

ECOLOGICAL CORRELATES OF FLYING SQUIRREL MICROHABITAT USE AND DENSITY IN TEMPERATE RAINFORESTS OF SOUTHEASTERN ALASKA

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We studied habitat relations of the Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*), an endemic of the temperate, coniferous rainforest of southeastern Alaska, because of concerns over population viability from extensive clear-cut logging in the region. We used stepwise logistic regression to examine relationships between microhabitat use (i.e., captures among traps spaced at 40-m intervals) and 26 vegetative and structural habitat features measured in plots centered on trap stations. Seasonal (spring, autumn) models were created for two old-growth forest types: upland, western hemlock (*Tsuga heterophylla*)–Sitka spruce (*Picea sitchensis*) forests (upland-OG); and peatland-scrub–mixed-conifer forests (peatland-MC). Density of trees with diameter at breast height (dbh) >74 cm and abundance of *Vaccinium* were positively correlated with microhabitat use in peatland-MC during both seasons. During spring and autumn, the odds of capturing a flying squirrel increased by factors of 2.7 and 16.9, respectively, with an increase in mean density of 10 large trees/ha. Microhabitat use of upland-OG during autumn was positively correlated with density of snags with a dbh of 50–74 cm and negatively correlated with percentage cover of understory herbaceous vegetation; microhabitat use during spring was inversely correlated with percentage surface cover of water. At the macrohabitat (13-ha replicate of forest type) scale, large (>74-cm dbh) trees explained 65% of the variation in density between forest types; percent cover of moss and volume of down wood in decay classes I–IV explained 70% and 63–77% of the variation, respectively. Our findings corroborate general patterns reported for western coniferous forests, but suggest that *G. sabrinus* in temperate rainforests of southeastern Alaska differ ecologically from populations in the Pacific Northwest in important ways.

Key words: density, *Glaucomys sabrinus griseifrons*, logistic regression, macrohabitat, microhabitat use, northern flying squirrel, old growth, southeastern Alaska, temperate rainforest

The northern flying squirrel (*Glaucomys sabrinus*) has been identified as a keystone species for forests of the Pacific Northwest (Carey 2000a; Maser et al. 1978) because of its role in the dissemination of ectomycorrhizal fungi, which are essential symbionts of Douglas-fir (*Pseudotsuga menziesii*), and because it is primary prey of the spotted owl and various mustelids (Carey 1995; Carey et al. 1999; Forsman et al. 1984; Maser and Maser 1988; Maser et al. 1978, 1985, 1986). The life history of the northern flying squirrel also has been linked to numerous attributes of old forest of the Pacific Northwest (Carey 1989, 1995; Carey et al. 1992; Waters and Zabel 1995; Witt 1992).

This species is more abundant in old-growth and complex young forests than conventionally managed stands in a variety of coniferous forests across the Pacific Northwest (Carey 1995; Carey et al. 1992; Waters and Zabel 1995; Witt 1992; but see Ransome and Sullivan 2003; Rosenberg and Anthony 1992). Thus, its close association with several facets of late-seral forest structure and process purportedly renders the northern flying squirrel a good indicator of old forest condition (Carey 2000a; Carey et al. 1999). Therefore, understanding its life history and habitat relations is fundamental to successfully managing second-growth forests for biological diversity (Carey 1998, 2000a, 2000b).

Northern flying squirrel abundance has been correlated with micro- and macrohabitat (stand-level) attributes that are common among forest types across several locations in the Pacific Northwest (Carey et al. 1999). However, no single habitat variable or suite of individual variables thoroughly explained variation in abundance across geographic regions.

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Rather, the relationship between habitat and flying squirrel abundance appears to be multifactorial, where populations increase with increasing forest complexity (Carey 2001; Carey et al. 1999; Weigl et al. 1992). The ecological value of individual habitat features increases synergistically as forests develop, and additional key habitat elements coincide at spatial scales that allow flying squirrels to readily incorporate them within their home ranges (Carey 2000a, 2000b; Carey et al. 1999). Habitat features that consistently explain significant variation in flying squirrel abundance among stands, or captures within stands, are forest characteristics associated with snags and down, dead wood or "decadence" (Carey et al. 1999:54).

In southeastern Alaska, old-growth temperate rainforests are similar in plant composition and structural attributes to coastal coniferous forests of the Pacific Northwest (e.g., large trees and snags, and abundant coarse woody debris—Carey et al. 1999). Old-growth rainforests of southeastern Alaska support mean densities of flying squirrels comparable to or higher than those reported for mesic or wet coniferous forests of California, Washington, and Oregon (Smith and Nichols 2003; Smith et al. 2003). However, little is known about northern flying squirrel habitat relations in southeastern Alaska (Bakker and Hastings 2002), especially the attributes of forests that are associated with the selection of microhabitats or forest types (Smith and Nichols 2003). Restoration of managed landscapes to sustain viable populations of *G. s. griseifrons* requires thorough understanding of its habitat relations.

The purpose of this study was to provide the first quantitative analysis of northern flying squirrel habitat relations in temperate rainforests of southeastern Alaska. Specific objectives of the study were to evaluate trap stations with and without flying squirrel captures relative to vegetative and structural features, and to quantify variation in flying squirrel density relative to stand-level conditions. We studied flying squirrel populations in two old-growth forest types that overlapped in plant composition and structural attributes, but differed substantially in fine-scale (<100 m) heterogeneity, especially with respect to the overall abundance and spatial distribution of large live and dead trees, coarse woody debris, woody shrubs, and canopy closure.

MATERIALS AND METHODS

Study area.—Southeastern Alaska has naturally fragmented landscapes with coastal temperate rainforest distributed among islands of the Alexander Archipelago or isolated along a narrow mainland by mountains, glaciers, and associated ice fields. The region has a cool, wet (200–600 cm precipitation) maritime climate with mean monthly temperatures ranging from 13°C in July to 1°C in January (Searby 1968). Coniferous rainforest dominates the landscape from shoreline to about 600 m elevation, with about 90% of highly productive forest in western hemlock (*Tsuga heterophylla*)–Sitka spruce (*Picea sitchensis*) forests; remaining areas are alpine, muskeg, or riparian (Hutchinson and LaBau 1974).

We studied northern flying squirrel (*G. sabrinus griseifrons*) populations on Prince of Wales Island, the largest island in the Alexander Archipelago. Since 1954, approximately 25% of the old-growth forests on Prince of Wales Island have been logged, mostly at low (<300 m) elevations (United States Department of Agriculture, Forest Service 1997). Six study sites were selected in north-central

Prince of Wales Island (55°42'–55°48'N, 132°47'–132°52'W—Smith and Nichols 2003) within largely unmanaged landscapes; 3 replicates in upland-old growth (OG) forest (Julin and Caouette 1997); and 3 in peatland-scrub-mixed-conifer (MC) forest (Neiland 1971). Replicates were established in the same watershed to minimize geographical variation, but were ≥800 m apart to achieve independence. These habitats were selected because they represent endpoints of a natural continuum of forest cover and productivity in southeastern Alaska.

The more productive old-growth forests on Prince of Wales Island have an uneven-aged, multilayered overstory, with dominant trees generally >300 years old, and extensive structurally diverse understories (Hanley and Brady 1997; Ver Hoef et al. 1988). Forest habitats vary in structure from scrub or low-volume communities of short (<10 m), small (<0.5 m bole diameter) trees with open canopies and a dense, shrubby understory on poorly-drained sites with organic soils (peatland), to highly productive sites that support high-volume stands with a closed canopy of tall (>60 m) and large (>3 m bole diameter) trees, and a mostly herbaceous understory (Alaback 1982; Harris and Farr 1974). The *Tsuga-Picea* forest type (upland-OG) constitutes most of the closed canopy-forests in the region (Alaback 1982). It is spatially heterogeneous at scales <1 ha (Schoen et al. 1984) and typically occurs on low elevation, well-drained sites, frequently as a mosaic with muskegs (i.e., sparsely forested peatland—Neiland 1971). Overstory dominants include Sitka spruce and western hemlock, and to a lesser extent red cedar (*Thuja plicata*) and yellow cedar (*Chamaecyparis nootkatensis*). Dense patches of blueberry (*Vaccinium*) typically dominate the understory.

