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## Original Investigation

## Winter site occupancy patterns of the northern flying squirrel in boreal mixed-wood forests

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## ABSTRACT

We assessed habitat use by the northern flying squirrel (*Glaucomys sabrinus*) to test the hypothesis that the species is not a late-seral coniferous forest specialist in boreal mixedwood forests of northwestern Québec. We monitored 149 pairs of nest boxes over 3 visits during February–April 2008. A total of 31 pairs of nest boxes were occupied during the study. The average (3.7, 2.8, and 1.8) and maximum (8, 6, and 4) numbers of individuals in nest boxes decreased from the first to last visit. Average air temperatures were below freezing and increased with the arrival of spring (−23.9, −14.5, and −3.7 °C). Using GIS software, we created a 430-m (median dispersal distance) buffer around each pair of nest boxes and extracted landscape composition variables from digital forest inventory maps. We created models that potentially explained site occupancy by the northern flying squirrel as well as detection probability. Model selection indicated that the area of coniferous forests negatively affected site occupancy by flying squirrels while temperature positively influenced detection probability. Our results support the hypothesis that the northern flying squirrel is not a habitat specialist, but can occupy a wider range of forest cover types than previously recognized in various landscape contexts.

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## Introduction

The northern flying squirrel, *Glaucomys sabrinus*, is a nocturnal arboreal rodent common across forested landscapes of northern North America (Wells-Gosling and Heaney, 1984). As the main prey item of the northern spotted owl (*Strix occidentalis caurina*) in the Pacific Northwest, it has been largely studied in this region and its optimal habitat is described as old-growth coniferous forest (Carey, 1991; Witt, 1992; Carey, 1995; Smith and Nichols, 2003). This selection is explained by its important consumption of truffles, i.e., hypogeous fruiting bodies (Maser et al., 1986; Pyare et al., 2002; Lehmkühl et al., 2004), of ectomycorrhizal fungi associated with the roots of conifers in the Pinaceae (Maser and Maser, 1988), and by its use of tree cavities (Smith, 2007). Although preference for multi-storied, structurally complex old forest may also be due in large part to predator avoidance (Carey 2002), this hypothesis has less empirical support than food and nest limitations (Smith 2007; Hough and Dieter 2009a). In the Appalachians, northern flying squirrel habitat has also been defined as coniferous-dominated forest at high

elevation or conifer-hardwood ecotones (Weigl et al., 1992; Odom et al., 2001; Menzel et al., 2006), where it may avoid competition with the southern flying squirrel, *Glaucomys volans* (Weigl 1978). However, recent studies in continental regions suggest that this species is less specialized in its habitat use than previously expected, as shown by its presence in mixed or deciduous forests (Wheatley et al., 2005; Holloway, 2006; Ritchie et al., 2009), and in residual stands fragmented after logging (Bayne and Hobson, 1998; Côté and Ferron, 2001). Such results highlight the apparent need for further studies to enhance our understanding of the habitat requirements of northern flying squirrel in regions where pure coniferous forests, old-growth forests, or a combination of these two are not common (Patterson and Malcolm 2010).

Few studies have examined the habitat characteristics of the northern flying squirrel in the northern part of its range, particularly in the boreal forest. As this region is characterized by a continental climate with average temperatures below freezing for 5–6 months per year, a considerable energetic demand is imposed on small mammals, including the northern flying squirrel, which is active year-round. It is generally recognized that cavities represent better winter nest choices than do external nests (Wells-Gosling and Heaney, 1984), as the former offers better protection from precipitation, wind, and cold temperatures. However, a study recently

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showed that external nests and even ground nests are more likely to be used than cavities on days following cold nights in our study area (Trudeau et al. 2011). Flying squirrels are also known to aggregate in nests (Mowrey and Zasada, 1984; Gerrow, 1996), and thus, large cavities are necessary for cohabitation. Availability of suitable cavities has therefore been proposed as a factor limiting this species (Smith, 2007). When available, nest boxes are readily used by flying squirrels (Maser et al., 1981; Carey, 2002; Ransome and Sullivan, 2004). As such, nest boxes represent an effective way to assess site occupancy and habitat use (Fokidis and Risch, 2005).

