



Research Article

Site Occupancy and Cavity Use by the Northern Flying Squirrel in the Boreal Forest

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ABSTRACT Tree cavities are used as shelter and breeding nests by numerous avian and mammalian species. In cold environments, tree cavities are often proposed as the best winter nest choice because of the superior protection they offer from precipitation, wind, cold temperatures, and predators. As such, they represent a critical resource, which has the potential to limit population size of non-excavating species. We assessed factors affecting site occupancy in the boreal forest by northern flying squirrels, a secondary user of tree cavities, and to identify which nest type is preferred during the colder days of the autumn–winter period. We trapped flying squirrels twice in 59 aspen-dominated stands in the autumn period using low- (1.5 m above ground-level) and high-mounted (4 m) traps to determine site occupancy. A total of 85 individuals were captured on 2,880 trap-nights. During the winter period, we radio-tracked 26 individuals to 87 diurnal nests in 220 locations. None of the habitat variables considered (cavity availability, woody debris, and lateral cover) explained site occupancy. Detectability decreased with precipitation, and was lower using high traps than low traps. Both females and males used tree cavities (26%), external nests (39%), and ground nests (35%). In cold weather, females preferred ground nests, whereas males preferred external nests. Our results do not support the hypothesis that tree cavities represent a limiting factor to northern flying squirrels in cold environments. Instead, this species seems to be a generalist and is opportunistic, using a variety of nest types. Nevertheless, practices ensuring the persistence of large diameter live cavity trees, providing better insulative properties, are likely to increase the relative use of tree cavities as nest sites by northern flying squirrels. © 2011 The Wildlife Society.

KEY WORDS boreal mixedwoods, cavity availability, detection probability, *Glaucomys sabrinus*, habitat use, nest web, northern flying squirrel, site occupancy.

Tree cavities are used as shelter and breeding nests by numerous avian and mammalian species. As such, they represent a critical resource around which cavity-nesting communities are structured in nest webs (Martin and Eadie 1999). These nest webs are hierarchical networks, which consist of excavators that create the resource and secondary users that rely on available tree cavities (Martin et al. 2004). Creation of cavities also occurs to a lesser extent through natural processes such as wood decay, whereas loss is achieved through deterioration, resealing, and tree fall (Sedgwick and Knopf 1992). Thus, cavity availability is influenced by many factors including the rates of creation, cavity reuse by excavators, and loss, together with territoriality and competition among cavity-nesters (Aitken et al. 2002). As obligate secondary users must use existing tree

cavities for reproduction or shelter, cavity availability represents a key element that has the potential to limit their population size (Newton 1994).

The northern flying squirrel (*Glaucomys sabrinus*) is a secondary user of tree cavities and is common across forested regions of North America. Its distribution ranges from Alaska to California, through central Canada and extends to North Carolina (Wells-Gosling and Heaney 1984). Until recently, the northern flying squirrel was reputed to be a lateral coniferous forest specialist (Carey 1995, Smith 2007). This habitat preference was explained by two main factors. First, an important portion of the diet of northern flying squirrels consists of hypogeous fungi (Pyare et al. 2002), which are often associated with coarse woody debris (Amaranthus et al. 1994), reaching their maximum volume in old forests (Harmon et al. 1986). Second, the species relies on tree cavities for nesting and shelter (Wells-Gosling and Heaney 1984, Smith 2007), and most tree excavators in the boreal forest also reach their maximum abundance in old

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forests (Imbeau et al. 2001, Drapeau et al. 2003, Schieck and Song 2006). More generally, disturbances that reduce structural complexity, canopy cover, or the availability of large, decaying trees result in lower population densities by limiting the availability of food, den sites, or by increasing predation risk (Smith 2007). Recently, however, the flying squirrel was described as a habitat generalist, abundant in mixed or deciduous forests (Wheatley et al. 2005, Holloway and Malcolm 2007, Weigl 2007, Patterson and Malcolm 2010) and in even-aged managed or second-growth stands (Rosenberg and Anthony 1992). It nests mainly in tree cavities throughout its range but is not considered to be an obligate secondary cavity user, because it also uses external nests built on branches in the forest canopy (Smith 2007). External nests can sometimes be located inside witches' brooms, which are deformities of conifer branches caused by dwarf mistletoe (*Arceuthobium* spp.) or spruce rust (*Chrysomyxa* spp.; Wells-Gosling and Heaney 1984, Smith 2007). There are also anecdotal accounts of nests in stumps or underground (Gerrow 1996, Bakker and Hastings 2002, Hackett and Pagels 2003).

Tree cavities may represent more than 90% of nest sites used (Pyare et al. 2010). Thus, cavities may be a limiting resource for this species in managed landscapes as well as in regions where the availability of this resource is naturally low. Nevertheless, most recent studies involving the addition of nest boxes failed to detect significant effects on population size or reproductive rates (Carey 2002, Ransome and Sullivan 2004). Similar results were also obtained for the southern flying squirrel (Brady et al. 2000), suggesting that other factors, such as food and predation, might have stronger effects on the distribution and abundance of flying squirrels.