The peatland-scrub-mixed-conifer (peatland-MC) forest type is heterogeneous at a scale of tens of meters, a complex of open- to sparsely-canopied muskegs intermixed with patches of mixed-conifer vegetation that occur on gently sloping, elevated accretions of well-drained, mineral soil (DeMeo et al. 1992; Neiland 1971). Conifer vegetation includes yellow cedar, red cedar, western hemlock, mountain hemlock (*Tsuga mertensiana*), and lodgepole pine (*Pinus contorta* var. *contorta*). Understory vegetation varies considerably. Open areas with little overstory typically are comprised of a mixture of herbaceous and woody species, including sedges, grasses, skunk cabbage (*Lysichiton americanum*), and Labrador tea (*Ledum glandulosum*); blueberry dominates areas with well-developed overstories.

Livetrapping and density estimation.—Our livetrapping protocol (Smith and Nichols 2003) closely followed Carey et al. (1991). Study grids encompassed approximately 13 ha and consisted of a 10 × 10 array of 100 trap stations at 40-m intervals (360 × 360 m). We trapped each grid twice per year for 3 years (1998–2000). We selected early spring (March–April) and early autumn (September–October) because we wanted estimates of abundance immediately following winter (lowest annual density) and during the period when most reproduction and weaning had occurred, but juveniles likely had not dispersed (highest annual density—Carey et al. 1991; Villa et al. 1999). During a trapping session, grids usually were operated for 14 days, an initial 6-day marking period, a 2-day period when traps were closed to allow animals to recover from trap-related stress, and another 6-day recapture period. An adjustment for traps that were closed or inoperable was used to compute sampling effort (i.e., trap nights—Nelson and Clark 1973).

We used the modified Lincoln-Petersen index to estimate population density (Smith and Nichols 2003). We selected the Lincoln-Petersen estimator because it provides relatively precise estimates of population size with low biases and it performs well over many different conditions, but without many constraints of program models (Menkens and Anderson 1988). Additionally, we calculated mean maximum distance moved (MMDM) seasonally to estimate edge effect (Wilson

TABLE 1.—Habitat features measured within study grids where trap stations were centers of a 20-m circular plot in old-growth western hemlock (*Tsuga heterophylla*)–Sitka spruce (*Picea sitchensis*) forests and peatland-scrub–mixed-conifer forests, Prince of Wales Island, southeastern Alaska during 1999–2000.

Habitat variable	Description
Vacc 1	Mean percentage cover of <i>Vaccinium</i> ≤ 0.3 m tall
Vacc 4.5	Mean percentage cover of <i>Vaccinium</i> between 0.3 m and 1.5 m tall
Decid 1	Mean percentage cover of deciduous shrubs (except <i>Vaccinium</i>) ≤ 0.3 m tall
Decid 4.5	Mean percentage cover of deciduous shrubs (except <i>Vaccinium</i>) between 0.3 m and 1.5 m tall
Conifer 1	Mean percentage cover of conifer seedlings ≤ 0.3 m tall
Conifer 4.5	Mean percentage cover of conifer saplings between 0.3 m and 1.5 m tall
Moss	Mean percentage cover of moss
Herb	Mean percentage cover of herbaceous vegetation ≤ 1.5 m tall
Wood	Mean percentage cover of down wood ≥ 1 m long and < 25 cm diameter at the midpoint diameter
Water	Mean percentage cover of surface water
Decay I	Volume (m^3)/ m^2 of down wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a I
Decay II	Volume (m^3)/ m^2 of down wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a II
Decay III	Volume (m^3)/ m^2 of down wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a III
Decay IV	Volume (m^3)/ m^2 of down wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a IV
Decay V	Volume (m^3)/ m^2 of down wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a V
Stumps	Density of stumps ^b
Tree 74	Density of trees > 1.5 m tall and with dbh > 74 cm
Tree 50-74	Density of trees > 1.5 m tall with dbh between 50 and 74 cm
Tree 10-49	Density of trees > 1.5 m tall with dbh > 10 to 49 cm
Tree 5-10	Density of trees > 1.5 m tall with dbh between 5 and 10 cm
Soft snag 74	Density of snags ^c > 1.5 m tall and > 74 cm dbh with $< 2\%$ of limbs ≥ 30 cm remaining
Soft snag 50-74	Density of snags ^c > 1.5 m tall and between 50 and 74 cm with $< 2\%$ of limbs ≥ 30 cm remaining
Soft snag 10-49	Density of snags ^c > 1.5 m tall and > 10 to 49 cm with $< 2\%$ of limbs ≥ 30 cm remaining
Hard snag 74	Density of snags ^c > 1.5 m tall and > 74 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining
Hard snag 50-74	Density of snags ^c > 1.5 m tall and between 50 and 70 cm with $\geq 2\%$ of limbs ≥ 30 cm remaining
Hard snag 10-49	Density of snags ^c > 1.5 m tall and > 10 to 49 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining

^a Decay classes according to Fogel et al. (1973), as modified by Sollins (1982).

^b Base of a topped off dead tree that is between 0.3–1.5 m tall.

^c Standing dead tree > 1.5 m tall.

and Anderson 1985). We added a strip equal to one-half MMDM as a border to each grid to estimate effective area sampled.

Habitat variables and sampling.—To describe microsite characteristics, we measured 26 vegetative and structural habitat elements using two nested plots (Carey 1995; Rosenberg and Anthony 1992; Spies et al. 1988) at trap stations where flying squirrels were captured and at every 3rd trap station without a capture. Major habitat elements included snags and live trees, understory vegetation, and volume and decay class (Fogel et al. 1973) of down woody material (Table 1). Percentage cover (estimated to the nearest 5%) of understory habitat variables were visually estimated in 1×1 m subplots centered at the trap station and at 4 and 7-m distances from the trap station in each of the 4 cardinal directions. Understory variables included herbaceous vegetation, moss, down wood (< 25 cm in diameter), surface water, and 3 groups of woody vegetation within each of 2 vertical strata (< 30 cm and 30–150 cm): 1) all *Vaccinium* species, of which the most common were red huckleberry (*Vaccinium parvifolium*) and 2 species of blueberry (*V. alaskaense* and *V. ovalifolium*); 2) other deciduous species; and 3) conifer species, which were primarily western hemlock, mountain hemlock, and Sitka spruce. *Vaccinium* were separated from other deciduous species because they are commonly the dominant understory woody vegetation in southeastern Alaska (Hanley and Brady 1997), and because of the significance of ericaceous shrubs in explaining variation in northern flying squirrel abundance in the Pacific Northwest (Carey et al. 1999). Average values of the 9 subplots were used to describe the understory at each trap station.

We also quantified density of snags and live trees. A snag was defined as a standing dead tree with diameter at breast height (dbh) ≥ 10 cm and > 1.5 m tall (Spies et al. 1988). Snags were classified as

hard snags when $> 2\%$ of their limbs > 30 cm in length remained, and as soft snags when $< 2\%$ of their limbs > 30 cm in length remained (Rosenberg and Anthony 1992). Within a 12.6 m radius, we recorded number of live trees of each species in each of 2 dbh categories, 5–10 cm and 11–49 cm, and number of hard and soft snags 10–49 cm dbh. Within a 20-m radius, we recorded snags and live trees in each of 2 larger dbh classes: 50–73 cm and ≥ 74 cm (Table 1).

All pieces of down wood 25–50 cm (midpoint diameter) were counted within a 12.6-m radius plot, whereas all larger pieces (> 50 cm) were counted in a 20-m radius plot. For each piece of down wood > 10 cm midpoint diameter, we collected midpoint diameter (cm), decay class (I–V—Sollins 1982), and length. Length and midpoint circumference ($\pi \times$ diameter) were used to calculate volume. Amount of down wood for each trapping station was estimated as volume (m^3) per m^2 ground area for each of the 5 decay classes.

