

Nesting patterns of southern flying squirrels in managed northern hardwoods

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Southern flying squirrels (*Glaucomys volans*) use multiple nest trees for foraging and protection, but nest trees can become scarce following harvests of hardwood forests. In northern Wisconsin, the Managed Old-growth Silvicultural Study tested techniques to remediate logging impacts on forest-dependent wildlife. Three types of canopy treatments were applied (multicohort harvest [0.4-ha and 1.2-ha irregular group shelterwoods], medium gaps [18-m- and 24-m-diameter gaps], and small gaps [11-m-diameter gaps]). To evaluate the effects of treatment on nest tree selection by southern flying squirrels, we tracked 33 radiocollared southern flying squirrels once a week for 5 weeks in late summer, locating 82 nest trees ($\bar{X} = 2.73$ nest trees per southern flying squirrel [95% confidence interval: 2.28–3.18 nest trees]). Canopy treatments were important predictors of nest tree switching. Probability of switching differed by canopy treatment (listed from lowest to highest probability): multicohort harvest: 0.29 (0.17–0.42), medium gaps: 0.44 (0.32–0.56), control: 0.57 (0.41–0.73), and small gaps: 0.73 (0.61–0.85). Lower nest tree switching in the multicohort harvest compared to the small gaps likely reflected availability of habitat resources. Spatial arrangement of canopy gaps and associated effects on southern flying squirrels should be considered when planning timber harvests in northern hardwoods.

Key words: canopy gaps, *Glaucomys volans*, optimal foraging, radiotelemetry, uneven-aged silviculture

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Southern flying squirrels (*Glaucomys volans*) rely on nest trees for shelter, foraging centers, and social gatherings (Holloway and Malcolm 2007; Muul 1968; Weigl 1968; Wells-Gosling 1985). Nests protect southern flying squirrels from predators such as owls (*Strigiformes*), raccoons (*Procyon lotor*), weasels (*Mustela*—Wells-Gosling 1985), and rat snakes (*Elaphe*—Rudolph et al. 2009; Taulman et al. 1998). Tree cavities in particular provide secure resting places for northern flying squirrels (*Glaucomys sabrinus*) because these dens are less penetrable by predators than leaf nests (Carey et al. 1997). Nest sites also shelter southern flying squirrels during cold precipitation events (Bendel and Gates 1987), and nest cavities that can be shared by multiple southern flying squirrels are important for seasonal thermoregulation (Muul 1968; Stapp et al. 1991). Additionally, southern flying

squirrels often select nest trees in close proximity to food resources such as mast-producing trees (i.e., oaks [*Quercus*] and hickories [*Carya*]—Fridell and Litvaitis 1991; Holloway 2006). With nearby food resources, nest trees serve as important sites for breeding and gestation, affecting recruitment rates of southern flying squirrels (Wells-Gosling 1985).

Stand structure and age of northern hardwood forests directly impact the abundance of suitable nest trees for southern flying squirrels. Even-aged, 2nd-growth forests have fewer snags and cavity trees for nest structures compared to uneven-aged, old-growth forests (Fan et al. 2005; Goodburn



and Lorimer 1998). Relatively young, even-aged stands tend to have homogenous canopies with suppressed trees in the midstory and understory (Nyland 2002). Suppressed trees were those overtopped by canopy trees that prevented direct sunlight from reaching them. Small, suppressed trees are less likely to have adequately sized cavities for southern flying squirrels. In contrast, uneven-aged stands have ≥ 2 canopy layers and a greater diversity of tree size classes. Varied canopy layers can allow growth of larger, unsuppressed trees over time. In general, larger trees tend to have larger cavities for flying squirrels, particularly northern flying squirrels (Bakker and Hastings 2002). Along with canopy structure, stand age can influence nest density. The likelihood of cavity formation increases with tree age, hence relatively young, 2nd-growth forests tend to have lower numbers of prospective nest sites compared to old-growth forests (Bakker and Hastings 2002; Goodburn and Lorimer 1998). Promoting development of characteristics found in uneven-aged, old-growth forests should help provide nest trees for flying squirrels.

