

2018

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Abstract

Southern flying squirrels (*Glaucomys volans*; SFS) nest in naturally formed cavities in snags and hardwoods found in mature, oak (*Quercus* spp.)–hickory (*Carya* spp.) forests. Intensive forest fragmentation of the Midwest United States limits the number of available nesting trees. We quantified annual nest-site selection patterns by southern flying squirrels across fragmented landscapes of west-central Illinois, USA. We used radiotelemetry to measure nest-tree use by 55 SFS (30 males, 25 females) captured during 2014–2016. Of 105 nest trees used by SFS, live trees and snags comprised 75% and 25%, respectively. Probability of diurnal nest-tree use increased 1.08/1.00-cm increase in diameter-breast-height and by 1.50/1-unit increase in the number of overstory mast trees between random and nest-tree habitat areas (i.e., 300-m² circular plots). Similarly, probability of diurnal nest-tree use increased 1.29/1-unit increase in the number of snags between random and nest-tree habitat areas. Our results revealed no intersexual differences in patterns of nest-site selection, which may reflect the tendency for SFS to compensate for reduced availability of key structural attributes (i.e., snags, overstory trees) across fragmented forests by exhibiting similar intersexual patterns of nest-tree use. Use of natural cavities for denning is encouraging, but also underscores the importance of unharvested oak–hickory forests in contributing essential habitat to SFS populations in fragmented Midwestern landscapes.

Keywords

diurnal nest trees, fragmentation, *Glaucomys volans*, Illinois, nest-site selection, southern flying squirrel

Disciplines

Animal Sciences | Ecology and Evolutionary Biology | Forest Sciences | Natural Resources and Conservation | Natural Resources Management and Policy

Comments

This article is published as Zweep, James S., Christopher N. Jacques, Sean E. Jenkins, Robert W. Klaver, and Shelli A. Dubay. "Nest tree use by southern flying squirrels in fragmented Midwestern landscapes." *Wildlife Society Bulletin* (2018). doi: [10.1002/wsb.901](https://doi.org/10.1002/wsb.901).

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Original Article

Nest Tree Use by Southern Flying Squirrels in Fragmented Midwestern Landscapes

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ABSTRACT Southern flying squirrels (*Glaucomys volans*; SFS) nest in naturally formed cavities in snags and hardwoods found in mature, oak (*Quercus* spp.)–hickory (*Carya* spp.) forests. Intensive forest fragmentation of the Midwest United States limits the number of available nesting trees. We quantified annual nest-site selection patterns by southern flying squirrels across fragmented landscapes of west-central Illinois, USA. We used radiotelemetry to measure nest-tree use by 55 SFS (30 males, 25 females) captured during 2014–2016. Of 105 nest trees used by SFS, live trees and snags comprised 75% and 25%, respectively. Probability of diurnal nest-tree use increased 1.08/1.00-cm increase in diameter-breast-height and by 1.50/1-unit increase in the number of overstory mast trees between random and nest-tree habitat areas (i.e., 300-m² circular plots). Similarly, probability of diurnal nest-tree use increased 1.29/1-unit increase in the number of snags between random and nest-tree habitat areas. Our results revealed no intersexual differences in patterns of nest-site selection, which may reflect the tendency for SFS to compensate for reduced availability of key structural attributes (i.e., snags, overstory trees) across fragmented forests by exhibiting similar intersexual patterns of nest-tree use. Use of natural cavities for denning is encouraging, but also underscores the importance of unharvested oak–hickory forests in contributing essential habitat to SFS populations in fragmented Midwestern landscapes. © 2018 The Wildlife Society.

KEY WORDS diurnal nest trees, fragmentation, *Glaucomys volans*, Illinois, nest-site selection, southern flying squirrel.

The southern flying squirrel (*Glaucomys volans*; SFS) is a secondary cavity nester, and commonly found in forested regions throughout eastern and central United States and Canada (Muul 1968, Bendel and Gates 1987, Taulman 1999, Holloway and Malcolm 2007). Nest sites are important habitat features for SFS and provide diurnal refugia from inclement weather and predation and feeding sites during nocturnal activity periods (Weigl 1978, Taulman 1999, Brady et al. 2000, Holloway and Malcolm 2007, Steinhoff et al. 2012). The spatial distribution and abundance of large, diseased, or damaged trees have been linked directly to SFS nesting strategies (Carey et al. 1997, Menzel et al. 2004). Several types of nests have been identified, including natural or excavated tree cavities, external leaf nests, and subterranean nests under downed logs and tree roots (Hackett and Pagels 2003). Cavity nests tend to be most prevalent in areas with high snag densities, with incidence of cavity use especially high in northern

populations, possibly because SFS are better able to minimize heat loss during cold climates in cavities than in external nests (Bendel and Gates 1987, Carey et al. 1997, Bakker and Hasting 2002, Lavers 2004, Menzel et al. 2004). Large cavity trees appear to be especially important as winter den sites and for pregnant females (Carey et al. 1999, Lavers 2004). Therefore, cavities may be critical for overwinter survival of SFS in low-productivity habitats characterized by smaller forest patches and relatively low snag densities (Jacques et al. 2017a). Consequently, knowledge of nest-tree characteristics is critical to conserving adequate nesting habitat for SFS, particularly along the western edge of their geographic range (DeGraaf and Shigo 1985, Naylor et al. 1996).

