

Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska

V.J. Bakker and K. Hastings

Abstract: Northern flying squirrel (*Glaucomys sabrinus*) dens are reportedly associated with features characteristic of older forests, and den availability is a potential limiting factor in younger forests. We assessed den sites used by northern flying squirrels in southeastern Alaska, where we expected den-site selection to differ from more southerly forests, owing to increased thermal stress but reduced predation and competition. We located 27 squirrels in 76 dens and compared den trees with 1875 matched random trees. Most dens ($\geq 73\%$) were in cavities and 21% were at heights of ≤ 3 m. This high rate of cavity use, including cavities low in the bole, likely reflects the importance of weatherproof dens in this cool wet region. Northern flying squirrels preferentially used trees with indicators of cavity presence, selecting for snags and for larger diameter trees with bole entries, conks, abundant mistletoe, and dead tops. Although cavity availability is probably not limiting populations in this region currently, cavity-supporting trees would be one of the last elements of old-growth forests to develop in intensively logged stands. Retention of small groups of large snags and live trees exhibiting evidence of disease or physical defects would ensure availability of denning structures after logging.

Résumé : Les repaires des grands polatouches (*Glaucomys sabrinus*) sont, semble-t-il, associés à des structures caractéristiques des forêts âgées et leur disponibilité peut être un facteur limitant dans les forêts plus jeunes. Nous avons évalué les sites utilisés par les polatouches pour établir leur repaire dans le sud-est de l'Alaska et nous nous attendions à ce que la sélection des sites à cet endroit diffère de celle qui existe dans les régions plus australes à cause du stress thermique plus grand ainsi que de la prédation et de la compétition réduites. Nous avons localisé 27 polatouches dans 76 repaires et comparé les arbres à repaires à 1875 arbres équivalents choisis au hasard. La plupart des repaires ($\geq 73\%$) sont aménagés dans des cavités et 21 % ont été trouvés à des hauteurs ≤ 3 m. La fréquence élevée d'utilisation des cavités, y compris les cavités basses sur les troncs, reflète probablement l'importance d'avoir des repaires à l'épreuve des intempéries dans cette région froide et humide. Les grands polatouches cherchent surtout les arbres qui comportent des signes de la présence de cavités, recherchant les enchevêtrements et les arbres de gros diamètre avec des ouvertures sur le tronc, des faux carpophores, du gui en abondance et des cimes mortes. Bien que la disponibilité des sites ne semble pas être un facteur limitant actuellement dans cette région, les arbres à cavités risquent de compter parmi les derniers éléments de vieille forêt à se développer dans les boisés où la coupe est importante. La préservation de petits groupes d'enchevêtrements importants et d'arbres vivants affichant des signes de maladie ou de défauts physiques assurerait la présence de structures utilisables pour l'établissement de repaires après la coupe de la forêt.

[Traduit par la Rédaction]

Introduction

Habitat-selection theory predicts that organisms will select habitat to maximize their fitness. Both abiotic and biotic factors may influence fitness potential, altering patterns of selection locally and regionally. For example, individuals should adjust their use of habitats in response to spatial and temporal differences in climate to achieve energy balance (Wilbert et al. 2000; Martin 2001). Similarly, individuals should respond to differences in competitor or predator densities, with some individuals using lower quality habitats because competition or predation is reduced there (Fretwell

and Lucas 1970; Lima and Dill 1990; Morris 1995; Rosenzweig and Abramsky 1997).

Understanding the ecological basis for habitat preferences can help natural-resource managers protect or enhance habitats important to species of concern. Individuals select habitat on multiple spatial scales, in the choice of a new home range, as well as in the nonrandom use of microhabitats within that home range (Hutto 1985; Morris 1992). Although there is debate about whether macrohabitat or microhabitat selection exerts more control over population densities (Morris 1987), clear examples exist where a scarce microhabitat limits populations in human-altered landscapes, especially

Received 12 March 2002. Accepted 22 August 2002. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 16 October 2002.

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the presence of nest trees for old growth associated species (e.g., Smith and Lindenmayer 1988; Newton 1994; James et al. 1997). Finding suitable nest sites is critical to maintaining thermal energy balance and avoiding predation and, thus, should be subject to strong selective pressures.

Northern flying squirrels (*Glaucomys sabrinus*) are an old growth associated species (Witt 1992; Carey 1995; Waters and Zabel 1995; but see Rosenberg and Anthony 1992) distributed across North America in boreal forests and western temperate rainforests (Wells-Gosling and Heaney 1984). When not engaged in nightly foraging, northern flying squirrels rest in tree cavities or in external nests, and females give birth and raise young there (Carey et al. 1997). These dens are reported to be associated with structural features characteristic of late-seral forests, including large-diameter trees with deformities (Cowan 1936; Martin 1994; Carey 1995; Clark 1995; Gerrow 1996; Carey et al. 1997). Most den-selection studies have been conducted in younger forests in the Pacific Northwest, where den availability has been proposed as a factor limiting the densities of northern flying squirrels (Carey 1991; Carey et al. 1997).

We studied den selection by northern flying squirrels in southeastern Alaska. Biologists identified flying squirrels as one of the region's old growth associated vertebrates most vulnerable to logging (L.H. Suring et al. 1993),² and forest planning has incorporated measures to protect the species from logging impacts (e.g., U.S. Department of Agriculture 1997), largely on the basis of studies conducted elsewhere. In southeastern Alaska, however, abiotic and biotic conditions could produce different patterns of den selection, altering optimal management practices for the species locally and shedding light on the mechanisms governing habitat selection generally.

The climate of the temperate rainforests of southeastern Alaska is more thermally demanding than that of Pacific Northwest forests, because it is cooler and lacks a pronounced summer dry season (Alaback 1994). Biotic stresses, on the other hand, are reduced in southeastern Alaska. Heterospecific competition for cavity sites is likely to be lower relative to more southerly forests, because decay is abundant (>30% of wood volume; Farr et al. 1976) and there are few competitors for cavities. Similarly sized secondary cavity nesters include red squirrels (*Tamiasciurus hudsonicus*), western screech owls (*Otus kennicottii*), and northern saw-whet owls (*Aegolius acadicus*; Armstrong 1990; Walsh 1993³), and none appear to be at high densities relative to elsewhere in their ranges. Conspecific densities are expected to be comparable with those in similar habitats in the Pacific Northwest (W.P. Smith and J.V. Nichols 2002).⁴ Northern flying squirrels, however, are known to den communally as a social and thermoregulatory strategy (Wells-Gosling and Heaney 1984) and, consequently, it is unclear how or if conspecific densities should influence

den selection. Predation on northern flying squirrels is likely lower in southeastern Alaska. The northern spotted owl (*Strix occidentalis occidentalis*), the squirrel's primary predator in many regions, is absent. Local terrestrial predators include marten (*Martes americana*) and ermine (*Mustela erminea*; Wells-Gosling and Heaney 1984; Carey 1991), both of which appear to be at low to moderate densities relative to more southerly forests (L.H. Suring et al. 1993²; British Columbia Ministry of Environment, Lands, and Parks 1998).

