

THE NORTHERN FLYING SQUIRREL AS AN INDICATOR SPECIES OF TEMPERATE RAIN FOREST: TEST OF AN HYPOTHESIS

WINSTON P. SMITH,¹ SCOTT M. GENDE,² AND JEFFREY V. NICHOLS³

U.S. Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 2770 Sherwood Lane, Suite 2A, Juneau, Alaska 99801-8545 USA

Abstract. Management indicator species (MIS) often are selected because their life history and demographics are thought to reflect a suite of ecosystem conditions that are too difficult or costly to measure directly. The northern flying squirrel (*Glaucomys sabrinus*) has been proposed as an MIS of temperate rain forest of southeastern Alaska based on previous studies in the Pacific Northwest that demonstrated its habitat is multi-factorial, i.e., an emergent property of old-growth forest. We evaluated the suitability of flying squirrels as MIS in temperate rain forests of Alaska by modeling seasonal (spring, autumn) microhabitat use with stepwise logistic regression (SLR) using either individual habitat variables ($n = 26$) or multivariate habitat “factors,” which were linear combinations of individual habitat variables generated from factor analysis. We compared the efficacy of single variable vs. multivariate factor models in explaining variation in microhabitat use to test the hypothesis that the habitat of flying squirrels in southeastern Alaska was an emergent property of old-growth rain forest. The underlying premise was that if factors were more thorough in explaining microhabitat use, the habitat of flying squirrels was multifactorial; that is, it consisted of multiple late-seral forest attributes occurring coincidentally at usable spatial scales (e.g., home range). SLR models with multivariate factors performed poorer in predicting capture sites than models of individual habitat variables. Two variables, density of large (>74 cm dbh) trees and understory cover of *Vaccinium*, explained much of the variation in microhabitat use. We conclude that the habitat of *G. sabrinus* in southeastern Alaska does not reflect emergent properties of old-growth forest in southeastern Alaska and hypothesize that this pattern may be related to regional ecological differences that facilitate a more general lifestyle than populations in the Pacific Northwest. Furthermore, the effectiveness of *Glaucomys sabrinus* as an MIS in north temperate rain forest is suspect, illustrating that regional differences in ecology of a species warrant caution when considering the suitability of MIS among geographic areas.

Key words: density; *Glaucomys sabrinus* griseifrons; logistic regression; microhabitat use; northern flying squirrel; old growth; southeastern Alaska; temperate rain forest.

INTRODUCTION

Whether land management planning (e.g., habitat conservation plans; Loehle et al. 2002) will facilitate a long-term goal of maintaining biological diversity is foremost among many issues challenging forest managers today (Szaro and Johnston 1996). The recent shift from single-species management toward consideration of ecological communities signifies an increasing appreciation for maintaining functional relationships and processes in forested ecosystems (Carey and Curtis 1996, Willson 1996, Williams et al. 2002). However, the value of species with unique life histories and ecological attributes, or significant community relation-

ships, should not be ignored (Carey 1991, 1995, Schmitz et al. 2000, Soulé et al. 2003). Some species have relatively complex life histories and their habitat is multi-factorial; their presence indicates the presence of complex habitat conditions, such as old-growth forests (Carey et al. 1999, Carey 2000a). Others have evolved keystone roles linked to fundamental processes (Maser et al. 1978, Willson et al. 1998). Equally important are interspecific relationships, such as competitive (e.g., Smith 1981) or predator-prey interactions (e.g., Carey et al. 1992, Soulé et al. 2003). Cascading effects to vertebrate assemblages of losing species that play keystone roles or have complex life histories can be substantial, including a reduction of ecosystem stability or resiliency through a loss of additional species or diminished ecosystem function (Borrvall et al. 2000, Schmitz et al. 2000).

Regardless of whether the focus is ecosystem processes or multi-species relationships within communities, challenges of managing forest ecosystems are intensified by the fact that many vertebrates of late-seral forests are habitat or trophic specialists and thus

Manuscript received 29 January 2003; revised 28 June 2004; accepted 21 July 2004. Corresponding Editor: G. H. Aplet.

¹ E-mail: WinstonSmith@fs.fed.us

² Present address: National Park Service, Glacier Bay Field Station, 3100 National Park Road, Juneau, Alaska 99801 USA.

³ Present address: Alaska Department of Fish and Game, Division of Sport Fish, Southeast Regional Office, P.O. Box 240020, Douglas, Alaska 99824 USA.

are sensitive to cumulative disturbance (Carey 1991, 1995, Laurance 1991, Patton 1992, Lomolino and Perault 2000). Nowhere has the challenge of sustainable management of multiple forest values been more evident recently than in landscapes of western North America, especially the Pacific Northwest, where several wildlife species apparently achieve their highest densities in old-growth coniferous forests (Forsman et al. 1984, Carey 1989, Huff et al. 1992). Extensive modification of old-growth forests has generated much concern over biological diversity (Szaro and Johnston 1996, Carey 1998, 2000a, b), especially the viability of late-seral habitat specialists (Forest Ecosystem Management Assessment Team 1993, Everest et al. 1997). Add to this the practical challenges and less than stellar accomplishments of single-species management, and the prospect of maintaining biological diversity in managed forests is disappointing (Simberloff 1998).

