

# Northern and southern flying squirrel use of space within home ranges in central Ontario

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## Abstract

Partial harvesting can reduce the supply of dead and diseased trees in forests and as a result is predicted to negatively influence flying squirrel habitat. In this study, we measured the home range and habitat use of 13 radio-collared southern flying squirrels (*Glaucomys volans*) in selection logged and uncut hardwood forests, and 14 radio-collared northern flying squirrels (*G. sabrinus*) in unlogged coniferous forest in Algonquin Provincial Park, Ontario. Locations were collected on southern flying squirrels in 2003, and on northern flying squirrels in 2004. Southern flying squirrel home range and core area size showed no differences between unlogged and recent selection-harvested sites. Compared to available locations, southern flying squirrels radio-locations in uncut sites were associated with higher densities of decayed and mast trees, and greater overstory tree diversity, whereas in recent cuts, they were associated with higher densities of mast producing shrubs. Northern flying squirrel used locations that were characterized by older, decaying conifer trees with high understory sapling density and abundant spruce trees. Southern flying squirrel core areas were near nests, whereas northern flying squirrel core areas appeared to be used for foraging activity. Selection harvesting appears to support sufficient food resources for southern flying squirrels in the short term to maintain populations. However, we obtained evidence that the supply of nest trees may be limited in cuts, which may negatively impact future flying squirrel populations. The close association between northern flying squirrels and decayed trees may explain why we found no northern flying squirrels in two partially logged stands, where logging reduced the number of decaying trees.

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## 1. Introduction

Northern hardwood and pine forests in northeastern North America are often managed through the use of partial harvesting silvicultural methods. These techniques typically result in reductions in the density of diseased and dead trees (snags) and of stand structural complexity (McGee et al., 1999; Costello et al., 2000). Populations of many arboreal wildlife species, including northern and southern flying squirrels, can be negatively affected by these changes (Waters and Zabel, 1995; Taulman et al., 1998; Costello et al., 2000). Because flying squirrels use trees and snags for food, travel, and nesting, they may be one of the groups most impacted by the harvesting (Selonen et al., 2001; Taulman and Smith, 2004). Previous studies in the Pacific Northwest, New Brunswick, and

Maryland have linked flying squirrel habitat use to features typically characteristic of mature unharvested forests, such as large trees, snags, and multi-layered canopies (Bendel and Gates, 1987; Carey, 1995; Gerrow, 1996; Carey et al., 1999). Additionally, food availability strongly influences flying squirrel densities and movement patterns: flying squirrel activity is associated with areas of high mast tree densities, abundant understory shrubs, and high hypogeous fungi biomass (Sonenshine and Levy, 1981; Fridell and Litvaitis, 1991; Carey, 1995; Waters and Zabel, 1995; Taulman and Smith, 2004).

Understanding flying squirrels fine-scale habitat requirements and use of space is crucial to ensuring that populations are maintained in managed landscapes. Unfortunately, few studies have investigated flying squirrel micro-habitat use (see Fridell and Litvaitis, 1991). Instead, most work on flying squirrel habitat use has been undertaken at the stand-level and has been based on trapping data (Carey, 1995; Taulman et al., 1998): the importance of particular within-stand habitat features has been largely inferred. Knowledge of micro-habitat

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use may be particularly important for northern flying squirrels, whose population densities are two to four times greater in unlogged stands than in post-logged stands (Carey, 1995; Holloway and Malcolm, 2006). Investigating their habitat use within home ranges in unharvested forest may provide insights into why northern flying squirrels are uncommon in harvested stands.

In this study, we investigate flying squirrel home range, movements, and fine-scale habitat use in partially harvested stands (southern flying squirrels) and uncut sites (southern and northern flying squirrels). Flying squirrel home range size and movements appear to be larger in harvested compared with unharvested areas, with the largest home ranges ever reported for flying squirrels in managed landscapes (Taulman and Smith, 2004; Menzel et al., 2006). Flying squirrel nighttime activity is hypothesized to be: (1) associated with old forest characteristics (larger trees and structurally diverse canopies), which reduce predation risk and (2) areas that potentially have higher food availability (high spruce tree, mast tree, mast producing shrubs, and understory shrub density). Spruce is predicted to be a strong correlate of food availability because the sporocarps (truffles) of hypogeous fungi that dominate the diet of northern flying squirrels are associated with spruce (Loeb et al., 2000).

## 2. Methods

### 2.1. Study area

We conducted the study in Algonquin Provincial Park (45°35'N, 78°30'W) in central Ontario. Forest cover in the study area is dominated by sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Smaller pockets of white and red pine (*Pinus strobus* and *P. resinosa*) also occur in association with white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). The forest is mature-to-old with an average age of 126 years (Ontario Ministry of Natural Resources [OMNR] unpublished data). Algonquin Provincial Park was established as a multiple-use park in 1893 and logging continues to the present day. Tolerant hardwood stands are managed under single-tree selection silviculture (OMNR, 1998a). Under this system, stands are harvested every 20–25 years when approximately one-third of the over-story basal area is removed, resulting in uneven aged stands with single- and multiple-tree canopy gaps.