A key conservation issue pertaining to SFS relates to effects of habitat fragmentation on fine-scale habitat use (Bendel and Gates 1987, Taulman et al. 1998, Holloway and Malcolm 2007, Steinhoff et al. 2012). Fragmentation of forested ecosystems over the past 200 years has been extensive, and particularly evident across Midwestern landscapes (Lomolino and Perault 2001, Desrochers et al. 2003, Taulman and Smith 2004, Koprowski 2005, Smith and Person 2007). In Illinois, USA, forested landscapes have

Received: 18 December 2017; Accepted: 13 May 2018

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been reduced by 64% and currently characterized by young (<61 yr old) oak (*Quercus* spp.)–hickory (*Carya* spp.) forests limited to the southern and western regions of the state (Crocker 2015). Recently, Jacques et al. (2017a) noted the importance of large (≥ 35 cm diameter-at-breast height [DBH]) overstory mast trees in predicting home range use and spatial activity patterns of SFS across fragmented forest landscapes; such may also be the case for diurnal nest-site selection. Southern flying squirrels are used as indicators of forest ecosystem sustainability; therefore, a greater understanding of nest-tree characteristics across fragmented Midwestern landscapes may aid in future conservation of cavity resources for forest-dependent wildlife (McLaren et al. 1998, Holloway and Malcolm 2007).

In general, southern flying squirrels are communal nesters during winter months, forming mixed-sex aggregations consisting primarily of adults, though they may contain mixed-age groups of related or unrelated individuals (Layne and Raymond 1994). Communal nesting behavior has an obvious thermoregulatory function across the northern part of the range by reducing energy expenditure for maintaining body temperature (Muul 1968, Stapp et al. 1991). In southern states, high levels of aggregative behavior may aid in thermoregulation and play a significant role in the social organization of SFS populations (Layne and Raymond 1994). Seasonal patterns of communal nesting and seasonal dissolution of aggregations of SFS across their range are triggered primarily by reproductive factors (Muul 1968, Raymond and Layne 1988, Layne and Raymond 1994). Increased female aggression may be a proximate cause of the breakup of aggregations, because females exhibit strong territoriality before and after parturition (Madden 1974, Layne and Raymond 1994). Increasing aggression between males at the onset of the breeding season may contribute to the decline of communal nesting behavior (Layne and Raymond 1994). In addition, SFS use multiple trees in a home range for roosting and frequently switch between nest trees. On average, SFS switch nest trees approximately twice a month during summer months in northern hardwood forests in response to increasing parasite loads and limited food availability (Holloway and Malcolm 2007, Steinhoff et al. 2012). However, excessive nest switching from one nest to another by SFS increases the likelihood of predation and infection with internal parasites (Wetzel and Weigl 1994, Carey et al. 1997). Consequently, these life-history strategies may increase the vulnerability of SFS to local extinction in closed populations and fragmented forest patches with few individuals (Nupp and Swihart 2000).

Given such unique life-history strategies, the SFS is an ideal species for evaluating seasonal associations among habitat features and nesting ecology. To date, no published studies have concurrently evaluated summer and winter nesting patterns of southern flying squirrels across Midwestern landscapes. Our primary objectives were to 1) quantify potential effects of tree (e.g., tree type, crown condition, snag decay class, DBH) and forest stand (e.g., densities of overstory mast trees and snags, basal area, canopy cover, shrub density) characteristics on nest presence and occupancy

patterns of SFS; and 2) determine whether nest-tree use differed between male and female SFS in west-central Illinois. Given notable changes in social behavior and reproductive activities (i.e., territoriality and high energy demands on females during parturition and rearing of young; Madden 1974, Bendel and Gates 1987, Fridell and Litvaitis 1991) between sexes, we hypothesized that tree characteristics at diurnal nest sites would vary seasonally between male and female SFS. We also hypothesized that given the importance of habitat characteristics in predicting home range use and spatial activity patterns of SFS (Jacques et al. 2017a), nest-site selection patterns also may be influenced by microhabitat characteristics such as DBH, snag density, tree height, and availability of mast trees. Evaluation of these hypotheses may contribute to a greater understanding of the nesting ecology of SFS across fragmented Midwestern landscapes, and provide insight into future conservation strategies for this species.