Statistical analysis and habitat modeling.—We used a combination of descriptive statistics and explanatory models to relate habitat conditions within a radius of 20 m of trap stations to flying squirrel captures, and stand-level condition to flying squirrel density in each forest type. At the microsite scale, we examined relationships between use and habitat features of trap stations with ≥ 1 capture versus a sample of trap stations without captures in the 3 upland-OG and 3 peatland-MC forest sites. Initially, we used histograms to examine the frequency distribution of captures per station for each habitat and season. For both forest types, distribution of captures was skewed toward 0 because a substantial proportion of trap stations ($\bar{X} = 35.4\%$) did not capture a flying squirrel. The remaining proportion was distributed among sites with captures ranging from 1 to 6, of which about 25% had a single capture and 30% had 2 captures. To determine

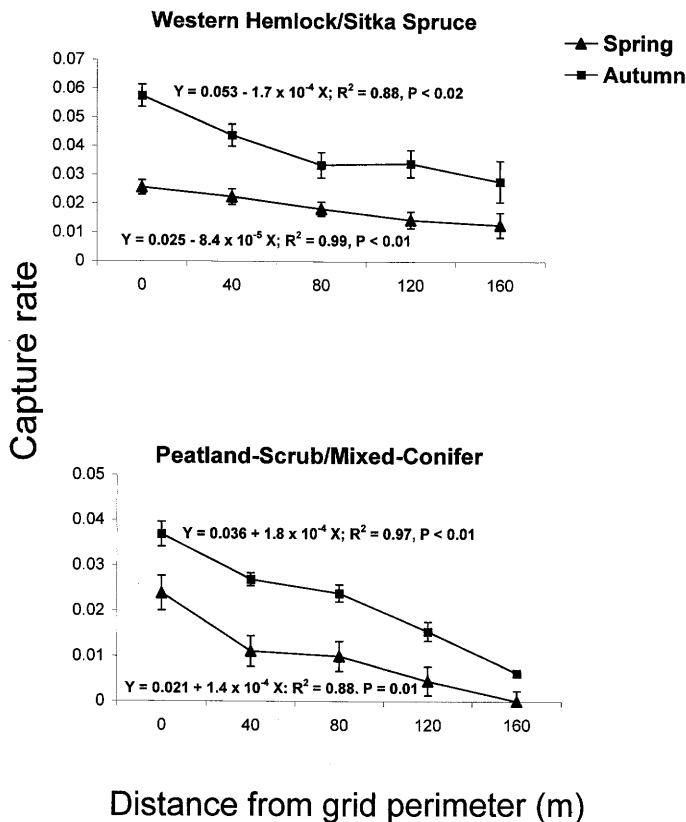


FIG. 1.—Likelihood of capturing (capture rate) northern flying squirrels (*Glaucomys sabrinus griseifrons*) as a function of distance of trap stations from perimeter of sampling grids in peatland-scrub-mixed conifer and western hemlock–Sitka spruce rainforest during spring (March–April) and autumn (September–October) 1998–2000, north-central Prince of Wales Island, southeastern Alaska.

if captures were influenced by a positive edge effect (Carey et al. 1999), we used simple linear regression (SAS 2000) and plotted the likelihood of capture relative to distance from the grid perimeter. Likelihood of capturing a flying squirrel (i.e., capture rate) at each trap station was computed as total number of captures at a station divided by total number of trap nights (Nelson and Clark 1973). We used ANOVA to compare vegetative and structural features among concentric sets of traps ($n = 5$) to determine if capture edge effect could possibly bias our habitat analyses. We pooled capture data across years to improve precision because seasonal densities of flying squirrels within forest types were similar among years with 1 exception (upland-OG in autumn 1998—Smith and Nichols 2003). We compared means with Duncan's multiple range test when significant variation was indicated.

To model habitat use, each trap station was categorized as either realized habitat when a squirrel was captured or unrealized habitat (Carey et al. 1999). We used a dichotomous response because of anticipated problems with model convergence using a polytomous response (no captures compared to 1 capture compared to >1 capture) when the likelihood of capturing a flying squirrel is greatly skewed toward 1 response level (e.g., 0 captures—Stokes et al. 1995); and because we had little ecological justification for delineating distinct categories for multiple captures, especially differentiating between trap stations with 1 versus 2 captures. For each of the 26 habitat elements, we used summary statistics, box and whisker plots, and histograms to examine distribution and variance structure. All habitat

measurements recorded as percentage cover were arc sine transformed prior to examining density among study grids with linear regression (Zar 1999).

Stepwise logistic regression was used to examine relationships between habitat characteristics of trap stations and the likelihood of capturing squirrels (0 compared to ≥ 1 captures) in each habitat and season (4 models). Variables were entered into a model if the $P \leq 0.25$, but were retained in the final model only if $P \leq 0.05$. We repeated the logistic regression analysis using the best subsets selection procedure (Cody and Smith 1997) and obtained similar results. For each significant variable in the final logistic regression models, we calculated confidence intervals on the odds-ratios, which were based on the profile likelihood (SAS 2000; Stokes et al. 1995). Thus, odds-ratio estimates were interpreted as the odds of capturing a flying squirrel given a specified unit increase in the habitat parameter (e.g., density of trees per ha) after being adjusted for the effects of other habitat elements in the model. We used the Hosmer and Lemeshow test to evaluate the suitability of each model, and examined several measures of goodness-of-fit (e.g., R^2) to evaluate the association of predicted probabilities and observed responses (SAS 2000). We also used prior probabilities (proportion of traps that captured squirrels) for each habitat $\times$ season combination to generate classification tables within PROC LOGISTIC in SAS to evaluate the performance of models in predicting captures among trap stations.

Lastly, to examine the relationship between population density and habitat elements at the stand level, we regressed mean density (pooled across years) of squirrels in replicate grids ($n = 6$) against the mean value of each habitat variable. Because of concerns over error rates, we limited regression analysis to habitat elements that from an inspection of plots appeared to have a linear relationship with mean density. We accepted $P \leq 0.10$ as the experiment-wise error rate. We performed multiple simple linear regressions during each season and used a Bonferroni-adjusted comparison-wise error rate to evaluate significance of select habitat elements (Zar 1999).

RESULTS

We caught 163 and 237 unique flying squirrels in peatland-MC and upland-OG forests, respectively. Corresponding total captures were 778 and 1,176, with 41,198 and 39,199 trap nights of effort, respectively. Capture probability (number captured $\div$ estimated number present) was relatively high across habitats, seasons, and years (range, 0.51–0.78). Recapture probability averaged 0.33 ($SE = 0.04$) and ranged 0.30–0.39. Capture rates in peatland-MC ranged 0–0.11 during spring and 0–0.14 during autumn; corresponding values in upland-OG were 0–0.12 and 0–0.20. Squirrel density in peatland-MC during spring ranged 0.4–1.9 squirrels/ha ($\bar{X} = 1.2$, $SE = 0.33$) among replicates and across years; corresponding values in upland-OG were 1.1–2.8 squirrels/ha ($\bar{X} = 1.8$, $SE = 0.35$). Autumn density ranged 0.4–3.3 squirrels/ha ($\bar{X} = 1.8$, $SE = 0.64$) and 2.2–5.3 squirrels/ha ($\bar{X} = 3.2$, $SE = 0.61$) in peatland-MC and upland-OG, respectively.