### 2.2. Trapping and telemetry

We live-trapped and radio-collared southern flying squirrels on five grids dominated by sugar maple and yellow birch in May 2003. Three grids were located in uncut hardwoods (stands not logged at least since the 1950's), two of which had a minor American beech component (c. 20% of tree basal area [BA] based on the Forest Resource Inventory); the third had an eastern hemlock component (38% of BA). The remaining two grids were in sites harvested by single-tree selection 8–9 years

previously that contained a minor American beech component (c. 10% of tree BA). The following summer southern flying squirrel populations crashed (see Bowman et al., 2005), and we were unable to capture any individuals despite 5758 trap nights in hardwood stands. As a result, we switched our efforts to studying northern flying squirrels in uncut and harvested conifer forests. However, despite 1545 trap nights in white pine shelterwood stands, we did not capture any northern flying squirrels, and therefore restricted our telemetry work to five grids in uncut, conifer-dominated stands. None of these sites were those studied for southern flying squirrels the previous year. The forest cover in three of these sites was dominated by white and red pine and the other was dominated by eastern hemlock, sugar maple and yellow birch. White spruce was relatively common at all five sites (c. 12% of BA).

We used large grids (either 6-by-11 [8.0 ha] or 8-by-9 [9.0 ha]) with 40-m spacing between grid stations to capture squirrels. At each station we placed one large Sherman trap (10-by-11-by-38 cm) on two large nails in the tree trunk at approximately 1.5 m in height and secured it on top using an elastic cord. We baited traps with apple, peanut butter, and unshelled sunflower seeds soaked in water. We fitted squirrels with Holohil<sup>®</sup> PD-2C radio-collars, which weighed 3.3 g. We only collared adult flying squirrels, which ranged in weight from 65 to 88 g (mean = 72.1 g) for southern flying squirrels and 86–130 g (108.1 g) for northern flying squirrels. We equipped 28 southern flying squirrels with radio-collars in 2003, and 17 northern flying squirrels in 2004.

We located radio-collared squirrels during 28 May to 15 August in 2003 and 12 June to 20 August in 2004, and tracked animals with Telonics<sup>®</sup> TR-2 receivers and 3-element Yagi<sup>®</sup> antennas via triangulation. To facilitate work at night, we marked grid stations with reflective tape. Two observers in radio contact took two-three bearings for a given individual within a 12 min period to triangulate flying squirrel locations. Triangulations were undertaken only at night (30–60 min after sunset to 60 min before sunrise), and we randomized the order in which locations were collected on individual animals from night to night throughout the study. Fixes were spread more-or-less evenly throughout this nighttime period, with 42% occurring in the first 3 h after sunset, and 58% occurring during the next 3–4 h before sunrise. In 2003, we located southern flying squirrels twice per night, two times a week, with a minimum of 2 h between successive nighttime locations. In 2004, we located all radio-collared flying squirrels once per night 5–6 times per week. Additionally, we tracked flying squirrels to diurnal nests once per week in both 2003 and 2004.

We estimated squirrel locations via maximum likelihood using the LOAS 2.11 software package. The angular error and the size of the error ellipse ( $\pm$ S.D.), respectively, were  $3.5 \pm 2.9^\circ$  and  $0.09 \pm 0.13$  ha in 2003, and  $3.1 \pm 2.8^\circ$  and  $0.06 \pm 0.12$  ha in 2004. We also conducted a beacon study (see White and Garrott, 1990) by placing transmitters on the ground and in the understory to test the accuracy of fixes. The average distance between the estimated and true locations was 26 m ( $\pm 22$  m).

### 2.3. Home range and spatial overlap analyses

We used the Animal Movement Extension on ArcView 3.2 (Hooge et al., 1999) to calculate home ranges (95% fixed kernel estimates) and core areas (50% fixed kernel estimates) by use of the least squares cross validation (LSCV) technique (see Kernohan et al., 2001 for details). We also provide 95% minimum convex polygon (MCP) home range estimates because they are commonly reported in the literature. To determine the minimum sample size needed for kernel home range estimates, we ran 100 bootstrap simulations per sample size (with replacement). Thirty locations are recommended as a minimum sample size (Kernohan et al., 2001); however, our simulations indicated that home range size had reached an asymptote by 24 locations. Indeed, for nine southern flying squirrels with  $\geq 30$  locations, 95% fixed kernel estimates did not differ significantly between 24 and 30 locations (paired *t*-test:  $t = 0.26$ ,  $P = 0.81$ ). All southern flying squirrels that had  $< 24$  locations were excluded from home range and core area analyses.

To investigate use of space within home ranges, we calculated percentage overlaps of home range and core areas for (1) pairs of same-sex and different-sexed neighbouring squirrels and (2) each individual with all neighbouring squirrels. To characterize movement patterns, we calculated average distances moved between successive locations. We used analysis of variance (ANOVA) to compare home ranges, core areas, and movement patterns between (1) male and female squirrels (both species separately) and (2) southern flying squirrels on uncut and recently cut sites. Assumptions of normality and homogeneity were justified based on examinations of residuals.

### 2.4. Habitat sampling

To quantify flying squirrel habitat use, we measured the habitat characteristics of sites where flying squirrels were located at night by radio-telemetry (hereafter referred to as “used” locations) and of random locations (hereafter referred to as “available” locations). We sampled 10 used locations/individual on average for both southern flying squirrels (range = 5–15) and northern flying squirrels (8–10). For some individuals, we sampled  $< 10$  sites in order to avoid any overlap in habitat sampling (sites had to be located at least 40 m apart). Available locations were selected in two ways: (1) stratified sampling across the entire grid (4–5 randomly selected stations per grid line for a total of 30–36 locations per site) and (2) sites selected by walking a random distance (between 50 and 100 m) and bearing from used locations.