In this study, our main objective was to investigate habitat use by the northern flying squirrel in boreal mixedwood forests using nest boxes. Since (1) cavity availability is an important limiting factor for the northern flying squirrel (Carey, 2002), (2) that most cavities in the boreal forest are excavated by woodpeckers rather than of natural origin (Aitken and Martin, 2007), and (3) that cavities are mainly excavated in trunks of trembling aspen (*Populus tremuloides*) in boreal mixedwood forests (Drapeau et al., 2009), we hypothesized that the flying squirrel is not associated with coniferous forest cover types in our study area but instead inhabits a wide range of forest cover types that include deciduous forests dominated by trembling aspen (Hough and Dieter 2009b). Large trees have also been associated with the presence of the northern flying squirrel in the boreal forest (McDonald, 1995) and we expected that the cover of mature and older forests would be positively associated with site occupancy probability. We also expected that sites surrounded by open habitats would be associated with lower occupancy because such habitats limit movement and dispersal of flying squirrels (Bendel and Gates, 1987), reducing the probability of such sites of being colonized and occupied.

## Material and methods

### Study area

The study took place in the boreal mixedwood forest of northwestern Québec (47°46'–49°00'N, 79°53'–78°22'W), which is located on the northern Clay Belt and characterized by clay soils and low rocky hills. Mean annual temperature is 1°C and average annual precipitation is 914 mm (Environment Canada, 2009). This region is part of the balsam fir–white birch bioclimatic domain of the boreal forest (Robitaille and Saucier, 1998), and consists of trembling aspen, 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*). The landscape is characterized by a mixture of coniferous, mixed, and deciduous forests interspersed with agricultural fields and clear-cuts, as well as numerous lakes and rivers.

### Nest boxes

We monitored 149 forest stands in which two nest boxes were installed in 2003 primarily for northern saw-whet owl (*Aegolius acadicus*) and boreal owl (*Aegolius funereus*) nesting, but these nest boxes were also used as winter shelter by northern flying squirrels. All nest boxes previously used by nesting birds were cleaned at the end of each summer by removing their content and adding a new layer of sawdust. The location of each nest box pair was determined using a stratified sampling design to ensure adequate representation of the variation in forest cover occurring over the region (mean = 77%, range = 26–100% forest in 430-m buffer), as well as existing forest cover types (coniferous, mixed, and deciduous). The nest boxes (19.8 cm × 19.8 cm × 44 cm height; 7.15 cm dia. entrance) were handmade with ca. 1.5 cm thick plywood and designed with a side door to access the interior. They were installed

at a 4-m height on a dominant tree and the bottom of the boxes was covered with wood chips. Nest boxes were distributed at approximately 50 m from roads with an average distance of 20 m between the nest boxes of a pair and 3 km between each pair.

Each pair of nest boxes was visited 3 times during winter and early spring 2008 (between February 14th and April 12th) to determine the presence and number of northern flying squirrels. As this species is strictly nocturnal (Cotton and Parker, 2000), the nest boxes were visited at any time of the day except 30 min after sunrise or before sunset to ensure that nests were being used at the time of checking. Using a ladder, each nest box was inspected for northern flying squirrels following the same procedure: (1) a few knocks were given on the door; (2) the door was opened; (3) if it contained a squirrel's nest, the latter was shaken; and finally, (4) the nest was inspected to ensure that no individual was missed. This exercise was performed with a second observer on the ground with an unobstructed view of the nest box entrance. This observer was able to count flying squirrels coming out of the nest box. All 149 nest box pairs were checked during the first visit. However, 2 and 14 pairs could not be checked during the second and third visits, respectively, due to difficult access and warmer weather affecting snow conditions.