Experimental results from nest box additions were obtained in relatively mild climates, where mean temperatures in cold months ranged between 0° C and 2.5° C for studies on the northern flying squirrel (Carey 2002, Ransome and Sullivan 2004), and approximately 12° C in the case of the southern flying squirrel (Brady et al. 2000). However, much of the geographic range of the northern flying squirrel overlaps with the complete extent of the boreal biome. As flying squirrels are active all year-round, individuals face extremes of cold weather during the winter, with temperatures as low as -33° C recorded in some northern studies (Mowrey and Zasada 1984, Cotton and Parker 2000a). To reduce heat loss and energy expenditure, flying squirrels build and use thermally insulated nests (Weigl 1974, Wells-Gosling and Heaney 1984), aggregate in them with many individuals (Mowrey and Zasada 1984, Gerrow 1996), and forage for shorter time periods (Cotton and Parker 2000a). Although the benefits of cavities over external nests remain uncertain (Guillemette et al. 2009), it is generally believed that cavities provide a superior protection from wind and precipitation (Carey and Sanderson 1981, Maser et al. 1981, Carey et al. 1997, Menzel et al. 2004) as well as from predators (Carey and Sanderson 1981). Coombs et al. (2010) recently reported, from their study conducted in northern hardwood forests during winter, that cavities within living trees of a large diameter at breast height cooled down less than others

located in snags or within trees of smaller diameter. Such observations suggest that if tree cavities are more insulated than other nest types, their availability may influence site use by northern flying squirrels to a greater extent in the northern part of its range, in colder climates.

We assessed factors affecting site use by northern flying squirrels in the boreal forest to determine whether the availability of tree cavities is a better predictor of site occupancy than other habitat variables potentially linked with factors such as food availability and predator avoidance (well-decayed coarse woody debris and lateral cover). Detectability is a problematic component of animal sampling and not accounting for it in wildlife studies could lead to spurious conclusions (Anderson 2001, Mazerolle et al. 2007). To control for this potential problem, we estimated detectability in relation to factors known to affect trapping success (trap height, minimal temperature, and precipitation). We also followed radio-collared individuals during the colder days of the autumn-winter period to determine the effects of temperature on nest use. We hypothesized that tree cavities would represent a limiting factor positively affecting habitat occupancy in the boreal forest because of their limited availability. We also expected that tree cavities, especially those available within large diameter living trees, would be preferred over other external nest types in cold temperatures because of their superior thermal insulation value.

STUDY AREA

We studied northern flying squirrels in northwestern Quebec at 59 sites located within 50 km of the city of Rouyn-Noranda (48°18'N, 79°05'W), from September 2008 to June 2009. This area experiences short mild summers and dry cold winters characteristic of a subarctic climate (mean annual temperature = 1.2° C; precipitation = 914 mm; 158 days with minimum temperature >0° C; Environment Canada 2009). We selected even-aged deciduous stands that were dominated by trembling aspen (*Populus tremuloides*). The sites also consisted of tree species such as balsam poplar (*Populus balsamifera*), white or paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and balsam fir (*Abies balsamea*). Although this region is located mainly in the balsam fir-white birch bioclimatic domain of the boreal forest (Robitaille and Saucier 1998), forests are dominated by aspen resulting from overexploitation and repeated uncontrolled slash fires during colonization (Vincent 1995).

In this region, tree cavities were mainly created by woodpeckers, and were primarily located (98%) in trembling aspen (Drapeau et al. 2009). This shade-intolerant deciduous species reaches maturity at 60 yr and is subsequently prone to fungal rot (Pothier et al. 2004), which renders wood fibers soft and easy to break down by cavity-excavating birds (Jackson and Jackson 2004). We selected sites representing a gradient in stand age (10–70 yr), and consequently, a gradient in snags and cavity availability. Stand age was determined from 1995 digitized topographic forest maps (1:20,000 scale) produced by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF) using

ArcView[®] 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA). Other criteria considered for the selection of stands included adjacency to a road that was accessible year-around, a stand area ≥ 3.6 ha to ensure a 100-m buffer of homogeneous habitat around the site, and a distance of at least 400 m between sites. The aforementioned values were chosen based on a mean maximum distance of about 100 m for movements of flying squirrels captured on trapping grids in the Pacific Northwest (Carey 1995). Woodpeckers observed at our sites included the northern flicker (*Colaptes auratus*), yellow-bellied sapsucker (*Sphyrapicus varius*), and downy (*Picoides pubescens*), hairy (*Picoides villosus*), and pileated (*Dryocopus pileatus*) woodpeckers.

METHODS

Flying Squirrel Trapping

We traced an 80-m linear transect that ran perpendicularly to the road at each site. We established a trapping station every 10 m along the line transect, for a total of 8 stations. We attached a single Tomahawk live trap (Model 201; Tomahawk Live Trap Co., Tomahawk, WI) to the trunk of the closest tree at each trapping station, positioning the trap horizontally. Because we expected that trap height had an effect on capture success, as shown for the southern flying squirrel (*Glaucomys volans*; Risch and Brady 1996), we established traps at either 1.5 m or 4 m above ground level. In any given transect, we randomly assigned the height of the first trap and alternated trap height between 1.5 m and 4 m along the 8 trapping stations. We reversed height attribution for the second visit (a tree with a trap at 4 m for the first visit received a trap at 1.5 m for the second, and vice versa). Traps were baited with apple and peanut butter and provided with polyethylene stuffing and white corrugated plastic cover for protection. As flying squirrels are solely active at night, traps were opened at dusk between 16:00 and 21:00, depending on the time of sunset, and checked every morning from 0600 to 1200. We trapped 10 sites per week for a period of 3 consecutive nights until all the sites were visited. We repeated this exercise a second time for a total of 2 visits over 12 weeks from September to December 2008. We recorded the detection of flying squirrels at each visit for all sites.