We focused habitat measurements on tree, snag, and shrub populations. At each used or available site, we recorded the diameter at breast height (dbh) of all trees and snags  $\geq 10$  cm dbh in a BAF 2 prism sweep. We assessed tree condition as healthy (intact canopy), declining ( $\geq 50\%$  of canopy showing signs of die-back or extensive fungal infection), or dead (snag), and we inspected all trees and snags for the presence of cavities. From these data, we calculated the basal area (BA) and average dbh (AverDBH) of all trees (variable acronyms in parenthesis). In addition, for three structural and five taxonomic categories, we

calculated the average density of trees  $\geq 10$  cm dbh/ha and of large trees  $\geq 25$  cm dbh/ha. They were: declining trees (Declin, Declin  $> 25$ ), conifer trees (Conifer, Conifer  $> 25$ ), hardwood trees (Hardwd, Hardwd  $> 25$ ), maple trees (Maple, Maple  $> 25$ ), mast trees (Mast, Mast  $> 25$ ), spruce trees (Spruce, Spruce  $> 25$ ), snags (Snags, Snag  $> 25$ ) and cavity trees (CavTree, CavTree  $> 25$ ). Mast trees were those that produce nuts (American beech, and red oak [*Quercus rubra*]). We counted the number of understory stems (trees  $< 10$  cm dbh and  $\geq 1$  m tall) in a 3-m radius plot as a measure of understory stem density (Understory) and stem densities of shrubs that produce abundant food crops (Foodstems; beaked hazel [*Corylus cornuta*], raspberry [*Rubus idaeus*], pin cherry [*Prunus pensylvanica*] and choke cherry [*Prunus virginiana*]) were counted. We also calculated tree species richness of trees  $\geq 10$  cm dbh (TreeSp\_rich) at each site. The density of maple and mast were only considered for southern flying squirrels, whereas spruce density was only included in analysis for northern flying squirrels. The net effect was a total of 19 variables for southern flying squirrels and 17 for northern flying squirrels.

### 2.5. Habitat analyses

Data for each species were analyzed separately; no direct comparisons of the two species were undertaken because data for the two were collected in different years. Because several of the habitat variables we calculated had the potential to be highly correlated, we used principal components analysis (PCA) to determine which habitat variables had similar loadings. When two variables were highly correlated (as indicated by similar vectors in the PCA biplot), we removed the one with the smaller loadings (i.e., the variable with the shortest vector). Using this procedure, we removed 7 habitat variables each for southern and northern flying squirrels.

In order to develop resource selection models, we first investigated whether or not harvesting significantly influenced southern flying squirrel habitat use and habitat availability by use of Multivariate Analysis of Variance (MANOVA). For this analysis, and in all following MANOVA and univariate tests, we rank transformed variables since the assumptions of normality and homogeneity were not always met. For southern flying squirrels, we compared habitat variables using a two-factor MANOVA with interaction, in which the factors were logging history (uncut or recent-selection cut) and habitat use (used or available). Because all three terms were highly significant (see results below), we conducted separate analyses for uncut sites and recent selection cut for southern flying squirrels. In order to compare used and available locations for: (1) southern flying squirrels in uncut sites; (2) southern flying squirrels in recent selection cuts; and (3) northern flying squirrels in uncut sites, we used a MANOVA test followed by univariate *t*-tests if the MANOVA was significant (i.e.,  $P < 0.05$ ).

We developed logistic regression models using the used-vs.-available design (Design I; see Manly et al., 2002 for further details), which is commonly used in wildlife habitat modeling. Under this design, flying squirrel used sites were compared with all possible available sites, and each site is considered a

Table 1

The top AIC models predicting flying squirrel used locations compared with those available for southern and northern flying squirrels, and comparing core vs. non-core locations for northern flying squirrels in Algonquin Park, Ontario

Spp/Model	Rank	$\Delta$ AIC
<i>G. volans</i> – uncut sites		
Overstory + nest + food <sup>a</sup>	1	0.0
Nest + food	2	3.5
<i>G. volans</i> – recent selection cuts		
Food <sup>a</sup>	1	0.0
Overstory	2	26.3
<i>G. sabrinus</i> – uncut Sites		
Overstory + nest <sup>a</sup>	1	0.0
Overstory	2	10.0
<i>G. sabrinus</i> – core vs. non-core		
Overstory + nest + food <sup>a</sup>	1	0.0
Overstory + food <sup>a</sup>	2	1.5
Overstory	3	3.4

<sup>a</sup> We give parameter estimates for these models in Table 4

replicate. To validate this approach, we also undertook used-vs.-unused analyses (Design III; Manly et al., 2002) in which individual flying squirrels were used as the unit of replication. In this analysis, we calculated habitat means for sites used by a given individual and compared them against means from same-grid locations outside its home range (“unused” sites).

We combined classical and information theoretic approaches in constructing logistic regression models. Habitat variables were classified *a priori* into three sets (overstory, food, and nest; see Tables 3 and 5), which provided seven possible models that examined the sets singly or in combination. For each of these seven combinations, we used stepwise logistic regression to create the “best” model (where  $P = 0.10$  for variable entry and  $P = 0.15$  for variable removal; Hosmer and Lemeshow, 2000). Subsequently, these models were compared by calculating Akaike’s Information Criterion (AIC or AIC<sub>c</sub> where appropriate) and the difference between the each model and the minimum AIC ( $\Delta$ AIC) was used to gauge the relative plausibility of candidate models (Burnham and Anderson, 1998). One model was clearly the “best” in AIC comparisons (where  $\Delta$ AIC<sub>c</sub> > 2.0), except for the analysis of

core versus non-core areas for northern flying squirrel where two models were ranked as equivalent (see Table 1).

In a final analysis, we used logistic regression to compare used locations in northern flying squirrel core areas against those used elsewhere in the home range. Because of the relatively small number of squirrel locations, we also included available locations that fell within flying squirrel home ranges, classifying them as core or non-core as appropriate. We used the same approach to construct regression models as described above. We did not undertake similar analyses for southern flying squirrels because comparisons of core versus non-core locations would be redundant with tests of nest and non-nesting habitat reported elsewhere (Holloway and Malcolm, 2007).