Owing to the thermally stressful abiotic environment and reduced competition and predation, we hypothesized that den choices in southeastern Alaska would be controlled by thermoregulatory needs. Specifically, we predicted that northern flying squirrels would use more cavities than external nests, because cavities are better insulated from moisture and cold temperatures (Collias 1964; Martin and Ghalambor 1999), and that the relative use of cavities in this region would exceed rates in late-seral forests in more temperate parts of the species' range. We expected that squirrels would select dens in the most thermally insulated cavities, which occur in large-diameter trees or low in the bole (Bunnell et al. 1999; Wiebe 2001), despite the increased risk of predation on these latter dens by terrestrial predators (Collias 1964; Nilsson 1984; Li and Martin 1991; Gerrow 1996). Finally, we expected that group denning would occur more frequently during winter and in more weatherproof cavities.

Cavity-denning squirrels should use specific tree types preferentially. Cavities are more abundant in large-diameter trees (Mannan et al. 1980; Bunnell et al. 1999), in well-decayed snags (Bunnell et al. 1999; Parks et al. 1999), and in live trees with defects or diseases that facilitate the entry of rot into the bole (Hennon and Demars 1997; Gunn and Hagan 2000; U.S. Department of Agriculture 2001). Hemlock dwarf mistletoe (*Arceuthobium tsugense*), for example, is a prevalent disease in southeastern Alaska that increases rates of bole deformities, dead tops, and heart rot (U.S. Department of Agriculture 2001). Cavities may also be more abundant in rot-prone species, such as western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), relative to rot-resistant species, such as Alaska-cedar (*Chamaecyparis nootkatensis*; Hennon and Demars 1997; U.S. Department of Agriculture 2001).

Northern flying squirrels using external nests construct them on branches using sticks and epiphytes (Cowan 1936; Carey et al. 1997). External nests, therefore, should be associated with platforms and materials for nest building, such as high epiphytic loads (Bailey 1936) and numerous witches' brooms (branch deformities caused by diseases such as mistletoe; Mowrey and Zasada 1984; Gerrow 1996; Cotton and Parker 2000). Owing to our expectation of low rates of external nesting, however, we predicted den trees would show no association with epiphytic loads. Mistletoe is associated

²L.H. Suring, D.C. Crocker-Bedford, R.W. Flynn, C.S. Hale, G.C. Iverson, M.D. Kirchoff, T.E. Schenck, L.C. Shea, and K. Titus. 1993. A proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in southeast Alaska; report of an interagency committee; final review draft. Available from U.S. Department of Agriculture, Forest Service, Alaska Region, P.O. Box 21628, Juneau, AK 99802-1628, U.S.A.

³P.J. Walsh. 1993. Unpublished checklist of the birds of Mitkof Island, southeast Alaska. Available from Juneau Audubon Society, P.O. 021715, Juneau, AK 99802, U.S.A.

⁴W.P. Smith and J.V. Nichols. 2002. Demography of the Prince of Wales Island flying squirrel: an endemic of southeastern Alaska temperate rainforest. *J. Mammal.* In press.

with both cavity formation and external nest platforms and, thus, we expected a positive relationship between den trees and mistletoe infection, regardless of external nesting rates.

Study area and methods

Study area and den-tree locations

The study was conducted on Mitkof Island (56°N, 133°W), the most northerly island supporting flying squirrels within the Tongass National Forest (MacDonald and Cook 1996), which encompasses nearly all the Alexander Archipelago in southeastern Alaska. The 518-km² island is mountainous, has a wet maritime climate (mean annual temperature 6°C, precipitation 2600 mm), and supports perhumid rainforest (Alaback 1994). Forest types range from low stature forests (10–20 m) composed of shore pine (*Pinus contorta* var. *contorta*), Alaska-cedar, western red cedar (*Thuja plicata*), mountain hemlock (*Tsuga mertensiana*), western hemlock, or Sitka spruce to forests dominated by tall (30–40 m) western hemlock and Sitka spruce and containing commercial volumes of timber. A well-developed ericaceous shrub layer is found throughout most late-seral forests. Peat bogs are common, and forests are often linearly aligned along beaches and riparian corridors in areas of better drainage (Concannon 1995). Clearcut logging has occurred in most of the island's watersheds, and 20% of the original forest containing commercial timber has been harvested since 1960.

We restricted our trapping to late-seral forests with commercial volumes of timber (>47 m³/ha), because northern flying squirrel densities are highest here (W.P. Smith and J.V. Nichols 2002)⁴ and because we sought information forest managers could use to manage habitat for flying squirrels in stands subject to selective logging. We trapped intermittently in forests within 1 km of a road and below a 150-m elevation from September 1996 through November 1999. Except for one squirrel trapped and two dens located in old second-growth forest (~100 years old; Fig. 1, site D), all traps and all dens were in old growth, although all sites included peat bogs and some contained clearcut patches (<30 ha; Fig. 1). We captured flying squirrels in Tomahawk live traps (13 × 13 × 41 cm) baited with peanut butter, oats, and molasses. Trap stations were spaced approximately 40 m apart in 1–3 transect lines. Each station consisted of a tree trap (1.5 m high) and a ground trap, two ground traps, or a single trap of either type. We fitted all captured flying squirrels ≥120 g (Carey et al. 1997) with radio collars (Holohil MD-2C and PD-2C) that were <3% of body mass. During midwinter through summer 1997, fall 1998, and midwinter through fall 1999, we located flying squirrels in their dens during the daytime 1–4 times monthly. We pinpointed squirrels to a specific tree using a Wildlife Materials Inc. TR1000 receiver and a hand-held three-element Yagi antenna. We did not climb trees or otherwise seek to inspect dens to confirm locations because Carey et al. (1997) reported that northern flying squirrels abandoned dens permanently after this type of disturbance.

