Red Squirrels Snags
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Research Article

# 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 $m^2$/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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*Table 3.* Mean (± 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] | | |
|---|---|---|---|---|---|---|---|
| | Mean | SE | Mean | SE | Mean | SE | $P$ |
| 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 | 6.1 | 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.

11.1 → 4.7 = −58%

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 nonsignificant $P$-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 multivariate 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., $\Delta AIC_c$) 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.

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 interspersion 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 northern 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 $\geq$25 cm dbh and 15 hardwood trees/ha $\geq$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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*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 $m^2$/ha (SE = 1.43), 18.96 $m^2$/ha (SE = 1.16), and 20.65 $m^2$/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 $m^2$/ha (SE = 1.28) and 20.01 $m^2$/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 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] | $\Delta AIC_c$ | $w_i$ | $r^2$ | $P$ |
|---|---|---|---|---|---|---|
| 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 | 0.46 | 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 | 0.56 | <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] | $\Delta AIC_c$ | $w_i$ | $r^2$ | $P$ |
|---|---|---|---|---|---|---|
| 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 | 0.68 | 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.

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