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Sciurid Habitat Relationships in Forests Managed Under Selection and Shelterwood Silviculture in Ontario

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Abstract

Although partial forest harvesting is practiced over large areas, managers know little about its impacts on sciurid rodents, particularly on northern (*Glaucomys sabrinus*) and southern flying squirrels (*G. volans*) in the northeastern United States and Canada. We examined habitat relationships of sciurid rodents (northern flying squirrels, southern flying squirrels, red squirrels [*Tamiasciurus hudsonicus*], and eastern chipmunks [*Tamias striatus*]) at 2 spatial scales in managed and unmanaged coniferous and hardwood forests of Algonquin Provincial Park, Ontario, Canada. We live-trapped rodents in 26 northern hardwood stands and in 16 white pine (*Pinus strobus*) stands from 2002 to 2004. Northern flying squirrel and red squirrel densities were significantly lower in recently harvested (3–10 yr since harvest) shelterwood stands than in unmanaged stands. In contrast, southern flying squirrel densities were higher in selection-harvested stands than in old-forest areas. The densities of northern flying squirrels and red squirrels had a strong relationship with the density of large spruce (*Picea* sp.) and hardwood trees and snags in conifer sites. Southern flying squirrel numbers had a positive association with the density of mast trees at the landscape level but not at the stand level in hardwood forests. Eastern chipmunk density had a positive correlation with the volume of old downed woody debris and the stems per hectare of declining trees. We recommend forest managers retain more large spruce and hardwood trees to mitigate the impacts of shelterwood harvesting on northern flying squirrels and red squirrels, and that they maintain high mast availability at the landscape level to ensure the persistence of southern flying squirrels. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1735–1745; 2006)

Key words

eastern chipmunk, *Glaucomys sabrinus*, *Glaucomys volans*, habitat use, northern flying squirrel, Ontario, partial harvesting, red squirrel, southern flying squirrel, stepwise regression, *Tamias striatus*, *Tamiasciurus hudsonicus*.

Many jurisdictions in North America, including Ontario, Canada, have selected flying squirrels (*Glaucomys* spp.) as indicators of sustainable forest management practices. This designation has resulted in a relatively large body of research on these and other tree squirrels in landscapes managed under clearcut logging (Rosenberg and Anthony 1992, Witt 1992, Carey 1995, 2000, Martin and Anthony 1999, Cote and Ferron 2001). However, partial harvesting techniques, such as selection and shelterwood logging, have received less attention. These are common silvicultural techniques employed in temperate mixedwood forests in northeastern Northern America. In these systems, forest operators remove a portion of the overstory at relatively shorter intervals (approx. 20 yr), creating a more frequent, but less intensive disturbance regime, than under clearcut logging. The effects of partial harvesting on canopy-dwelling organisms are likely to differ from those resulting from clearcutting because partial harvesting maintains a relatively closed-canopy mature forest throughout the harvest cycle. Unfortunately, only 2 studies have examined the effects of partial harvesting (shelterwood harvesting) on flying squirrels (Waters and Zabel 1995, Taulman et al. 1998). These studies found that relatively high harvest intensities (<10 m²/ha residual basal area) negatively affected flying squirrel populations. Researchers have not examined the effects of

selection harvesting systems in hardwood forests, which typically leave greater residual basal areas than shelterwood logging.

Although partial harvesting systems retain canopy cover on sites, impacts on tree squirrel populations may manifest through other logging-induced changes in forest structure. Partial harvesting typically involves a reduction in the abundance of diseased and dead trees (McComb and Lindenmayer 1999, McGee et al. 1999, Costello et al. 2000) and often results in more homogenous forest structure, with reduced tree density and size (Costello et al. 2000). These changes may be important for arboreal mammals (Gerrow 1996, Carey 2000) and could result in negative effects for cavity nesters (Imbeau et al. 2001).

Most past studies on sciurids have only considered local (site-level) effects; however, organisms may demonstrate different responses to the same factor at different scales (Wiens 1989). Studies in fragmented landscapes suggest that flying squirrels may be sensitive to area effects (Nupp and Swihart 2000) and indicate that large clearcuts may act as barriers to dispersal and movement (Bendel and Gates 1987). Taulman (1999) found that flying squirrels nested in adjacent unharvested forest following partial harvesting, suggesting that the amount and configuration of unharvested stands might modulate flying squirrel responses to forest harvesting. In concert, these studies raise the possibility that local responses to forest harvesting might,

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in part, reflect harvest-induced changes at the broader landscape (i.e., changes in the amount and configuration of primary habitats).

Four squirrel species occur in central Ontario: southern flying squirrels (*Glaucomys sabrinus*), northern flying squirrels (*G. volans*), eastern chipmunks (*Tamias striatus*), and red squirrels (*Tamiasciurus hudsonicus*). Southern flying squirrels and eastern chipmunks are most common in hardwood forests (Sonenshine and Levy 1981, Snyder 1982), whereas northern flying squirrels and red squirrels are typically associated with coniferous forest (Obbard 1987, Gerrow 1996). Both flying squirrel species tend to be associated with older forests or second-growth stands with old-growth legacies (large-diam downed woody debris, snags, and tall trees; Bendel and Gates 1987, Witt 1992, Taulman et al. 1998, Carey 2000). Mast availability also strongly influences southern flying squirrels (Weigl et al. 1999), as they subsist solely on stored mast over the winter. Eastern chipmunks show highest abundances in sites with high understory stem densities (Bennett et al. 1994, Zollner and Crane 2003). Red squirrel populations are associated with areas of high conifer seed production (Kemp and Keith 1970) and are more abundant in unharvested forests than in clearcut areas (Obbard 1987).

We investigated the effects of 2 partial harvesting systems (selection and shelterwood harvesting) on squirrel populations (particularly flying squirrels), and we examined effects at both the site and landscape levels. Foresters implement these 2 harvesting systems to create suitable conditions for the regeneration and growth of desirable timber species. We examined correlations between squirrel densities and various habitat features, including the densities of snags and diseased trees. We predicted that cavity-nesting squirrel species (both flying squirrel species and red squirrels) would respond negatively to logging at both scales, with the level of response proportional to harvesting intensity. In contrast, we expected eastern chipmunk density to be highest in harvested stands because of greater understory development. We also predicted southern flying squirrel densities to show a positive relationship with increasing mast tree density. We expected northern flying squirrel and red squirrel densities to show a positive relationship with increasing amounts of conifers in stands, whereas we expected southern flying squirrel and eastern chipmunk densities to demonstrate the reverse.