Characterization of dens and den trees

To ensure that study results would be useful to managers, we chose readily observable tree features to test our ecologi-

cal hypotheses about den-tree selection. To test our prediction that squirrels would den in cavities, we recorded whether a den was an external nest or an internal cavity whenever possible. Because height and density of the forest canopy generally prevented us from visually locating high dens, we also recorded indicators of cavity presence. Cavity indicators were tree characteristics associated with invasion by heart-rot fungus, specifically: tree diameter (diameter at breast height (DBH) to the nearest centimetre), whether the tree was a snag, and whether it had fruiting bodies of tree-rot fungi (i.e., conks; Kimmey 1956), visible bole entries large enough for a northern flying squirrel to fit through (>5 cm; Mowrey and Zasada 1984), scars breaching the bark, or a broken top (Hennon and Demars 1997). For snags, we recorded decay level (five level ordinal ranking scale: least decayed to most decayed; Hennon et al. 2002). For live trees, we recorded hemlock dwarf mistletoe infection level (ordinal ranking scale modified from Hawksworth 1977: light, few or no branches infected; medium, about one-half of the branches infected; heavy, nearly every branch infected) and presence of a dead top. To determine if rot-prone trees were selected, we recorded tree species.

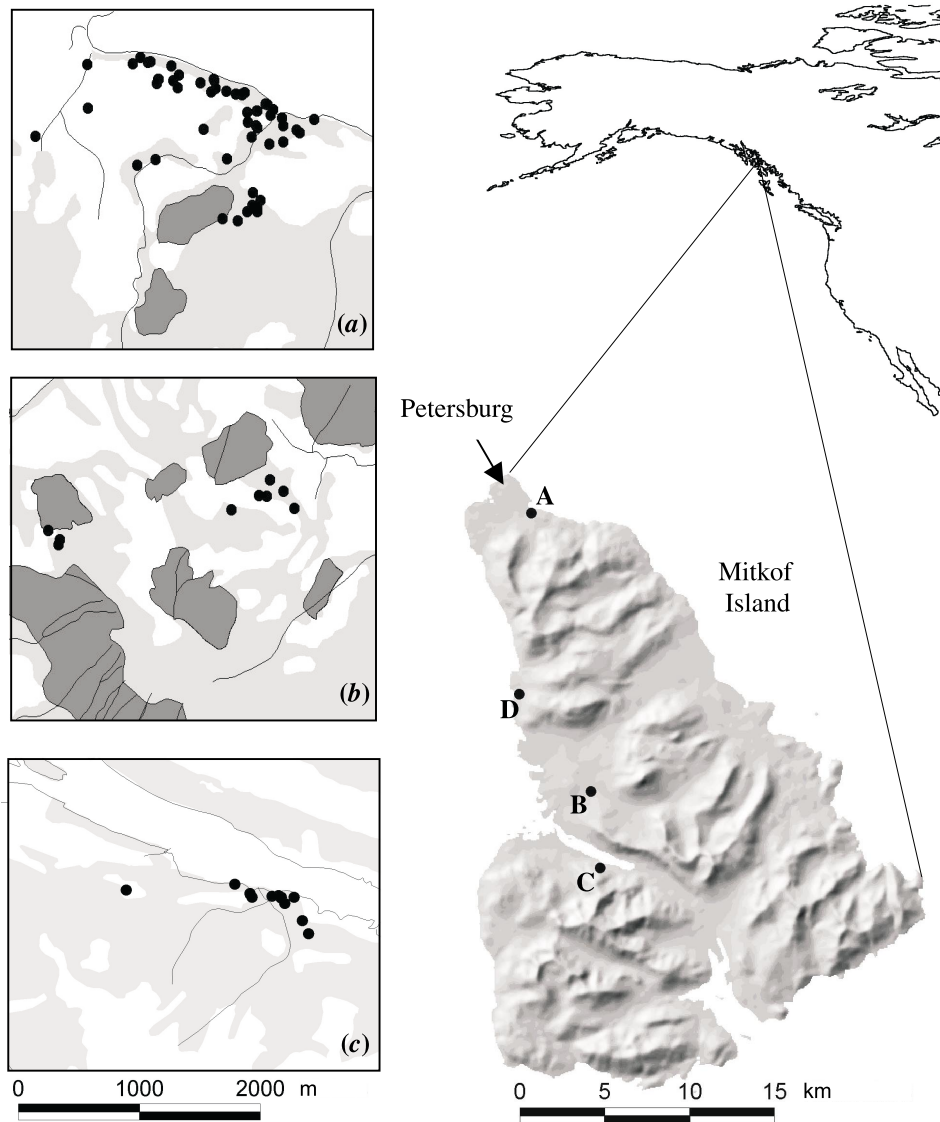
To determine if northern flying squirrels selected trees with extensive external nest platforms, we recorded epiphytic load (ordinal ranking scale: light, few or no epiphytes present; medium, epiphytes present on most branches; heavy, diameter of most branches at least doubled by epiphytes) and mistletoe infection level. To test our prediction that squirrels would use low-level dens, we estimated den height (<0, 0–3, 3–9, and >9 m) where possible, using telemetry, and also estimated den-tree height to the nearest 5 m.

Determination of availability and selection

To assess whether northern flying squirrels selected trees with cavity indicators or high epiphytic loads, we identified a sample of trees available to squirrels and compared these with the den trees actually used. Because of the spatial heterogeneity of the landscape and because we had different numbers of dens at each study site, we employed a matched case – control design, so that each den was compared with a unique sample of available trees matched on spatial proximity. We compared each den tree with up to 10 available trees in a 30 m radius plot immediately surrounding the den (hereinafter, the den setting; comparison 1 in Fig. 2). Available trees, which we defined as live trees or snags ≥45 cm DBH (the minimum size of den trees found during the early part of our study) and ≥2 m tall, were sampled for the same variables as den trees. We restricted our sample of available trees to those ≥45 cm DBH, to compare den trees with trees large enough to support dens, thereby allowing a more subtle discrimination of attributes important to flying squirrels.

We also compared the den tree with 20 trees in two matched settings (30 m radius plots) located 60 m away in random directions (comparison 2 in Fig. 2), to help identify important characteristics that might be masked by fine-scale spatial autocorrelation in tree attributes such as size, disease, and physical damage. Finally, we compared the characteristics of all the available trees in the den setting (actual den and available trees) with those of the available trees in the two matched random settings (comparison 3 in Fig. 2).

Fig. 1. Mitkof Island study area. The relief map shows the locations of the study sites (A–D). On corresponding site maps (a–c) heavy shading represents clearcuts, light shading is forest with commercial volumes of timber, and unshaded areas are either scrub forest or peat bog. Dens are shown as small dots. (a) Site A data are 46 traps, 1244 trap-nights, 22 squirrels, 45 den trees, 1 den not associated with a tree, and 7 non-pinpointed den sites. (b) Site B data are 56 traps, 1096 trap-nights, 3 squirrels, 7 den trees, and 2 non-pinpointed den sites. (c) Site C data are 60 traps, 924 trap-nights, 10 squirrels, 11 den trees, and 1 den not associated with a tree. The data for site D (no site map included) are 8 traps, 72 trap-nights, 1 squirrel, and 2 den trees.