STUDY AREA

We conducted our study within a 4.9-km² area of land owned by the Illinois Department of Natural Resources and Western Illinois University within Hancock County of west-central Illinois. Landscape characteristics consisted primarily of flat upland prairies, bluffs, and valleys near the Illinois and Mississippi River watersheds (Walker 2001). For a detailed description of the study area, see Jacques et al. (2017a, b).

METHODS

Flying Squirrel Capture, Handling, and Monitoring

We captured SFS using Sherman traps and artificial nest boxes situated along systematically placed transects during summer 2015 and autumn 2014–2016, respectively (Jacques et al. 2017b). We checked all Sherman traps daily (0600–0900) to minimize time in traps, stress, and capture-related mortalities. We checked nest boxes bi-weekly during diurnal hours (1000–1400) to maximize the likelihood of occupancy by individuals; all nest boxes were closed at the end of each capture season (i.e., 30 Nov) to prevent subsequent use throughout the year. We fitted adult (≥ 55 g; Sollberger 1943) animals with radiocollars (collar mass = 4.2 g; $\leq 7\%$ total body mass; 165 MHz, model M1540; Advanced Telemetry Systems, Isanti, MN, USA) and 2 metal ear tags (Number 1; National Band and Tag Company, Newport, KY, USA) prior to release. We used standard ground-telemetry techniques to monitor movement status of radiocollared SFS 2–3 times per week from October 2014 through April 2016, after which time field work was terminated. For detailed descriptions of capture, handling, and monitoring of study animals, see Jacques et al. (2017a, b). Animal capture and handling methods were approved by the Institutional Animal Care and Use Committee at Western Illinois University (approval number 15-01) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes et al. 2016).

Habitat Measurements

We used habitat data (i.e., densities of large [≥ 35 -cm DBH] overstory mast trees [NO_MT] and snags

[NO_SN]) collected by Jacques et al. (2017a) to evaluate potential effects of habitat characteristics on nest site use by SFS. From October 2014 to April 2016, we further quantified habitat characteristics of diurnal nest trees and paired random trees situated within core areas of radio-collared individuals. Our random tree locations were selected by walking a random distance (between 25 m and 50 m) and bearing from nest-tree locations and selecting the nearest tree ≥ 10 -cm diameter DBH. We used 10-cm DBH based on minimum nesting-tree size of SFS reported in previous studies (Bendel and Gates 1987, Hackett and Pagels 2003). For each nest tree, we also recorded type of nest or nest hole present (i.e., natural cavity, excavated cavity, or external nest; Holloway and Malcolm 2007). We defined natural cavities as holes with visible cracks or noncircular, jagged openings (Holloway and Malcolm 2007). In contrast, excavated cavities were classified as those with small circular entrance holes created by primary cavity nesters (e.g., woodpeckers [i.e., Picidae]; Holloway and Malcolm 2007). External leaf nests were characterized by the presence of leaves or sticks on tree branches and boles (Holloway and Malcolm 2007).

We also characterized local habitat features in areas surrounding nest and random trees. Within 300-m² (9.8-m radius) circular plots centered on nest or random tree locations, we identified to species and measured all trees >10 -cm DBH (Steinhoff et al. 2012). We also recorded tree type (TT; live or snag), tree height (TH; cm), snag decay class (SDC; 0–1 = little or no decay; 2–3 = moderate decay; 4–5 = advanced decay; Steinhoff et al. 2012), canopy cover (CC; %), basal area (BA; m²), and densities (no. stems/300 m²) of shrubs (SD; stems ≤ 2.5 -cm DBH), understory trees (UD; 2.5–8.8-cm DBH), lower midstory trees (LMTD; 8.9–16.5-cm DBH), upper midstory trees (UMTD; 16.6–24.1-cm DBH), and overstory trees (OTD; >24.1 -cm DBH; Taulman et al. 1998).

Data Analyses

Given the relatively large number ($n = 15$) of forest stand variables collected and potential comparisons, we used multivariate analysis of variance (MANOVA) to evaluate main effects of sex, season (winter [Oct through Mar], summer [Apr through Sep; Mumford and Whitaker 1982, Raymond and Layne 1988, Jacques et al. 2017a]), and plot type (nest vs. random tree) on continuous variables (e.g., no. of mast trees [NO_MT], no. of snag trees [NO_SN], diameter at breast height [DBH], tree height [TH], basal area [BA], overstory tree density [OTD]; Table 1). Our analyses revealed no significant 2- or 3-way interactions between plot type (nest trees vs. random trees), sex, and season on habitat characteristics at nest locations; thus, we limited our reporting of univariate test results and regression models to main effects. We determined duration of seasons from data on reproductive condition and emergence of offspring (Raymond and Layne 1988, Jacques et al. 2017a). Given the relatively short life-expectancy (i.e., 10 months) of radiocollars, few animals captured during 2014 were available for evaluating nest-site characteristics in subsequent years; thus, we did not conduct direct comparisons between years. In cases where MANOVAs were significant ($\alpha = 0.05$), we used chi-square analyses or t tests to test for differences between dependent and independent variables. We used Bonferroni correction factors to maintain experiment-wide error rates when performing multiple chi-square analyses and t tests (Dunn 1961, Mittlehammer et al. 2000). Prior to analyses, we screened all dependent and independent variables for collinearity using Pearson's correlation coefficient ($|r| > 0.5$; Jacques et al. 2017b); we excluded collinear variables from analyses. Additionally, we used residual plots, quantile plots, and a Shapiro–Wilk test to evaluate assumptions of normality (Shapiro and Wilk 1965).