Flying squirrels switch between nest trees at regular rates. On average, southern flying squirrels switch nest trees almost twice a month during the summer (May–August) in uncut forests (Holloway and Malcolm 2007). Nest switching changes temporally due to flying squirrel activities. For example, distances moved between nest trees were lower for female northern flying squirrels during lactation (July–September) compared to other seasons in the Pacific Northwest (Carey et al. 1997). Siberian flying squirrels (*Pteromys volans*), especially males, were most active in August, likely gathering forage resources for winter (Hanski et al. 2000). Long photoperiods and warm temperatures of summer often increase southern flying squirrel activity, whereas short photoperiods and cold temperatures of winter tend to reduce activity (Muul 1968).

Southern and northern flying squirrels rotate between select groups of nest trees, often to access resources and reduce parasite loads that infest bedding (Bendel and Gates 1987; Carey et al. 1997; Muul 1968). Southern flying squirrels are more likely to remain in a nest tree if resources are abundant and if external parasite loads are low (Charnov 1976; Wetzel and Weigl 1994). However, infrequent nest tree switching increases susceptibility of southern flying squirrels to predation by mammalian predators that use scent to locate nest trees (Wetzel and Weigl 1994). Therefore, southern flying squirrels switch trees if food resources are limited and if external parasite loads are high (Weigl 1968). Excessive switching from one nest to another by southern and northern flying squirrels increases the likelihood of contracting internal parasites and encountering predators (Carey et al. 1997; Wetzel and Weigl 1994). Southern flying squirrels acquire internal parasites through indirect contact with feces of conspecifics and other squirrels. In thinned forests, southern and northern flying squirrels often switch to previously used nest that may contain feces from previous inhabitants (Bendel and Gates 1987; Carey et al. 1997; Holloway and Malcolm 2007). Suitable habitat should provide southern flying

squirrels the option of switching but not force southern flying squirrels to switch nest trees.

Moderate nest tree switching (Holloway and Malcolm 2007) is expected under favorable conditions (i.e., suitable nest trees, sufficient habitat resources, and relatively healthy southern flying squirrels). Deviating rates of switching may indicate suboptimal conditions. Predictors of nest tree switching are not mutually exclusive in that effects of individual southern flying squirrels and habitat conditions on switching may be additive or antagonistic. This study was designed to determine how nesting patterns are influenced by habitat conditions of uneven-aged silvicultural treatments in northern hardwoods. The goal was to identify and quantify factors that dictate rates of nest tree switching by southern flying squirrels in late summer.

MATERIALS AND METHODS

Study area.—Study stands were located in the Northern Highland American Legion State Forest in Vilas County, Wisconsin (46°03'26"N, 089°26'32"W). Stands were even-aged, 2nd-growth northern hardwoods 80–100 years old. Pretreatment basal area, snag density, and down woody debris (DWD) volume in study stands resembled those of other even-aged hardwood stands in northern Wisconsin (Table 1; Goodburn and Lorimer 1998).

Study design.—Managed Old-growth Silvicultural Study treatments were implemented between November 2007 and March 2008. Treatments entailed 3 canopy alterations with differing size and frequency of gaps. The multicohort treatment included 0.4-ha and 1.2-ha irregular group shelter-wood harvests with light thinning to replicate mesoscale wind disturbances (Fig. 1; Frelich and Lorimer 1991; Hanson and Lorimer 2007). The medium-gap treatment contained alternating 18-m- and 24-m-diameter gaps to simulate smaller multitree wind throws (Fig. 1). The small-gap treatment included 11-m-diameter gaps with 10 gaps/ha to mimic openings created by toppling of individual senescent trees (Fig. 1).

All treatments included single-tree thinning between gaps (Nyland 2002) and retained approximately 16–20 m²/ha basal area. Cut trees were marked prior to harvest with an emphasis on maintaining less abundant native tree species and to maintain the 12 largest diameter at breast height (DBH) trees per hectare. Densities of DWD and snags were supplemented within each canopy treatment. To create additional DWD, designated trees were double-girdled and live trees were cut and left on site (Martin et al. 2006). The 49-ha, experimental control stand was similar to the treatment stands but with no anthropogenic canopy alteration, DWD manipulation, or snag creation (Fig. 1). DWD volume remained intact; basal area and snag density slightly decreased overall in treatment stands postapplication (Table 1).