### Environmental variables

We determined habitat use by the northern flying squirrel using seven different landscape composition variables, known to be better predictors of flying squirrel distribution than forest configuration variables (Ritchie et al., 2009). The variables were chosen in order to test seven different hypotheses relating to the specialization of flying squirrel habitat use in terms of forest composition (conifer versus deciduous tree cover) and developmental stages (greater than 7 or 12 m in height; Table 1). These variables were extracted using ArcView® 3.2 (ESRI, 1999) from 1995 digitized forest cover maps (1:20,000 scale) that were produced by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF) and which were updated with recent clear-cuts (1993–2007). We created a 430-m buffer around each pair of nest boxes and extracted areas corresponding to each variable within the buffer. This buffer value was chosen as it represents the median dispersal distance for flying squirrels (D'eon et al., 2002). We expected that the landscape context defined by habitat composition within this radius would have an effect on the probability that a stand would be colonized in the fall, and thus occupied when we conducted our nest box surveys in winter.

### Statistical analysis

We analyzed flying squirrel detection at nest boxes using single season occupancy models that were fit in R version 2.13.0 using the unmarked package (Ihaka and Gentleman 1996; Fiske et al. 2011; MacKenzie et al., 2006). This method estimates a probability of detection using data from repeated visits to account for false absences (MacKenzie et al., 2002). In this analysis, each stand with a nest box pair was considered an independent site, whereas nest box pairs provided the detection histories for each site. On a given visit, each nest box pair contributed a single binary observation: squirrels were either detected or not at each site. Each one of our seven main hypotheses on habitat use (Table 1) constituted independent models on site occupancy and were compared with air temperature and area of coniferous forest as covariates potentially affecting detection, for a total of fourteen different models. For temperature, we used the minimal temperature between 0:00 and 6:00 on the day of observation. All data were acquired from the closest meteorological station, which was located in the city of Val-d'Or (48°03'N, 77°47'W), and downloaded from the Environment Canada website

**Table 1**  
Description of the landscape composition variables extracted from digitized forestry maps. Values for mean area and range are expressed in hectares and calculated within the 430-m buffer of each site.

Variables	Description and hypothesis on habitat use	Mean (range)
Coniferous (Con)	Stands dominated <sup>a</sup> by conifers (coniferous or mixed) > 7 m; conifer specialized species	17.3 (0–57.8)
Deciduous (Dec)	Stands dominated <sup>a</sup> by deciduous trees (deciduous or mixed) > 7 m; deciduous specialized species	21.8 (0–56.1)
Open	Open habitats including; forested stands < 2 m, water, agricultural fields, fallows, deforested and urban areas; species avoiding open areas	12.1 (0–42.7)
Forest (For)	All forested stands (coniferous, deciduous and mixed) > 7 m; generalist forest species	44.4 (15.1–57.8)
Mature (Mat)	All forested stands (coniferous, deciduous and mixed) > 12 m; mature forest specialized species	26.4 (0–53.5)
Mature Coniferous (MatCon)	Stands dominated <sup>a</sup> by conifers (coniferous or mixed) > 12 m; mature coniferous forest specialized species	8.9 (0–47.5)
Mature Deciduous (MatDec)	Stands dominated <sup>a</sup> by deciduous trees (deciduous or mixed) > 12 m; mature deciduous forest specialized species	17.5 (0–53.5)

<sup>a</sup> Dominance is described as >50% of total basal area of the stand.

(Environment Canada, 2009). Because cavity use decreases at low temperatures (Trudeau et al. 2011), we expected a similar effect on nest box use, yielding a positive effect of temperature on probability of detection at our study sites. Because leaf nests are apparently constructed only in conifers in our study area (Trudeau et al. 2011), we also expected that probability of detection of flying squirrels using nest boxes would be higher in sites where the availability of conifers is low.

All variables were centered prior to analysis. Strong correlations ( $r \geq 0.7$ ) occurred among certain landscape composition variables. To avoid including highly correlated variables in the same models, we considered a final set of 19 models to explain the presence of the northern flying squirrel at our sites, which included a null model and 10 global models. We tested the fit of each of 10 global models to the data by using a parametric bootstrap approach with 10,000 bootstrap samples ( $\hat{c} > 1.0$  indicated overdispersion of the data) using program PRESENCE 2.4 (Hines 2006; MacKenzie et al., 2006). We used Akaike's Information Criterion, adjusted for small sample size (i.e., total number of sites), to compare candidate models (Burnham and Anderson, 2002). We considered models with  $\Delta AIC_c$  values  $\leq 2$  to have 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). We used the AICcmodavg package (Mazerolle 2011) to compare models and implement multimodel inference to assess the effect of variables on either occupancy or detection probability.