Squirrels were anesthetized at first capture with an isoflurane-inhaled anesthetic (Desmarchelier et al. 2007), sex was determined, and they were weighed using either a spring or an electronic scale. Squirrels were marked with paired, numbered metal ear tags (Monel No.1; National Band and Tag Co., Newport, KY) for individual identification. A subgroup of 46 individuals that weighed >100 g were fitted with radio collars that weighed 4 g (model PD-2C; Holohil Systems, Ltd, Woodlawn, Canada), and which were attached with plastic cable ties encased in flexible plastic tubing. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the institutional animal care review committee at the Université du Québec en Abitibi-Témiscamingue (UQAT, permit # 2004-03-01).

Nest Use

We radio-tracked flying squirrels while they occupied nests during the day, using a digital receiver (Model R-1000; Communications Specialists, Inc., Orange, CA) and a hand-held 3-element Yagi antenna. We occasionally radio-tracked squirrels in the autumn after the attachment of the collars, and we located animals regularly twice a week from January to April 2009. We used this frequency of sampling as Carey et al. (1997) showed that 2 locations per week permitted identification of 95% of flying squirrel nests. As flying squirrels never leave their nests during daylight hours (Mowrey and Zasada 1984, Cotton and Parker 2000a), we conducted radio-tracking at any time of day except 30 min after dawn or before dusk to ensure that animals were in their nests at the time of radio-tracking. Every time an individual was located, we recorded the type of nest being used, together with characteristics of the tree such as species, diameter at breast height, and status (alive or dead; following Imbeau and Desrochers 2002). We monitored flying squirrels until death, loss of signal, or removal of collar (from 3 days to 203 days). We trapped animals at their nest locations in spring 2009 to remove collars.

Environmental Variables

We measured 3 habitat variables at each site in May and June 2009 to assess which factor influenced site occupancy by flying squirrels. First, we counted available tree cavities by conducting a systematic inventory over an area of 1.6 ha using 4 contiguous transects (200 m long \times 20 m wide) perpendicular to the trapping transect. Each of the 4 transects intersected the trapping transect at a trapping station. All tree trunks were checked for abandoned woodpecker holes (small circular entrances) or natural cavities using binoculars while walking back and forth on the transects, to estimate the total number of tree cavities per site. All cavity types known to be used by the northern flying squirrel were thus counted (Gerrow 1996). Second, we quantified woody debris since they provide optimal microhabitat for mushroom growth and because food is also known as a potential limiting factor to northern flying squirrels (Ransome and Sullivan 2004). Such structures might also be used as natal dens (Carey et al. 1997). Using the line intersect sampling method (Marshall et al. 2000) on a 60-m triangular transect crossing the trapping transects at the second and sixth stations, we measured the diameters of all intersecting logs at the point of intersection and estimated the volume of woody debris per hectare (m^3/ha). We estimated decay stages of logs following Fraver et al. (2002), and only those in advanced stages of decay with high moisture levels (class 3 and 4) were retained for subsequent analyses. Third, we estimated vegetation cover to assess potential escape from predators. We measured the percentage of lateral cover using the vegetation profile board technique of Nudds (1977) on both sides of the trapping transect at a perpendicular distance of 15 m from the second and fourth stations. We estimated visually the percentage of obstruction for each 0.5 m section of the 2-m profile board and then, pooled all 16 measurements for each site to obtain a

mean percentage. We took these measurements in spring before leaf out to characterize the same conditions as those occurring when trapping was conducted in fall.

We assessed the impact of climatic variables on flying squirrel capture success and nest site selection. We acquired all data from the closest meteorological station located in the city of Val-d'Or (48°03'N, 77°47'W) and downloaded from the Environment Canada website (Environment Canada 2009). For trapping data, we used the minimal temperature from 0000 to 0600 over the 3-night sampling periods at a site. We also considered total precipitation for these same periods, including the water equivalent of snowfall (i.e., snowfall divided by 10). For telemetry data, we used the minimum temperature from 0000 to 0600 on the day of nest location.

Statistical Analysis

We estimated site occupancy rates using the single season model with program PRESENCE 3.1 (Version 3.1, www.mbr-pwrc.usgs.gov/software/presence.html, accessed 1 November 2010). This method addresses the problem of imperfect detection of animals, common in many species, by estimating a probability of detection of the species conditional on presence, using data from repeated visits. We considered each period of 3 consecutive nights of trapping at a site as a visit, and each site as independent. We centered all numerical site and environmental variables prior to analysis. We formed a limited set of 11 candidate models based on the scientific literature to identify the variables that might explain site occupancy by flying squirrels and which affect the probability of detection at each visit, according to 5 main hypotheses (Table 1). Possible variables influencing site occupancy included habitat measurements: number of tree cavities (hypothesis 1), lateral cover (hypothesis 2), and woody debris (hypothesis 3). We considered weather (temperature, precipitation; hypothesis 4) and trap height (hypothesis 5) as variables potentially influencing detectability. To quantify the effect of trap height within each site, we split each of the 2 visits into low or high traps using the design matrix. We ran 10,000 bootstrap samples to test the fit of the global model to the data (where $\hat{c} > 1.0$ indicated overdispersion of the data) and compared candidate models using

Akaike's Information Criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002). We considered models within 2 AIC_c from the top ranked model as having strong support and we also calculated model probabilities from the AIC_c values to indicate the level of support for each model considered (Burnham and Anderson 2002). Following model fitting, we programmed and implemented multimodel inference in R software (R Version 2.12.1, www.R-project.org, accessed 1 November 2010) to assess the effect of variables on either occupancy or detection probability.