Study Area

We conducted our study in Algonquin Provincial Park in central Ontario, which was one of the largest protected areas in southern Canada, encompassing nearly 775,000 ha. Forest cover was contiguous and road density is low. The west side of the park (45°35'N, 78°30'W) sat on the Algonquin dome (elevation = 320–400 m), an area of relatively cold winters and high precipitation (average Dec–Feb temp = –10° C; annual precipitation = 983 mm). Sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), and American beech

(*Fagus grandifolia*) dominated the forest cover. The forest was mature to old, with an average age of 126 years (as estimated from aerial photo-based Forest Resource Inventories [FRI]; Ontario Ministry of Natural Resources, unpublished data). The east side of the park (45°53'N, 77°44'W) was lower in elevation (130–180 m), characterized by drier, nutrient-poor, sandy soils (average Dec–Feb temperature = –11°C and annual precipitation = 813.7 mm) along a glacial outwash plane (Chambers et al. 1997). White and red pines (*Pinus strobus* and *Pinus resinosa*) and mixed pine–trembling aspen (*Populus tremuloides*) forest dominated the area. Sugar maple, white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and large-tooth aspen (*Populus grandidentata*) were common associates. The east-side forest was somewhat younger, with an average age of 96 years.

The province of Ontario established Algonquin Provincial Park as a multiple-use park in 1893, and logging continues to the present. Managers use single-tree selection to manage hardwood forests on the west side (Ontario Ministry of Natural Resources [OMNR] 1998a). Every 20–25 years logging crews enter stands and remove approximately one-third of the overstory basal area in a pattern that produces single- and multiple-tree canopy gaps. Foresters use the uniform shelterwood silvicultural system to manage the white pine forest on the east side of Algonquin Park (OMNR 1998b). Here, logging crews remove the overstory in a series of 3–4 cuts at approximately 20-year intervals to encourage the development of an even-aged cohort of pine regeneration in the shade of the residual overstory. As both shelterwood and selection harvesting only became prevalent in the 1970s, most areas have only undergone 1–2 harvest cycles. Under the shelterwood system, pine stands have typically only received seeding or first removal cuts. Pileated woodpecker (*Dryocopus pileatus*) guidelines address the retention of microhabitat features (cavity trees and snags) implemented for both silvicultural systems in Ontario (Naylor et al. 1996). These guidelines mandate the retention of a minimum of 6 cavity trees ≥ 25 cm diameter at breast height (dbh)/ha. The park has set aside unlogged reserves where no harvesting has occurred in several decades. However, during the late 19th and early 20th centuries, loggers high-graded much of the park, especially for white pine.

Methods

Sampling Sites

We conducted fieldwork for 3 years (2002–2004) from 1 May to 31 August, during which time we live-trapped 42 grids: 26 in hardwood stands on the west side of the park and 16 in white pine stands. In the western hardwood stands, we selected 3 logging histories for study: old forest (defined as stands with no known history of logging after 1975), recent selection cuts (defined as stands harvested on average 5 yr ago [range: 3–10 yr]), and old selection cuts (defined as stands cut on average 15 yr ago [range: 13–18 yr]). Many of the old-forest sites were in areas unlogged

Table 1. Variables used in a priori habitat model building for northern and southern flying squirrels, eastern chipmunks, and red squirrels at site and landscape scales in logged and old hardwood and pine forest sites in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Scale	Species	No. of models	Variables ^a
Hardwood			
Site	Southern flying squirrel	15	Year, BA, Mast ≥ 25 , Conifer, Declin ≥ 25
Landscape	Southern flying squirrel	15	LMast, LAverBA, LConifer
Site	Northern flying squirrel	15	CanClos, Conifer, Spruce ≥ 25 , Snags, DWD ≥ 25
Landscape	Northern flying squirrel	6	LAverBA, LConifer, LSpruce
Site	Eastern chipmunk	15	Year, Conifer, Declin ≥ 25 , Understory, DWD ≥ 25 , DWDdc45
Landscape	Eastern chipmunk	4	LAverBA, LMast, LConifer
Site	Red squirrel	15	CanClos, Conifer, Spruce ≥ 25 , Snags, DWD ≥ 25
Landscape	Red squirrel	8	LAverBA, LConifer, LSpruce
Pine			
Site	Southern flying squirrel	21	BA, Conifer, Hardwd, Hwd ≥ 25 , Mast ≥ 25 , Snags ≥ 25
Landscape	Southern flying squirrel	8	LAverBA, LMast, LMixed
Site	Northern flying squirrel	21	CanClos, Hwd ≥ 25 , Spruce ≥ 25 , Snags ≥ 25 , DWD ≥ 25
Landscape	Northern flying squirrel	4	LAverBA, LSpruce, LAreaCut
Site	Eastern chipmunk	15	Year, Hardwd, Conifer, Snags ≥ 25 , Hunderstory, DWDdc1–3
Landscape	Eastern chipmunk	4	LAverBA, LMast, LConifer
Site	Red squirrel	10	Year, Hwd ≥ 25 , Spruce ≥ 25 , Snags ≥ 25 , DWD ≥ 25
Landscape	Red squirrel	9	LSpruce, LAreaCut, LMixed

^a See text for definition of habitat variables.

since the 1950s. Average forest age in the 3 logging histories (from FRI data) was 148, 142, and 135 years, respectively, and average basal area was 30.98 m²/ha (SE = 1.43), 18.96 m²/ha (SE = 1.16), and 20.65 m²/ha (SE = 0.82), respectively. In addition, within each logging history we attempted to systematically sample grids from a diverse array of mast and conifer compositions. We defined mast trees as those producing mast (both hard and soft mast; American beech, red oak [*Quercus rubra*], and black cherry [*Prunus serotina*]). Specifically, we selected approximately equal numbers of stands where the forest composition was 1) sugar maple–dominated, 2) mixed sugar maple–beech stands, or 3) mixed sugar maple–conifer stands. The dominant conifer species in hardwood stands was eastern hemlock, with smaller amounts of white spruce, balsam fir, and eastern white cedar (*Thuja occidentalis*).

In the eastern pinelands, we only sampled old-forest white pine stands and recent (3- to 10-yr-old) pine shelterwood cuts. Average FRI-based ages of both stand types was 100 years, and average basal areas were 30.68 m²/ha (SE = 1.28) and 20.01 m²/ha (SE = 1.79), respectively.

Sciurid Trapping

We sampled 10 grids in 2002, an additional 26 in 2003, and an additional 6 in 2004. We trapped all grids for 5 consecutive nights twice per summer, for a total of 10 trap-days/grid, with an interval of 4–7 weeks between trapping sessions. We attempted to sample recent cuts, old cuts, and old-forest sites equally in each trap session. For all grids, the average nearest neighbor distance between grids was 2.1 km (range: 0.6–13.6 km).