Habitat surveys.—We analyzed nest tree use by flying squirrels using data on vegetation structure, including tree characteristics and DWD volume (Martin et al. 2006). Square

TABLE 1.—Habitat conditions of study stands before and after treatments in the Northern Highland American Legion State Forest, Wisconsin, in 2007–2009, compared to other even-age northern hardwood stands. Study stands included multicohort harvest (0.4-ha and 1.2-ha irregular group shelterwoods), medium gaps (18-m and 24-m diameter), small gaps (11-m diameter), and an untreated control.

Stand	Time	Habitat conditions before and after treatments					
		Basal area (m ² /ha)		Snag density (m ² /ha)		DWD ^a volume (m ³ /ha)	
		\bar{X}	95% CI	\bar{X}	95% CI	\bar{X}	95% CI
Even-age ^b		35.1	NA ^c	2.8	NA ^c	24.6	16.6–32.6
Multicohort	Before	36.34	34.71–37.97	1.53	1.11–1.96	44.71	34.49–54.93
Medium-gap	Before	34.61	33.07–36.14	2.21	1.65–2.76	51.45	31.57–71.33
Small-gap	Before	30.94	29.51–32.37	1.84	1.38–2.31	41.64	33.80–49.48
Control	Before	40.30	38.46–42.13	2.45	1.82–3.08	37.87	29.67–46.07
Multicohort	After	24.44	22.47–26.40	1.36	0.86–1.87	29.02	22.48–35.56
Medium-gap	After	23.50	21.54–25.46	1.09	0.66–1.51	32.12	23.44–40.80
Small-gap	After	25.39	23.84–26.95	0.94	0.56–1.33	30.26	23.83–36.69
Control	After	35.05	33.46–36.65	2.40	1.78–3.01	25.94	19.40–32.48

^a DWD = down woody debris.

^b Adapted from Goodburn and Lorimer (1998).

^c NA = not applicable; standard error not given.

tree plots ($n = 152$, area = 1,557 m²) were placed systematically 100 m apart throughout the treatments and control. Within tree plots, all trees ≥ 10 -cm DBH were identified by species, measured for DBH, classified as live or snag, and categorized as suppressed or not. Snags were dead trees standing upright and were defined by decay class (0–1 being none to little external decay, 2–3 being moderate decay, and 4–5 being highly decayed). Using DBH measurements, we calculated basal area for each tree plot (Avery and Burkhart 2002). Numbers of red oak (*Quercus rubra*) trees ≥ 35 -cm DBH indexed mast production (Auchmoody et al. 1993). Numbers and diameters of DWD pieces > 10 cm, including stumps and roots, were quantified on 4 transects (22.26-m and 40-m length) arrayed perpendicularly from each tree plot center. We determined DWD volume for individual tree plots by squaring the diameter of DWD pieces, summing these values for each transect, and calculating a weighted average (Marshall et al. 2000).

Livetrapping.—We established 5 × 5 trapping grids with 40-m spacing between grid points and a 40-m perimeter buffer in stratified, randomly selected locations in each canopy treatment and the control stand ($n = 4$) in 2008 and 2009. High DWD areas were designated for trapping to increase the probability of catching flying squirrels (Carey et al. 1991). In 2008 we expanded the trapping grid in small-gap treatment (11-m gaps) to a 7 × 7 array to increase the total number of captures. Otherwise, livetrapping methods did not differ between 2008 and 2009. At each grid point, we placed 2 Tomahawk 201 live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin).

Trapping occurred from late May through July 2009 until >6 southern flying squirrels were fitted with radiocollars in each stand. All trapping and handling procedures conformed to an animal use protocol that followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Research Animal Resource Center at the University of Wisconsin–Madison (protocol A070769 A1343). We recorded characteristics of captured southern

flying squirrels (i.e., sex, age, reproductive status, and mass—Wells-Gosling 1985) and ear-tagged each individual.

Radiotelemetry.—We anesthetized southern flying squirrels in a sealed container using 7 ml of isoflurane injected into a cotton ball soaked in mineral oil and placed in a porous canister. We fitted southern flying squirrels with radiocollars (model M1530; Advanced Telemetry Systems, Isanti, Minnesota) weighing $\leq 7\%$ total body mass. Once a week for 5 weeks (28 July–24 August 2009), we tracked southern flying squirrels to diurnal nest trees. Nest trees were categorized and measured according to habitat survey protocol. We also classified crown condition of nest trees as intact (with no apparent broken branches) or declining (with a structural defect) and measured tree height (m, using a clinometer).