We compared characteristics of nest trees supporting cavities and trees supporting external nests. First, we used a 2-sided t -test on log-transformed values of diameter at breast height (dbh) to assess the difference in means. Second, we used separate chi-square tests to verify that the proportions observed within each category of nest trees were different from a 1:1 ratio for type (deciduous vs. coniferous) and status (alive or dead). Similarly, we assessed the independence of nest type use and sex using a chi-square test. Characteristics of cavity trees used by at least 1 flying squirrel (dbh, status) were compared to those available found on systematic inventories using t -test and chi-square tests. We fit mixed logistic regressions separately on each sex to test the influence of temperature on the probability of utilization of each of the 3 nest types (i.e., tree cavities, external nests, and ground nests). Had observations been independent, a multinomial logistic regression would have been appropriate to model this type of data. Because we had several locations for each individual, we used a mixed-model counterpart of the multinomial logistic regression instead to reflect the structure of our data (i.e., several observations for each individual). This was achieved by making 2 comparisons using tree cavities as the reference level with 2 logistic regressions and specifying individual as a random effect for each sex. In essence, this is similar to fitting a multinomial logistic regression (see Agresti 2002). The inclusion of animal identity as a random effect in the regressions allowed us to control for possible individual squirrel preferences in nest use. We fit these models with the `glmer` function of the `lme4` package in R (`lme4: Linear mixed-effects models using Eigen and CRAN.R-project.org/package=lme4`, accessed 17 February

Table 1. List of 11 candidate models and a priori hypotheses (5) for northern flying squirrel occupancy (ψ) and detection probability (P) in Abitibi, Québec, Canada, during autumn 2008.

Models tested	Hypotheses
1. $\psi(\text{Cavities}), P(\cdot)$	H1: Positive effect of cavity availability on site occupancy
2. $\psi(\text{Lateral cover}), P(\cdot)$	H2: Positive effect of lateral cover on site occupancy
3. $\psi(\text{Coarse woody debris}), P(\cdot)$	H3: Positive effect of coarse woody debris on site occupancy
4. $\psi(\text{Cavities}), P(\text{precipitation} + \text{temperature})$	H4: Detection affected by weather (negative effect of precipitation; positive effect of temperature) + H1
5. $\psi(\text{Lateral cover}), P(\text{precipitation} + \text{temperature})$	H4 + H2
6. $\psi(\text{Coarse woody debris}), P(\text{precipitation} + \text{temperature})$	H4 + H3
7. $\psi(\text{Cavities}), P(\text{trap height})$	H5: Detection affected by trap height + H1
8. $\psi(\text{Lateral cover}), P(\text{trap height})$	H5 + H2
9. $\psi(\text{Coarse woody debris}), P(\text{trap height})$	H5 + H3
10. $\psi(\cdot), P(\cdot)$	Null model
11. $\psi(\text{Cavities} + \text{lateral cover} + \text{coarse woody debris}), P(\text{precipitation} + \text{temperature} + \text{trap height})$	Global model

2011). We assessed the fit of mixed logistic regression models with a parametric bootstrap approach based on the sum of squared errors (SSE) as a measure of lack of fit. Specifically, we generated 1,000 data sets from each model to determine significance based on the number of SSE from simulated data sets that were as large or larger than the observed test statistic from the original data set (Gelman and Hill 2007).

RESULTS

Environmental Variables

We observed considerable variability in the 3 habitat variables. Mean number of tree cavities was 6.9 cavities/site (range 0–27), mean volume of woody debris was 24.6 m³/ha (range 2.6–100.9) and mean lateral cover was 57.3% (range 23.6–88.8). During autumn trapping, the mean minimum temperature was 0.0° C during the first visit (range –7.4° C to 6.4° C) and –9.3° C during the second visit (range –19.1° C to 0.3° C). Mean total precipitation for this same period was 6.2 mm for the first visit (range 0 mm to 16.5 mm) and 7.3 mm for the second visit (range 1.0 mm to 13.5 mm). During telemetry, minimum temperature averaged –14.3° C (range –40.2° C to 4.8° C).

Site Occupancy

We surveyed 59 sites twice between 10 September and 5 December 2008 and captured 85 northern flying squirrels (47 M, 38 F) for 102 captures over 2,880 trap-nights. The average mass of the animals at the time of capture was similar between sexes (113.5 ± 1.5 g for M, 118.1 ± 2.4 g for F, $t_{82} = 1.6425$, $P = 0.104$). We recorded flying squirrels at least once on 34 sites (58%) with the following detection histories: on both visits at 17 sites (29%), on the first visit only at 14 sites (24%), and on the second visit only at 3 sites

(5%). We captured 0–7 flying squirrels per site on each of the 2 visits, with an average of 1.1 individuals (SD = 1.6) on the first visit and 0.6 individuals (SD = 1.2) on the second visit.

There was considerable uncertainty regarding the most parsimonious model for the analysis of site occupancy and detectability. Indeed, the top-ranked model had an Akaike weight of only 0.29. We deemed 4 models equivalent, having most of the support, including all the variables considered, with Akaike weights ranging from 0.29 to 0.10 (Table 2). These 4 models were the only ones in our set that included variables linked to our hypothesis that detection was affected by weather. Indeed, the β estimates from model averaging (Table 3) indicate that occupancy is not affected by any of the habitat variables considered in our models. Detection probability decreased with increasing precipitation ($\beta = -0.09$, unconditional SE = 0.03) and was lower using high traps than low traps ($\beta = -0.74$, unconditional SE = 0.35). However, detectability did not vary with temperature. Parametric bootstrap suggested that the global model had a good fit to the data ($P = 0.927$) and there was no overdispersion in the data ($\hat{c} = 0.5$).

