Loeb. 1997. Southern flying squirrel displaces a red-cockaded woodpecker from its cavity. Chat 61:112–115.

Rudolph, D. C., R. N. Conner, and J. Turner. 1990*a*. Competition for red-cockaded woodpecker roost and nest cavities: effects of resin age and entrance diameter. Wilson Bulletin 102:23–36.

Rudolph, D. C., H. Kyle, and R. N. Conner. 1990*b*. Red-cockaded woodpeckers vs rat snakes: the effectiveness of the resin barrier. Wilson Bulletin 102:14–22.

Rudolph, D. C., R. R. Schaefer, J. B. Pierce, D. Saenz, and R. N. Conner. 2009. Texas ratsnake predation on southern flying squirrels in red-cockaded woodpecker cavities. Southeastern Naturalist 8: 41–46.

Sonenshine, D. E., and G. F. Levy. 1981. Vegetative associations affecting *Glaucomys volans* in central Virginia. Acta Theriologica 26:359–371.

Stabb, M. A., M. E. Gartshore, and P. L. Aird. 1989. Interactions of southern flying squirrels, *Glaucomys volans*, and cavity-nesting birds. Canadian Field-Naturalist 103:401–403.

Stober, J. M., and L. M. Conner. 2007. Scent deterrence to reduce southern flying squirrel kleptoparasitism of red-cockaded woodpecker cavities. Human-Wildlife Conflicts 1:45–48.

Stober, J. M., and S. B. Jack. 2004. Down for the count? Red-cockaded woodpecker restoration on Ichauway. Pages 347–354 *in* R. Costa and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, Washington, USA.

Taulman, J. F. 1999. Selection of nest trees by southern flying squirrels (Sciuridae: *Glaucomys volans*) in Arkansas. Journal of Zoology 248:369–377.

Taulman, J. F., and K. G. Smith. 2004. Home range and habitat selection of southern flying squirrels in fragmented forests. Mammalian Biology 69:11–27.

Taulman, J. F., K. G. Smith, and R. E. Thill. 1998. Demographic and behavioral responses of southern flying squirrels to experimental logging in Arkansas. Ecological Applications 8:1144–1155.

U.S. Fish and Wildlife Service. 2003. Recovery plan for the red-cockaded woodpecker (*Picoides borealis*): second revision. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Walters, J. R. 1990. The red-cockaded woodpecker: a "primitive" cooperative breeder. Pages 67–101 *in* P. B. Stacey and W. D. Koenig, editors. Cooperative breeding in birds: longterm studies of ecology and behavior. Cambridge University Press, Cambridge, England.

Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. Bulletin of Tall Timbers Research Station 24:1–93.

Wharton, C. H. 1978. The natural environments of Georgia. Geologic and Water Resources Division and Georgia Department of Natural, Resources, Atlanta, Georgia, USA.

Yarrow, G. K., and D. T. Yarrow. 1999. Managing wildlife on private lands in Alabama and the southeast. Sweet Water Press, Birmingham, Alabama, USA.

Associate Editor: Amy Kuenzi.