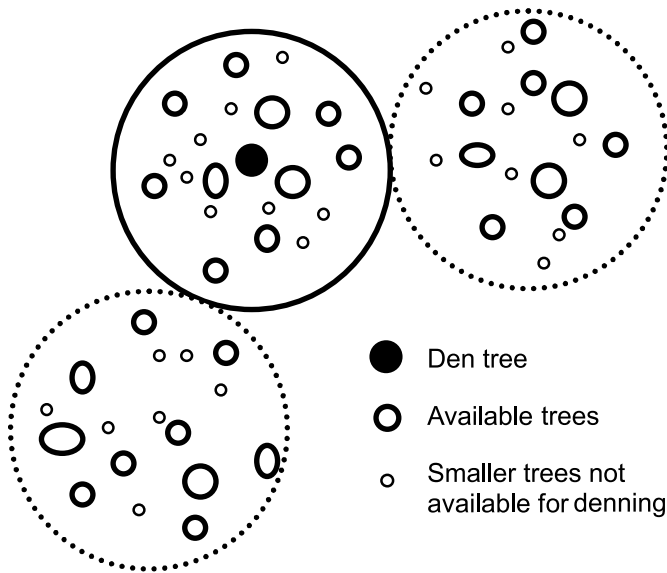
Data analyses

We used conditional logistic regression (CLR) to identify the variables (cavity indicators, epiphytic load, tree height) that best predicted the den trees that northern flying squirrels selected. CLR is used for highly stratified data, such as the many den strata in our matched design, because it uses conditioning arguments to eliminate strata effects (Hosmer and Lemeshow 1989; Stokes et al. 1995), analogous to a paired t test. CLR is frequently employed in analyses of epidemiological matched case – control studies to eliminate the effect of the treatment clinic, but has recently been used in studies of habitat selection (e.g., Hershey et al. 1998; Compton et al. 2002). The test is conceptually similar to using differences between cases and controls as predictors (Stokes et al. 1995). Like logistic regression, CLR identifies significant predic-

tors of a particular outcome (e.g., being a den), the slope of the relationship between the predictor and the outcome (the regression coefficient, β), and the odds ratio for each predictor. The odds ratio is the exponentiation of the regression coefficient (e^β), and it indicates the increased likelihood of the outcome with each unit increase in the predictor. In multivariate CLR, the odds ratio for each variable adjusts for all other variables in the model (Hosmer and Lemeshow 1989; Stokes et al. 1995).

Prior to CLR analyses, we used SAS 8.1 (SAS Institute Inc. 2000) to examine Spearman's rank correlations between variables (PROC CORR) and tolerance values for each variable (PROC REG), to identify potential collinearity problems (i.e., $r > 0.7$, tolerance < 0.3 ; Menard 1995). We performed CLR using PROC PHREG, building our model using forward step-

Fig. 2. We compared the den tree with the 10 nearest available trees (≥ 45 cm DBH) in the den setting (large circle with an unbroken outline) (comparison 1), the den tree with the 10 nearest available trees in two matched random settings (large circles with a broken outline) 60 m away (comparison 2), and the den tree and the 10 available trees in the den setting with the 10 available trees in the matched random settings (comparison 3). Den settings and random settings were 30 m radius plots.



wise selection. Because we built many CLR models and evaluated the importance of numerous variables in each, we used the more stringent criteria of $P = 0.05$ to enter and $P = 0.10$ to remove, rather than the recommended screening criteria of 0.15 and 0.20, respectively (Hosmer and Lemeshow 1989). After identifying significant main effects, we evaluated models that included these main effects and interaction terms. To assess model goodness of fit, we examined model residual χ^2 , residual diagnostics, and logit plots (Hosmer and Lemeshow 1989; Stokes et al. 1995).

Most den-tree characteristics we measured differed strongly between snags and live trees, and some applied only to one of these categories. Therefore, we first tested for selection for variables common to both tree types. We then divided the data set and compared snag dens only with available snags and live den trees only with available live trees. In assessing tree-species selection, we again separated our data set into snags and live trees. Because PROC PHREG does not permit the use of nominal variables, we analyzed tree-species selection in SYSTAT 7.0 (SPSS Inc. 1997) with McNemar's test of symmetry by cross-tabulating the den tree against the modal species in the den setting and in the matched random settings.

In addition to evaluating the predictive power of cavity indicators, we calculated the minimum rate of cavity usage as the proportion of dens known to be in cavities, owing to unimpeded views of the bole and crown. We also analyzed the subset of den trees that potentially held external nests (i.e., high dens with the view impeded by the canopy), comparing each with available live trees in the den setting and matched random settings using CLR, to determine if these den trees

had high levels of epiphytic loads or whether they showed indicators of internal cavity presence.

To determine if group denning occurred in more weather-proof dens, we used logistic regression (PROC LOGISTIC) to evaluate whether tree diameter and cavity indicators predicted group-den sites. We defined a group den as any den used by two or more squirrels simultaneously. One group den could not be included in our CLR analysis of group-den characteristics because it was not associated with a tree; two squirrels denned together underground below a highly decayed stump.

Results

We captured 36 northern flying squirrels (20 male, 16 female) in 3336 trap-nights at four sites (Fig. 1). We collared 32 squirrels and located at least one den site for 27 individuals, for a total of 76 unique den sites in 238 telemetry locations (January–March, 19 dens; April–June, 29 dens; July–September, 28 dens; October–November, 15 dens; 19 dens were used in more than one season). We pinpointed 65 dens to a specific tree. Two more den sites were pinpointed exactly but were ≥ 1 m from a live tree or snag: one was under a large root wad and another was below a highly decayed 30 cm diameter moss-covered stump. These two dens, not associated with trees, along with nine den sites not pinpointed exactly, were used only for analyses of setting-wide tree characteristics (comparison 3 in Fig. 2).

Live den trees ($n = 26$) ranged from 29 to 113 cm DBH and snags containing dens ($n = 39$) ranged from 37 to 173 cm DBH (Table 1). Squirrels denned in five structures < 45 cm DBH. Four of these were broken top snags 37–41 cm DBH. The fifth was a 29-cm live tree, at which the den was either low in the bole or in an adjacent moss mound at < 1 m. Because our sample of available trees was limited to trees ≥ 45 cm DBH, our den tree analyses may have been biased toward detection of characteristics associated with smaller trees. To assess potential bias, we ran all our analyses with and without the smaller den trees and report any instances in which different variables predict den trees when the smaller trees are excluded. Similarly, because we could not confirm that the last den location for each squirrel ($n = 17$ dens) was actually a squirrel den and not a predator cache, we also reran all our analyses with and without these unconfirmed dens and report discrepancies in results; we do not report instances where variables fail to enter predictive models owing to loss of power, if significance levels indicate that the relative importance of variables remains constant.