The proportion of stations with captures was highest (86%) in upland-OG during autumn and lowest (46%) in peatland-MC during spring; squirrels were captured at 64% of upland-OG and 63% of peatland-MC trap stations during spring and autumn, respectively. Traps on the perimeter of grids were more likely ($F = 21.1$ – 222.5 , $P < 0.02$) to catch flying squirrels than traps stations within the interior of the grid (Fig. 1) in both

TABLE 2.—Stepwise logistic regression models of habitat variables correlated with flying squirrel (*Glaucomys sabrinus griseifrons*) microhabitat use in peatland-MC (peatland-scrub-mixed-conifer) and upland-OG (western hemlock–Sitka spruce) rainforest during spring and autumn 1998–2000, Prince of Wales Island, southeastern Alaska.

Model	Variable ^a	<i>P</i>	Parameter estimate (<i>SE</i>)	Odds ratio ^b (95% CI)	Model goodness of fit ^c
Spring					
Peatland-MC					<i>P</i> = 0.23
	Vacc 4.5	0.001	0.035 (0.01)	1.4 (1.1–1.8)	
Upland-OG	Tree 74	0.007	0.098 (0.04)	2.7 (1.3–6.8)	<i>P</i> = 0.60
	Water	0.005	−0.087 (0.04)	0.4 (0.2–0.8)	
Autumn					
Peatland-MC					<i>P</i> = 0.85
	Tree 74	0.003	0.283 (0.12)	16.9 (2.8–615.5)	
Upland-OG	Vacc 1	0.029	0.064 (0.03)	1.9 (1.1–3.5)	<i>P</i> = 0.30
	Herb	0.013	−0.040 (0.02)	0.7 (0.5–1.0)	
	Soft 10-49	0.034	0.017 (0.01)	1.2 (1.1–1.4)	
	Tree 10-49	0.014	−0.003 (0.01)	1.0 (0.9–1.0)	
	Hard 50-74	0.045	0.083 (0.04)	2.3 (1.1–5.7)	

^a See Table 1 for a description of habitat variables.

^b Effect of a 10 unit increase in the value of the variable (e.g., percentage cover) on the probability of capture (SAS 2000).

^c Hosmer and Lemeshow test (SAS 2000), reported as the probability that the model will be improved by an additional habitat variable.

forest types during both seasons ($R^2 = 0.83$ – 0.98 , $P \leq 0.01$). However, with only one exception, mean values of habitat parameters in both forest types did not differ significantly ($F = 0.20$ – 3.12 , $df = 3$, $P \geq 0.026$) relative to distance from grid perimeter. In upland-OG, traps stations along the grid perimeter had a higher ($F = 4.78$, $P = 0.003$) density of hard snags with dbh 10–49 cm than the remaining sets of stations, which did not differ ($P > 0.05$). We measured habitat variables at 136 and 185 unique trap stations where squirrels were captured in peatland-MC during spring and autumn, respectively; corresponding values for upland-OG were 160 and 213 stations. We also measured habitat features at 149 and 100 systematically selected microsites where flying squirrels were not captured in peatland-MC during spring or autumn, respectively; corresponding sample sizes for trap stations without captures in upland-OG were 90 and 37 sites.

Stepwise logistic regression models of flying squirrel captures among trap stations.—We obtained 4 significant logistic regression models (Table 2). Density of large (>74 cm dbh) live trees was significant in both spring and autumn models of flying squirrel capture in peatland-MC. The estimated ecological impact of large trees on flying squirrels was substantial, especially during autumn when an increase in mean density of 10 trees/ha (2–12 trees/ha) increased the odds of capturing a squirrel by a factor of 17 (Table 2). In upland-OG, surface water was the only significant spring variable and a 10% increase in cover of water reduced the odds of capturing a squirrel by a factor of 2.5 ($1.0 \div 0.4$). The autumn upland-OG model included 4 habitat variables, but only density of hard snags 50–74 cm dbh and herb cover had a notable (odds ratio departed from 1.0) ecological impact on where flying squirrels were captured. Flying squirrel captures were positively correlated with density of hard snags, but inversely related to

herb cover. An increase of 10 snags/ha of hard snags with dbh 50–74 cm increased the odds of capturing a flying squirrel by a factor of 2.3, whereas a 10% increase in understory cover of herbs decreased the odds of capture by a factor of about one-half (i.e., $[1.0-0.7] \div 0.7$; Table 2).

The proportion of trap stations classified correctly ranged from 62.1–85.0% (Table 3). The percentage of capture sites correctly classified (sensitivity) and fraction of noncapture sites classified correctly (specificity) ranged between 61.4–100 and 0–62.7, respectively. With the exception of upland-OG during autumn, which performed best in predicting capture sites, about one-third of the trap stations were incorrectly classified as capture sites. Neither autumn model misclassified an observed capture site; however, in the spring a relatively large number of observed capture sites were misclassified (Table 3).

Flying squirrel density.—From an inspection of graph plots of flying squirrel density and stand-level averages of vegetative and structural features, we identified 4 variables during each season that warranted further analysis with linear regression. We obtained a significant positive relationship ($F = 13.1$, $P = 0.02$) during spring with amount of down wood in decay class III (Fig. 2), which explained 77% ($R^2 = 0.77$) of the variation in squirrel density across the 6 study sites. Similarly, percentage cover of moss and down wood in decay classes I and IV explained 70% ($P = 0.04$), 75% ($P = 0.025$), and 74% ($P = 0.029$) of the variation in spring squirrel density, respectively. Mean (and SE) percent cover of moss in upland-OG and peatland-MC was 73.5 (1.0) and 81.8 (0.7), respectively. Corresponding mean (and SE) densities (m^2) of down wood volume (m^3) for decay classes I, III, and IV were as follows: 0.31 (0.13) and 0.02 (0.02); 18.32 (1.43) and 4.06 (0.46); and 30.79 (1.83) and 4.62 (0.47), respectively. During autumn, density of trees >74 cm dbh explained 65% ($P = 0.05$) of the

TABLE 3.—Performance of logistic regression models of habitat variables in predicting flying squirrel (*Glaucomys sabrinus griseifrons*) microhabitat use in peatland-MC (peatland-scrub-mixed-conifer) and upland-OG (western hemlock-Sitka spruce) rainforest spring and autumn 1998–2000, Prince of Wales Island, southeastern Alaska.

Model	Probability level ^a	Correct ^b (%)	Sensitivity ^c (%)	Specificity ^d (%)	False positive ^e (%)	False negative ^f (%)
Spring						
Peatland-MC	0.51	62.1	61.4	62.7	36.8	39.0
Upland-OG	0.64	65.6	99.4	5.6	34.8	16.8
Autumn						
Peatland-MC	0.70	70.0	100	0	30.0	—
Upland-OG	0.85	85.0	100	0	15.0	—

^a Expected probability of a capture, which is based on the observed or prior probability.

^b Fraction of trap stations that were correctly classified.

^c Fraction of capture sites that were correctly classified.

^d Fraction of noncapture sites that were correctly classified.

^e Fraction of trap stations predicted to capture an animal that were incorrectly classified as a capture site.

^f Fraction of trap stations predicted to not be a capture site that were incorrectly classified as a noncapture site; dash denotes rate was not computable.

variation in population density among grids (Fig. 2). Also, trees with dbh 10–49 cm and 5–10 cm, which were negatively correlated with trees >74 cm ($r = -0.81$, $P = 0.05$ and $r = -0.91$, $P = 0.01$, respectively), explained 73% ($P = 0.03$) and 72% ($P = 0.03$) of the variation in squirrel density during autumn. Mean density (SE) of trees (ha) >74 cm, 10–49 cm, and 5–10 cm in upland-OG and peatland-MC, respectively, were as follows: 24.9 (1.0) and 1.4 (0.3); 308.2 (8.2) and 472.3 (13.6); and 150.1 (6.9) and 342.0 (11.1). When we compared stand-level means of habitat variables with t -tests ($n = 26$), all but 3 (Stump, Vacc 1, Water) differed significantly ($t = 3.50$ – 22.7 , $df = 347$ – 584 , $P < 0.01$) between upland-OG and peatland-MC.