We used different trapping methodology in 2002 and in 2003–2004. In 2002, following Carey et al. (1991), we sampled each site using a 9 × 9 grid with 40-m spacing. We established 6 grids in hardwood stands (2 old forest, 2 recent cut, and 2 old cut), and 4 in white pine (2 old forest and 2 recent cut). We set 2 traps at every station, one attached to a

tree at 1.5 m in height and one on the ground. We placed tree traps on top of 2 large nails and secured them with an elastic cord. We set extra-large Sherman traps (10.2 × 11.4 × 38.1 cm) in the trees and standard-sized Sherman traps (5.1 × 6.4 × 22.9 cm) on the ground. We baited traps with a peanut butter and oats mixture and a slice of apple.

We modified this method in 2003–2004 for several reasons. First, we found that even within a treatment type, sciurid densities varied considerably among grids. Therefore, we increased replication of our trapping grids. In order to trap more grids, given a limited trap supply and limited person-power, we decreased the grid size. Second, because ground traps contributed little to captures of tree squirrels, we used only one extra-large Sherman tree trap per grid station. Finally, we changed our baiting regime due to extensive black bear (*Ursus americanus*) depredation: we used soaked, unshelled sunflower seeds and a slice of apple inside the trap, and peanut butter smeared on the tree near the trap door. In 2003, we live-trapped 18 grids in hardwood sites (6 old forest, 6 recent cut, and 6 old cut) and 8 in white pine sites (5 old forest and 3 recent cut). Twenty-three grids were small (4 × 9) with 40-m spacing and 3 were larger (either 6 × 11 or 8 × 9). We established the large grids in support of radiotelemetry studies (Holloway 2006). We live-trapped 6 sites in 2004, consisting of 2 old-forest white pine stands (4 × 9 grids), 2 recent shelterwood cuts (4 × 9 grids), and 2 old-forest hardwood grids (6 × 11 grids).

Habitat Measurements

Site-level measurements.—We used prism sweeps (basal area factor = 2) to quantify forest composition and structural characteristics at each of the 42 sites. In the sweeps, we measured all trees and snags with dbh above 10 cm and identified them to species. We made prism sweeps at 4–5 randomly selected stations/grid line for a total of 16–36 sweeps/grid, depending on grid size. We noted live trees as declining if more than one-half of the canopy showed signs

Table 2. Mean densities (min. no. known alive/ha \pm SE) for northern and southern flying squirrels, eastern chipmunks, and red squirrels in logged and old hardwood and pine forest sites and ANOVA statistics comparing logging histories and sampling year in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Species	Recent cut $n = 8$, 7 ^a		Old cut $n = 8$ ^b		Old forest $n = 10$, 9 ^a		Logging history P^c	Year P
	Mean	SE	Mean	SE	Mean	SE		
Hardwood								
Southern flying squirrel	1.19	0.34	1.04	0.36	0.08	0.08	0.224	0.040
Northern flying squirrel	0.11	0.12	0.13	0.04	0.03	0.02	NA	NA
Eastern chipmunk	5.78	0.91	6.00	1.09	5.44	1.26	0.950	<0.001
Red squirrel	0.14	0.19	0.06	0.04	0.03	0.02	NA	NA
Pine								
Southern flying squirrel	0.23	0.07	NA	NA	0.20	0.06	0.814	0.444
Northern flying squirrel	0.09	0.07	NA	NA	0.44	0.08	0.012	0.400
Eastern chipmunk	4.85	1.20	NA	NA	3.23	0.80	0.120	0.009
Red squirrel	0.20	0.07	NA	NA	0.62	0.24	<0.001	<0.001

^a Sample sizes for hardwood and pine forests, respectively.

^b We did not sample old cut stands in pine forests.

^c We did not test northern flying squirrels and red squirrels in hardwood forests because of low captures.

of die-back or obvious fungal infection (presence of conks). We calculated the average stems per hectare of living conifer trees and hardwood trees and snags for all trees ≥ 10 cm dbh (Con, Hwd, and Snags, respectively) and for stems per hectare ≥ 25 cm dbh (Con ≥ 25 , Hwd 25, and Snags ≥ 25 , respectively), as well as total basal area (BA; m^2/ha) for each grid. Additionally, we calculated the stems per hectare ≥ 25 cm dbh for spruce trees, mast trees, and declining trees (Spruce ≥ 25 , Mast ≥ 25 , and Declin ≥ 25 , respectively). We measured percent canopy closure (CanClos) with a spherical densitometer, averaging 4 readings in each of the cardinal directions at each station. We estimated the volume of downed woody debris (DWD) using the line intercept technique. We ran a 60-m-long transect line at a random orientation for 4–9 randomly selected stations per grid depending on grid size, giving a total of 360–560 m of line intercept. For each item of DWD that intersected the line, we recorded the species (where possible), diameter, and decay class (see Maser et al. 1979). We calculated the volume of DWD using equations developed by Van Wagner (1968) for 1) all pieces of DWD > 10 cm dbh (m^3/ha ; DWD), 2) DWD ≥ 25 cm dbh (DWD ≥ 25), 3) recent decay class DWD (decay classes 1–3; DWDdc1–3), and 4) old decay class DWD (decay classes 4 and 5; DWDdc45). We counted the number of understory saplings (trees < 10 cm dbh and ≥ 1.0 m tall) in a 3-m-radius plot centered at the tree in which the trap was placed as a measure of understory stem density for all stems (Understory) and hardwood stems (Hunderstory). In total, we measured 17 habitat variables for analysis.

Landscape-level measurements.—We derived 7 landscape composition variables based on the digital FRI in an area extending 500 m beyond each trapping grid. In the absence of prior knowledge on the appropriate scale, we used 500 m because it corresponded to the mean maximum distance moved by radiocollared northern flying squirrels during the summer of 2004 (Holloway 2006). We derived 5 variables that measured the proportional area within each landscape buffer: 1) high mast abundance (mast tree species

composed $\geq 20\%$ of the overstory; LMast), 2) high conifer abundance (conifer tree species composed $\geq 30\%$ of overstory; LConifer), 3) high spruce abundance (spruce composed $\geq 20\%$ of the overstory; LSpruce), 4) high hardwood abundance (hardwood tree species composed $\geq 80\%$ of overstory; LHardwd), and 5) areas with mixed-forest composition (conifer tree species composed $\geq 20\%$ and $\leq 80\%$ of the overstory; LMixed). The remaining 2 variables we measured were the proportion of the area logged within the last 20 years (LAreaCut) and the average basal area (m^2/ha) of the forest in the surrounding buffer (LAverBA).