Cavity use

We had an unimpeded view of all snags used as dens. Thus, we are confident that all 39 snag dens were in internal cavities, as were two dens under stumps or root wads. Likewise, we determined that 8 of 26 dens in live trees were internal dens, because we pinpointed them to below-ground locations or to low in the bole. Therefore, cavity use occurred at a rate of at least 73% (95% confidence interval of 61–83).

When the 18 trees that might have contained external nests were compared with available live trees in the den setting, external nest platforms predicted den presence. Both mistletoe

Table 1. Characteristics of den trees and available trees (≥ 45 cm DBH) in the den setting and in matched random settings 60 m away (Fig. 2); snags represented 60% (95% confidence interval of 47–72) of the 65 den trees and 27% (25–29) of the 1875 available trees.

| (a) Diameter* (cm). | | | | | | | | | |
|--|------------|--------------------------|-----------------|----------|--------------------------|-----------------------|--------------------------|----------|--|
| Live trees | | | | | Snags | | | | |
| Den trees | | Available trees | | | Den trees | | Available trees | | |
| Median diameter (95% CI) | <i>n</i> | Median diameter (95% CI) | <i>n</i> | | Median diameter (95% CI) | <i>n</i> [†] | Median diameter (95% CI) | <i>n</i> | |
| 68 (60–82) | 26 | 58 (57–59) | 1367 | | 71 (57–82) | 38 | 60 (58–60) | 508 | |
| (b) Species and other characteristics. | | | | | | | | | |
| | Live trees | | | | Snags | | | | |
| | Den trees | | Available trees | | Den trees | | Available trees | | |
| | % (95% CI) | <i>n</i> | % (95% CI) | <i>n</i> | % (95% CI) | <i>n</i> [†] | % (95% CI) | <i>n</i> | |
| Species [‡] | | | | | | | | | |
| Western hemlock | 73 (52–88) | 26 | 76 (63–87) | 51 | 62 (45–77) | 39 | 71 (59–81) | 72 | |
| Alaska-cedar | 15 (4–35) | 26 | 16 (7–29) | 51 | 21 (9–36) | 39 | 22 (13–34) | 72 | |
| Sitka spruce | 12 (2–30) | 26 | 4 (0–13) | 51 | 5 (1–17) | 39 | 4 (1–12) | 72 | |
| Mountain hemlock | 0 (0–13) | 26 | 4 (0–13) | 51 | 0 (0–9) | 39 | 0 (0–5) | 72 | |
| Unknown | 0 (0–13) | 26 | 0 (0–7) | 51 | 13 (4–27) | 39 | 3 (0–10) | 72 | |
| Other characteristics | | | | | | | | | |
| Visible bole entries | 38 (20–59) | 26 | 13 (11–14) | 1363 | 53 (36–69) | 38 | 40 (35–44) | 508 | |
| Broken top | 15 (4–34) | 26 | 6 (5–8) | 1367 | 79 (64–91) | 39 | 70 (66–74) | 508 | |
| Conks | 8 (1–25) | 26 | 2 (1–3) | 1367 | 45 (29–62) | 38 | 36 (32–41) | 508 | |
| Scars | 73 (52–88) | 26 | 48 (45–51) | 1367 | 89 (75–97) | 38 | 85 (82–88) | 508 | |
| Dead top | 19 (7–39) | 26 | 10 (8–12) | 1366 | | | | | |
| Epiphytes | | | | | | | | | |
| None | 0 (0–13) | 26 | 3 (2–4) | 1367 | | | | | |
| Light | 27 (12–48) | 26 | 29 (27–32) | 1367 | | | | | |
| Medium | 58 (37–77) | 26 | 60 (58–63) | 1367 | | | | | |
| Heavy | 15 (4–35) | 26 | 8 (6–9) | 1367 | | | | | |
| Mistletoe | | | | | | | | | |
| None | 46 (27–67) | 26 | 69 (67–72) | 1366 | | | | | |
| Light | 19 (7–39) | 26 | 17 (15–19) | 1366 | | | | | |
| Medium | 15 (4–35) | 26 | 9 (7–10) | 1366 | | | | | |
| Heavy | 19 (7–39) | 26 | 6 (4–7) | 1366 | | | | | |
| Decay class (1→5) | | | | | | | | | |
| 1 (least decayed) | | | | | 5 (1–17) | 39 | 12 (9–15) | 508 | |
| 2 | | | | | 28 (15–45) | 39 | 26 (22–30) | 508 | |
| 3 | | | | | 23 (11–39) | 39 | 24 (21–28) | 508 | |
| 4 | | | | | 21 (9–36) | 39 | 20 (17–24) | 508 | |
| 5 (most decayed) | | | | | 23 (11–39) | 39 | 17 (14–21) | 508 | |

*When den trees <45 cm DBH are excluded, live den tree median diameter is 68 cm (61–82 cm) and snag den median diameter is 72 cm (60–83 cm).

[†]Some data are missing for one snag den that collapsed prior to sampling.

[‡]The modal species of available trees in the den setting and of available trees in the two random settings combined are tabulated, resulting in twice as many available tree species as den tree species. For one live den tree and six snag dens, a den or random setting had no modal species. McNemar's test, described in the text, compared the den tree species with the mode of available trees in the den and random settings, excluding unknown species.

($P = 0.002$, odds ratio = 4.060) and epiphytic load ($P = 0.029$, odds ratio = 2.943) were positive predictors of den presence ($G = 18.476$, model $P < 0.001$). However, comparing these trees with available live trees in random settings 60 m away, cavity indicators predicted den presence. Mistletoe ($P = 0.003$, odds ratio = 2.853), diameter ($P = 0.030$, odds ratio = 1.029), and dead tops ($P = 0.051$, odds ratio = 3.802) were positive predictors of den presence ($G = 21.436$, $P < 0.001$). We observed likely external dens (e.g., a mound of epiphytes on a limb consistent with the telemetry signal) only four times.