Nest Use

We radio-tracked collared individuals from 87 different nests between 18 October 2008 and 13 April 2009. For nests located within trees, 31 were in tree cavities (25 woodpecker holes and 6 natural cavities), whereas 33 were external nests, 2 of which were located inside a witches' broom. We observed a clear difference in tree selection for the above-mentioned nest types (Fig. 1). Tree cavities were exclusively in deciduous trees (90% trembling aspen), whereas we only observed external nests in conifers ($\chi^2_3 = 52$, $P < 0.001$). A greater number of cavities were located in the sampled larger diameter trees ($t_{39} = 6.387$, $P < 0.001$). Tree cavities were

Table 2. Model selection results with $\Delta AIC_c \leq 4$ for northern flying squirrel occupancy (ψ) and detection probability (P) in Abitibi, Québec, Canada, during autumn 2008. The global model fit the data well ($P = 0.927$) and there was no evidence of overdispersion.

Models	K^a	AIC_c^b	ΔAIC_c^c	ω_i^d
Cavity availability (ψ) and weather (P)	5	259.33	0.00	0.29
Lateral cover (ψ) and weather (P)	5	259.44	0.12	0.28
Coarse woody debris (ψ) and weather (P)	5	259.97	0.64	0.21
Global model	8	261.45	2.12	0.10

^a K = no. of parameters.

^b AIC_c = Akaike's Information Criterion corrected for small sample sizes.

^c ΔAIC_c = AIC_c relative to the most parsimonious model.

^d ω_i = AIC_c model weight.

Table 3. Model-averaged parameter estimates (β_i) on the logit scale for northern flying squirrel detection probability and site occupancy models in Abitibi, Québec, Canada, during autumn 2008. We show reference levels in parentheses for qualitative covariates. Asterisks identify parameters for which confidence intervals excluded 0.

Parameter	Estimate	Unconditional SE	Lower 95% CL	Upper 95% CL
Occupancy				
Cavity availability	–0.06	0.06	–0.18	0.07
Lateral cover	0.02	0.02	–0.03	0.07
Woody debris	–0.01	0.02	–0.05	0.03
Detection				
Height (low)*	–0.74	0.35	–1.42	–0.06
Precipitation*	–0.09	0.03	–0.16	–0.03

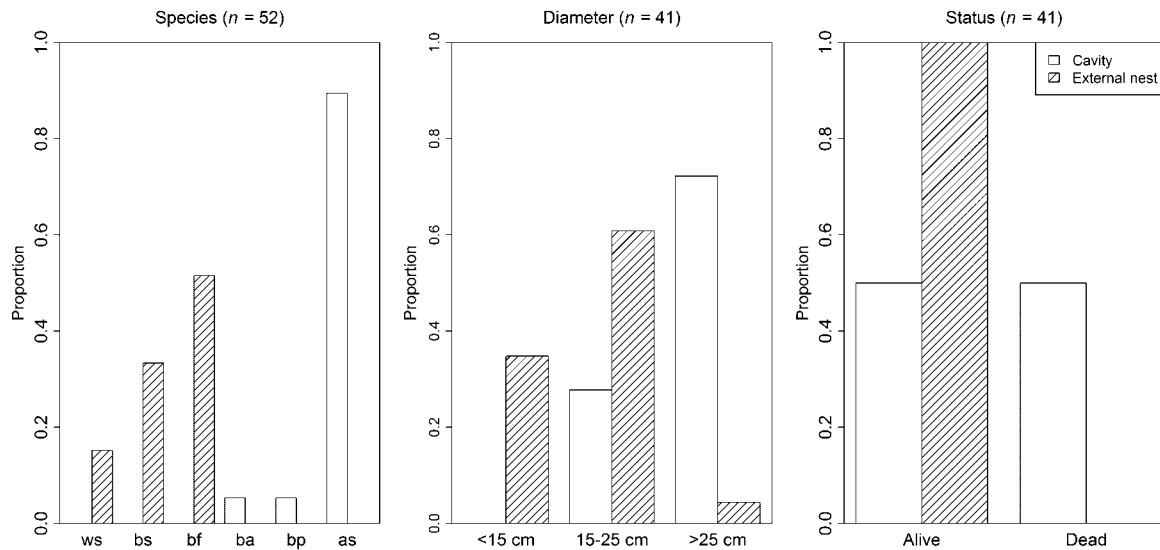


Figure 1. Comparison of species, diameter, and status of trees selected by northern flying squirrels for nesting in Abitibi, Québec, during the autumn–winter period of 2008–2009. Species abbreviations: ws = white spruce, bs = black spruce, bf = balsam fir, ba = black ash, bp = balsam poplar, and as = trembling aspen.

equally frequent in live or dead trees, but external nests exclusively occurred in live trees ($\chi^2_3 = 23.040$, $P < 0.001$). Compared to the 301 available trees with cavities inventoried in the trapping sites, used cavities occurred in trees with a greater dbh (30.0 cm vs. 26.5 cm; $t_{317} = -1.940$, $P = 0.053$), were more often found on live trees (50.0% vs. 23.4%; $\chi^2_1 = 4.934$, $P = 0.026$), but were found in trembling aspen in similar proportions (88.9% vs. 93.7%, $\chi^2_1 = 0.061$, $P = 0.804$). We also located 20 ground nests, 4 of which were positioned under logs or stumps beneath the snow cover. The remaining ground nests were located below-ground up to depths of 1 m, as determined by excavations on 7 cases where predation had occurred. There were 3 nests located inside the walls of private houses due to the proximity of our sites to residential areas but they were not included in our analysis.