We used conditional logistic regression to compare nest and random trees with respect to forest-stand characteristics.

Table 1. Tree and habitat characteristics (mean \pm SE) of nest trees and random trees of male and female southern flying squirrels (*Glaucomys volans*) in west-central Illinois, USA, 2014–2016. Characteristics were measured at the tree or habitat levels.

| Level | Variable description ^a | Nests ($n = 105$) | Random trees ($n = 105$) | P^b | Male ($n = 53$) | Female ($n = 52$) | P |
|--------------|--|---------------------|----------------------------|--------|-------------------|---------------------|-----|
| Tree | Tree type (live, snag) | | | 0.021 | | | NS |
| | Live | 79 | 92 | | 34 | 39 | |
| | Snag | 26 | 13 | | 19 | 13 | |
| Tree | Snag decay class | | | NS | | | NS |
| | Low (0–1) | 83 | 93 | | 40 | 43 | |
| | Moderate (2–3) | 10 | 4 | | 5 | 5 | |
| | Advanced (4–5) | 12 | 8 | | 8 | 4 | |
| Tree | Diameter at breast height (cm) | 54.4 \pm 1.7 | 34.1 \pm 1.5 | <0.001 | 53.8 \pm 2.6 | 54.9 \pm 2.3 | NS |
| Tree | Tree height (m) | 23.5 \pm 0.7 | 19.8 \pm 0.6 | <0.001 | 23.5 \pm 1.0 | 23.4 \pm 0.9 | NS |
| Forest stand | Basal area (m ² /300 m ²) | 0.89 \pm 1.7 | 0.98 \pm 0.04 | NS | 0.91 \pm 0.1 | 0.88 \pm 0.1 | NS |
| Forest stand | Canopy cover (%) | 89.7 \pm 1.7 | 90.9 \pm 1.5 | NS | 85.3 \pm 2.4 | 90.4 \pm 1.8 | NS |
| Forest stand | No. of species | 4.7 \pm 0.2 | 4.6 \pm 0.2 | NS | 4.9 \pm 0.2 | 4.5 \pm 0.3 | NS |
| Forest stand | Shrubs (no./300 m ²) | 10.4 \pm 1.2 | 11.6 \pm 1.8 | NS | 9.1 \pm 1.5 | 11.6 \pm 1.9 | NS |
| Forest stand | Understory trees (no./300 m ²) | 9.6 \pm 0.8 | 9.5 \pm 0.9 | NS | 8.6 \pm 1.0 | 10.6 \pm 1.2 | NS |
| Forest stand | Lower midstory trees (no./300 m ²) | 5.2 \pm 0.3 | 5.4 \pm 0.4 | NS | 5.5 \pm 0.5 | 4.9 \pm 0.5 | NS |
| Forest stand | Upper midstory trees (no./300 m ²) | 2.5 \pm 0.2 | 2.5 \pm 0.2 | NS | 2.5 \pm 0.2 | 2.4 \pm 0.3 | NS |
| Forest stand | Overstory trees (no./300 m ²) | 5.2 \pm 0.3 | 5.3 \pm 0.2 | NS | 5.4 \pm 0.4 | 5.1 \pm 0.4 | NS |

^a The first 2 variables were analyzed using chi-square tests; remaining variables were analyzed with t tests on rank-transformed values.

^b P values were reported for significant comparisons ($P \leq 0.05$); NS = not significant.

Conditional logistic regression is used when observations are matched or otherwise grouped in some way, and are thus analogous to a paired *t*-test (Hosmer and Lemeshow 2000, Bakker and Hastings 2002, Holloway and Malcolm 2007). In our case, a diurnal nest-tree location and its associated random tree location were not independent observations, and thus, comprised a matched pair (Holloway and Malcolm 2007). Our MANOVA analyses revealed no significant interactions between sex and our dependent variables; therefore, we did not conduct logistic regression comparing forest stand or tree characteristics of nest-tree locations between male and female squirrels. Prior to conditional regression analyses, we posited biologically plausible models of how plot type (nest vs. random) may be influenced by tree type, DBH, tree height, number of snags, number of tree species (NO_SP), snag decay class (SDC), percent canopy cover, overstory tree density, crown condition (CROWN), and number of mast trees. Our model set consisted of 9 *a priori* models (excluding global and intercept-only models) that grouped logically into habitat effects (Table 2). We selected the set of habitat factors that we considered biologically meaningful to SFS nest-tree use (9 variables; Table 2). Further, these variables have been identified as