Den-tree characteristics

When comparing the 65 den trees with the 642 available trees within the den settings, three cavity indicators (diameter, snag, and bole entries) were significant positive predictors of den presence (all $P \leq 0.002$; a in Table 2). Odds ratios indicate that a tree was more than three times more likely to be a den if it was a snag and nearly three times more likely to be a den if it had bole entries. Each 10-cm increase in diameter increased the probability of a tree having a den by 23%. Comparing den trees with the 1233 available trees in random settings yielded similar results, although a

Table 2. Predictors of northern flying squirrel den trees using forward stepwise selection conditional logistic regression ($P = 0.05$ to enter and $P = 0.10$ to remove).

| Variable | P | Odds ratio |
|---|--------|------------|
| Den trees relative to nearby trees (a) | | |
| Snag | <0.001 | 3.259 |
| Bole entries | <0.001 | 2.820 |
| Diameter | 0.002 | 1.023 |
| Scars | 0.337 | |
| Conks* | 0.520 | |
| Snag dens relative to nearby snags (b) | | |
| Diameter | 0.027 | 1.026 |
| Bole entries | 0.076 | |
| Scars | 0.207 | |
| Broken top | 0.240 | |
| Decay class | 0.677 | |
| Conks | 0.849 | |
| Live den trees relative to nearby live trees (c) | | |
| Mistletoe | 0.001 | 2.920 |
| Bole entries | 0.003 | 5.005 |
| Epiphytic load | 0.158 | |
| Conks | 0.199 | |
| Diameter | 0.405 | |
| Scars | 0.435 | |
| Broken top | 0.523 | |
| Dead top | 0.602 | |
| Live den trees relative to live trees in random settings (d) [†] | | |
| Bole entries | <0.001 | 6.800 |
| Mistletoe | 0.004 | 2.163 |
| Conks | 0.010 | 10.900 |
| Dead top | 0.057 | 3.192 |
| Diameter | 0.101 | |
| Scars | 0.136 | |
| Broken top | 0.431 | |
| Epiphytic load | 0.866 | |
| Trees in den settings relative to trees in random settings (e) | | |
| Conks | 0.009 | 1.419 |
| Scars | 0.247 | |
| Bole entries | 0.248 | |
| Diameter | 0.687 | |
| Snag | 0.858 | |

Note: Odds ratios are presented only for significant variables. Nonsignificant interaction terms are not shown. Models predict (a) den trees from available (≥ 45 cm DBH) trees in a den setting ($G = 51.727$, $P < 0.001$; comparison 1 in Fig. 2), (b) snags containing dens from available snags in a den setting ($G = 5.435$, $P = 0.020$; comparison 1 in Fig. 2), (c) live den trees from available live trees in a den setting ($G = 18.415$, $P < 0.001$; comparison 1 in Fig. 2), (d) live den trees from available live trees in random settings ($G = 30.784$, $P < 0.001$; comparison 2 in Fig. 2), and (e) the den and available trees in a den setting from available trees in random settings ($G = 6.756$, $P = 0.009$; comparison 3 in Fig. 2).

*Conks ($P = 0.025$, odds ratio = 2.175) are a significant predictor in the model when den trees are compared with trees in random settings ($G = 48.772$, $P < 0.001$). All other predictors remain in the model.

[†]Diameter ($P = 0.025$, odds ratio = 1.029) replaces dead top when den trees < 45 cm DBH are excluded ($G = 31.414$, $P < 0.001$).

fourth cavity indicator, conks ($P = 0.025$), was also included in the model, more than doubling the probability of den presence. When dens < 45 cm DBH were censored, scars

($P = 0.052$, odds ratio = 2.126) replaced bole entries as a positive predictor of den presence (a in Table 2).

Large diameter predicted den presence in snags when comparing them with available snags in the den setting ($P = 0.027$; b in Table 2). Diameter ($P = 0.003$, odds ratio = 1.028) was also a positive predictor of dens relative to snags in random settings ($G = 9.380$, model $P = 0.002$).

Among live trees, mistletoe abundance and bole entries were the best predictors of den presence (all $P \leq 0.003$; c in Table 2). Each unit increase in abundance of mistletoe nearly tripled the probability of a tree containing a den, while the presence of visible bole entries increased the probability of a tree containing a den by more than five times. When we compared live den trees with live trees in random settings, conks and dead tops were positive predictors of den presence in addition to mistletoe and bole entries (all $P \leq 0.057$; d in Table 2). When only dens ≥ 45 cm DBH were considered, diameter replaced dead top in the model ($P = 0.025$; d in Table 2).

Northern flying squirrels denned in live and dead western hemlock, Sitka spruce, and Alaska-cedar (Table 1) and did not select rot-prone species preferentially. They denned in the modal species of the den setting 93% of the time and in the modal species of random settings 69% of the time. When squirrels chose other than the modal species, their choices did not differ from random (vs. den-setting mode, $\chi^2 = 2.00$, $P = 0.572$; vs. random-settings mode, $\chi^2 = 1.377$, $P = 0.711$).

When assessing whether all the available trees in the den setting differed from the available trees in random settings (comparison 3 in Fig. 2), only the presence of conks was a significant predictor of den setting trees (e in Table 2). Conk presence also predicted snags in den settings ($P = 0.042$, odds ratio = 1.452, $G = 4.147$, model $P = 0.042$). Excluding the den trees < 45 cm DBH, both conks ($P = 0.038$, odds ratio = 1.467) and diameter ($P = 0.026$, odds ratio = 1.010) predicted snags in den settings ($G = 9.557$, model $P = 0.008$).

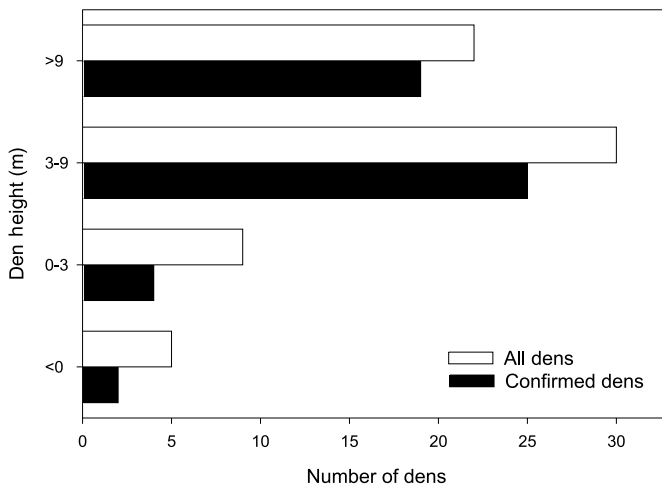
Low epiphytic load ($P < 0.001$, odds ratio = 0.546) was the most significant predictor of live trees in den settings. Each incremental increase in average epiphytic load decreased the probability of a setting having a den by nearly half. More dead tops ($P < 0.001$, odds ratio = 1.914) and mistletoe ($P = 0.008$, odds ratio = 1.204) were also found on live trees in den settings ($G = 54.109$, model $P < 0.001$).