Data Analyses

Squirrel densities.—We estimated squirrel density as the minimum number known alive (MNKA) over the 2 trap sessions per grid divided by the effective trapping area of a grid. We calculated effective trap area as the grid area plus a buffer of one-half the mean maximum distance moved between recaptures for animals caught ≥ 2 times (102 m for southern flying squirrels [$n = 109$ recaptured individuals], 117 m for northern flying squirrels [$n = 52$], 49 m from eastern chipmunks [$n = 907$], and 107 m for red squirrels [$n = 51$]). We decided upon MNKA per hectare as the most appropriate estimator because the low number of recaptures between grid sessions would bias population density estimators (Krebs 1999). Additionally, MNKA per hectare estimates had a strong correlation with the Chapman-modified Lincoln–Peterson index ($r = 0.95$ for southern flying squirrels, $r = 0.99$ for northern flying squirrels, $r = 0.86$ eastern chipmunks, and $r = 0.98$ for red squirrels [all $P < 0.001$]). In 2002 and 2003, the proportion of animals recaptured between trap sessions was 0.58 and 0.50 for northern flying squirrels, and 0.24 and 0.27 for southern flying squirrels, respectively. We accounted for any potential effect of the reduction in grid size by including year effects. In addition, by controlling for interannual variation, we accounted also for biases due to methodological changes. Moreover, we attempted to sample all forest types and

Table 3. Mean (\pm SE) values for site-level habitat variables that differed among logged and old hardwood and pine forest sites in Algonquin Provincial Park, Ontario, Canada, 2002–2004. Variable units are the number of stems per hectare unless otherwise stated.

Habitat variable ^c	Recent cut $n = 8$, 7 ^a		Old cut $n = 8$ ^b		Old forest $n = 10$, 9 ^a		<i>P</i>
	Mean	SE	Mean	SE	Mean	SE	
Hardwood							
BA (m ² /ha)	19.0	1.2	20.7	0.8	31.0	1.4	<0.001
Conifer	13.1	7.7	11.5	5.9	39.9	8.4	0.020
Con ≥ 25	8.1	5.4	5.0	2.5	23.6	5.8	0.028
Hwd ≥ 25	54.5	3.8	62.4	5.0	70.4	4.0	0.044
Spruce ≥ 25	0.5	0.4	0.5	0.3	3.5	1.1	0.014
Snags	10.8	3.7	13.3	3.5	28.8	4.6	0.008
Snags ≥ 25	3.0	0.7	6.0	1.4	10.1	1.1	<0.001
Pine							
BA (m ² /ha)	20.0	1.8	NA	NA	30.7	1.3	<0.001
CanClos (%)	76.2	3.2	NA	NA	89.4	1.6	0.001
Conifer	153.8	21.5	NA	NA	229.3	25.4	0.047
Hwd ≥ 25	12.4	3.9	NA	NA	27.4	3.9	0.018
Spruce ≥ 25	3.2	1.0	NA	NA	8.1	2.1	0.080
Snags ≥ 25	4.7	1.1	NA	NA	11.1	2.0	0.022

^a Sample sizes for hardwood and pine forests, respectively.

^b We sampled old cut stands only in hardwood forests.

^c See text for definition of habitat variables.

logging histories evenly between years, and hence allow equal application of any biases among comparisons.

Habitat variable reduction and variance partitioning.—The various sciurid species tended to be more or less abundant in one forest type (hardwood or conifer), but uncommon in the other; hence, we undertook community analyses separately for hardwood and white pine sites. Because squirrel densities differed between trap years (see Table 1), we first partialled it out of the models. To examine species–habitat relationships, we performed partial redundancy analysis (RDA), which served to reduce the number of site-level habitat variables (some of which were highly correlated with each other). Initially, we entered the 17 site habitat variables into the RDA (see Habitat Measurements, above). We computed the statistical significance of each variable using Monte Carlo simulations and a forward selection routine (9,999 permutations). We sequentially removed variables that contributed little (highest non-significant *P*-value) until the inflation factor was <10 (ter Braak and Smilauer 1998). We retained 11 variables in the hardwood model and 9 in the white pine model.

We investigated the relative importance of site and landscape variables using variance partitioning (Borcard et al. 1992, Cushman and McGarigal 2004). This analysis measures the variation in a community matrix, explained independently and jointly by different sets of explanatory variables. We calculated the unique variation at each level (site and landscape) by partialling out (as a covariate) variation due to the other level. We performed all multi-variate analyses with CANOCO 4.5 for Windows (ter Braak and Smilauer 1998).

Individual species responses.—We plotted the density of each squirrel species against all habitat variables to ensure that assumptions of normality and homogeneity were satisfied and to check for the possibility of curvilinear relationships. We ln-transformed southern flying squirrel

densities in hardwood sites and red squirrel densities in pine sites to normalize the variance. We performed analysis of variance (ANOVA) with Bonferroni-corrected post hoc tests for each species to compare densities among years. Where a significant year effect existed ($P \leq 0.050$), we included it in all the following regression and ANOVA analyses. We analyzed the influence of logging history on squirrel density and habitat variables with ANOVA.

We used linear regression to develop sciurid habitat relationship, except in 2 instances (northern flying squirrels and red squirrels in hardwood sites) where densities were low and we therefore used logistic regression (on presence/absence). For all species, if a year effect was significant, we included it in all models. To develop site-level habitat models, we used 2 methods, stepwise regression and a priori selection of candidate variables followed by use of Akaike's Information Criterion (AIC; Burnham and Anderson 1998) to compare among models created from these candidate variables. In the former method, we used the site-level habitat variables remaining after the RDA forward selection routine. In the latter method, we picked 5–6 variables for each species that we reasoned to be most important based on relationships observed or hypothesized in the literature (listed in Table 1). From these candidate variables, we constructed all possible models of up to 3 terms and used AIC_c to compare among them. Specifically, we calculated the difference between the *i*th model and the minimum AIC_c (i.e., ΔAIC_c) and the Akaike weight (w_i) for each model.