Table 2. Akaike's Information Criterion model selection of *a priori* conditional logistic regression models for comparing habitat variables at nest-tree locations for southern flying squirrels in west-central Illinois, USA, 2014–2016.

| Model covariates ^a | K ^b | AIC _c ^c | ΔAIC ^d | w _i ^e | ROC ^f |
|-------------------------------|----------------|-------------------------------|-------------------|-----------------------------|------------------|
| DBH + NO_MT + NO_SN | 3 | 82.212 | 0.000 | 0.922 | 0.916 |
| TT + DBH + TH + NO_SN | 4 | 87.885 | 5.672 | 0.059 | 0.907 |
| DBH | 1 | 92.133 | 9.920 | 0.007 | 0.876 |
| DBH + NO_SP + NO_SN | 3 | 92.438 | 10.225 | 0.006 | 0.885 |
| DBH + SDC | 2 | 92.855 | 10.642 | 0.005 | 0.882 |
| GLOBAL | 9 | 92.887 | 10.674 | 0.005 | 0.941 |
| DBH + CC | 2 | 94.065 | 11.852 | 0.002 | 0.875 |
| INTERCEPT-ONLY | 1 | 106.760 | 24.547 | 0.000 | 0.500 |
| NO_MT + NO_SN | 2 | 129.492 | 47.279 | 0.000 | 0.741 |
| NO_SN | 1 | 136.967 | 54.754 | 0.000 | 0.659 |
| OTD | 1 | 145.614 | 63.401 | 0.000 | 0.512 |

^a DBH = diameter at breast height (cm); NO_MT = no. of mast trees ≥35 cm DBH recorded; CC = canopy cover (%); NO_SN = no. of snags recorded; TT = tree type (live vs. dead); TH = tree height (m); NO_SP = no. of tree species recorded; SDC = snag decay class (0–1 = low, 2–3 = moderate, 4–5 = advanced); GLOBAL = fully saturated (global) regression model; CC = canopy cover (%); OTD = no. of overstory trees ≥24.1 cm DBH recorded; INTERCEPT-ONLY = model consisting of the intercept term only, serving as a null model for comparisons. All habitat variables represented the total numbers recorded per 300-m² plot centered on male and female nest-tree locations.

^b No. of parameters.

^c Akaike's Information Criterion adjusted for small sample sizes (Burnham and Anderson 2002).

^d Difference in AIC_c relative to minimum AIC_c.

^e Akaike weight (Burnham and Anderson 2002).

^f Area under the receiver operating characteristic (ROC) curve. Values between 0.7 and 0.8 were considered acceptable discrimination, and values between 0.8 and 1.0 were considered excellent discrimination. We considered ROC values between 0.5 and 0.7 low discrimination, and values ≤0.5 indicated that model predictive capabilities were no better than random (Grzybowski and Younger 1997, Hosmer and Lemeshow 2000).

important factors influencing microhabitat partitioning and resource selection of SFS across the eastern and central United States (Bendell and Gates 1987, Fridell and Litvaitis 1991, Taulman 1999, Holloway and Malcolm 2007).

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models that best described these data and used Akaike weights (*w_i*) as a measure of relative support for model fit (Burnham and Anderson 2002, Jacques et al. 2017b). We considered models differing by ≥4 ΔAIC from the highest-ranked model as noncompetitive and thus excluded them from further consideration (Burnham and Anderson 2002). We determined associations between response and predictor variables using odds ratios. The odds ratio for a predictor variable is the relative amount by which the odds of the outcome increase (odds ratio >1.0) or decrease (odds ratio <1.0) with each unit increase in the predictor variable (Hosmer and Lemeshow 2000, Freund and Wilson 2003, Jacques et al. 2017b). Thus, odds ratios approximated the likelihood of a predicted outcome among associated variables. The appropriate interpretation of odds ratios obtained from model parameters for continuous (predictor) variables was that multiplicative effects on the odds of a 1-unit increase in the response variable was associated with fixed levels of other predictor variables (Hosmer and Lemeshow 2000, Freund and Wilson 2003, Jacques et al. 2017b). We assessed discriminatory capability of fitted models using area under the receiver operating characteristic (ROC) curve; ROC values between 0.7 and 0.8 are considered acceptable discrimination and values exceeding 0.8 are considered excellent discrimination. We considered ROC values between 0.5 and 0.7 low discrimination, and values ≤0.5 indicated that model predictive capabilities were no better than random (Grzybowski and Younger 1997, Hosmer and Lemeshow 2000). We conducted statistical analyses using Program R (R Core Team 2015); statistical tests were conducted at α = 0.05.