Spearman's correlation coefficients (r) were < 0.50 for all pairs of variables used together in CLR analyses, both overall and when snags and live trees were considered separately. Broken top was highly correlated with snag ($r = 0.68$, $P < 0.001$) and, consequently, it was not used in overall analyses of den trees, which included snag as an independent variable. Snag was also correlated with conks ($r = -0.48$, $P < 0.001$). The most highly correlated variables among snags were decay class and broken top ($r = -0.47$, $P < 0.001$) and decay class and bole entries ($r = 0.32$, $P < 0.001$). For live trees, correlated variables were scars and bole entries ($r = 0.33$, $P < 0.001$) and dead top and broken top ($r = 0.27$, $P < 0.001$).

Den height

Dens were frequently at low heights (Fig. 3). Of 66 dens for which we obtained den-height estimates, 5 were at or below ground level and 9 were at a height of 0–3 m (21% of

Fig. 3. Estimated heights of northern flying squirrel dens. Confirmed dens exclude telemetry locations after which no subsequent movement was detected.



dens ≤ 3 m). The median height of structures in which these low dens were found was 15 m. When we censored unconfirmed dens (final locations for squirrels), 12% of the remaining dens were still ≤ 3 m, including two underground dens: a group den under a highly decayed stump and a solitary den under a 25 m tall live western hemlock.

Group denning

Group denning was observed 23 times (20 groups of 2, 3 groups of 3) between January and early May in two different years, or 35% of locations during this part of the year and 21% of all locations. Eight flying squirrels denned with conspecifics in five dens during this period. Denning partners varied over time, and both same-sex and different-sex groupings were observed. Two other dens were occupied sequentially by two to three squirrels. Although 42% of den locations were made from late May to December, group denning was never observed during this time period in the 3 years of the study. Den trees used by groups did not differ statistically from other den trees. Neither diameter ($P = 0.062$) nor whether the tree was a snag or had conks, scars, or a dead top was important (all $P > 0.321$).

Discussion

Cavity use

As expected, northern flying squirrels used more internal cavities ($\geq 73\%$) than external nests in southeastern Alaska. Fewer than 27% of dens were in the canopy and may have been external nests. These dens were in trees that had higher epiphytic loads and more mistletoe than nearby live trees, consistent with external nesting. Mistletoe induces witches' brooms, which provide structures for external nesting in other regions. In dry interior boreal forests, for example, spruce broom rust (*Chrysomyxa* spp.) creates witches' brooms consisting of dense clumps of branches up to 1 m in diameter in which northern flying squirrels frequently nest (Mowrey and Zasada 1984; Gerrow 1996; Cotton and Parker 2000). At our study sites, however, witches' brooms result from hemlock dwarf mistletoe and most appear as an open proliferation of

branches on a two-dimensional plane (V.J.B., personal observation). When compared with live trees in random settings 60 m away, trees with canopy dens had more cavity indicators, including more mistletoe, larger diameters, and more dead tops. Consequently, we suspect that some of these dens may have been in internal cavities and that the actual rate of external nest use was lower than 27%.

Climate may have influenced denning locations, because the proportion of cavity dens in this region was greater than most reported rates elsewhere in the northern flying squirrel's range, including mature boreal mixed conifer-hardwood forests (32% in interior Alaska, Mowrey and Zasada 1984; 58% in southern New Brunswick, Gerrow 1996) and more southerly temperate rainforests ($\leq 55\%$ in old growth and second growth in the Oregon Cascades, Rosenberg et al. 1996; 51% in second growth in the Puget Trough, Carey et al. 1997; 69% in second growth on the Olympic Peninsula, Clark 1995). Similarly, cavity use was below that observed in winter in interior British Columbia (84% in a mosaic of mature and younger subboreal forest; Cotton and Parker 2000).

Den-tree characteristics

Cavity indicators consistently predicted den presence. A snag was over three times more likely than a live tree to be a northern flying squirrel den. Ours is the first study to document preferential use of snags by northern flying squirrels in temperate rainforests (Martin 1994; Clark 1995; Carey et al. 1997). Adjusting for the effect of being a snag, three other correlates of cavity presence (tree diameter, visible bole entries, and conks) were additional positive predictors of den presence. Cavity indicators also predicted den presence for snags and live trees separately; both had larger diameters, and live-tree dens had heavier mistletoe infections and more frequent bole entries, conks, and dead tops.

Northern flying squirrels did not choose rot-prone species over rot-resistant species. In late-seral forests where heart rot is prevalent, such as in southeastern Alaska (U.S. Department of Agriculture 2001), cavities may be abundant in all species.

The importance of tree diameter is underestimated in most results we report, owing to the presence of five den trees < 45 cm DBH in our experimental sample, despite none in our random samples. Censoring these smaller trees from analyses always increased the odds ratios and decreased significance levels associated with tree diameter. Because few qualitative changes occurred, however, we primarily report results that include these smaller trees. The importance of bole entries could be a sampling effect, because we may have searched the den tree more thoroughly than random trees for entries.

Several discrepancies between comparisons of the den tree with trees in den settings and with trees in random settings likely resulted from spatial autocorrelation in measured characteristics. For example, conks were important indicators of den presence when comparing den trees with trees in random settings but not when comparing den trees with trees in the den setting (a in Table 2). When comparing all trees within den settings to those in random settings, however, trees in the den setting had more conks (e in Table 2). Live trees and snags showed similar patterns, although the relationships were not significant for snags. These results sug-

gest that northern flying squirrels are denning in trees with conks and that conk occurrence is spatially autocorrelated. The same trend was found for broken tops on snags and dead tops on live trees. All these features can result from factors that strike a multitude of nearby trees, such as wind or disease. Although mistletoe prevalence varied from tree to tree locally and was a strong predictor of den presence within the den setting, spatial autocorrelation in the distribution of mistletoe infection may also explain the relative importance of mistletoe on live trees in den settings relative to random settings. Dead tops may have been caused by mistletoe infection (Hawksworth and Wiens 1996; U.S. Department of Agriculture 2001).

Although we predicted no relationship between den trees and epiphytic load, we were surprised to find that den settings had significantly lighter epiphytic loads overall than did random settings. Nonetheless, the relationship between epiphytic loads and den trees was positive, although non-significant, within the den setting.