DISCUSSION

Our study provides the first quantitative analysis of northern flying squirrel microhabitat use and density relative to micro-site and stand-level characteristics in southeastern Alaska temperate rainforest. We documented significant relationships between flying squirrel captures and vegetative and structural features surrounding trap stations, and identified several stand-level characteristics that explained variation in population density between forest types. The findings of this study contribute to our knowledge of the region's natural history and to a more general understanding of the autecology of *G. sabrinus* populations in coastal coniferous forests of north-western North America. This information also is important to land managers in southeastern Alaska, who are seeking reliable means of assessing ecosystem management of temperate rainforest (United States Department of Agriculture, Forest Service 1997). However, because our study was conducted in natural rainforest in largely unmanaged landscapes and because the fitness value of individual habitat features to northern flying squirrels might vary among macrohabitats and region (Carey et al. 1999), we recommend that caution be exercised in generalizing ecological patterns documented in this study beyond unmanaged forest types of southeastern Alaska.

An important finding of our study was a positive edge effect on captures of flying squirrels. That flying squirrels are

captured at higher rates along the perimeter of a trapping grid is not unusual (Carey et al. 1999), but it has significant implications for estimating population density (Wilson and Anderson 1985) and it can contribute bias in analyses of habitat relations. An inherent assumption of our analysis was that squirrel captures largely were a proximate response to habitat conditions within 20 m of trap stations. Any phenomenon that influences capture rates independent of habitat potentially contributes confounding variation to such analyses, especially if variation in habitat conditions is coincidentally correlated with variation in capture rates. Fortunately, the habitat condition of trap stations in our study was independent of their location relative to the grid perimeter in both forest types. Therefore, we believe that our analysis of habitat use was not biased by capture rates of flying squirrels that were higher along the perimeter than in the central interior of the grid.

Smith and Nichols (2003) concluded that western hemlock–Sitka spruce forest was primary habitat for *G. sabrinus* in southeastern Alaska because multiple demographic parameters were higher in upland-OG than peatland-MC. In this study, we quantified variation in population density among stands relative to differences in vegetative or structural features to identify habitat correlates of flying squirrel demography in southeastern Alaska. When averaged across microsites, 23 of 26 habitat variables differed between upland-OG and peatland-MC forests. Density of flying squirrels appeared to be correlated with 4 variables during spring and 4 variables during autumn. Strictly speaking, however, only down wood in decay classes III and I were statistically significant ($P \leq 0.025$) variables. Rosenberg and Anthony (1992) found no significant relationship between population density and habitat features among old-growth and second-growth stands in Oregon and concluded that the northern flying squirrel was a habitat generalist. We do not believe that the limited number of statistically significant correlates in our study indicates this species is a habitat generalist of temperate rainforest. Rather, we think that study design constrained our ability to detect significant correlations between habitat variables and population density. We used multiple, simple linear regressions (rather than multiple

regression) to investigate relationships between population density and 26 habitat variables because there were only 6 observations (study grids) of squirrel density. We used a Bonferroni-adjusted comparison-wise error rate to protect the experiment-wise Type-I error, but at the expense of statistical power (SAS 2000). For that reason, we think that trees with 10–49 cm dbh, trees with 5–10 cm dbh, and down wood in decay class IV, all of which had P -values near the adjusted error rate and $R^2 > 70\%$, were ecologically significant correlates of flying squirrel density in our study.

A somewhat surprising result of our study was that squirrel capture in upland-OG was not significantly correlated with trees >74 cm dbh, given its apparent significance in peatland-MC and reputed fitness value to flying squirrels elsewhere (Bakker and Hastings 2002; Carey et al. 1997, 1999). However, the absence of a statistically significant relationship does not necessarily preclude ecological importance. Discriminating statistically significant features when modeling habitat use is as much a function of resource availability as use, and vital resources might not appear valuable simply because they are widely abundant. In our study, density of trees with >74 cm dbh was an order of magnitude higher in upland-OG (25 trees/ha) than in peatland-MC (<2 trees/ha). Thus, large trees likely are a valuable resource in both forest types, but only limiting in peatland-MC. This conclusion is supported further by the fact that trees with dbh >74 cm explained 65% of the variation in squirrel density among study sites.

Large trees and snags are important features of northern flying squirrel habitat (Bakker and Hastings 2002; Carey 1991, 1995; Carey et al. 1997; Cowan 1936). *G. sabrinus* typically selects large, old trees for denning (Bakker and Hastings 2002; Carey et al. 1997; Cotton and Parker 2000) and has a strong preference for tree cavities as den sites (Bakker and Hastings 2002; Carey et al. 1997; but see Mowrey and Zasada 1984). In intensively managed landscapes, cumulative broad-scale disturbances such as clear-cut logging can eliminate large trees and snags for extended periods (Carey et al. 1997; Cotton and Parker 2000), and den availability has been proposed as a limiting factor of flying squirrel populations in younger forests (Carey 1991; Carey et al. 1997). However, empirical evidence of den availability limiting flying squirrel populations is limited and conflicting. Witt (1991) reported that carrying capacity of second-growth forests can be increased with supplemental dens, but more recent evidence suggests that northern flying squirrels can exhibit considerable plasticity in den tree use (Cotton and Parker 2000); consequently dens probably are not limiting flying squirrel populations in second-growth coniferous forest of the Pacific Northwest (Carey 2002).

In southeastern Alaska, flying squirrels used snags more than live trees for denning, and those that denned in live trees or snags chose larger diameter structures (Bakker and Hastings 2002). The majority of nests (72%) were in cavities, but up to 28% of dens were external nests such as in dwarf mistletoe (*Arceuthobium tsugense*). Cavities were abundant and trees that supported medium to high epiphytic loads were common (Bakker and Hastings 2002). Based on their results, we believe

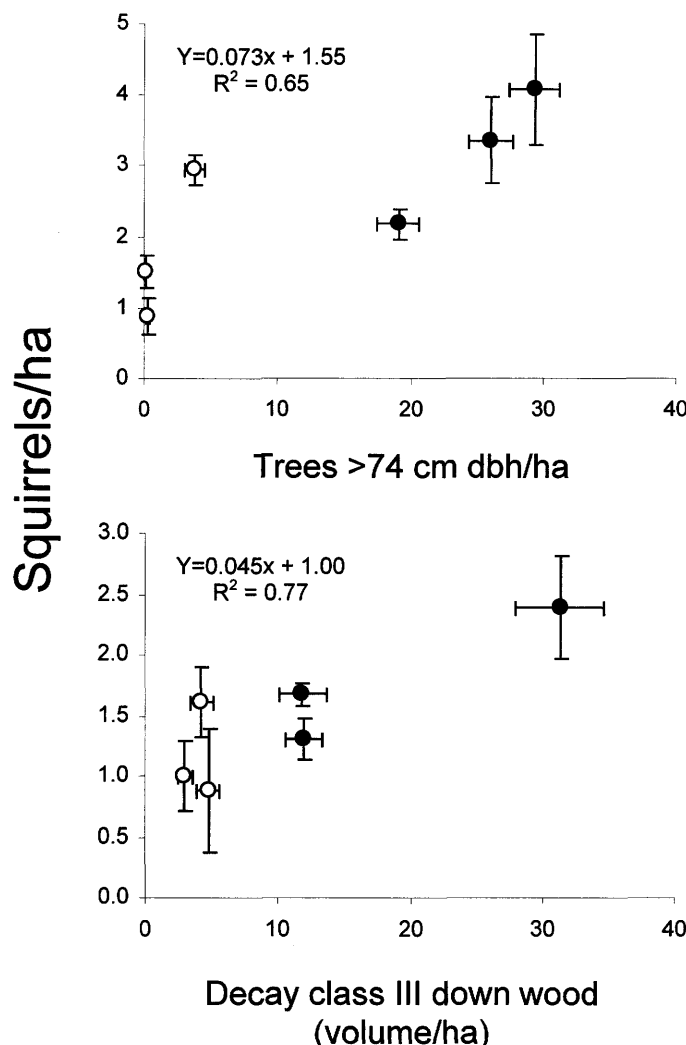


FIG. 2.—Relationship between density of northern flying squirrels (*Glaucomys sabrinus griseifrons*) during autumn and density of large (>74 cm) trees, and flying squirrel density during spring and abundance of down wood in decay class III. Decay classes delineated according to Fogel et al. (1973), as modified by Sollins (1982). Data points constitute average values ($\bar{X} \pm SE$) for upland-OG (●) and peatland-MC (○) habitats. Standard error bars denote variation in both the predictor (x) and response (Y) variables.