## Results

A total of 31 sites were occupied over the 3 visits, with fewer sites occupied during the first (12) and second (17) visits compared to the third (25). The average number of flying squirrels in occupied sites was 2.8 per nest box over the 3 visits, and this average number decreased with more individuals observed during the first (3.7) and second (2.8) visits compared to the third (1.8). We also observed an aggregation of 8 flying squirrels in a nest box during the first visit, while the maximum numbers of individuals in subsequent visits were 6 (second visit) and 4 (third visit) animals, respectively. The mean temperature over the 3 visits was  $-14.3^\circ\text{C}$ ; consistent with expectation, average air temperature increased as the season progressed, from  $-23.9^\circ\text{C}$  on the first visit to  $-14.5^\circ\text{C}$  on the second visit, and to  $-3.7^\circ\text{C}$  on the third.

None of the 10 global models in our candidate model set suggested overdispersion in the data as  $\hat{c}$  was close to 1. A single occupancy model had most of the support with an Akaike weight of 0.87 (Table 2) and it included the variables conifer cover (coniferous) on occupancy and minimal air temperature (temperature) on detection. This model was 17 times more likely than the second-ranked model, which consisted of mature conifer cover on occupancy and temperature on detectability.

The area of coniferous habitat surrounding each pair of nest boxes negatively affected the probability of site occupancy (model-averaged  $\beta = -0.10$ , 95% CI =  $-0.15, -0.05$ ; Fig. 1). As for detection probability, it was positively affected by temperature (model-averaged  $\beta = 0.07$ , 95% CI =  $0.03, 0.12$ ; Fig. 2).

## Discussion

Our results support recent studies suggesting that the northern flying squirrel is not a coniferous forest specialist and can use a wider variety of forest cover types than previously thought (Wheatley et al., 2005; Weigl, 2007; Ritchie et al. 2009). Site use, as determined by nest box detections, was negatively related to the area of coniferous habitat within a 430-m buffer, but there were no effects of stand age or open habitats. This indirectly supports the hypothesis that deciduous and mixedwood forests are high-quality habitats. Indeed, sites occupied by flying squirrels had a greater area of deciduous or mixed forest habitats, reflecting the potential importance of deciduous trees, particularly trembling aspen, in their habitat use. The absence of an effect of mature forest or open habitats also suggests that flying squirrels can use various landscape contexts.

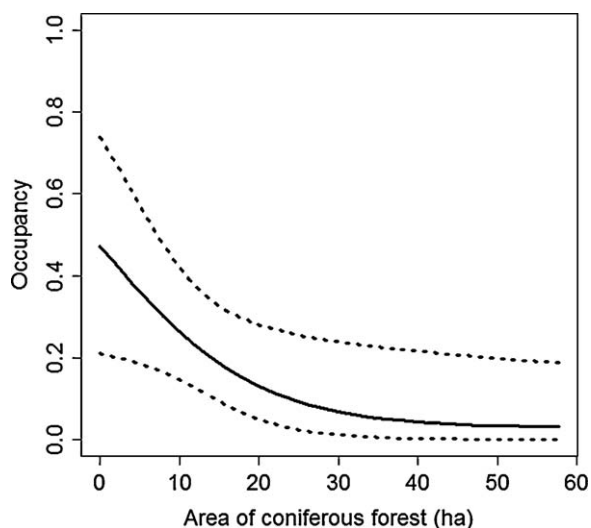
Site occupancy by northern flying squirrels was negatively influenced by the area of coniferous forest surrounding each nest

**Table 2**

Model selection results for northern flying squirrel occupancy ( $\psi$ ) and detection probability ( $p$ ) in northwestern Québec, Canada, during winter and early spring 2008 ( $K$ : no. of parameters,  $AIC_c$ : Akaike's Information Criterion corrected for small sample sizes,  $\Delta AIC_c$ :  $AIC_c$  relative to the most parsimonious model,  $w_i$ :  $AIC_c$  model weight). Variable codes are described in Table 1.