Twenty-six individuals (13 M, 13 F) were located alive in nests 220 times, with 1–32 locations per animal. Each flying squirrel used 1–6 nests over the tracking period. Both males and females used tree cavities, external nests, and ground nests. However, females used a greater proportion of ground nests, whereas males used mainly external nests ($\chi^2_2 = 18.654$, $P < 0.001$; Fig. 2). Based on a parametric bootstrap approach with 1,000 simulated data sets, there were no indications of lack of fit of the logistic regression models with random effects, as all models had $P > 0.497$. The probability of using an external nest rather than a cavity increased with decreasing temperature for males ($\beta = -0.18$, $SE = 0.07$, 95% CI = -0.32 to -0.04) but there was no significant effect for females ($\beta = -0.02$, $SE = 0.06$, 95% CI = -0.14 to 0.10 ; Fig. 3). Females were approximately 2 times more likely to select an external nest than a cavity at -30°C than at 0°C , whereas males were approximately 257 times more likely to select an external nest than a cavity at -30°C than at 0°C . The probability of using a ground nest rather than a cavity also

increased with decreasing temperature for females ($\beta = -0.15$, $SE = 0.04$, 95% CI = -0.23 to -0.07 ; Fig. 3); females were approximately 79 times more likely to select a ground nest than a cavity at -30°C than at 0°C . Problems of model convergence prevented the analysis of the probability of using ground nests over cavities for males.

DISCUSSION

Site Occupancy

We captured northern flying squirrels on more than half our sampled sites (58%) and as many as 7 individuals per site, suggesting high population abundances in aspen-dominated stands of the Abitibi region. Both our occupancy and

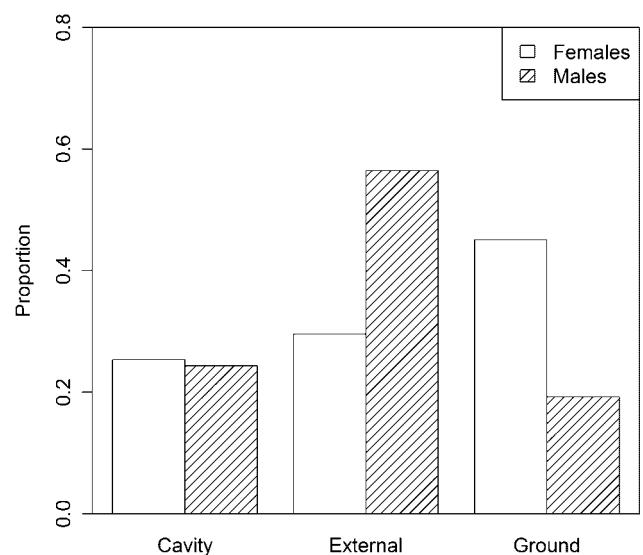


Figure 2. Proportion of telemetry locations in each nest type by sex: female ($n = 142$) and male ($n = 78$) northern flying squirrels in Abitibi, Québec, Canada, during the autumn–winter period of 2008–2009.

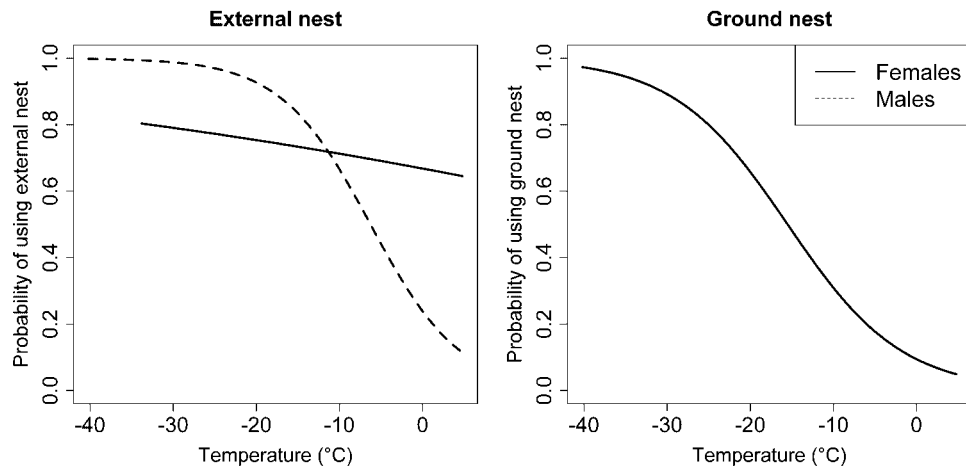


Figure 3. Effect of temperature on the probability of using an external and a ground nest by females and males northern flying squirrel in Abitibi, Québec, Canada during autumn–winter 2008–2009. Reference level for comparisons is cavity. Limited use of ground nests by males prevented analysis.