To incorporate landscape-level variables into these analyses, we first forced the best site-level model into the analysis and then evaluated the value of the landscape variables in explaining additional variation in squirrel densities. We followed this hierarchical procedure for 2 reasons: 1) site-level variables proved to be more important than landscape-level variables in explaining squirrel captures

(see Results, below; see also Cushman and McGarigal 2004), and 2) in a forested landscape, we reasoned that a first-order model would incorporate local site features, whereas any landscape-level effects would be additive to these local effects. As before, we undertook both stepwise and AIC-based approaches. If results of the site-level AIC evaluation were equivocal—that is, ≥ 2 models were of approximately equal explanatory value—then we evaluated all combinations of these site models and landscape variables. For example, if 2 site-level models were equivalent, then in combination with 3 landscape variables, we evaluated 8 models (the 2 best site-level models plus 6 combinations of 1 site model plus 1 landscape variable). We performed all analyses with SPSS 11.0 (SPSS Inc., Chicago, Illinois).

Results

Over 3 summers we captured 274 individual southern flying squirrels, 83 northern flying squirrels, 1,709 eastern chipmunks, and 110 red squirrels during 28,548 trap-nights (21,091 grid-station nights). In general, small mammal populations were intermediate in abundance in 2002, high in 2003, and low in 2004. In hardwood sites, southern flying squirrel density was significantly lower in 2002 compared with 2003 (ANOVA $P = 0.044$; mean MNKA/ha [\pm SE] = 0.35 [0.15]), and 1.12 [0.20] for 2002 and 2003, respectively). We only analyzed grids sampled in 2002 and 2003 for southern flying squirrels because, remarkably, we did not capture a single individual in 2004. This dramatic crash in numbers appeared to be a widespread phenomenon across the far northern range of the species (Bowman et al. 2005). Similarly, eastern chipmunk density was significantly higher in 2003 than in 2002 or 2004 ($P < 0.001$; mean MNKA/ha [\pm SE] = 2.98 [0.55], 7.16 [0.63], and 0.90 [0.28] for 2002, 2003, and 2004, respectively). In pine stands, eastern chipmunk densities in 2004 were significantly lower than in 2002 and 2003 ($P = 0.048$; mean MNKA/ha [\pm SE] = 4.20 [1.51], 5.20 [0.88], and 1.16 [0.51] for 2002, 2003, and 2004, respectively). In contrast, red squirrel densities were significantly high in 2004, compared with densities in 2002 or 2003 ($P = 0.025$; mean MNKA/ha [\pm SE] = 0.33 [0.12], 0.17 [0.05], and 1.08 [0.46] for 2002, 2003, and 2004, respectively).

Partial harvesting appeared to have little effect on densities of southern flying squirrels or eastern chipmunks. Densities of both species were slightly higher in cut sites of both ages than in old-forest stands, although not significantly so for either the hardwood or the white pine stands ($P > 0.120$; Table 2). In pine sites, both northern flying squirrels and red squirrels had significantly higher densities in old-forest sites than in recent cuts (Table 2). However, there was a significant interaction between trap year and logging history ($P < 0.001$) for red squirrels because of especially high abundances in old-forest stands in 2004 compared with 2002 and 2003. We did not perform any analyses for northern flying squirrels or red squirrels in hardwood stands because of low captures.

In both hardwood and pine sites, logging history changed the habitat structure present (Table 3). In hardwood sites, 6 habitat variables were significantly higher in old-forest sites than in either age of cut sites: basal area, spruce stems/ha ≥ 25 cm dbh, total conifer stems per hectare, conifer stems/ha ≥ 25 cm dbh, total snag stems per hectare, and snag stems/ha ≥ 25 cm dbh. Stems per hectare of hardwood trees ≥ 25 cm dbh were significantly higher in old-forest stands than in recent cuts. In pine sites, 5 habitat variables were significantly higher in old-forest sites than in recently harvested sites: basal area, canopy closure, total conifer, hardwood stems/ha ≥ 25 cm dbh, and snags/ha ≥ 25 cm dbh. Although not significant, stems per hectare of spruce ≥ 25 cm dbh were greater in old-forest sites than in cut sites.

Habitat Associations

Habitat variable reduction.—Eleven habitat variables remained in the site-level hardwood data set after collinearity was reduced to acceptable levels: basal area, canopy closure, conifer density, hardwood density ≥ 25 cm dbh, spruce density ≥ 25 cm dbh, mast density ≥ 25 cm dbh, declining tree density ≥ 25 cm dbh, snag density, understory stem density ≤ 10 cm dbh, volume of DWD ≥ 25 cm dbh, and volume of old decay class DWD. The 9 habitat variables remaining in the pine habitat data set were canopy closure, conifer density, hardwood density, hardwood density ≥ 25 cm dbh, spruce density ≥ 25 cm dbh, mast density ≥ 25 cm dbh, snag density ≥ 25 cm dbh, hardwood understory density ≤ 10 cm dbh, and the volume of recent decay class DWD.

Variance partitioning: site and landscape habitat associations.—In the variance partitioning analysis, site-level factors were more important than landscape-level factors, accounting for nearly twice as much explained variance. The unique site-level variance accounted for 46.4% and 43.7% of the explained variance in the squirrel community (in hardwood and pine sites, respectively), whereas the landscape-level variance accounted for only 22.0% and 22.5%, respectively. The remaining variance (31.6% and 33.8%, respectively) represented joint and unexplained variance.

Species-specific habitat models.—The stepwise regression models compared favorably with those chosen through the AIC_c procedure (Tables 4, 5). We ranked them as the best or second best model in all pine sites; when they were second best, the ΔAIC_c value was ≤ 0.64 . In hardwood sites, in 6 of 7 instances the stepwise model was one of the best 3 models, with ΔAIC_c values of < 1.29 . The only discrepancy was the model for red squirrels in hardwood sites, with the best AIC_c model adding an additional term (snag stems/ha) in comparison to the stepwise model. As a result, below we describe in more detail the results of the stepwise regression analyses, except for red squirrels in hardwood sites, for which we describe the top-ranked AIC_c model instead.