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$\psi(\text{Con}), p(\text{Temp})^a$	4	238.52	0.00	0.87
$\psi(\text{MatCon}), p(\text{Temp})$	4	244.44	5.92	0.05
$\psi(\text{MatCon}), p(\text{Con})$	4	245.78	7.26	0.02
$\psi(\text{MatDec} + \text{MatCon} + \text{Open}), p(\text{Temp})^a$	6	246.64	8.11	0.02
$\psi(\text{Dec}), p(\text{Temp})^a$	4	247.52	9.00	0.01
$\psi(\text{Mat}), p(\text{Con})$	4	248.21	9.68	0.01
$\psi(\text{Con}), p(\text{Con})^a$	4	248.24	9.71	0.01
$\psi(\text{Dec}), p(\text{Con})^a$	4	248.49	9.97	0.01
$\psi(\text{MatDec}), p(\text{Con})$	4	249.04	10.52	0.00
$\psi(\text{Open}), p(\text{Con})$	4	249.17	10.65	0.00
$\psi(\text{For}), p(\text{Con})^a$	4	249.18	10.66	0.00
$\psi(\text{MatDec} + \text{MatCon} + \text{Open}), p(\text{Con})^a$	6	249.66	11.13	0.00
$\psi(\text{Mat} + \text{Open}), p(\text{Con})^a$	5	250.18	11.65	0.00
$\psi(\text{MatDec}), p(\text{Temp})$	4	256.09	17.57	0.00
$\psi(\text{For}), p(\text{Temp})^a$	4	266.13	27.61	0.00
$\psi(\text{Open}), p(\text{Temp})$	4	266.49	27.97	0.00
$\psi(\text{Mat}), p(\text{Temp})$	4	266.97	28.44	0.00
$\psi(\text{Mat} + \text{Open}), p(\text{Temp})^a$	5	268.10	29.58	0.00
$\psi(\cdot), p(\cdot)$	2	275.84	37.32	0.00

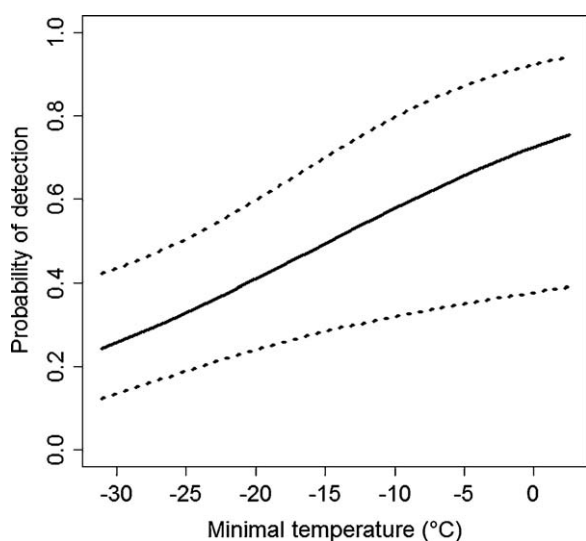
<sup>a</sup> Global models.



**Fig. 1.** Effect of the area of coniferous forest within 430-m buffers around each site on occupancy of nest boxes by northern flying squirrels in northwestern Québec, Canada, during winter and early spring 2008. Results are based on model-averaged predictions. Dashed lines indicate 95% confidence limits.

box pair. This result differs from a study conducted by Wheatley et al. (2005) in mixedwood forests of the boreal plain of Alberta, where no relationships were found between squirrel abundance and conifer-dominance in stand composition, stand age, or non-forested openings at the landscape scale (50-, 150- and 300-m) using data from digital map inventories. These authors did capture flying squirrels in all of the habitats sampled (coniferous, mixed, and deciduous stands). Our findings corroborate their conclusions that flying squirrel populations do not seem to be associated with old-aged or conifer forests. In contrast, McDonald (1995) observed a positive relationship between flying squirrel abundance and density of white spruce in aspen mixedwood forests of Alberta, but all of the stands that she selected had >80% aspen canopy cover.