Comparing nest use by canopy treatment.—The initial nest tree found for a southern flying squirrel was considered the baseline nest site. Following location of this initial nest tree, there were 4 subsequent location attempts. Nest switching was characterized as the count of nest switches ($0 \leq n \leq 4$) by radiocollared southern flying squirrels in each treatment. Nest tree suitability parameters included tree type (live or snag), tree species (sugar maple [*Acer saccharum*] or other), decay class (0–5), crown condition (intact or broken and declining), DBH, and tree height (Table 2). We grouped tree species into 2 levels because sugar maple dominated our study area. Squirrel characteristics included both categorical (age and sex) and continuous parameters (mass and length of the right hind foot—Madden 1974). Treatment was categorical with 4 levels (Table 2), 1 for each treatment type and the control.

We checked normality assumptions of continuous parameters using quantile plots, equal variance assumptions using residual-fitted plots, and made transformations as appropriate. Nest switches, nest tree characteristics, and flying squirrel condition were dependent variables. We used analysis of variance (ANOVA) tests to compare dependent variables by treatment, sex, and treatment–sex interaction. To compare numbers of flying squirrels by treatment and by sex, we used Wilcoxon tests.

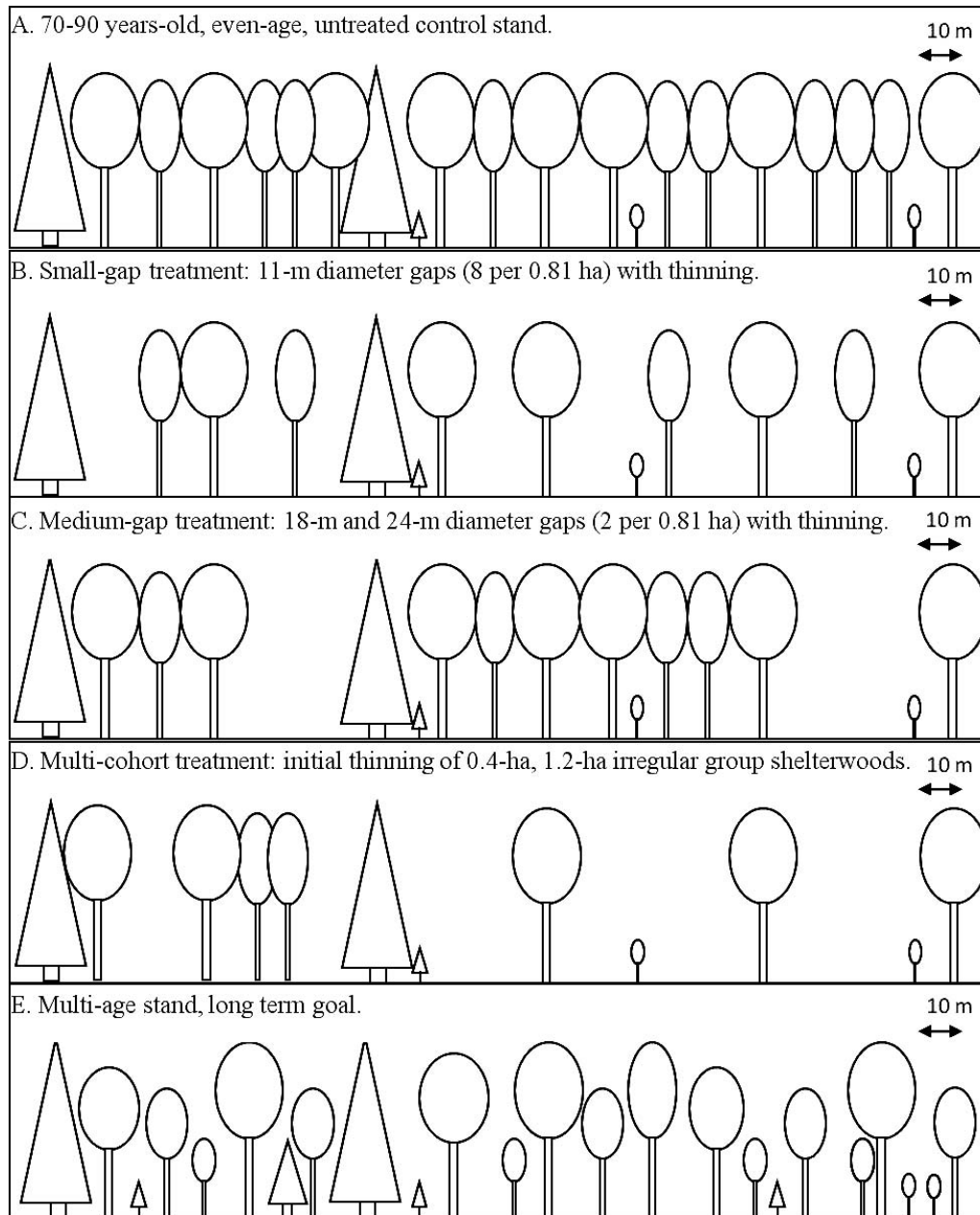


FIG. 1.—A–E) Managed Old-growth Silvicultural Study stands in mixed hardwoods of the Northern Highland American Legion (NHAL) State Forest, Wisconsin. B–D) All canopy treatments retained 16–21-m²/ha residual basal area.

Numbers of shared nest trees (i.e., trees occupied by >1 southern flying squirrel concurrently or serially) were compared by treatment using ANOVA. We evaluated shared nest trees as a group because our primary interest was in the traits of nest trees that received high amounts of use rather than the causal social behavior of such use. We tested whether available trees and habitat characteristics differed by treatment using ANOVA and examined the magnitude of differences using post hoc Tukey honestly significant difference ($\alpha = 0.05$). Basal area and snag density defined availability of nest trees under the assumption that both of these measures were associated positively with cavity occurrence. Habitat charac-

teristics included number of red oak trees ≥ 35 cm DBH and DWD volume.

Modeling determinants of nest tree switching.—Multilevel logistic regression was used to model important determinants of nest tree switching. Potential regressors included individual southern flying squirrel as a random effect and fixed effects grouped into 3 categories: silvicultural treatment, squirrel characteristics, and nest tree suitability (Table 2). The null model was switching as a function of the random effect from individual southern flying squirrels. The global model included all potential regressors. Another 6 models were different arrangements of parameter groupings (i.e., treatment,