In hardwood forest, southern flying squirrel densities had a negative correlation with several habitat variables, including basal area (Fig. 1b) and conifer stems per hectare ($r = -0.52$,

Table 4. The best 3 Akaike's Information Criterion adjusted for small sample size (AIC_c) models predicting densities for northern and southern flying squirrels, eastern chipmunks, and red squirrels at site and landscape scales in hardwood forest in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

Species ^a	Model rank	Variables ^b	ΔAIC _c	w _i	r ²	P
Site scale						
Southern flying squirrel	1	Year, Snags, Conifer	0.00	0.27	0.48	0.001
	2	Year, Snags, Mast ≥ 25	0.18	0.25	0.48	0.001
	3	Year, Snags ^{c,d}	0.94	0.17	0.51	<0.001
Northern flying squirrel	1	CanClos	0.00	0.17	0.04	0.369
	2	Spruce ≥ 25	0.33	0.15	0.03	0.488
	3	Conifer	0.67	0.13	0.07	0.710
Eastern chipmunk	1	Year, DWDdc45, Declin ≥ 25 ^{c,d}	0.00	0.54	0.64	<0.001
	2	Year, DWDdc45	1.79	0.22	0.59	<0.001
	3	Year, DWDdc45, Conifer	4.36	0.06	0.58	<0.001
Red squirrel	1	Spruce ≥ 25, Snags ^d	0.00	0.27	0.49	0.003
	2	Spruce ≥ 25 ^c	0.45	0.22	0.37	0.004
	3	Snags	1.72	0.11	0.32	0.009
Landscape scale						
Southern flying squirrel	1	Year, Snags, Conifer, LAverBA	0.00	0.20	0.56	0.001
	2	Year, Snags, LMast ^{c,d}	0.05	0.20	0.58	<0.001
	3	Year, Snags, LAverBA	0.32	0.17	0.51	0.001
Northern flying squirrel	1	LAverBA ^{c,d}	0.00	0.35	0.24	0.023
	2	LAverBA, LSpruce	1.03	0.21	0.16	0.205
	3	LAverBA, LConifer	1.64	0.15	0.20	0.134
Eastern chipmunk	1	Year, DWDdc45, Declin ≥ 25, LConifer	0.00	0.48	0.69	<0.001
	2	Year, DWDdc45, Declin ≥ 25 ^{c,d}	1.29	0.25	0.64	<0.001
	3	Year, DWDdc45, Declin ≥ 25, LAverBA	1.79	0.20	0.66	<0.001
Red squirrel	1	Spruce ≥ 25, LConifer	0.00	0.15	0.49	0.003
	2	Spruce ≥ 25, Snags ^d	0.01	0.15	0.49	0.003
	3	Spruce ≥ 25, Snags, LSpruce	0.27	0.13	0.58	0.003

^a Models for southern flying squirrels and eastern chipmunks, and those for northern flying squirrels and red squirrels were developed using linear and logistic regression, respectively.

^b See text for definition of habitat variables.

^c Best model predicted by stepwise linear/logistic regression.

^d We give parameter estimates for this model in text.

Table 5. The best 3 Akaike's Information Criterion adjusted for small sample size (AIC_c) models predicting densities for northern and southern flying squirrels, eastern chipmunks, and red squirrels at the site and landscape scales in pine forest in Algonquin Provincial Park, Ontario, Canada, 2002–2004.

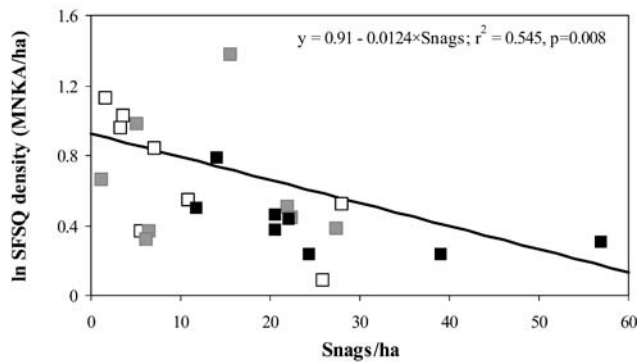
Species	Model rank	Variables ^a	ΔAIC _c	w _i	r ²	P
Site scale						
Southern flying squirrel	1	Hwd ≥ 25, Snags ≥ 25	0.00	0.32	0.53	0.014
	2	Mast ≥ 25 ^{b,c}	0.42	0.26	0.35	0.025
	3	Mast ≥ 25, Conifer	3.05	0.07	0.39	0.043
Northern flying squirrel	1	Spruce ≥ 25, Hwd ≥ 25, DWDdc13 ^{b,c}	0.00	0.53	0.75	<0.001
	2	Spruce ≥ 25, DWD ≥ 25	2.33	0.16	0.65	<0.001
	3	Spruce ≥ 25, Hwd ≥ 25	2.78	0.13	0.64	0.001
Eastern chipmunk	1	Year, Conifer ^{b,c}	0.00	0.30	0.55	0.002
	2	Year, Conifer, Hunderstory	1.02	0.18	0.60	0.003
	3	Year, Hunderstory	1.91	0.12	0.49	0.005
Red squirrel	1	Year, Spruce ≥ 25, DWDdc13	0.00	0.28	0.63	0.002
	2	Year, Snags ≥ 25 ^{b,c}	0.64	0.20	0.57	0.002
	3	Year, Spruce ≥ 25	1.29	0.15	0.56	0.002
Landscape scale						
Southern flying squirrel	1	Hwd ≥ 25, Snags ≥ 25	0.00	0.44	0.53	0.014
	2	Mast ≥ 25 ^{b,c}	0.42	0.36	0.35	0.025
	3	Mast ≥ 25, LAverBA	4.41	0.05	0.32	0.070
Northern flying squirrel	1	Spruce ≥ 25, Hwd ≥ 25, DWDdc13 ^{b,c}	0.00	0.79	0.75	<0.001
	2	Spruce ≥ 25, Hwd ≥ 25, DWDdc13, LMixed	4.33	0.09	0.74	0.001
	3	Spruce ≥ 25, Hwd ≥ 25, DWDdc13, LSpruce	5.12	0.06	0.73	0.001
Eastern chipmunk	1	Year, Conifer, LMast ^{b,c}	0.00	0.88	0.74	<0.001
	2	Year, Conifer	5.58	0.05	0.55	0.002
	3	Year, Conifer, LConifer	6.49	0.03	0.61	0.002
Red squirrel	1	Year, Snags ≥ 25, LAreaCut ^{b,c}	0.00	0.63	0.76	<0.001
	2	Year, Spruce ≥ 25, DWDdc13, LAreaCut	1.93	0.24	0.74	0.001
	3	Year, Spruce ≥ 25, DWDdc13	5.30	0.05	0.63	0.002

^a See text for definition of habitat variables.

^b Best model predicted by stepwise linear regression.

^c We give parameter estimates for this model in text.