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) and that ectomycorrhizal fungi, especially those producing truffles, are mostly



**Fig. 2.** Effect of minimal air temperature on detection probability of northern flying squirrels at nest boxes in northwestern Québec, Canada, during winter and early spring 2008. Results are based on model-averaged predictions. Dashed lines indicate 95% confidence limits.

symbiotic with the roots of conifers (Maser and Maser, 1988). Therefore, conifers may be associated with a high abundance of food for the northern flying squirrel at the microhabitat scale (Pyare and Longland, 2002). Aspen also exhibits an ectomycorrhizal habit, but it tends to associate with mycobionts that produce aboveground sporocarps (Cripps, 2001) and rarely, if ever, forms associations with genera that produce belowground fruiting bodies, such as *Rhizopogon* (Godbout and Fortin, 1985) or *Tuber* (Visser et al., 1998). In this study, northern flying squirrels were more likely to occupy deciduous dominated and mixed forests of the boreal mixedwoods and avoided purely coniferous sites. Although the forest maps that we used did not discriminate between black and white spruces, white spruces are usually found sparsely within deciduous or mixed forests, while black spruce and jack pine are often found in pure stands. This occupancy pattern may therefore be in agreement with the association of northern flying squirrel to sites where large white spruces are found (Holloway and Malcolom 2006), a species that could be a key mycorrhizal host tree in boreal forests at the northern range of the northern flying squirrel.

There was no effect of the area of mature and older forests in the landscape on site occupancy. Although our study is not based on analyses of northern flying squirrel abundances, it is noteworthy that in Alberta, northern flying squirrels were more abundant in old stands than younger stands (McDonald, 1995). However, old stands (>120 years) represented only 1.5% of the total area considered for the analysis of our 149 sites. Our sites (10–90 years) were comparable to the stands considered as mature (50–70 years) or young (<30 years) in the Alberta study, which had medium to low abundance of flying squirrels. It is possible that the characteristics associated with old-growth forests, and which are of interest to northern flying squirrels, such as abundant cavities and highly decomposed woody debris used as growth substrates for fungi, were not frequently encountered in our study area.

Contrary to our hypothesis, we did not observe any effect of habitat type on the probability of detection. However, as expected based on a recent study (Trudeau et al. 2011), we observed a positive effect of temperature on detection probability. The latter result is consistent with the observations of McComb and Noble (1981) on temperature being on average 6.5 °C colder inside nest boxes than inside cavities in a bottomland hardwood stand in Louisiana. Thus, the thermal insulation of a nest box might not be sufficient for winter use in cold nights by the northern flying squirrel in the boreal forest. Nest box use in our study increased from the first to the third visit (12, 17 and 25 occupied pairs) with increasing air temperature (−23.9 °C, −14.5 °C and −3.7 °C). An alternative to compensating for the low insulation value of nests is to cohabit with other individuals. Northern flying squirrels aggregate in nests after a sharp drop in temperature (Mowrey and Zasada, 1984; Gerrow, 1996; Cotton and Parker, 2000). Moreover, such aggregations have been shown to reduce energy expenditure up to 33% in southern flying squirrels (Stapp et al., 1991). Interestingly, we recorded the maximum number of flying squirrels that were observed to be sharing a nest box during the first visit, which was also the coldest. This would also affect detection probability as fewer nests are used during the cold winter period due to aggregations, limiting the probability of a nest box to be used by at least one squirrel. Flying squirrels could either prefer other nest types in cold weather and only use nest boxes in warmer temperature, or aggregate in nest boxes when the temperature is colder, which would also limit detection success.

In conclusion, although we acknowledge that this study is based on 149 sites but for only one year of data, it supports the hypothesis that the northern flying squirrel is not associated with late-seral coniferous forests in the boreal mixedwood forest of eastern Canada. Results also show that the northern flying squirrel can use a wider variety of forest cover types than previously

recognized and this in varying landscape contexts. Although conifers provide a fine-scale food resource, deciduous or mixed forests can represent a suitable habitat for this species. Our study suggests that digital forest inventory maps are appropriate to assess habitat use by this species at a median dispersal distance in boreal mixedwoods. We showed that temperature affects nest box use, and we suggest that this variable should be taken into consideration with suitable methods when site occupancy is the state variable of interest.