that availability of suitable den trees probably is not limiting flying squirrel populations in southeastern Alaska. Still, the results of our study suggest that highly preferred den sites might be much less available in peatland-MC than upland-OG. Not only were large trees and snags less abundant, within-stand variability was much higher in peatland-MC ($CV = 360\%$) than upland-OG ($CV = 69\%$). Capture sites in peatland-MC averaged twice the density of large trees than sites without captures. Also, the mosaic nature of peatland-MC likely reduces flying squirrel access to suitable den trees because large trees and snags are clumped in highly productive microsites that are interspersed among open-canopy muskegs (Neiland 1971). More importantly, select timber harvest of more productive portions of peatland-MC, which has been

proposed to mitigate logging pressure in upland-OG (United States Department of Agriculture, Forest Service 1997), will further reduce availability of large trees within peatland-MC and likely reduce the capability of those stands to support northern flying squirrel populations. This is a key finding because of the potential role of peatland-MC in maintaining viable populations of *G. sabrinus* in managed landscapes (Smith and Nichols 2003).

Microhabitat use by flying squirrels also was highly correlated with understory cover of *Vaccinium*. This was most evident in peatland-MC, where the odds of capturing flying squirrels increased substantially during both seasons with increasing percent cover of *Vaccinium*. The ecological link between *Vaccinium* abundance and flying squirrel capture rate is unknown but could be related to increased foraging opportunities or cover from predation. Carey (1995) reported that ericaceous shrubs influence diversity of mycorrhizal fungi (i.e., truffles), the primary food of flying squirrels in the Pacific Northwest (Carey et al. 1999; Pyare et al. 2002; Rosentreter et al. 1997; Waters et al. 2000). It is unclear to what extent *Vaccinium* species are associated with hypogeous mycorrhizal fungi in temperate rainforests. Flying squirrels in southeastern Alaska included truffles in their diet, but they were not as dependent on truffles as flying squirrel populations in the Pacific Northwest (Pyare et al. 2002). This was especially true of flying squirrels in peatland-MC, whose diets included only one genus of truffle. Alternatively, the fruit of *Vaccinium* might be an important source of food for flying squirrels, especially during late summer–early autumn when blueberries and huckleberries become abundant. The extent to which *G. sabrinus* in southeastern Alaska includes fruit in its diet is unclear, but northern flying squirrels in the Pacific Northwest frequently consume fruits (Thysell et al. 1997).

Another potential benefit of abundant *Vaccinium* ground cover is avoidance of predators such as owls (Strigidae) or the northern goshawk (*Accipiter gentilis*). Several investigators reported that flying squirrels in the Pacific Northwest selected microsites with greater understory cover (Carey 1995; Carey et al. 1999; Pyare and Longland 2002). Populations of *G. sabrinus* in the Pacific Northwest might experience high predation rates from the northern spotted owl (*Strix occidentalis*), a specialized predator of flying squirrels in old-growth coniferous forests (Forsman et al. 1984). Southeastern Alaska has few (if any) predators that specialize on *G. sabrinus* and predation rates might be relatively low. Still, the perceived risk of predation might influence microhabitat use (Lima et al. 1985), especially in peatland-MC where typically *Vaccinium* species represent the only cover available to flying squirrels foraging on the ground.

Interestingly, the habitat space realized by flying squirrels fluctuated between forest types and seasons. During both seasons, flying squirrels were caught at fewer stations in peatland-MC than in upland-OG, the latter of which had fewer correlates of microhabitat use. Also, flying squirrels were caught at more stations during autumn than spring in both forest types. The disparity between forest types might have been related to differences in spatial heterogeneity and

resource availability. Upland-OG was more homogeneous and key resources (e.g., large trees) were more abundant and more uniformly distributed than in peatland-MC. This might in part explain why we observed fewer ecologically significant variables in upland-OG than peatland-MC. That is, flying squirrels perhaps showed less discrimination in upland-OG because of less within-stand variability. Factors responsible for seasonal variation are less clear. Increasing realized habitat space during autumn might have been in response to phenological changes that facilitate use of more sites by flying squirrels. *Vaccinium* species undergo a marked transformation between spring and autumn with a dramatic increase in vegetative cover and production of fruit. Perhaps flying squirrels were captured at more stations during autumn because food resources were more widely available; or, access to resources was less constrained because predation risks were lower (Carey et al. 1999; Pyare et al. 2002). Alternatively, we might have caught flying squirrels at more locations during autumn because there were more flying squirrels with higher probabilities of capture (Smith and Nichols 2003).

On the Olympic Peninsula, Carey (1995) reported higher abundance of flying squirrels only where densities of large snags were >5 snags/ha and prevalence (proportion of sites with dense cover) of ericaceous shrub cover was $\geq 40\%$. Coarse woody debris and prevalence of ericaceous shrubs also were attributes of 19 stands in southwestern Oregon that were correlated with squirrel abundance or carrying capacity (i.e., maximum density—Carey et al. 1999). However, not all stands that met these criteria achieved higher population levels and this pattern varied regionally, suggesting that the habitat of northern flying squirrels in the Pacific Northwest is multifactorial and varies among forest types (Carey 1995; Carey et al. 1999). In our study, mean density of snags >50 cm dbh contributed little toward explaining variation in squirrel density between forest types. However, availability of suitable den trees might be an important feature distinguishing upland-OG and peatland-MC, which differed markedly in density and dispersion of large trees. Bakker and Hastings (2002) reported that a large ($\sim 40\%$) proportion of dens used by flying squirrels in southeastern Alaska were in live trees. Perhaps the prominent use by northern flying squirrels of large live trees for denning in southeastern Alaska (Bakker and Hastings 2002) precludes the need for large snags.

We did not measure percentage cover or prevalence of ericaceous shrubs, but understory cover of deciduous woody vegetation (many of which were ericaceous species) and *Vaccinium* were higher among study grids with higher flying squirrel densities. Additional understory features associated with higher population density were volume of decayed down wood and percent cover of moss. Admittedly, the value of moss or decayed down wood to flying squirrel populations in southeastern Alaska is not immediately apparent, but perhaps they are ecological correlates of important resources. In temperate rainforest, moss typically occurs on wetter sites and nutrient-poor soils (Alaback 1982; Neiland 1971) and in our study it was directly correlated with percentage cover of

Vaccinium in both forest types. In upland-OG, where its prevalence typically indicates a more open canopy, moss cover was inversely correlated with density of large trees. Thus, the ecological significance to northern flying squirrels might be that moss cover is a correlate of open-canopied sites with an abundance of *Vaccinium* in the understory.

The ecological significance of higher densities of soft snags of 10–49 cm, or lower densities of trees 10–49 cm and lower percentage cover of surface water or herbs in upland-OG eludes us. Documenting a significant correlation between these variables and flying squirrel captures is a unique finding of our study. Density of trees 10–49 cm and soft snags 10–49 cm have odds ratios that did not depart appreciably from unity, indicating that the influence on habitat use was negligible. However, percentage cover of surface water during spring, and to a lesser extent percentage cover of herbs during autumn, were highly significant variables to which flying squirrels responded with considerable sensitivity in upland-OG. The causal relationship between flying squirrel capture and amount of surface water or herb cover remain unclear, and perhaps these variables are ecological correlates of biotic or abiotic characteristics that were not measured.