RESULTS

From October 2014 to April 2016, we tracked 55 radio-collared SFS (30 males, 25 females) to 105 nest trees (79 live trees [87.6% available], 26 snags [12.4% available]; 1.91 trees/animal) throughout the study area; diurnal nest-tree locations included no instances where SFS were tracked to nest-box locations. We found diurnal nests in 16 tree species; the majority (≥83%) included oak (*Quercus* spp.), maple (*Acer* spp.), white ash (*Fraxinus americana*), black locust (*Robinia pseudoacacia*), and shagbark hickory (*Carya ovata*) overstory trees (Fig. 1). The majority (*n* = 96) of the 105 nests occurred in natural cavities; remaining nests occurred in excavated cavities (*n* = 7) or external leaf nests (*n* = 2). Natural cavities were generally located in noncircular broken branch holes or large, jagged openings, or visible cracks in the main tree trunk.

Habitat Measurements

Sex and season main effects were not significant (Wilks λ = 0.95, *F*_{9,194} = 1.69, *P* = 0.09; Wilks λ = 0.93, *F*_{9,194} = 1.89, *P* = 0.07, respectively), though the plot-type

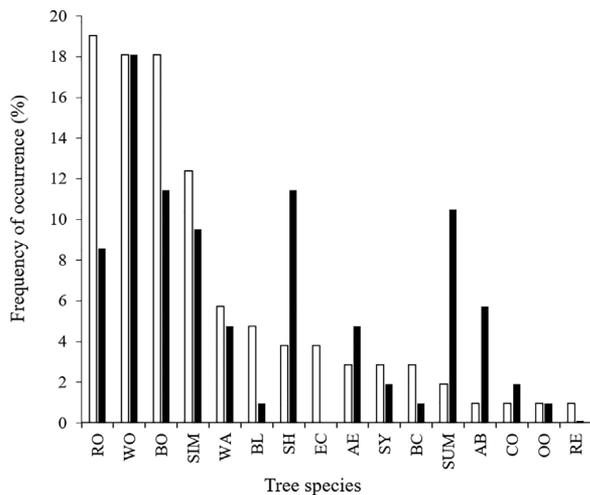


Figure 1. Frequency of occurrence (%) of diurnal nest-tree use (open vertical bars) relative to availability (solid vertical bars) by southern flying squirrels across west-central Illinois, USA, 2014–2016. Diurnal nests were found in 16 tree species, including northern red oak (RO; *Quercus rubra*), white oak (WO; *Q. alba*), black oak (BO; *Q. velutina*), silver maple (SIM; *Acer saccharinum*), white ash (WA; *Fraxinus americana*), black locust (BL; *Robinia pseudoacacia*), shagbark hickory (SH; *Carya ovata*), Eastern cottonwood (EC; *Populus deltoides*), American elm (AE; *Ulmus americana*), sycamore (SY; *Platanus occidentalis*), black cherry (BC; *Prunus serotina*), sugar maple (SUM; *A. saccharum*), American basswood (AB; *Tilia americana*), chinkapin oak (CO; *Q. muehlenbergii*), osage orange (OO; *Maclura pomifera*), and red elm (RE; *U. rubra*).

main effect was significant (Wilks $\lambda = 0.64$, $F_{9,194} = 12.65$, $P < 0.001$). Our results revealed that the majority (75%) of trees used for nesting were live trees (Table 1). Nevertheless, nest trees were taller, larger diameter, and characterized by relatively greater use of dead trees than random trees (Table 1). We documented no differences between tree type, snag decay class, DBH, tree height, or overstory tree density between male and female SFS (Table 1). Univariate analyses also revealed differences ($t_{103} = 2.22$, $P = 0.03$) in density of snags used by SFS between summer ($\bar{x} = 2.95$, $SE = 0.34$, $n = 40$) and winter ($\bar{x} = 2.12$, $SE = 0.20$, $n = 65$). Similarly, number of mast trees used by SFS varied ($t_{103} = 2.741$, $P = 0.007$) between winter ($\bar{x} = 2.85$, $SE = 0.29$, $n = 65$) and summer ($\bar{x} = 1.75$, $SE = 0.21$, $n = 40$).

Conditional regression analysis revealed that the highest-ranked model for predicting nest-tree use was DBH + NO_MT (no. of mast trees) + NO_SN (no. of snags); weight of evidence (w_i) supporting this model was 0.92, and predictive

capability was excellent (ROC = 0.92; Table 2). The β and 95% confidence intervals for parameter estimates for the DBH, number of mast trees (NO_MT), and number of snags (NO_SN) covariates did not overlap zero and all $P \leq 0.012$, indicating these variables were influential predictors of diurnal nest-tree use by SFS (Table 3). Probability of diurnal nest-tree use increased 1.08/1.00-cm increase in DBH and by 1.50/1-unit increase in the number of overstory mast trees between random and nest-tree habitat areas (i.e., 300-m² circular plots). Similarly, probability of diurnal nest-tree use increased 1.29/1-unit increase in the number of snags between random and nest-tree habitat areas (Table 3).