Weatherproof cavities

Northern flying squirrels in southeastern Alaska selected features associated with more weatherproof cavities, including larger-diameter snags and live trees. Tree diameter is correlated not only with cavity presence but also with the potential insulation of the cavities. Denning high in larger-diameter trees would have several advantages, because such cavities would be safer from predators as well (Bunnell et al. 1999). We saw considerable use of low-level dens, however, with one-fifth of all dens at a height ≤ 3 m and 8% at or below ground level (Fig. 3). Although some of these dens may have been predator caches, 12% of dens were low-level dens (≤ 3 m) used by squirrels known to be alive. Documented use of low-level dens in the Pacific Northwest has been restricted to females, primarily during the breeding season in second-growth forests ($\leq 9\%$; Clark 1995; Carey et al. 1997). Carey et al. (1997) speculated that females were forced into suboptimal low-level dens, because they sought solitary occupancy during the breeding season and cavities were scarce in second growth. In some bird species, the use of low-level cavities increases with increasing population density and, thus, with decreased cavity availability, despite higher predation on low-level nests (Nilsson 1984). In our region, however, cavity availability is likely not a limiting factor, and we observed the use of low-level dens by both sexes, including one instance of a male and female denning together below ground. All our confirmed low-level dens were occupied from October to March, which is outside the breeding season, suggesting a thermoregulatory basis to the use of low-level dens. Similarly, in southern New Brunswick, Canada, the frequency of below-ground nesting by northern flying squirrels was negatively related to mean temperature ($R^2 = 0.91$), despite high levels of weasel predation on these dens (Gerrow 1996). Although mustelids in southeastern Alaska readily climb trees, they are believed to hunt more frequently on the ground (Clark et al. 1987; British Columbia Ministry of Environment, Lands, and Parks 1998) and would be more likely to encounter dens near ground level. The relatively frequent use of low-level dens in southeastern Alaska suggests that thermoregulatory gains can outweigh the added predation risk of denning near ground level.

Group denning

Group-denning behavior also appeared to be influenced by thermoregulatory needs, being observed only during winter and spring. Group denning represented 35% of locations from January to early May but was not documented in the summer and fall months, despite a similar sampling effort during the two time periods. Because we did not have all flying squirrels in any of our study areas collared, our group-denning observations almost certainly underestimate the actual frequency of this behavior. The seasonal pattern is consistent with those reported for the Pacific Northwest (Clark 1995; Carey et al. 1997), where most cohabitation occurred in winter, and for interior British Columbia, where cohabitation began after the minimum nightly temperature dropped below freezing (Cotton and Parker 2000). Although group denning has been documented in all seasons in other regions (Carey and Sanderson 1981; Maser et al. 1981; Gerrow 1996) and may serve a social function, the seasonal pattern of the behavior in southeastern Alaska and elsewhere suggests that it also serves a thermoregulatory function. Group denning in winter reduced energy expenditures up to 33% in southern flying squirrels (*Glaucomys volans*; Stapp et al. 1991). The seasonal pattern also suggests that the behavior is not a response to limited den-site availability, although highly weatherproof dens might be limiting. Group-den characteristics did not differ from those of other dens, although our small sample size limits our power to detect differences. Tree diameter was a marginally significant predictor of group dens ($P = 0.062$), suggesting that flying squirrels may aggregate in more insulated dens.

Implications

Northern flying squirrels in southeastern Alaska likely experience fewer biotic pressures on den-site selection, including reduced competition and predation. In contrast, abiotic demands of climate are likely strong in the region. Given these conditions, habitat-selection theory predicts that northern flying squirrels will show a high level of selectivity and that den-use patterns will reflect climatic stresses. Consistent with theory, northern flying squirrels made extensive use of cavity dens, including cavities at low heights, and increased group denning during winter months.

These ecological patterns can inform management decisions. Currently, snags and diseased trees are abundant in most unharvested forests on the island (U.S. Department of Agriculture 2001) and cavity availability is probably not limiting populations. In intensively logged watersheds, however, cavity availability could be a limiting factor. Although northern flying squirrels in the Pacific Northwest make more extensive use of external nests in second-growth forests relative to old-growth forests (Carey et al. 1997), flying squirrels in southeastern Alaska may be less able to take advantage of external nests when cavities become limiting, owing to the thermal stresses of the region's cooler and wetter climate.

Retention of snags and live trees that support cavities or are likely to develop cavities could ameliorate the long-term effects of widespread logging on northern flying squirrel den availability. Otherwise, large cavity-supporting snags and live trees are likely to be one of the last features important to northern flying squirrels to develop in even-aged second-growth forests, particularly since decay occurs more slowly

in southeastern Alaska than in temperate rainforests to the south (Hennon and Demars 1997).

Retaining groups of trees in partially harvested areas may be a more efficient and effective strategy than identifying suitable individual trees (Bunnell et al. 1999). Groups of snags in den settings were larger in diameter than available snags outside the setting and were more likely to have conks. Live trees were more likely to have dead tops and abundant mistletoe. Thus, one strategy for ensuring the availability of appropriate denning structures would be to retain small groups of large snags and live trees with conks, heavy mistletoe infections, and top damage. Although foresters may prefer to remove all mistletoe from stands to prevent reinfestation, mistletoe infections spread slowly in southeastern Alaska, presenting an opportunity to manage infestation levels to enhance wildlife habitat while limiting timber loss (Trummer et al. 1998).

Identifying the scale of spatial autocorrelation in tree characteristics important to northern flying squirrels would provide managers with a tool for selecting groups of trees to retain for denning habitat. For autocorrelated features, foresters would only need to locate one or a few trees exhibiting predefined criteria, such as conk presence and mistletoe infection, at the core of a group. Other retained trees would also likely be diseased, and core trees could act as an inoculum source for neighboring trees to ensure continued den availability.

Other factors beyond protecting suitable denning trees are also important to sustaining northern flying squirrel populations in heavily logged watersheds, including maintenance of habitat that supports foraging, permits gliding, and provides adequate cover. Like denning behavior, other aspects of the species' ecology may differ in this cool wet region relative to areas where northern flying squirrels have been studied more intensively (e.g., diet; Pyare et al. 2002). More research into the population structure and dynamics, diet, and movement behavior of northern flying squirrels is needed to frame a comprehensive conservation strategy for this species in southeastern Alaska.

Acknowledgements

We thank E. DeGayner for guidance, reviews, and unflagging support. A. Hartshorn, D. Morris, W. Smith, D. Tallmon, and D. Van Vuren gave helpful reviews that greatly improved the quality of the manuscript. D. Magness, K. Topel, and O. Maiboroda provided expert field assistance in demanding conditions. Funding for the collection of field data was provided by the U.S. Department of Agriculture Forest Service. V.J.B. was supported by an Environmental Protection Agency Science to Achieve Results graduate research fellowship. K.H. was supported by the U.S. Department of Agriculture Forest Service and NSF-GRT No. 9553611 to P. Kukuk, C. Brewer, and F. Allendorf.

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