Although some of our findings corroborate results of earlier studies, there were notable differences. This was not surprising because correlates of flying squirrel density and habitat use vary considerably across western coniferous forests (Carey et al. 1999; Pyare and Longland 2002; Rosenberg and Anthony 1992; Smith et al. 2003). In the Sierra Nevada Range, flying squirrels preferred sites with understory (<2 m) cover; neither availability of snags nor coarse woody debris influenced flying squirrel occurrence (Pyare and Longland 2002). Captures in the Pacific Northwest were positively correlated with foliage height diversity and midstory cover (>2-m subcanopy), whereas prevalence (proportion of sites with dense cover) of ericaceous shrubs and coarse woody debris explained only 39% of the variability in captures across stands (Carey et al. 1999). Sites without squirrel captures typically had a higher density of conifers and snags with medium-sized dbh, whereas the maximum density of flying squirrels occurred in stands with the highest coarse woody debris and decadence (i.e., multivariate factor of old-forest features).

Similarly, we observed that flying squirrel captures increased with increasing cover of ericaceous shrubs (*Vaccinium*) in the understory, and that maximum flying squirrel density occurred in the stand with the largest amount of coarse woody debris. Sites across peatland-MC without captures typically had a higher density of conifer saplings and more herb cover, whereas unused upland-OG sites consistently had higher densities of all saplings. Unlike Carey et al. (1999), we found that a few key individual variables explained variation in flying squirrel captures. Furthermore, Smith et al. (in press), derived several multivariate habitat factors from our set of 26 habitat variables, including a factor comprised of several decadent features typical of old forest (snags, coarse woody debris), but these habitat factors added little ecological information about flying squirrel microhabitat use or abundance in peatland-MC or upland-OG.

In the Pacific Northwest, multivariate habitat factors such as decadence, habitat breadth (within-stand diversity), and moisture-temperature gradient values (MGV) largely explained variation in flying squirrel carrying capacity (Carey et al. 1999). In our study, several features typical of late-seral forest varied directly with flying squirrel density (e.g., down wood), or were correlated with microhabitat use (e.g., large snags). That we did not observe more variation in squirrel density or habitat use attributed to old-growth features might be related to the narrow range of habitat conditions we examined. Both peatland-MC and upland-OG contained a relatively large volume of down wood and relatively high density of snags and stumps. Had we included younger, less complex forest in our comparison, we suspect that more attributes typical of old forest would have emerged as correlates of population density. The significance of factors such as habitat breadth and MGV in the Pacific Northwest could be related to the diversity of small mammal communities (Verts and Carraway 1998) and the role of habitat diversity in facilitating resource partitioning among several ecologically similar small mammal species (Carey 1991, 1995, 1996, 2000a; Carey et al. 1999). Mesic to wet coniferous forests of the Pacific Northwest support several arboreal and semi-arboreal species that potentially share several resources (Carey 1991; Maser et al. 1978; Verts and Carraway 1998). In contrast, the mammal fauna of southeastern Alaska is relatively depauperate and *G. sabrinus griseifrons* is syntopic with only 1 other common rodent, *Peromyscus keeni* (MacDonald and Cook 1996).

Thus, *Glaucomys sabrinus* in southeastern Alaska seems to interact with a different biotic and abiotic environment than populations in the Pacific Northwest. The habitat of *G. sabrinus* in the Pacific Northwest apparently is an emergent property of old-growth forest (Carey et al. 1999), whereas evidence from southeastern Alaska suggests that the habitat of flying squirrels is not strictly multifactorial (Smith et al., in press). These differences are not trivial and are somewhat surprising, given regional similarities in climate and forest composition and structure, and suggest that *G. sabrinus* populations of southeastern Alaska differ ecologically from populations in the Pacific Northwest in several important ways (Smith and Nichols 2003; Smith et al., in press). The extent to which these differences are a consequence of genetic dissimilarities (Arbogast 1999) or result from regional differences in biotic and abiotic factors is unclear. The vertebrate community within which flying squirrel populations of southeastern Alaska interrelate (MacDonald and Cook 1996) is different from communities in the Pacific Northwest (Verts and Carraway 1998). Moreover, the dynamics of interspecific interactions, such as competition and predation might be quite different (Smith and Nichols 2003).

Nonetheless, if the habitat relations of *G. sabrinus* in southeastern Alaska differ from populations in the Pacific Northwest, explanations could lie in their more generalized diet or lifestyle (Pyare et al. 2002). A consistent predictor of northern flying squirrel captures and density across several studies in the Pacific Northwest has been frequency or abundance of hypogeous sporocarps (i.e., truffles—Carey et

al. 1999; Pyare and Longland 2002; Waters and Zabel 1995; Waters et al. 2000). Thus, the link between flying squirrel populations in the Pacific Northwest and decadence largely might be a function of their dependence on truffles (Carey et al. 1999). Several investigators have reported correlations between the abundance of truffles and mushrooms and old forest attributes, such as coarse woody debris or decayed down wood (Amaranthus et al. 1994; Smith et al. 2000, 2002). Features typical of old forest condition that were correlated with habitat use in southeastern Alaska and the Pacific Northwest (e.g., snags) might be related to other aspects of flying squirrel life history, without any apparent connection to truffle distribution and abundance. Evidence from southeastern Alaska is limited in scope and lacks an explicit empirical basis for conclusions about habitat use and diet. Additional studies of flying squirrels that investigate the interrelationships among habitat use, microhabitat structure, and preferred foods are needed to thoroughly examine this question.

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LITERATURE CITED

- ALABACK, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932–1948.
- ARBOGAST, B. S. 1999. Mitochondrial DNA phylogeography of the New World flying squirrels (*Glaucomys*): implications for Pleistocene biogeography. *Journal of Mammalogy* 80:142–155.
- AMARANTHUS, M. P., D. S. PARRISH, AND D. A. PERRY. 1994. Decaying logs as moisture reservoirs after drought and wildfire. Pp. 191–194 in *Stewardship of soil, air, and water resources: Proceedings of Watershed 89* (E. Alexander, ed.). United States Department of Agriculture, Forest Service, Region 10, Juneau, Alaska.
- BAKKER, V. J., AND K. HASTINGS. 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. *Canadian Journal of Zoology* 80:1623–1633.
- CAREY, A. B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. *Natural Areas Journal* 9:151–162.
- CAREY, A. B. 1991. The biology of arboreal rodents in Douglas-fir forests. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-276, Portland, Oregon.
- CAREY, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications* 5:648–661.
- CAREY, A. B. 1996. Interactions of northwest forest canopies and arboreal mammals. *Northwest Science* 70 (Special issue):72–78.
- CAREY, A. B. 1998. Ecological foundation of biodiversity: lessons from old growth and managed forests. *Northwest Science* 72 (Special issue 2):127–133.
- CAREY, A. B. 2000a. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. Pp. 45–66 in *Biology of gliding mammals* (R. L. Goldingay and J. S. Scheibe, eds.). Filander Verlag, Fürth, Germany.
- CAREY, A. B. 2000b. Effects of new forest management strategies on squirrel populations. *Ecological Applications* 10:248–257.
- CAREY, A. B. 2001. Experimental manipulation of spatial heterogeneity in Douglas-fir forests: effects on squirrels. *Forest Ecology and Management* 152:13–30.
- CAREY, A. B. 2002. Response of northern flying squirrels to supplementary dens. *Wildlife Society Bulletin* 30:547–556.
- CAREY, A. B., B. L. BISWELL, AND J. W. WITT. 1991. Methods for measuring populations of arboreal rodents. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-273, Portland, Oregon.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- CAREY, A. B., J. KERSHNER, B. BISWELL, AND L. DOMINGUEZ DE TOLEDO. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs* 142:1–71.
- CAREY, A. B., T. M. WILSON, C. C. MAGUIRE, AND B. L. BISWELL. 1997. Dens of northern flying squirrels in the Pacific Northwest. *Journal of Wildlife Management* 61:684–699.
- CODY, R. P., AND J. K. SMITH. 1997. Applied statistics and the SAS programming language. 4th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.
- COTTON, C. L., AND K. L. PARKER. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. *Journal of Mammalogy* 81:1071–1086.
- COWAN, I. M. 1936. Nesting habits of the flying squirrel, *Glaucomys sabrinus*. *Journal of Mammalogy* 17:58–60.
- DEMEO, T., J. MARTIN, AND R. A. WEST. 1992. Forest plant association guide: Ketchikan Area, Tongass National Forest. United States Department of Agriculture, Forest Service, Alaska Region R10-MB-210.
- FOGEL, R., M. OGAWA, AND J. M. TRAPPE. 1973. Terrestrial decomposition: a synopsis. Coniferous Forest Biome Internal Report 135. College of Forest Resources, University of Washington, Seattle.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87:1–64.
- HANLEY, T. A., AND W. W. BRADY. 1997. Understory species composition and production in old-growth western hemlock–Sitka spruce forests of southeastern Alaska. *Canadian Journal of Botany* 75:574–580.
- HARRIS, A. S., AND W. A. FARR. 1974. The forest ecosystem of Southeast Alaska: 7. Forest ecology and timber management. United States Department of Agriculture, Forest Service General Technical Report PNW-25, Portland, Oregon.
- HUTCHINSON, O. K., AND V. J. LABAU. 1974. The forest ecosystem of Southeast Alaska: 9. Timber inventory, harvesting, marketing, and trends. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-34, Portland, Oregon.
- JULIN, K. R., AND J. P. CAOUEITE. 1997. Options for defining old-growth timber volume strata: a resource assessment. Pp. 24–37 in *Assessments of wildlife viability, old-growth timber volume estimates, forested wetlands, and slope stability* (C. G. Shaw III, technical