### 3. Results

#### 3.1. Southern flying squirrel home range and core area

Southern flying squirrel home ranges averaged 5.1 ha (S.E. = 2.2), and home range and core area sizes did not differ significantly between recent cuts and uncut sites or between male and female flying squirrels (Table 2 and Fig. 1a and b). Similarly, mean distances between successive locations were nearly identical for recent cuts and uncut sites, and for males and females. Home range overlap between neighbouring southern flying squirrels averaged 13.8% for female–female pairs (S.E.  $\pm$  3.5,  $n = 10$ ), 23.6% for male–female pairs (4.3, 26), and 24.5% for male–male pairs (5.6, 8). Respective core area overlaps were 2.8% (1.5), 23.1% (6.1), and 25.2% (11.8). Neither home range nor core area overlaps differed significantly between any of the three pair types ( $P_s > 0.12$ ). The average home range and core area overlapped by one or more neighbouring squirrels were 55% and 56%, respectively (Table 2). Sex had no significant influence on total overlap area, however, core area overlap on recent cuts was significantly higher than on uncut sites ( $P = 0.049$ ).

Southern flying squirrels appeared to act as central place foragers (Orian and Pearson, 1979). Core areas were centred on nest sites, with all nests falling in the core area for 11 of 15 animals (Fig. 1a and b). The remaining four animals used the most nests (five or six each) and at least half of their nests were

Table 2

Home range characteristics (mean  $\pm$  S.E.) and the distance moved between successive radio-locations for male and female southern and northern flying squirrels in Algonquin Park, Ontario, 2003 and 2004.

Characteristics	Southern flying squirrels			Northern flying squirrels					
	Uncut ( $n = 8$ )	Cut ( $n = 5$ )	$P$ -value <sup>a</sup>	Female ( $n = 7$ )	Male ( $n = 6$ )	$P$ -value <sup>a</sup>	Female ( $n = 7$ )	Male ( $n = 7$ )	$P$ -value <sup>a</sup>
95% MCP (ha)	2.97 (0.35)	3.11 (0.69)	0.979	2.99 (0.54)	3.07 (0.40)	0.821	3.76 (0.57)	11.22 (3.40)	0.051
Home range (ha)	4.67 (0.66)	5.86 (1.21)	0.366	5.02 (0.87)	5.25 (2.14)	0.856	5.65 (1.3)	14.58 (4.0)	0.056
Core area (ha)	0.67 (0.15)	1.09 (0.27)	0.180	0.95 (0.24)	0.69 (0.28)	0.399	1.26 (0.4)	2.60 (1.0)	0.237
% Home range overlap	49.2 (10.1)	62.3 (3.8)	0.307	48.5 (8.4)	63.2 (7.6)	0.246	74.0 (6.1)	61.0 (3.9)	0.103
% Core area overlap	40.8 (13.3)	76.2 (4.7)	0.049	45.7 (14.1)	69.6 (7.2)	0.204	85.1 (8.9)	80.0 (9.1)	0.706
Mean successive distance moved (m)	99.21 (24.6)	105.8 (25.4)	0.921	102.4 (26.9)	101.7 (22.7)	0.604	105.6 (27.7)	153.4 (53.5)	0.058

For southern flying squirrels, values also are shown for uncut and recent selection-harvested stands. The number of locations per animal used to calculate home ranges for southern flying squirrels averaged 30 (range 24–38), while for northern flying squirrels the average was 36 (24–40).

<sup>a</sup>  $P$ -values from analysis of variance.