telemetry results corroborate those from nest box supplementation experiments that did not show an increase in population abundance or reproduction rate for either northern flying squirrels in the Pacific Northwest (Carey 2002, Ransome and Sullivan 2004) or southern flying squirrels in South Carolina (Brady et al. 2000). In our study, cavity availability, as estimated by binocular surveys of available trees, did not influence flying squirrel site occupancy, suggesting that cavities do not represent a limiting factor for this species. In coniferous and boreal forests of North America the majority of cavities are located on trunks and are excavated by woodpeckers (Aitken et al. 2002, Aitken and Martin 2004, Martin et al. 2004, Cooke 2009, Cadieux 2011). Woodpeckers may excavate incomplete cavities that are not wide or deep enough for being used by flying squirrels (Hoyt 1957, Hooper et al. 1991, Ojeda et al. 2007). Binocular surveys in systems where woodpeckers create most of the suitable cavities may thus lead to an overestimation of cavity abundance. A recent study conducted in the same region as our study found that only 36% of the potential cavities detected by binocular surveys were suitable cavities for nesting as determined by direct inspection (Ouellet-Lapointe et al., unpublished data). We consider, however, that although incomplete holes without chambers may result in an overestimation of available cavities, our results truly represent a crude index of available cavities at each site. Our results on collared individuals also show that northern flying squirrels are not obligate cavity-nesters in the autumn–winter period, as individuals used other nest types in cold weather. However, a more robust test of the hypothesis that cavities are a resource limiting population size of flying squirrels in boreal forests requires experimental manipulation of tree cavities as well as control of extraneous variables that potentially could confound the results, such as food availability, which has been proposed as the most important factor limiting these populations (Carey et al. 1997, Carey 2002, Ransome and Sullivan 2004).

Hypogeous fungi that are consumed by the northern flying squirrel are associated with ground surface woody debris in second-growth and mature stands of the Appalachians

and the Pacific Northwest (Amaranthus et al. 1994, Hackett and Pagels 2003). However, our stands had a low volume of woody debris with small diameters in early stages of decay. Logs in our aspen-dominated stands might not represent an adequate substrate for fungal growth, and therefore, they were possibly not an adequate proxy for food availability or an effective predictor of site occupancy for flying squirrels. Indeed, it is recognized that the northern flying squirrel consumes both truffles and aboveground fungal sporocarps in boreal mixedwood forests (Currah et al. 2000, Wheatley 2007). Ectomycorrhizal fungi, especially those producing truffles, are mostly symbiotic with the roots of conifers (Maser and Maser 1988). Aspen also exhibits an ectomycorrhizal habit, but it tends to associate with mycobionts that produce epigeous (aboveground) sporocarps (Cripps 2001) and rarely, if ever, forms associations with genera that produce hypogeous (belowground) fruiting bodies, such as the truffle-forming *Rhizopogon* spp. (Godbout and Fortin 1985) or *Tuber* spp. (Visser et al. 1998). Therefore, conifers may be associated with a high abundance of food for the northern flying squirrel at the microhabitat scale (Pyare and Longland 2002), which may explain why its densities had a strong relationship with the density of large spruce trees (*Picea* sp.) in some areas (Hollaway and Malcolm 2006).

A well-developed understory has been associated with the presence of northern flying squirrel on the west coast of North America (Rosenberg and Anthony 1992, Carey 1995). In this region, this relationship may be linked to predation avoidance as the spotted owl (*Strix occidentalis*) is a specialized predator of the northern flying squirrel, consuming up to 235 individuals per year, and it typically ambushes prey in open areas (Heinrichs 1983). However, resident owls found in our study area are mostly great horned owls (*Bubo virginianus*; Gauthier and Aubry 1996), known to specialize mostly on snowshoe hare (*Lepus americanus*; Houston et al. 1998). If mammalian predators are more important than owls, we can speculate that vegetation cover may not as greatly influence predation success or a flying squirrel's choice of habitat in our study area.

Precipitation has been shown to negatively influence the ability of northern flying squirrels to orient properly (Flaherty et al. 2008) and to increase latency in moving from release sites during relocation experiments (Rizkalla and Swihart 2007). This behavior might be coupled with increased thermoregulatory costs and mortality under adverse conditions, as suggested by the observation that Arctic ground squirrels (*Spermophilus parryii*) stay underground in their burrows on cold rainy days in Alaska (Long et al. 2005). Therefore, flying squirrels might be less active on rainy days, thereby reducing our ability to detect their presence with a trapping method.

The greater success of low (1.5-m) over high (4-m) traps at capturing flying squirrels is contradictory to Risch and Brady (1996), who found that 4- to 5-m high traps had more southern flying squirrel captures. We, however, found a weak effect of trap height on detectability, as models that included trap height ranked poorly relative to the entire set of candidate models. Our observations of flying squirrels landing on tree trunks and climbing up to the canopy implies that flying squirrels would encounter traps at any height, especially if the animal is attracted by a strong peanut butter smell. We recommend using low-mounted traps as they do not require the use of a ladder, making them easier to install and monitor.

Nest Use

Several studies have reported low use of external nests in favor of tree cavities (4% in Alberta, McDonald 1995; 16% in northwestern British Columbia, Cotton and Parker 2000b; <27% in southeastern Alaska, Bakker and Hastings 2002; 29% in central Ontario, Holloway and Malcolm 2007). In New Brunswick, external nests represented 40% of all nests found; however, they were avoided during winter (Gerrow 1996). This avoidance was explained by the wet, cold climate of the coast and the tendency of external nests to freeze after water absorption, limiting insulation qualities. In our study, external nests had the highest proportion of use, with 39% of all locations, and were preferred in cold weather by males. This result is similar to that of a study in interior Alaska, which reported a majority of nest locations (65%) in outside nests and an avoidance of tree cavities in conditions of extreme cold (Mowrey and Zasada 1984). As opposed to tree cavities, which cannot be created by northern flying squirrels, the construction of external nests does offer numerous advantages during the cold season. First, external nests can be located in structures that provide additional protection from inclement weather. In agreement with other studies, we observed external nests mainly in the dense foliage of live coniferous trees (Carey et al. 1997, Holloway and Malcolm 2007). Second, external nests can be located close to food sources, further reducing travel costs, energetic demands, and predation risks. Third, their adaptable internal dimension (as opposed to the maximum limit of a cavity chamber) increases the potential for aggregations. Aggregations have been correlated with drops in temperatures (Mowrey and Zasada 1984, Gerrow 1996, Cotton and Parker 2000a) and have been shown to reduce energy expen-

ditures up to 33% in southern flying squirrels (Stapp et al. 1991). In Abitibi, it is possible that external nests provide the northern flying squirrel with high insulation cover because of the dry climate, the choice of a strategic location, and the possibility to form aggregations.