- coordinator). United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-392, Portland, Oregon.
- LIMA, S. L., T. J. VALONE, AND T. CARACO. 1985. Foraging-efficiency-predation-risk trade-off in the gray squirrel (*Sciurus carolinensis*). *Animal Behaviour* 33:155–165.
- MACDONALD, S. O., AND J. A. COOK. 1996. The land mammal fauna of southeast Alaska. *Canadian Field-Naturalist* 110:571–598.
- MASER, C. E., AND Z. MASER. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Naturalist* 48:358–369.
- MASER, C. E., Z. MASER, J. W. WITT, AND G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Canadian Journal of Zoology* 64:2086–2089.
- MASER, Z., C. E. MASER, AND J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Canadian Journal of Zoology* 63:1084–1088.
- MASER, C. E., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799–809.
- MENKENS, G. E., JR., AND S. H. ANDERSON. 1988. Estimation of small-mammal population size. *Ecology* 69:1952–1959.
- MOWREY, R. A., AND J. C. ZASADA. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pp. 351–356 in *Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, April 12–15, 1982* (W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds.). American Institute of Fishery Research Biologists.
- NEILAND, B. J. 1971. The forest bog complex of Southeast Alaska. *Vegetatio* 22:1–63.
- NELSON, L., JR., AND F. W. CLARK. 1973. Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy* 54:295–298.
- PYARE, S., AND W. F. LONGLAND. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forestry Research* 32:1016–1024.
- PYARE, S., W. P. SMITH, J. V. NICHOLS, AND J. A. COOK. 2002. Dietary uniqueness of northern flying squirrels in southeast Alaska. *Canadian Field-Naturalist* 116 (1):97–102.
- RANSOME, D. B., AND T. P. SULLIVAN. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. *Canadian Journal of Forest Research* 33:587–596.
- ROSENBERG, D. K., AND R. G. ANTHONY. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology* 70:161–166.
- ROSENRETER, R., G. D. HAYWARD, AND M. WICKLOW-HOWARD. 1997. Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho. *Northwest Science* 71:97–102.
- SAS. 2000. SAS/STAT user's guide, Release 8.1 Edition. SAS Institute, Inc., Cary, North Carolina.
- SCHOEN, J. W., M. D. KIRCHHOFF, AND O. C. WALLMO. 1984. Sitka black-tailed deer/old-growth relationships in Southeast Alaska: implications for management. Pp. 315–319 in *Proceedings of a symposium: Fish and wildlife relationships in old-growth forests* (W. R. Meehan, T. R. Merrell, and T. A. Hanley, eds.). American Institute of Fishery Research Biologists. Juneau, Alaska, USA.
- SEARBY, H. W. 1968. Climate of Alaska. Climatography of the United States No. 60–49. *Climates of the States, Alaska*. United States Department of Commerce, Environmental Science Service Administration, Environmental Data Service.
- SMITH, J. E., R. MOLINA, M. M. P. HUSO, AND M. J. LARSEN. 2000. Occurrence of *Piloderma fallax* in young, rotation age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the cascade range of Oregon, U.S.A. *Canadian Journal of Botany* 78:995–1001.
- SMITH, W. P., R. G. ANTHONY, J. R. WATERS, N. L. DODD, AND C. J. ZABEL. 2003. Ecology and conservation of arboreal rodents of the Pacific Northwest. Pp. 157–206 in *Mammal community dynamics in western coniferous forests: management and conservation* (C. J. Zabel and R. G. Anthony, eds.). Cambridge University Press, Cambridge, United Kingdom.
- SMITH, W. P., S. M. GENDE, AND J. V. NICHOLS. In press. The northern flying squirrel as a management indicator species of north temperate rainforest. *Ecological Applications*.
- SMITH, W. P., AND J. V. NICHOLS. 2003. Demography of the Prince of Wales flying squirrel: an endemic of Southeastern Alaska temperate rainforest. *Journal of Mammalogy* 84:1044–1058.
- SMITH, J. E., ET AL. 2002. Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade range of Oregon, U.S.A. *Canadian Journal of Botany* 80:186–204.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forestry Research* 12:18–28.
- SPIES, T. A., J. F. FRANKLIN, AND T. B. THOMAS. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–1702.
- STOKES, M. E., C. S. DAVIS, AND G. G. KOCH. 1995. Categorical data analysis using the SAS System. SAS Institute Inc., Cary, North Carolina.
- THYSELL, D. R., L. J. VILLA, AND A. B. CAREY. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle food items. *Northwestern Naturalist* 78:87–92.
- UNITED STATES DEPARTMENT OF AGRICULTURE, FOREST SERVICE. 1997. Land and resource management plan: Tongass National Forest. United States Department of Agriculture, Forest Service R10-MB-338dd. Juneau, Alaska.
- VER HOEF, J. M., B. J. NEILAND, AND D. C. GLENN-LEWIN. 1988. Vegetation gradient analysis of two sites in southeast Alaska. *Northwest Science* 62:171–180.
- VERTS, B. J., AND L. N. CARRAWAY. 1998. *Land mammals of Oregon*. University of California Press, Berkeley, California.
- VILLA, L. J., A. B. CAREY, T. M. WILSON, AND K. E. GLOS. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. United States Department of Agriculture, Forest Service General Technical Report PNW-GTR-444, Portland, Oregon.
- WATERS, J. R., K. S. MCKELVEY, C. J. ZABEL, AND D. LUOMA. 2000. Northern flying squirrel mycophagy and truffle production in fir forests in northeastern California. United States Department of Agriculture, Forest Service General Technical Report PSW-GTR-178, Albany, California.
- WATERS, J. R., AND C. J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management* 59:858–866.
- WEIGL, P. D., T. W. KNOWLES, AND A. C. BOYNTON. 1992. The distribution of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. North Carolina Wildlife Resources Commission, Raleigh, North Carolina.
- WILSON, K. R., AND D. R. ANDERSON. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.

- WITT, J. W. 1991. Increasing the carrying capacity of second-growth stands for flying squirrels with the use of nest boxes. P. 529 in Wildlife and vegetation of unmanaged Douglas-fir forests (L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators). United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-285, Portland, Oregon.
- WITT, J. W. 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. *Journal of Mammalogy* 73:921-929.
- ZAR, J. H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.
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