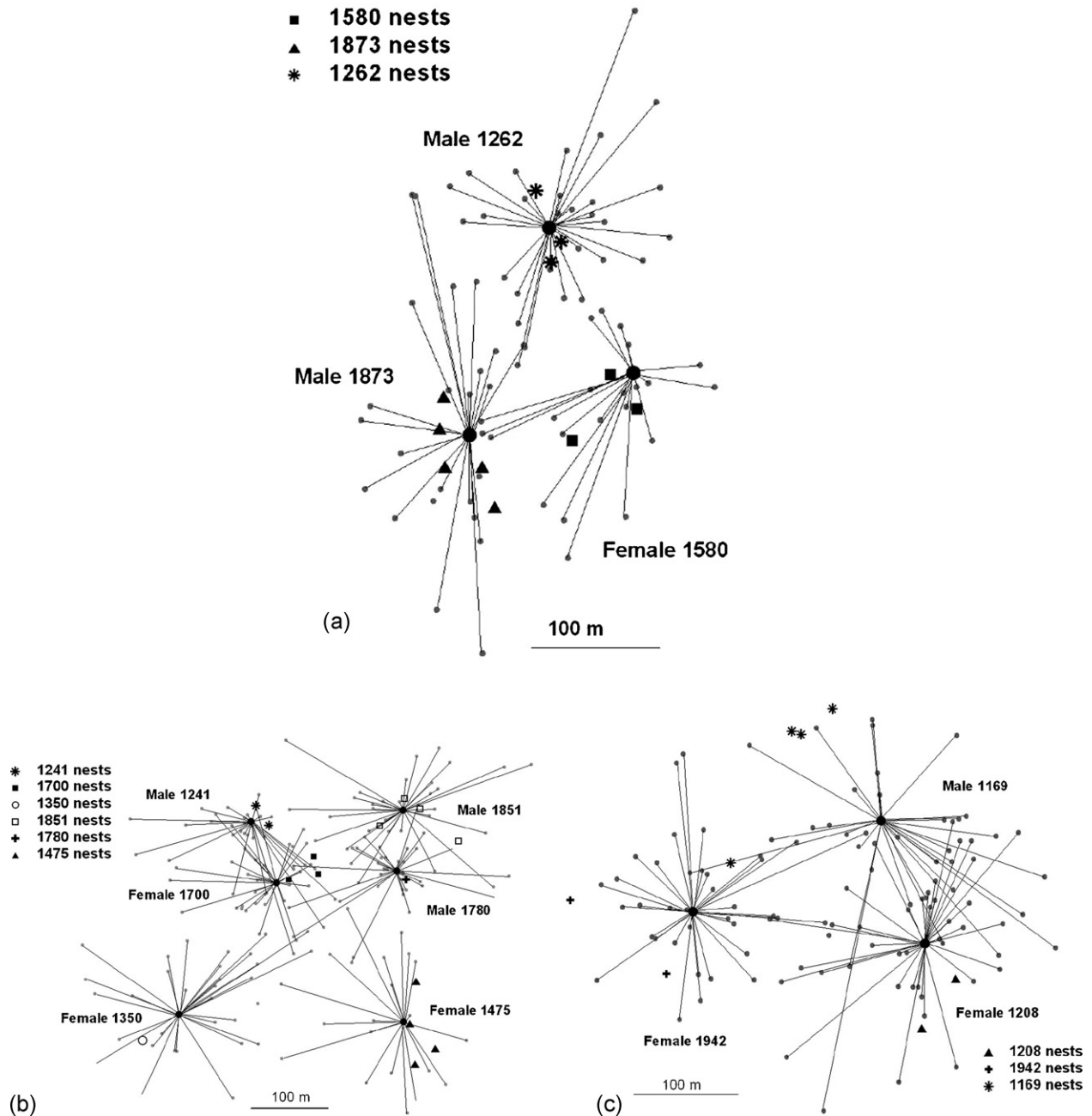


Fig. 1. Illustration of home ranges on 3 representative study grids for: (a) southern flying squirrels in selection-harvested forests; (b) southern flying squirrels in uncut forests; and (c) northern flying squirrels in uncut forests in Algonquin Provincial Park, Ontario, 2003 and 2004. The locations of night-time telemetry fixes (excluding those in daytime nests) for each individual are shown as small dots and are connected by lines to the geometric centre (large circles) of core areas. The shown home ranges are for all animals with  $\geq 24$  telemetry locations. Daytime nests are identified for each individual by use of unique symbols.

in their core areas. Southern flying squirrels were often near or in their nests, with 18.8% (S.D. = 4.3,  $n = 14$  individuals) of nighttime locations occurring in diurnal nests.

### 3.2. Southern flying squirrel resource selection

Selection harvesting had a significant effect on both southern flying squirrel habitat use and on the habitat characteristics in uncut sites and selection cuts. Logging history (Wilks' Lambda = 0.50,  $P < 0.001$ ), whether the site was used or available (Wilks' Lambda = 0.80,  $P < 0.001$ ), and interaction

between these two terms (Wilks' Lambda = 0.88,  $P < 0.001$ ) all were highly significant.

On uncut sites, three habitat variables were significantly greater at used than available locations: density of mast tree  $\geq 25$  cm dbh and of declining trees  $\geq 25$  cm dbh and tree richness, whereas three variables showed the opposite: density of maple and cavity trees, and average tree dbh (Table 3). The best logistic regression model predicting used locations from available locations had five terms, three positive (density of mast tree  $\geq 25$  cm dbh, declining trees  $\geq 25$  cm dbh and tree species richness) and two negative (understorey and cavity tree

Table 3  
Habitat characteristics (mean  $\pm$  SE) in Algonquin Provincial Park, Ontario, 2003, for southern flying squirrel nighttime locations (“used” locations) compared against all available locations in uncut sites and recent selection harvests

Variable set	Habitat variables <sup>a</sup> (per/ha)	Uncut sites			Recent selection cuts		
		Used ( $n = 101$ )	Available ( $n = 161$ )	$P$ -value <sup>b</sup>	Used ( $n = 71$ )	Available ( $n = 123$ )	$P$ -value <sup>b</sup>
Overstory	BA (m <sup>2</sup> /ha)	30.4 $\pm$ 0.8	30.1 $\pm$ 0.7	ns	21.1 $\pm$ 0.6	20.9 $\pm$ 0.5	ns
Overstory	Conifer $\geq$ 25	18.4 $\pm$ 2.5	20.2 $\pm$ 2.4	ns	4.8 $\pm$ 1.2	6.7 $\pm$ 1.5	ns
Overstory	Hardwd $\geq$ 25	77.5 $\pm$ 3.4	78.8 $\pm$ 2.8	ns	61.3 $\pm$ 2.9	58.9 $\pm$ 2.1	ns
Overstory	Maple	93.5 $\pm$ 8.5	119.3 $\pm$ 8.0	0.015	98.0 $\pm$ 9.0	110.2 $\pm$ 6.5	ns
Overstory	Understory	1866 $\pm$ 171	3582 $\pm$ 321	ns	2017 $\pm$ 214	1826 $\pm$ 192	ns
Food	Mast $\geq$ 25	20.9 $\pm$ 2.4	13.7 $\pm$ 1.6	0.013	6.3 $\pm$ 1.1	7.0 $\pm$ 1.0	ns
Food	Foodstems	3.5 $\pm$ 3.5	0.0 $\pm$ 0.0	ns	737 $\pm$ 193	26 $\pm$ 14	< 0.001
Food	TreeSp_rich (#)	3.8 $\pm$ 0.1	3.1 $\pm$ 0.1	< 0.001	2.8 $\pm$ 0.2	2.7 $\pm$ 0.1	ns
Nest	AverDBH (cm)	36.1 $\pm$ 0.7	38.1 $\pm$ 0.6	0.020	38.3 $\pm$ 0.9	35.9 $\pm$ 0.5	ns
Nest	Snags	22.4 $\pm$ 3.9	22.2 $\pm$ 2.6	ns	13.3 $\pm$ 3.1	9.6 $\pm$ 1.9	ns
Nest	Declin $\geq$ 25	39.9 $\pm$ 4.4	15.1 $\pm$ 1.4	< 0.001	21.6 $\pm$ 2.8	16.9 $\pm$ 2.3	0.045
Nest	CavTree	10.8 $\pm$ 1.4	15.7 $\pm$ 1.3	0.004	7.2 $\pm$ 1.3	8.7 $\pm$ 1.7	ns