DISCUSSION

The general pattern of nest-tree use in our study revealed that SFS appeared to depend nearly exclusively on natural cavities. Contrary to most previous studies, our results provided little support for the tendencies of SFS to utilize excavated cavities, as reflected by limited use of woodpecker holes and declining use of nest boxes over the duration of our study (Loeb 1993, Holloway and Malcolm 2007). Several factors may explain these patterns. First, SFS show a strong selection for cavities with small entrances and appear to avoid cavities that have been enlarged by other species (Loeb 1993). Natural cavities with small entrances presumably provide greater protection from predators (e.g., black rat snakes [*Pantherophilus obsoletus*]; Stickel et al. 1980) and may reduce accessibility (and thus competition) via arboreal routes from other larger sciurids such as fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*; Muul 1968, Bendel and Gates 1987). Our results corroborate previous hypotheses regarding nest-tree use by SFS and Siberian flying squirrels (*Pteromys volans*) in Finland, whereby cavities with small entrance holes were the most common nest source and prevented access by most natural predators (e.g., owls [*Strix uralensis*], pine marten [*Martes martes*]; Selonen et al. 2014, Selonen and Makelainen 2017). Similarly, Suzuki and Yanagawa (2013) reported the relative importance of cavity diameter and tree condition in nest use by Siberian flying squirrels, particularly the use of cavities in live trees with small entrance holes. In addition, natural cavities also may be less likely to fill with snow or water, reduce competitive interactions with sympatric populations of woodpeckers that have the ability to enlarge excavated cavities, and serve as important microsites for seasonal thermoregulation (Bendel and Gates 1987, Stapp et al. 1991, Loeb 1993).

Table 3. Parameter estimates (β), standard error (SE), odds ratio, odds ratio 95% upper and lower confidence limits, and associated P -values for the best approximating conditional regression model predicting nest-tree use by southern flying squirrels in west-central Illinois, USA, 2014–2016.

| Model covariate ^a | β | SE | Odds ratio ^b | Upper CL | Lower CL | P |
|------------------------------|---------|-------|-------------------------|----------|----------|--------|
| DBH | 0.072 | 0.015 | 1.075 | 1.106 | 1.045 | <0.001 |
| NO_MT | 0.403 | 0.140 | 1.496 | 1.966 | 1.138 | 0.004 |
| NO_SN | 0.254 | 0.092 | 1.289 | 1.544 | 1.075 | 0.012 |

^a DBH = tree diameter-at-breast-height (cm), NO_MT = no. of mast trees, NO_SN = no. of snag trees.

^b Odds ratios used to estimate measures of association between variables. A measure of association in which a value is near 1 indicates no relationship between variables (Hosmer and Lemeshow 2000).

Our results parallel nest-use studies of SFS in Maryland, USA, and central Ontario, Canada, where nest-tree use was characterized by greater use of live trees (70–75%) than snags (25–30%; Bendel and Gates 1987, Holloway and Malcolm 2007). As secondary cavity nesters, patterns of nest-tree use by SFS may be as much determined by excavators (i.e., woodpeckers) as by the squirrels themselves (Holloway and Malcolm 2007). Nest-use studies have indicated that the presence of decayed heartwood is required by virtually all species of primary cavity-nesting birds for nest-hole excavation, and occurs most frequently in softer hardwood species (e.g., trembling aspen [*Populus tremuloides*], paper birch [*Betula papyrifera*]; Harestad and Keisker 1989). Patterns of nest-tree use by SFS revealed that large-diameter, live oak trees were the most frequently used resources (i.e., 59% of diurnal nest sites) in our study site, which may reflect differences in decay patterns in hard, decay-resistance trees (i.e., oaks) relative to more decay-prone trees (Goodburn and Lorimer 1998, Holloway 2006). Woodpeckers occupying our study site may have been less likely to excavate cavities, thereby triggering increased use of live trees and natural cavities by SFS.

We predicted that availability of nest trees likely to contain cavities would be greater than associated random sites, which was supported. Our results indicated positive associations between forest stands with increasing DBH and mast-tree density with diurnal nest-tree use. Previous studies have noted selection for large-diameter trees and hypothesized that nest cavity selection was based on microclimate (Sedgeley 2001, Wiebe 2001, Willis et al. 2006). The presence of large dead or broken branches and greater abundance of natural-formed and excavated cavities have been strongly correlated with tree DBH (Bendel and Gates 1987, Carey et al. 1997, Holloway and Malcolm 2007). It is possible, however, that SFS may have selected larger, live trees for other reasons. For instance, Coombs et al. (2010) noted prominent effects of DBH and decay class on tree cavity temperature. Most notably, cavities in live trees were better insulated than cavities in dead trees. Further, cavities in larger trees stayed warmer during winter nights and cooler during summer days, which may be related to the increased time to conduct heat across live than dead wood (McComb and Noble 1981, Coombs et al. 2010). The propensity for SFS to select larger, live mast trees across our study site may have been associated with the concurrent benefits of minimizing energy expenditure during unfavorable ambient temperatures and proximity to food resources. The apparent selection for large, live trees also may be a result of larger (and presumably older) trees being more likely to contain more cavities than younger trees (Fan et al. 2003, Coombs et al. 2010). Nest-site selection patterns revealed during the present study may provide additional insight into future conservation of SFS, particularly with continued mesophication (i.e., replacement of forest stands dominated by more fire-adapted and shade-intolerant oaks with those consisting of fire-intolerant and shade-tolerant species; Nowacki and Abrams 2008), succession of forests, and low availability of snag trees across fragmented Midwestern landscapes.