(a)



(b)

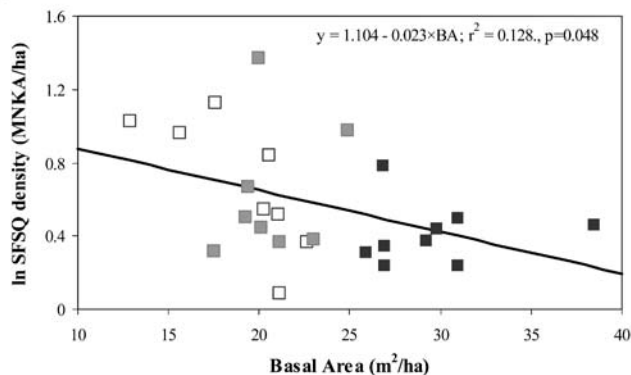


Figure 1. Southern flying squirrel (SFSQ) density in hardwood sites in Algonquin Provincial Park, Ontario, Canada, plotted against (a) snags/ha, and (b) basal area from summers 2002–2004. Black squares = old-forest sites, gray squares = old cuts, empty squares = recent cuts, and the solid line represents the linear regression line. We removed year effects by subtracting the year-specific deviation from the grand mean for both (a) and (b).

$P = 0.012$). Interestingly, highest densities had an association with sites with the lowest basal areas (range 12–20 m^2/ha). However, the best model predicting density had a negative relationship with total snags per hectare (Fig. 1a) and year: $y = 0.45 - [(1.24 \times 10^2) \times \text{Snags}] + (0.46 \times \text{Year})$. At the landscape level, a positive relationship with the area of high mast abundance was added to the model: $y = 0.32 - [(1.04 \times 10^2) \times \text{Snags}] + (0.45 \times \text{Year}) + (0.62 \times \text{LMast})$. Site-level habitat variables were poor predictors of northern flying squirrel density in the stepwise analysis, nor did any model fit the data well in the AIC_c comparison; all r^2 values explained $<8\%$ of the variance and P -values were ≥ 0.35 (Table 4). At the landscape level, the probability of northern flying squirrel occurrence was significantly greater in areas with larger basal area ($B_1 = 0.42$, where intercept = 0.24).

Eastern chipmunk density showed a positive relationship with year, the volume of old decay class DWD, and stems per hectare of declining trees ≥ 25 cm dbh: $y = -1.13 + (4.60 \times \text{Year}) + [(5.22 \times 10^2) \times \text{DWDdc45}] + (0.16 \times \text{Declin} \geq 25)$. Chipmunk density appeared to have a non-linear relationship to the presence of canopy gaps, whether natural or created by logging activity; a significant unimodal

(quadratic) relationship with canopy closure was shown ($r^2 = 0.32$, $F = 4.79$, $P = 0.010$ [$P = 0.029$ for the quadratic term]). As in the above stepwise model, we included a year ($P = 0.013$) term in the model for chipmunks. The probability of red squirrel presence at the site level was best predicted by a positive relationship with spruce stems per hectare ($B_1 = 0.51$) and snags ≥ 25 cm dbh ($B_2 = 0.07$, where intercept = -2.77). The addition of landscape variables did not significantly improve models predicting eastern chipmunk density or red squirrel presence.

In pine forests, southern flying squirrel densities had a positive relationship with the stems per hectare of mast trees ≥ 25 cm dbh: $y = 0.15 + [(1.36 \times 10^2) \times \text{Mast} \geq 25]$. Northern flying squirrel density had a positive correlation with the stems per hectare of snags ≥ 25 cm dbh ($r = 0.66$, $P = 0.003$) and a negative correlation with the area cut on the landscape ($r = -0.67$, $P = 0.002$). The best regression model for northern flying squirrels had a positive relationship with the stems per hectare of spruce and hardwood trees ≥ 25 cm dbh, and a negative association with the volume of recent DWD: $y = 0.13 + [(2.75 \times 10^2) \times \text{Spruce} \geq 25] + [(7.04 \times 10^3) \times \text{Hwd} \geq 25] - [(4.34 \times 10^3) \times \text{DWDdc13}]$. Old-forest sites contained the highest densities of large spruce (Fig. 2). For both flying squirrel species the inclusion of landscape variables did not significantly improve the explanatory power of the models. Chipmunks demonstrated a negative relationship with total conifer stems per hectare and year at the site level: $y = 8.46 - (3.60 \times \text{Year}) - [(1.85 \times 10^2) \times \text{Conifer}]$, and a positive relationship with the area of high mast abundance was added to the model, $y = 6.67 - (2.59 \times \text{Year}) - [(1.46 \times 10^2) \times \text{Conifer}] + (12.57 \times \text{LMast})$ at the landscape level. Red squirrels showed a positive relationship with snags/ha ≥ 25 cm dbh and year the stand level: $y = -1.39 \times 10^2 + (0.38 \times \text{Year}) + [(2.73 \times 10^2) \times \text{Snag} \geq 25]$, and a negative relationship with the area cut in the last 20 years at the landscape level, $y = 0.32 + (0.50 \times \text{Year}) + [(5.80 \times 10^3) \times \text{Snag} \geq 25] - (0.49 \times \text{LAreaCut})$.

Discussion

Contrary to our initial expectations, southern flying squirrels demonstrated little evidence of a negative response to partial harvesting. Southern flying squirrel densities were in fact higher in logged sites than in old-forest areas. High use of relatively open forest structure, such as that found in partial cuts, is not unprecedented for this species (Sonenshine and Levy 1981). We speculate that abundance of food, particularly hard and soft mast, may be higher in selection-harvested stands than in old-forest sites. Researchers have never examined the effect of selection logging on mast production in American beech; however, the production of oak mast and soft mast from understory shrubs was greater in partially harvested stands (5 yr postharvest) than in uncut areas in Arkansas (Perry et al. 1999, Perry and Thill 2003). Here, mast production was highest in areas with the most intense harvesting (group selection and shelterwood cuts), which supports the negative relationship we observed between southern flying squirrel

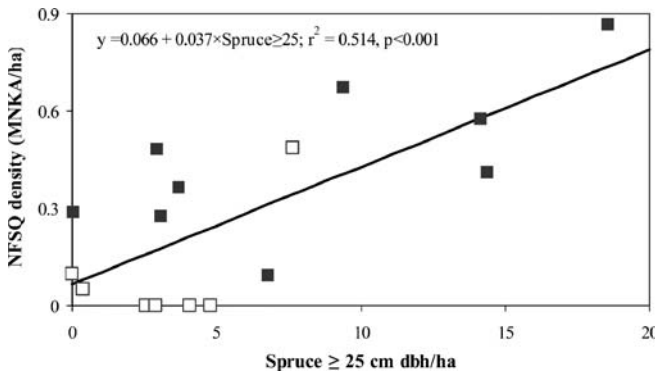


Figure 2. Northern flying squirrel (NFSQ) density in white pine sites in Algonquin Provincial Park, Ontario, Canada, plotted against stems/ha of spruce ≥ 25 cm diameter at breast height (dbh) from summers 2002–2004. Black squares = old-forest sites, empty squares = recent cuts, and the solid line represents the linear regression line.

density and basal area. However, our study measured density, not reproductive success or survival. Taulman et al. (1998) found that predation on radiocollared animals was more frequent in disturbed habitats; similarly, in a concurrent radiotelemetry study, we found that the loss of radiocollared animals was 2.5 times greater in selection cuts than in old-forest stands (Holloway 2006). Open stand structure may lead to easier movement, not only by flying squirrels, but also by their owl predators.