Used locations included those from additional seven squirrels that were not included in home range analyses because of small samples sizes. We performed univariate  $t$ -tests because MANOVA analyses indicated that at least one variable was significant both for uncut sites (Wilks' Lambda = 0.74,  $P < 0.001$ ) and recent selection cuts (Wilks' Lambda = 0.76,  $P < 0.001$ ).

<sup>a</sup> Unit given if different from stems/ha.

<sup>b</sup> From  $t$ -tests on rank transformed data.

density; Table 4). This result was supported by the used-vs.-unused analysis (validation model). Here only one model was significant (Nest model), which included one term (the density of declining trees  $\geq 25$  cm dbh; Table 4).

On recent selection cuts, under the used-vs.-available design, a positive relationship with the density of food producing shrubs and tree species diversity (Food model) best distinguished used and available locations (Table 4). These two variables were the only ones to differ significantly between used and available locations (Table 3). Similarly, in the validating used-vs.-unused analysis, only one model was significant (Food model), which showed a positive relationship with the density of food producing shrubs.

### 3.3. Northern flying squirrel home range and core area

Male northern flying squirrel home ranges were nearly three times larger than female home ranges and they moved further between successive locations than females, although the differences were not quite significant (Table 2 and Fig. 1c). Home range and core area overlap was high among all neighbouring squirrels (67.0% and 82%, respectively), and did not differ significantly between the sexes ( $P_s > 0.10$ ). Comparing pairs of neighbouring northern flying squirrels, home range overlap for female–female, male–female, and male–male pairs, respectively was 16.5% (S.E. = 6.8;  $n = 8$ ), 27.0% (4.1, 32), and 27.9% (7.9, 14), whereas core area overlap was 11.4% (6.7), 32.2% (6.6), and 35.6% (12.2). The overlap of home ranges and core areas did not differ significantly among the three pair types ( $P_s > 0.30$ ).

Unlike southern flying squirrels, northern flying squirrel nest sites usually were located outside core areas, with many occurring near home range edges (Fig. 1c). For 11 of 14 animals, no nests occurred within core areas. For the three remaining animals, 75% of nests on average were located outside core areas. Few nighttime locations occurred in diurnal nests (average = 4.2%, [S.D. = 3.8,  $n = 13$  individuals]).

### 3.4. Northern flying squirrel resource selection

In comparing the habitat at used and available locations for northern flying squirrels, 4 variables were significantly lower at used than available locations (basal area, tree species richness,

Table 4  
Parameter estimates from logistic regression analyses for northern and southern flying squirrels and two model designs in Algonquin Provincial Park, Ontario. Sample sizes are from 11 and 9 individual southern flying squirrels in uncut sites and recent selection cuts, respectively, and for 14 northern flying squirrels, in the used-vs.-unused models

Spp/Model	Variables	$B_1 \pm$ S.E.	Odds ratio	$P$
<i>G. volans</i> – uncut sites				
Use-vs.-available	Understory	−0.044 $\pm$ 0.020	0.96	0.029
	Mast $\geq$ 25	0.015 $\pm$ 0.007	1.01	0.042
	TreeSp_rich	0.331 $\pm$ 0.121	1.39	0.006
	Declin $\geq$ 25	0.031 $\pm$ 0.008	1.03	<0.001
	CavTree	−0.025 $\pm$ 0.011	0.98	0.029
Use-vs.-unused	Declin $\geq$ 25	0.26 $\pm$ 0.11	1.30	0.022
<i>G. volans</i> – recent selection cuts				
Use-vs.-available	Foodstems	0.92 $\pm$ 0.28	2.51	0.001
	TreeSp_rich	0.28 $\pm$ 0.12	1.32	0.024
Use-vs.-unused	Foodstems	4.45 $\pm$ 2.94	20.54	0.131
<i>G. sabrinus</i>				
Use-vs.-available	BA	−0.078 $\pm$ 0.015	0.925	<0.001
	Conifer $\geq$ 25	0.009 $\pm$ 0.004	1.009	0.014
	Understory	0.022 $\pm$ 0.013	1.022	0.085
	Declin $\geq$ 25	0.015 $\pm$ 0.004	1.015	<0.001
Use-vs.-unused	BA	−1.43 $\pm$ 0.79	0.24	0.015
	Declin $\geq$ 25	0.55 $\pm$ 0.34	1.74	0.025
Core-vs.-periphery (1)	Understory	0.036 $\pm$ 0.015	1.036	0.021
	Spruce	0.004 $\pm$ 0.002	1.004	0.029
	Declin $\geq$ 25	0.009 $\pm$ 0.005	1.009	0.065
Core-vs.-periphery (2)	Understory	0.037 $\pm$ 0.015	1.04	0.017
	Spruce	0.004 $\pm$ 0.002	1.01	0.047

Table 5

Habitat characteristics (mean  $\pm$  S.E.) in Algonquin Provincial Park, Ontario, 2004, for northern flying squirrel nighttime locations (“used” locations) compared against all available locations