TABLE 2.—Model parameters for analysis of southern flying squirrels (*Glaucomys volans*, $n = 33$) nesting in the Northern Highland American Legion State Forest, Wisconsin, in 2009. Treatments included multicohort harvest (0.4-ha and 1.2-ha irregular group shelterwoods), medium gaps (18-m and 24-m diameter), small gaps (11-m diameter), and an untreated control.

Levels	Parameters		
	Squirrel	Treatment	Tree
Categorical	Age	Multicohort	Alive versus snag
	Sex	Medium-gap	Tree species
		Small-gap	Decay class
Continuous	Mass (g) Right hind foot (mm)	Control	Crown condition
			DBH (cm)
			Tree height (m)

squirrel, and nest tree); each included individual southern flying squirrel as a random variable (Table 3).

We used 2nd-order Akaike's information criterion (AIC_c) because of a low sample-size to model-parameter ratio (Burnham and Anderson 2002a). Because of model uncertainty, beta values were averaged across all models based on Akaike weights to evaluate parameter estimates (Burnham and Anderson 2002b). We determined unconditional parameters and meaningful model structures through data simulations. The absolute probability of switching was calculated as a function of treatment parameters using Monte Carlo simulations with 100,000 replicates (Burnham and Anderson 2002b). To evaluate model fit to the data, we ran 1,000 sets of deviance simulations and compared the outcomes to expected values using a chi-square test (Gelman and Hill 2007).

RESULTS

In 2009, we trapped, radiocollared, and tracked 33 southern flying squirrels to 82 nest trees ($\bar{X} = 2.73$ nest trees per southern flying squirrel, 95% confidence interval [95% CI]: 2.28–3.18). Sixteen of the radiocollared squirrels were females, 8 of which were lactating at the time of capture. Reproductive status did not have a significant influence on female nest switching ($\chi^2_1 = 3.05$, $P = 0.08$). However, lactating females tended to switch nests less often ($\bar{X} = 0.37$, 95% CI: 0.11–0.64) than independent females ($\bar{X} = 0.66$, 95% CI: 0.40–0.91). During 4 weeks of observation, average number of switches per flying squirrel was 1.94 (range = 1.45–2.43). Seasonal weather changes did not appear to impact nest switching. Nest switching did not vary by number of civil-twilight daylight hours ($\chi^2_1 = 1.35$, $P = 0.25$, range = 14.52–16.08) or average minimum temperature ($\chi^2_1 = 0.31$, $P = 0.58$, range = 9–14°C). Mean occurrence of switching nest trees did not significantly differ by treatment ($F_{3,29} = 2.68$, $P = 0.06$).