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## References

- Aitken, K.E.H., Martin, K., 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. *J. Ornithol.* 148, S425–S434.
- Bayne, E.M., Hobson, K.A., 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Can. J. Zool.* 76, 62–69.
- Bendel, P.R., Gates, J.E., 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). *J. Mammal.* 68, 243–255.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.
- Carey, A.B., 1991. The Biology of Arboreal Rodents in Douglas-fir Forests. General Technical Report PNW-GTR-276. United States Department of Agriculture, Forest Service, pp. 1–46.
- Carey, A.B., 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecol. Appl.* 5, 648–661.
- Carey, A.B., 2002. Response of northern flying squirrels to supplementary dens. *Wild. Soc. Bull.* 30, 547–556.
- Côté, M., Ferron, J., 2001. Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. *Can. J. Forest Res.* 31, 1805–1815.
- Cotton, C.L., Parker, K.L., 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. *Can. J. Zool.* 78, 1896–1901.
- Cripps, C.L., 2001. Mycorrhizal fungi of aspen forests: Natural occurrence and potential applications. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Eds.), *Sustaining Aspen in Western Landscapes: Symposium Proceedings, Grand Junction, Colorado, 13–15 June, 2000*. USDA Forest Service, Fort Collins, pp. 285–298.
- Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M., Larsen, K.W., 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. *Can. J. Bot.* 78, 1514–1520.
- D'eon, R.G., Glenn, S.M., Parfitt, I., Fortin, M.-J., 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. *Conserv. Ecol.* 6, 10.
- Drapeau, P., Nappi, A., Imbeau, L., Saint-Germain, M., 2009. Standing deadwood for keystone bird species in the eastern boreal forest: managing for snag dynamics. *Forest Chron.* 85, 227–234.
- Environment Canada, 2009. Canadian Climate Normals 1971–2000 [online]. Available from: [climate.weatheroffice.ec.gc.ca/](http://climate.weatheroffice.ec.gc.ca/).
- ESRI, 1999. ArcView® GIS. Environmental Systems Research Institute, Inc., Redlands.
- Fiske, I., Chandler, R.B., Royle, J.A., 2011. Unmarked: models for data from unmarked animals. R package version 0.9-0. <http://CRAN.R-project.org/package=unmarked>.
- Fokidis, H.B., Risch, T.S., 2005. The use of nest boxes to sample arboreal vertebrates. *Southeast. Nat.* 4, 447–458.
- Gerrow, J.S., 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.Sc. thesis, Acadia University, Wolfville.
- Godbout, C., Fortin, J.A., 1985. Synthesized ectomycorrhizae of aspen: fungal genus level of structural characterization. *Can. J. Bot.* 63, 252–262.
- Hines, J.E., 2006. PRESENCE2-Software to estimate patch occupancy and related parameters [online]. (USGS-PWRC, ed.). Available from [mbr-pwrc.usgs.gov/software/presence.html](http://mbr-pwrc.usgs.gov/software/presence.html).
- Holloway, G.L., 2006. Flying squirrel (*Glaucomys sabrinus* and *G. volans*) habitat use and ecology in landscapes managed with partial harvesting silviculture in central Ontario. Ph.D. dissertation, University of Toronto, Toronto.
- Holloway, G.L., Malcolm, J.R., 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. *J. Wildl. Manage.* 70, 1735–1745.
- Hough, M.J., Dieter, C.D., 2009a. Summer nest tree use by northern flying squirrels in the Black Hills, South Dakota. *Am. Midl. Nat.* 162, 98–111.
- Hough, M.J., Dieter, C.D., 2009b. Resource selection habitat model for northern flying squirrels in the Black Hills, South Dakota. *Am. Midl. Nat.* 162, 356–372.
- Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. *J. Comput. Graph. Stat.* 5, 299–314.
- Lehmkuhl, J.F., Gould, L.E., Cázares, E., Hosford, D.R., 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. *For. Ecol. Manage.* 200, 49–65.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling – Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, New York.
- Maser, C., Anderson, R., Bull, E.L., 1981. Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation. *Murrelet* 62, 54–55.