Variable set	Habitat variables <sup>a</sup> (per/ha)	Used ( $n = 146$ )	Available ( $n = 172$ )	$P$ -value <sup>b</sup>
Overstory	BA (m <sup>2</sup> /ha)	24.0 $\pm$ 0.7	31.5 $\pm$ 0.7	<0.001
Overstory	Conifer $\geq 25$	48.9 $\pm$ 2.8	52.2 $\pm$ 3.1	ns
Overstory	Hardwd $\geq 25$	23.4 $\pm$ 2.3	40.1 $\pm$ 2.6	<0.001
Overstory	Understory	3876 $\pm$ 212	3276 $\pm$ 170	<0.001
Food	Spruce	45.1 $\pm$ 5.8	34.6 $\pm$ 4.4	0.045
Food	Foodstems	935 $\pm$ 160	570 $\pm$ 82	0.002
Food	TreeSp_rich (#)	3.4 $\pm$ 0.1	3.8 $\pm$ 0.1	0.003
Nest	AverDBH (cm)	38.7 $\pm$ 0.8	39.7 $\pm$ 0.6	ns
Nest	Snags	28.2 $\pm$ 3.2	32.8 $\pm$ 2.8	0.029
Nest	Declin $\geq 25$	21.8 $\pm$ 2.6	7.4 $\pm$ 0.8	<0.001

We performed univariate  $t$ -tests because MANOVA analyses (Wilks' Lambda = 0.904,  $P < 0.001$ ) indicated that at least one variable was significant.

<sup>a</sup> Unit given if different from stems/ha.

<sup>b</sup> From  $t$ -tests on rank transformed data.

snag density, and the density of hardwood trees  $\geq 25$  cm dbh) and four were significantly higher (understory density, the density of food producing shrubs, spruce trees, and declining trees  $\geq 25$  cm dbh; Table 5). The Overstory + Nest model best predicted used locations from available locations under the used-vs.-available design. Three terms in the model were positive (density of understory stems, conifer stems  $\geq 25$  cm dbh, and declining trees  $\geq 25$  cm dbh) and one was negative (basal area; Table 4). Results of the used-vs.-unused validation model were similar; the Overstory + Nest was the best model ( $\Delta$ AIC for the second ranked model was 12.2), and the significant terms were a subset of the same variables as the used-vs.-available design (the density declining trees  $\geq 25$  cm dbh and basal area).

Core areas ( $n = 108$ ) were best distinguished from the home range periphery ( $n = 164$ ) by greater densities of spruce trees, understory stems, and declining trees  $\geq 25$  cm dbh (Table 4). In this comparison two models were ranked as equivalent (Table 1); the Overstory + Food + Nest model (3 terms) and the Overstory + Food (2 terms). However, the smaller model was a subset large global model. The density of understory stems, spruces, and declining trees  $\geq 25$  cm dbh was 3887 (S.E. = 233), 56.4 (6.5) and 18.3 (2.5), respectively in core areas, compared with 3077 (251), 41.6 (5.5) and 12.9 (2.0) in non-core areas of home ranges.

## 4. Discussion

### 4.1. Southern flying squirrel home range characteristics and resource selection

Southern flying squirrel home ranges and movement patterns in this study were consistent with those from other eastern populations in forests of similar species composition and age. Male and female MCP home ranges in Maryland were 2.3 and 2.0 ha (Bendel and Gates, 1987), respectively, which were similar to our corresponding values of 3.1 and 3.0 ha. The 95% kernel home range from Arkansas for female southern flying squirrels (5.9 ha; Taulman and Smith, 2004) was nearly identical to that for females in our study. However, unlike

previous studies, we observed little differences in home ranges between the sexes. This variability in sex-specific home range sizes in part may be due to the substantial population fluctuations that flying squirrels commonly exhibit from year to year (Layne and Raymond, 1994). Larger male home range sizes are more typical at low population densities, as males must travel further to find females for mating opportunities (Fridell and Litvaitis, 1991). Southern flying squirrel core areas were centred on nest sites, and individuals often returned to their nests during the night. Possibly, the supply of suitable nesting trees influences the arrangement and location of home ranges. Suitable nesting areas may be a key resource for adult females, and one that they defend exclusively, given that the spatial overlap of core areas was lowest for female–female neighbours (also see Bendel and Gates, 1987).

Contrary to our predictions, selection logging did not have a strong influence on southern flying squirrel home range sizes. These results are based on a small sample sizes (5 animals on recent cuts and 8 on uncut sites), and thus must be interpreted cautiously. However, provided that a relatively high residual basal area is retained (a mean of 20.4 m<sup>2</sup>/ha in the current study) selection harvesting may not significantly alter southern flying squirrel habitat use. A threshold below which harvesting negatively affects use of space apparently exists, as more intensive harvesting (where residual basal areas were  $\leq 10$  m<sup>2</sup>) resulted in the largest southern flying squirrel home range ever reported (16.0 ha; Taulman and Smith, 2004).

Southern flying squirrels appear to compensate for the structural changes following selection harvesting at least in the short term. However, we obtained some evidence that nesting resources may be limited in selection cuts compared with uncut sites. Firstly, given that core areas provide important nest habitat, we observed more intensive use of core areas by multiple individuals (higher spatial overlap of core areas by neighbouring squirrels) on recent selection cuts than in uncut sites. Secondly, southern flying squirrels species nested nearly exclusively in live declining trees in the region (Holloway and Malcolm, 2007). In uncut stands, the strongest factors predicting southern flying squirrels habitat use was a positive association with the density of declining trees, but this relationship was not seen in recent cuts.