The relationship we observed for southern flying squirrels and snags in hardwood forest was the reverse of our initial predictions. The negative relationship this species showed with snags suggests southern flying squirrels are adaptable in regards to den use. In fact, cavities in live declining trees were the most common den substrate used by southern flying squirrels in our study area (Holloway 2006), and the density of declining trees did not differ between old-forest and cut sites. Mast density is a key habitat feature for southern flying squirrels (Sonenshine and Levy 1981, Bendel and Gates 1987, Taulman et al. 1998), but the availability of this resource appears to influence the spatial scale at which mast is most critical. In suboptimal habitat (mixed conifer–hardwood), mast density was important directly at the local site level. In more suitable hardwood stands, similar to those in Fridell and Litvaitis (1991), we observed a positive relationship between southern flying squirrel density and mast availability on the landscape. Flying squirrels are mobile animals, and presumably move into mast stands during the fall, but a supply of mast must exist either within an animal's home range or in the surrounding vicinity for overwinter survival. Low mast abundance the preceding fall, coupled with cold winter conditions, most parsimoniously explains the crash of the southern flying squirrel population at our study site in 2004 (Bowman et al. 2005).

Chipmunks were ubiquitous across our study sites and partial harvesting had little discernable effect on their populations. Declining trees, dense understory cover, and downed woody debris are important habitat features for eastern chipmunks (Bennett et al. 1994, Mahan and Yahner

1996, Zollner and Crane 2003, this study). Chipmunks use fallen logs and branches as travel runways, while high shrub density provides both protective cover and abundant food. These features in our study area were most abundant in sites with intermediate levels of canopy closure (particularly declining trees). Intermediate canopy closure shows a link to sites with intermediate gap sizes created by less intensive (or older) logging activity, or the mortality of overstory trees, which results in mosaic of gaps in old-forest stands.

This study affirmed the link between high densities of northern flying squirrels and red squirrels and older, undisturbed forests (Carey et al. 1999). Characteristics associated with old-forest areas (high snag density and basal area) were important predictors for these 2 species. Shelterwood harvesting resulted in significantly lower densities of standing trees, spruce, hardwoods, snags, and canopy closure, leading to an overall reduction in structural complexity. The loss of these features under shelterwood harvesting may be problematic for both northern flying squirrels and red squirrels because high structural diversity and overstory cover are associated with decreased predation risk (Vahle and Patton 1983, Carey 2000). Moreover, these changes will affect the availability of nesting habitat because northern flying squirrels and red squirrels commonly use hardwood trees and snags as nests in central Ontario (Obbard 1987, Holloway 2006). Finally, the removal of trees increases the habitat suitability for understory species such as eastern chipmunks at the expense of the arboreal sciurids.

The abundance and availability of foraging resources also may be a critical consideration for these species (Kemp and Keith 1970, Ransome and Sullivan 1997, Carey et al. 1999). Hypogeous fungi are major dietary items for northern flying squirrels and red squirrels, and both species act as primary dispersers of fungal spores (Maser et al. 1986, Vernes et al. 2004). Spruce density was a key habitat predictor for both species, supporting previous research both in the boreal forest and in the southern Appalachians (Fancy 1980, Payne et al. 1989, Cotton and Parker 2000, Ford et al. 2004). Spruce is important directly as a seed source (a major diet item for red squirrels; Kemp and Keith 1970) and indirectly because of its mycorrhizal associations with fungi. In the Appalachians, the presence of truffles was associated with red spruce (*Picea rubra*) abundances (Loeb et al. 2000), and the frequency of ectomycorrhizal fungi occurrence in red spruce stands was double that found in adjacent hardwood stands (Bills et al. 1986). In particular, the most common fungal genus, *Elaphomyces*, found in the Appalachians (Loeb et al. 2000) and in northern flying squirrel feces in this study (Holloway 2006), was associated with spruce (*Picea* sp.) and fir (*Abies* sp.) trees.

In addition to a reduction in spruce and snag densities, shelterwood harvesting may also decrease the microclimatic suitability in stands for fungi. Hypogeous fungal productivity is associated with old-growth features (such as a well-developed organic soil layer, abundant coarse woody debris, and the presence of large, old trees; North et al. 1997). The

abundance of flying squirrels and hypogeous fungi was significantly lower in shelterwood stands than in uncut old-growth stands in California (Waters and Zabel 1995). Beyond the local site-level effects of harvesting, we observed additive effects of logging on the surrounding landscape. This suggests that the interspersed of large harvested and unharvested blocks on the landscape may be important to ensure the persistence of red squirrels and northern flying squirrels.

We developed habitat models using both stepwise regression and models developed a priori. Stepwise regression has fallen into disfavor recently because of misuse of the technique (excessive data dredging), its reliance on arbitrary cutoffs (e.g., $\alpha = 0.05$), and model over-fitting (Burnham and Anderson 1998, Stephens et al. 2005). However, models developed a priori may be equally prone to problems when considering a large number of potential variables (i.e., model dredging; Stephens et al. 2005). Thoughtful model development is critical in both stepwise techniques and a priori model building. If researchers take care in developing models, we believe stepwise regression is a powerful tool and should continue to be used in habitat studies. Habitat studies often lead to the development of large sets of potential variables, and the inclusion of novel variables can lead to new insights.

Management Implications

Shelterwood harvesting decreased the density of large spruces and hardwoods below critical thresholds for north-

ern flying squirrels and red squirrels. In order to mitigate the structural changes resulting from logging, we recommend managers retain at least 4.5 spruce trees/ha ≥ 25 cm dbh and 15 hardwood trees/ha ≥ 25 cm dbh in white pine stands (levels predicted to maintain northern flying squirrel densities in shelterwood stands at 50% of their mean level in old-forest areas). The abundance of mast trees on the landscape appears to limit southern flying squirrel density. In hardwood stands, we recommend foresters maintain a minimum of 17% of the landscape area (to maintain 80% of their mean level in hardwood forests) with high mast tree abundance (i.e., where $\geq 20\%$ of the stand composition is a mast tree).

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