Our prediction that patterns of nest-tree use would vary by sex in response to seasonal differences in social behaviors and reproductive activities was not supported. As reported previously by Jacques et al. (2017a), the naïve SFS density was 0.30 animals/ha across our study site and on the lower end of observed densities for SFS (Sonenshine et al. 1979, Gilmore and Gates 1985, Taulman et al. 1998). Similarly, snag density (77–83/ha) and overstory mast-tree density (61–81 trees/ha) across our study site was consistent with relatively low availability and diversity of mast-producing trees and snag trees along the northern range limit of SFS (Fridell and Litvaitis 1991). Despite the low availability of snag trees across our study site, nearly 25% of diurnal nest-tree locations occurred in snags, thereby confirming the importance of standing snags in contributing nesting habitat for SFS populations in fragmented forests (Jacques et al. 2017a). Nevertheless, our results suggest that SFS may compensate for reduced availability of snags by selecting larger, live overstory trees across Midwestern landscapes.

The apparent use of live trees with natural cavities by SFS is encouraging, but also underscores the relative importance of unharvested live oak trees in contributing essential nesting habitat in fragmented Midwestern landscapes characterized by low availability of snag trees. In surrounding landscapes actively managed via timber harvesting, ensuring a suitable supply of cavity trees may be a challenge because of negative effects of overbrowsing by white-tailed deer (*Odocoileus virginianus*) on recruitment of hardwood (particularly oak) seedlings (Waller and Alverson 1997, White 2012). Furthermore, the expansion of maples and other shade-tolerant, mesic species in forests previously dominated by oaks is well-documented, though it remains uncertain whether mesophication of fragmented forested landscapes will alter the balance of limiting factors (e.g., food resources) for species such as SFS (Shotola et al. 1992, Ozier et al. 2006, Rogers et al. 2008). Large-scale declines in oak-mast production could reset the carrying capacity of maple-dominated forests in the future by reducing the availability of natural cavities in close proximity to food resources (Fridell and Litvaitis 1991, Lorimer 2003, Rogers et al. 2008), and, in turn, reduce recruitments rates of SFS in closed populations and fragmented landscapes (Wells-Gosling 1985). Lastly, the tendency for SFS to rotate between natural cavities was noted during our study, though evaluating the causative factors for nest switching behavior was beyond the scope of the current study. Predictors of nest-tree switching are not mutually exclusive in that potential effects of intrinsic factors (e.g., sex, age, nutritional condition), habitat conditions (e.g., tree species, decay class), season, and predation risk may be additive or antagonistic, and warrants investigation with future studies (Steinhoff et al. 2012).

MANAGEMENT IMPLICATIONS

Our results suggest that management practices that maintain live trees with cavities in addition to snags should be considered, because both resources appear to provide SFS with critical nesting habitat. Trees with cavities are undoubtedly important to SFS, particularly in relation to

female parturition and rearing of young. A greater understanding of the relative importance of live trees to parturient females may provide greater insight into intersexual differences in microhabitat partitioning in regions characterized by low habitat quality and low animal densities. Small fragments of available forests may be subject to less anthropogenic disturbance (e.g., timber harvest) than larger patches; therefore, remnant patches of primary habitat may potentially play an important role in future conservation planning to sustain SFS populations in fragmented landscapes along the western boundary of their geographic range. Quantifying availability of excavated cavities relative to their use also may facilitate a greater understanding of forest stand dynamics (i.e., overstory tree species composition and age structure), and, in turn, aid in the implementation of forest management plans that promote adequate cavity-nesting habitat for SFS population across Midwestern landscapes.

ACKNOWLEDGMENTS

Funding and logistical support was provided by Western Illinois University (WIU) and the Alice L. Kibbe Field Station at WIU. We thank E. Lampo, L. McNeely, and C. Waddle for assistance during animal captures; and J. Lamer for logistical support. We thank V. Selonen, R. Swihart, 3 anonymous reviewers, and the Associate Editor for their insightful reviews and editorial suggestions on earlier drafts of our manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Associate Editor: Neubauss.