In fact, the density of declining trees on sites used by southern flying squirrels in recent cuts was nearly one-half that on uncut sites. Nest availability is one of the structural features limiting southern flying squirrels under intensive harvesting (Taulman et al., 1998), and in the long term, this reduction in nest habitat may have serious implications, and forest managers should strive to increase the supply of potential nest substrates following harvesting.

As predicted, food availability had a significant affect on habitat use by southern flying squirrels. In uncut sites, individuals used areas with higher mast tree availability, a feature which is critical for southern flying squirrel over-winter survival (Fridell and Litvaitis, 1991). The crash we observed of the southern flying squirrel population in 2004 was caused by a mast crop failure the previous fall, followed by a cold winter (Bowman et al., 2005). However, this species also used sites with older trees, as evidenced by the association with declining trees (older trees demonstrate a greater incidence of decay (Parks and Shaw, 1996). Older trees are potentially associated with higher food availability as the production of pollen and seeds by trees is proportional to tree size (Greene and Johnson, 1994).

Southern flying squirrels also were active in areas with lower densities of maples, and higher tree species richness. This pattern is of interest because sugar maples are the dominant species in northern hardwood forests, and tree species diversity is inversely related to the density of maples (Spearman's  $r = -0.36$ ,  $P < 0.001$ ). Under mature canopies, sugar maple out-competes many other tree species because of its high shade tolerance (OMNR, 1998a). In our study area, southern flying squirrels consumed a diverse array of food stuffs, including hypogeous fungi and pollen (which combined comprised  $> 40\%$  of their diet; Holloway, 2006). The diversity of tree species is presumably related to the abundance of fungi and pollen because: (1) hypogeous fungi are predominately associated with the Pinaceae (pine and spruce), Fagaceae (beech and oak) and Betulaceae (birch) tree families (Maser et al., 1978), and (2) southern flying squirrels frequently consumed pollen from several hardwood and conifer tree species, but only rarely from sugar maple (Holloway, 2006).

In recent selection cuts, the density of food producing shrubs had a significant influence on southern flying squirrel habitat use. Soft-mast producing shrubs tend to be early-successional, light-demanding species (such as raspberries and pin cherries) which are most abundant on harvested sites (Perry et al., 1999). The high availability of these shrubs may be why we observed high densities of southern flying squirrels on recent selection cuts (Holloway and Malcolm, 2006), despite the lower density of density of declining trees and mast trees. Southern flying squirrels appear to be adaptable in their habitat use when given abundant food resources.

#### 4.2. Northern flying squirrel home range characteristics and resource selection

For northern flying squirrels, our home range estimates also were similar to those reported in other studies in contiguous forests. The MCP home range sizes of male (12.5 ha) and female

(2.8 ha) northern flying squirrels in New Brunswick (Gerrow, 1996) were similar to ours (11.2 and 3.8 ha, respectively). In our study, northern flying squirrels showed little evidence of territorial behaviour as they demonstrated high overlap in the both home ranges and core areas. We hypothesize that northern flying squirrel activity in core areas is related to foraging, particularly for hypogeous fungi. Hypogeous fungi tend to occur in small concentrated patches; however, the patches themselves are spatially disjunct (Johnson, 1996). As a result, truffles are a locally abundant, but highly dispersed resource (Cork and Kenagy, 1989), which may make defense of patches impractical.

Our results on habitat use indicate that old conifer forests are important habitats for this species. Northern flying squirrels used areas which were characterized by old, senescing trees with a mosaic of canopy gaps. We frequently observed that sites used by northern flying squirrels were located in or near tree fall gaps. These areas were characterized by low basal area, but abundant large declining trees, large conifers, and high understory stem density. Understory stem density increases as stands age and shift into the gap-dynamic phase with high tree mortality and frequent gap creation. Several investigators have reported northern flying squirrels selecting micro-sites with greater understory cover (Carey, 1995; Smith et al., 2004). High understory cover may provide protection from predators for squirrels foraging on the ground. Moreover, northern flying squirrels used areas with a high spruce density, particularly in their core areas, and hence sites which likely had a greater availability of hypogeous fungi. Spruce appears to be a key habitat characteristic in eastern populations, as this feature is consistently a strong predictor of northern flying squirrel presence (Payne et al., 1989; Ford et al., 2004; Menzel et al., 2006; Holloway and Malcolm, 2006). The site conditions described above characterising northern flying squirrel micro-habitat sites are impacted significantly by harvesting (Holloway and Malcolm, 2006): the density of conifers, particular spruce trees, snags and canopy cover are all reduced following shelterwood logging, which may account for the low density of northern flying squirrels found on harvested sites.

#### 4.3. Resource selection models

Resource selection models are influenced by the manner in which resource availability is defined (Manly et al., 2002). Accordingly, we undertook both used-vs.-available and used-vs.-unused analyses, with the former using locations as replicates and the latter using individuals as replicates. Results from the two analyses were consistent in that the used-vs.-unused models were subsets of the more complex used-vs.-available models. Used-vs.-unused models were unlikely to contain more than two terms because the number of individual squirrels was small (11 southern flying squirrel in uncut sites, 9 in recent cuts, and 14 northern flying squirrels in uncut sites).

#### 4.4. Conclusions

This study provides understanding of northern and southern flying squirrel use of space within home ranges, and the manner



in which it is affected by partial harvesting. In the short-term, given high residual basal area and abundant food, southern flying squirrels appear able to maintain populations in harvest stands. However, reductions in nest tree supply may eventually limit use of these stands, especially given multiple harvesting entries every 15–20 years. For northern flying squirrels, partial harvesting appears to negatively impact several structural features that are important features in core areas (density of dead/diseased trees, and understory and spruce density).

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