Nest trees.—As a group, characteristics of nest trees that southern flying squirrels switched to ($n = 66$) were similar across treatments ($F_{21,162} = 1.02$, $P = 0.44$). However, decay class was lower and crown condition more intact for nest trees in the multicohort treatment compared to those in the control

TABLE 3.—Second-order Akaike information criterion (AIC_c) selection of multilevel logistic regression models explaining nest tree switching by southern flying squirrels (*Glaucomys volans*, $n = 33$) in the Northern Highland American Legion State Forest, Wisconsin, in 2009.

Model ^a	AIC_c	Δ_i	L(g,lx)	w_i	(w_i/w_j)
Null	162.92	0.00	1.00	0.48	
Treatment	163.22	0.30	0.86	0.41	1.16
Treatment + Tree	167.47	4.56	0.10	0.05	9.75
Tree	167.94	5.02	0.08	0.04	12.32
Squirrel	169.87	6.95	0.03	0.01	32.26
Treatment + Squirrel	170.58	7.66	0.02	0.01	46.13
Squirrel + Tree	174.24	11.32	0.00	0.00	287.44
Global (Treatment + Squirrel + Tree)	174.65	11.73	0.00	0.00	352.57
Totals		47.55	2.10	1.00	

^a All models include individual squirrel as a random variable.

($t_{29} = 2.43$, $P = 0.02$). There was no difference in nest tree decay class between the medium-gap treatment, small-gap treatment, and control ($t_{51} < 1.49$, $P > 0.14$). Other traits of nest trees, including tree type (alive or snag), tree species (sugar maple or other), lower decay classes, DBH, and tree height, did not differ among treatments (Table 4).

Sixty-six percent ($n = 6$) of shared nest trees (i.e., those used by multiple southern flying squirrels) were occupied concurrently. No shared nest trees were found in the multicohort treatment. Characteristics of shared nest trees did not differ among medium-gap and small-gap treatments and the control ($F_{4,12} = 1.08$, $P = 0.52$). Southern flying squirrels shared birch (*Betula*) trees, sugar maple (*A. saccharum*) trees, and sugar maple snags. Intact crown canopies along with broken and declining crown canopies were equally represented among shared nest trees. Basal area ($F_{3,148} = 36.96$, $P < 0.01$) and snag density ($F_{3,148} = 11.97$, $P < 0.01$) of available trees were lower in treatments than in the control stand after treatment (Table 1). Numbers of red oaks ≥ 35 cm DBH ($F_{3,148} = 2.19$, $P = 0.09$; Tukey honestly significant difference: $P \geq 0.11$) and DWD volume ($F_{3,148} = 1.83$, $P = 0.27$) were similar in availability among treatments and the control.

Nesting patterns.—Model selection using AIC_c suggested that null and treatment models were the most parsimonious for nest tree switching. Collectively, these models accounted for 88% of Akaike weight of evidence (Table 3). The 2 best-supported models were close, differing by 0.30 AIC_c units, indicating uncertainty in model selection (Table 3; Burnham and Anderson 2002b). With model averaging, the probability of southern flying squirrels switching nest trees increased across the multicohort treatment, medium-gap treatment, control, and small-gap treatment (Table 5). Southern flying squirrels in the multicohort treatment had a lower probability of switching nest trees compared to those in the small-gap treatment ($Z_{12} = 2.37$, $P = 0.02$). Probability of switching nest trees for flying squirrels was similar in medium-gap and small-gap treatments ($Z_{13} = 1.64$, $P = 0.10$). Southern flying

TABLE 4.—Characteristics of nest trees used by southern flying squirrels (*Glaucomys volans*, $n = 33$) in the Northern Highland American Legion State Forest study stands, Wisconsin, in 2009. Stand treatments included multicohort harvest (0.4-ha and 1.2-ha irregular group shelterwoods), medium gaps (18-m and 24-m diameter), small gaps (11-m diameter), and an untreated control.