Only a few studies have observed the use of ground or subterranean nests by northern flying squirrels (9.8% in southern New Brunswick, Gerrow 1996; 8% in southeastern Alaska, Bakker and Hastings 2002; 27% for males in southwest Virginia, Hackett and Pagels 2003; 0.02% in central Ontario, Holloway and Malcolm 2007). This is surprising, as we found that ground nests were the second-most used nests, with 36% of all locations, and they were preferred by females in cold temperatures. Gerrow (1996) also found an increased use of ground nests with decreasing temperature in winter. It is very possible that the insulation provided by a ground nest is superior to any other nest type because of the insulative properties of snow and that the use of ground nests may represent normal winter behavior in a cold climate. There might also be a compromise between insulation and predation, as we observed 8 mortalities in underground nests over the course of the study. Gerrow (1996) suggested weasels were the only predators capable of getting into underground nests and observed that weasel predation upon flying squirrels increased with the latter's increased use of ground nests. In Alaska, the relatively frequent use of below-ground nests suggests that thermoregulatory gain can outweigh the added predation risk of denning near ground-level (Bakker and Hastings 2002).

Nest choice was clearly differentiated by sex, with males selecting external nests and females preferring ground nests. Females have been observed to use low structures such as stumps and slash piles as natal dens during the reproductive period in the Pacific Northwest (Carey et al. 1997) and it is known that females isolate themselves to raise their young (Gerrow 1996). Carey et al. (1997) hypothesized that only suboptimal nests are available when the number of tree cavities is low and competition is high. We made all our observations of ground nest use outside the breeding season (parturition: late May through June; Wells-Gosling and Heaney 1984), suggesting a thermoregulatory basis to the use of ground nests. Further, we believe the difference in nest use by sex might have been due to sample size, as most collared males did not survive through the winter. In fact, 76% of male locations in temperatures <0° C ($n = 63$) were made on 3 males, and 1 of these did not use ground nests at all. Spatial and temporal use of nests varies among individuals (Cotton and Parker 2000b, Hackett and Pagels 2003). There might have been an individual preference towards external nests in the cold, and thus, our small sample size showed low use of ground nests by males.

It is possible that tree cavities do not provide sufficient insulation for the cold winter period in the boreal forest, even though flying squirrels used preferentially those with the greatest insulative properties (large diameter, living trees; Coombs et al. 2010). Tree cavities are used by both males (24%) and females (25%), but they are less likely to be used compared to external and ground nests as temperature

decreases. In New Brunswick, the use of excavated cavities decreased with decreasing temperature in winter (Gerrow 1996). Wiebe (2001) has demonstrated that cavities in live and large trembling aspen heat and cool more slowly than small and dead trees, resulting in more stable temperatures during the day. This response is partly because large trees have thick walls surrounding the cavity, thereby providing better insulation. This temperature moderating effect is illustrated by tree cavities being 6.5° C warmer than nest boxes (McComb and Noble 1981). Interestingly, the only 2 tree cavities used below -15° C were in large trees of 49- and 34-cm dbh, which were among the 4 largest cavity trees used for nesting by northern flying squirrels during our study. Although tree cavities were largely preferred (96%) during the autumn-winter period in Alberta, trees had an average diameter of 36.5 cm and live trees were selected (McDonald 1995). This suggests they were better insulated than in our sites. Therefore, cavities in large trees are probably limited in our study area and small trees might not offer adequate thermal insulation for winter.

Our results concur with those from other studies having shown the flying squirrel to be opportunistic in its choice of structures to use for nesting, even though it generally seeks larger trees (McDonald 1995, Gerrow 1996, Cotton and Parker 2000b, Hackett and Pagels 2003). Tree cavities used by flying squirrels were located mostly in large trembling aspen, reflecting the selection by woodpeckers for this deciduous species, which is commonly infected by heartwood rot (Wiebe 2001, Savignac and Machtans 2006, Cadieux 2011). Similarly, heartwood decay and tree size were important in determining nest-trees for northern flying squirrels in central Ontario and these characteristics were determined by the excavators (Holloway and Malcolm 2007).

MANAGEMENT IMPLICATIONS

Our hypothesis that tree cavities represent a limiting factor for northern flying squirrel during winter months in the boreal forest was not supported; we found only 25% of nests within tree cavities. Nevertheless, practices ensuring the persistence of large diameter live cavity trees, providing better insulative properties, are likely to increase the relative use of tree cavities as nest sites by northern flying squirrels. Like any secondary hole-user, practices aiming at providing suitable conditions to excavators, such as partial cuts or retention of structural legacies within clear-cuts, should be favored to ensure a long-term availability of suitable cavities (Drapeau et al. 2009). We suggest that the ability of northern flying squirrels to use a diversity of nest types explains the abundance and broad distribution of the species across a wide range of environments and its distributional range reaching high northern latitudes.

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