- Maser, C., Maser, Z., 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Nat.* 48, 358–369.
- Maser, C., Maser, Z., Witt, J.W., Hunt, G., 1986. The northern flying squirrel: a mycophagist in south western Oregon. *Can. J. Zool.* 64, 2086–2089.
- Mazerolle, M.J., 2011. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.17. <http://CRAN.R-project.org/package=AICcmodavg>.
- McComb, W.C., Noble, R.E., 1981. Microclimate of nest boxes and natural cavities in bottomland hardwoods. *J. Wildl. Manage.* 45, 284–289.
- McDonald, L., 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. In: Stelfox, J.B. (Ed.), *Relationships Between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta*. Alberta Environmental Centre (AECV95-R1)/Canadian Forest Service, Vegreville/Edmonton, pp. 227–240.
- Menzel, J.M., Ford, W.M., Edwards, J.W., Terry, T.M., 2006. Home range and habitat use of the Vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA. *Oryx* 40, 204–210.
- Mowrey, R.A., Zasada, J.C., 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. In: Mechan, W.R., Merrell, T.R.J., Hanley, T.A. (Eds.), *Fish and Wildlife Relationships in Old-growth Forests: Proceedings of the Symposium, Juneau, Alaska, April 1982*. American Institute of Fishery Research Biologists, Morehead city, pp. 351–356.
- Odum, R.H., Ford, W.M., Edwards, J.W., Stihler, C.W., Menzel, J.M., 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. *Biol. Cons.* 99, 245–252.
- Patterson, J.E.H., Malcolm, J.R., 2010. Landscape structure and local habitat characteristics as correlates of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus* occurrence. *J. Mammal.* 91, 642–653.
- Pyare, S., Longland, W.S., 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Can. J. Forest Res.* 32, 1016–1024.
- Pyare, S., Smith, W.P., Nicholls, J.V., Cook, J.A., 2002. Diets of northern flying squirrels, *Glaucomys sabrinus*, in Southeast Alaska. *Can. Field Nat.* 116, 98–103.
- Ransome, D.B., Sullivan, T.P., 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *J. Mammal.* 85, 206–215.
- Ritchie, L.E., Betts, M.G., Forbes, G., Vernes, K., 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *For. Ecol. Manage.* 257, 1920–1929.
- Robitaille, A., Saucier, J.-P., 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec, Sainte-Foy.
- Smith, W.P., 2007. Ecology of *Glaucomys sabrinus*: Habitat, demography, and community relations. *J. Mammal.* 88, 862–881.
- Smith, W.P., Nichols, J.V., 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. *J. Mammal.* 84, 1044–1058.
- Stapp, P., Pekins, P.J., Mautz, W.W., 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Can. J. Zool.* 69, 2548–2555.
- Trudeau, C., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2011. Site occupancy and cavity use by the northern flying squirrel in the boreal forest. *J. Wildl. Manage.* 75, 1646–1656.
- Visser, S., Maynard, D., Danielson, R.M., 1998. Response of ecto- and arbuscular mycorrhizal fungi to clear-cutting and the application of chipped aspen wood in a mixedwood site in Alberta, Canada. *Appl. Soil Ecol.* 7, 257–269.
- Weigl, P.D., 1978. Resource overlap, interspecific interactions and the distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*. *Am. Midl. Nat.* 100, 83–96.
- Weigl, P.D., Knowles, T.W., Boynton, A.C., 1992. The Distribution and Ecology of the Northern Flying Squirrel, *Glaucomys sabrinus coloratus*, in the Southern Appalachians. North Carolina Wildlife Resources Commission, Raleigh.
- Weigl, P.D., 2007. The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge. *J. Mammal.* 88, 897–907.

- Wells-Gosling, N., Heaney, L.R., 1984. *Glaucomys sabrinus*. Mammalian species No. 229, pp. 1–8.
- Wheatley, M., 2007. Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. *Northwest Sci.* 81, 265–273.
- Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., Boutin, S., 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. *J. Appl. Ecol.* 42, 577–586.
- Witt, J.W., 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. *J. Mammal.* 73, 921–929.