Stand	Type		Species		Decay class			Crown		Dimensions			
	Live	Snag	A.s. ^a	Other	0–1	2–3	4–5	Intact	B-D ^b	DBH (cm)	95% CI	Height (m)	95% CI
Multicohort	11	1	8	4	11	1	0	11	1	43.43	34.25–52.61	29.03	23.03–35.04
Medium	15	3	14	4	15	0	3	14	4	45.14	39.21–51.08	26.92	22.97–30.88
Small	11	6	15	2	11	1	5	10	7	40.17	34.10–46.24	22.84	19.15–26.52
Control	12	7	15	4	11	1	7	10	9	49.59	43.55–55.63	24.92	21.27–28.57
F^c	1.59	1.59	0.64	0.64	2.01	2.01	2.25	2.30	2.30	1.74		1.64	
$d.f.$	3,62	3,62	3,62	3,62	3,62	3,62	3,62	3,62	3,62	3,62		3,62	
P	0.20	0.20	0.59	0.59	0.12	0.73	0.09	0.09	0.09	0.17		0.19	

^a A.s. = *Acer saccharum* (sugar maple).

^b B-D = broken–declining.

^c From ANOVA, null hypothesis: characteristic did not differ by treatment.

squirrel patterns of nest tree switching did not vary between multicohort and medium-gap treatments ($Z_{20} = 0.89$, $P = 0.37$). Nest tree switching in the control did not differ from that in the medium-gap ($Z_{33} = 0.31$, $P = 0.76$), small-gap ($Z_{40} = 1.44$, $P = 0.15$), and multicohort ($Z_{14} = 1.22$, $P = 0.22$) treatments.

Variation in the model did not vary from that expected by chance ($t = 609$, $P = 0.71$). The chi-square distribution aligned with the deviance of the selected model ($\chi^2_{113} = 153.1$, $P = 0.99$) meaning it was an approximation of model fit. Thus, simulations suggest that the treatment model accurately described the data.

DISCUSSION

Nesting patterns of southern flying squirrels among silvicultural treatments in late summer were influenced by resource availability. In the multicohort treatment, switching of nest trees by southern flying squirrels was less frequent than in the small-gap treatment. Within treatments, sugar maple and birch were key tree species that served as shared nest sites for southern flying squirrels. Spatial arrangement of trees had more influence on nest switching than either southern flying squirrel condition or nest tree characteristics providing further

evidence of the importance of forest structure for southern flying squirrels. Managed Old-growth Silvicultural Study treatments favorably changed the canopy structure and allowed southern flying squirrels to continue usual nesting patterns.

Two non-exclusive explanations may account for reduced nest switching by southern flying squirrels in the multicohort treatment compared to the small-gap treatment. Assuming an optimal foraging scenario in the multicohort treatment, moving less may indicate sufficient resources locally and no need to expend extra energy (Charnov 1976). However, evidence supporting higher resource availability in multicohort compared to other treatments was lacking because red oak abundance and DWD volume did not differ among stands. Alternatively, limited availability of nest trees may have prevented switching among trees. Lower density of highly decayed nest trees than in the other treatments (Table 4) most likely reduced switching frequency in the multicohort treatment.

Southern flying squirrels use a wide range of tree sizes (DBH range = 3.0–69.1 cm) but prefer nesting in snags with cavities (Taulman 1999). Most nest trees in the multicohort treatment did not resemble cavity trees of old-growth forest. Cavity trees in late-successional forests tend to have more advanced decay than even-aged or selection-cut stands (Goodburn and Lorimer 1998). Because decayed nest trees appeared less available in the multicohort treatment (Table 4), southern flying squirrels probably used alternative (e.g., less decayed with fewer developed cavities) trees. Southern flying squirrels in Ontario, Canada, that used alternative nest trees in thinned hardwood stands (18-m²/ha residual basal area) were more susceptible to predators (Holloway 2006).

Predators and other factors influencing nest switching of southern flying squirrels (e.g., parasites and seasonality) warrant further investigation. Predator pressure may function in combination with resource availability in determining nesting behavior and survival (McNamara and Houston 1987) of southern flying squirrels. How predators directly affect nest switching rates is unknown. Risk of being detected by predators in a nest tree may motivate a southern flying squirrel to switch, but risk of encountering predators may

TABLE 5.—Unconditional parameter estimates of logistic regression models predicting the probability of nest switching by southern flying squirrels (*Glaucomys volans*, $n = 33$) in the Northern Highland American Legion State Forest, Wisconsin, in 2009. Treatments included multicohort harvest (0.4-ha and 1.2-ha irregular group shelterwoods), medium gaps (18-m and 24-m diameter), small gaps (11-m diameter), and an untreated control.

Treatment	Unconditional parameter estimates of nest switching ^a			
	$\tilde{\beta}^b$	95% CI ($\tilde{\beta}$)	Simulated β	Simulated 95% CI (β)
Multicohort	0.29 ^A	0.17–0.42	0.35 ^C	0.32–0.38
Medium-gap	0.44 ^{A,B}	0.32–0.56	0.49 ^D	0.46–0.52
Small-gap	0.73 ^B	0.61–0.85	0.73 ^E	0.70–0.76
Control	0.57 ^{A,B}	0.41–0.73	0.54 ^F	0.52–0.56

^a Means followed by the same capital letters are not significantly different ($P > 0.05$).

^b Beta values calculated across all candidate models (Burnham and Anderson 2002b).

cause nest philopatry. Predation risk may depend on the amount of habitat cover (Carey et al. 1997; Kotler and Blaustein 1995; Mysterud and Ims 1998). Type of predators and their hunting strategies vary regionally, which calls for evaluation of several study sites.

Another habitat element linked to nest switching is nest condition. External parasite loads in nests seem to be a causal factor for southern and northern flying squirrels to switch nest trees (Carey et al. 1997; Krichbaum et al. 2010; Wells-Gosling 1985). Although switching nest trees may help southern flying squirrels escape external parasites, this movement may increase the likelihood of contracting internal parasites. Spread of gut parasites such as *Strongyloides robustus* from southern flying squirrels could harm populations of northern flying squirrels unaccustomed to this parasite (Pauli et al. 2004; Weigl 2007; Wetzel and Weigl 1994). Shared nests greatly increase the potential for transmission of internal parasites (Weigl 1978). The roles of external and internal parasites in nest switching dynamics, including nest sharing, need additional study for flying squirrel conservation.

Only sugar maple and birch tree species were used as nest trees by multiple radiocollared southern flying squirrels in our study area. Sugar maple might have been used by southern flying squirrels as a shared nest tree because of its abundance. Southern flying squirrels also seemed to use birch trees as shared nest sites over other tree species. Soft bark of live birch trees and rapid decay of birch tree snags may facilitate cavity formation, making this tree species more likely to have nest sites (Goodburn and Lorimer 1998; Holloway 2006). Tree species can affect the suitability of an individual tree as a shared nest tree depending on the combination of diameter and wood tensile strength (Nyland 2002).

Nest tree sharing by southern flying squirrels is higher in the winter than in summer at temperate latitudes (Gilmore and Gates 1985; Muul 1968; Stapp 1991). Monitoring nest tree use and associated factors throughout the year for southern flying squirrels would increase understanding of how nest switching and its determinants fluctuate over time. This knowledge will enable wildlife managers to better evaluate effects of forest practices on flying squirrels.

The small-gap and medium-gap treatments did not drastically alter nest tree use compared to the untreated control stand. Spatial arrangements of trees in these treatments were conducive to switching patterns of southern flying squirrels. Our findings suggest that southern flying squirrels maintain expected nest switching with canopy gaps ≤ 80 m in northern hardwoods. The multicohort treatment initially had lower rates of nest switching and likely had lower densities of suitable nest trees because of tree removal at the hectare scale. According to our study, the multicohort technique should be adapted in northern hardwoods to increase cavity trees available for southern flying squirrels immediately following treatment. Additional residual cavity trees with decay in thinned areas may help preserve spatial distribution of nest trees (Kenefic and Nyland 2007). Forest managers should maintain densities of trees with cavities at 6.5–9/ha for flying

squirrels (Holloway 2006). Future studies are planned to evaluate the long-term effects of these old-growth silvicultural treatments on nesting patterns of southern flying squirrels.

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