Ecosystem management recently emerged as a broad-scale ecological paradigm for maintaining biological diversity across federal (Rauscher 1999) and many industrial forests (Loehle et al. 2002), largely because of both theoretical and empirical strengths over managing single species (Simberloff 1998). However, there are many practical challenges to maintaining the ecological and functional integrity of entire watersheds, not the least of which is monitoring a myriad of ecosystem elements and processes (Landres et al. 1988, Niemi et al. 1997, Simberloff 1998). Because monitoring ecosystems is problematical, managers have selected surrogates, most notably "indicator" species, to assess environmental conditions or evaluate the response of forest ecosystems to external perturbations (Simberloff 1998). The concept of indicator species is not novel (Hall and Grinnell 1919), but its prominence in natural resource management emerged during the mid-1970s and mid-1980s, when its application became formally integrated into procedures used by the USDI Fish and Wildlife Service (U.S. Department of Interior 1980) and USDA Forest Service. Regulations pursuant to the National Forest Management Act of 1976 (Code of Federal Regulations 1985) require that National Forests incorporate management indicator species (MIS) in effects analyses of management plan alternatives during forest planning (e.g., Tongass National Forest; Everest et al. 1997).

Criteria for selecting MIS may vary according to management goals, but typically species whose populations are thought to reflect the "health" of an ecosystem are primary candidates (Landres et al. 1988, Simberloff 1998). In practical terms, ecosystem health represents a myriad of habitat attributes and processes, which often are too difficult or costly to measure. Accordingly, species with complex life histories are good MIS candidates, particularly in forest ecosystems, because healthy populations of these taxa are thought to indicate that many facets of ecosystem condition exist (Carey 2000a).

The northern flying squirrel (*Glaucomys sabrinus*) has been proposed as an MIS for north temperate rain forests because its populations become increasingly abundant with increasing forest complexity (horizontal and vertical heterogeneity in vegetation and structural features) in the Pacific Northwest (Carey et al. 1999, Carey 2001) and elsewhere (Weigl et al. 1992). Densities of flying squirrels were more abundant in old-growth and complex young forests than conventionally managed stands in a variety of coniferous forests across the Pacific Northwest (Carey et al. 1992, Carey 1995, Waters and Zabel 1995, Witt 1992; but see Rosenberg and Anthony 1992, Ransome and Sullivan 2003). Its life history reputedly is linked to numerous attributes of old forest (Carey 1989, 1995, Carey et al. 1992, Waters and Zabel 1995, Witt 1992).

In the Pacific Northwest, *G. sabrinus* density and microhabitat use have been correlated with vegetative and structural attributes that are common among forest types across several locations (Carey et al. 1999). However, no single habitat variable or group of habitat attributes thoroughly explained variation across geographic areas. Rather, the relationship between habitat and flying squirrel abundance appears to be multifactorial—a consequence of increasing synergism among habitat elements as forests develop and additional key habitat elements coincide at spatial scales that facilitate inclusion within a flying squirrel's home range (Carey et al. 1999, Carey 2000a). Habitat conditions that consistently explained variation in squirrel activity (i.e., captures) within stands, and differences in abundance among stands, were forest attributes such as "decadence" (prevalence of dying, dead, or decaying trees), which were habitat "factors" that incorporated unique ecological information from multiple variables (Carey et al. 1999:54).

In southeastern Alaska, temperate coniferous rain forests have many structural attributes that reflect the coastal coniferous forests of the Pacific Northwest (e.g., large trees and snags, coarse woody debris; Carey et al. 1999) and are similar in plant composition. *Glaucomys sabrinus* is one of two arboreal rodents that occur throughout most of the region (MacDonald and Cook 1996), and its life history was believed to be similar to populations in the Pacific Northwest (Suring 1993). Mean densities of flying squirrels are comparable to (or higher than) those reported for mesic or wet coniferous forests of California, Washington, and Oregon (Smith et al. 2003, Smith and Nichols 2003), but little is known about its habitat relations in southeastern Alaska, particularly correlates of microhabitat use and density (Bakker and Hastings 2002, Smith et al. 2004). A thorough understanding of the demography and habitat relations of *G. sabrinus* is fundamental to determining its suitability as an MIS of temperate rain forests (Carey et al. 1999, Carey 2000a, Jorgensen 2002, Morris 2003, Simberloff 1998).

The purpose of this study was to evaluate the suitability of *G. sabrinus* as an MIS of temperate rain forest through a quantitative analysis of its habitat relations in southeastern Alaska. Specifically, we asked whether the habitat of *G. sabrinus* in southeastern Alaska was an emergent property of old-growth rain forests by comparing the efficacy of models developed from individual variables vs. multivariate factors to test the hypothesis that its habitat is multifactorial (Carey et al. 1999). If the optimal habitat of *G. sabrinus* is multifactorial, then multivariate habitat factors should more thoroughly explain variation in microhabitat use than individual habitat variables (Carey 2000a).

METHODS

Study area

Southeastern Alaska 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). The region is unique with numerous naturally fragmented landscapes, a dynamic geological history (MacDonald and Cook 1996), and coastal temperate coniferous rain forest (Alaback 1982, Harris and Farr 1974). The rain forest is distributed among islands of the Alexander Archipelago or isolated along the narrow mainland by mountains and ice fields. Topography, geology, climate, and other environmental features create a variety of isolated habitats; spatial heterogeneity occurs at multiple spatial scales in a manner rarely found elsewhere. Fragmentation of natural forest habitats has increased markedly since the middle of the 20th century because of land use; most notably from extensive clearcut logging (50% of low elevation, old-growth forest on some islands) throughout the region (USDA Forest Service 1997, Smith and Nichols 2003).

We studied populations of *Glaucomys sabrinus griseifrons* in the north-central region of Prince of Wales Island (55°42'–55°48' N, 132°47'–132°52' W; Smith and Nichols 2003) in the two dominant forest habitats: upland old-growth (upland-OG) and peatland-scrub/mixed-conifer forests (peatland-MC). Upland old growth is represented by several plant associations of western hemlock (*Tsuga heterophylla*)–Sitka spruce (*Picea sitchensis*) forests (DeMeo et al. 1992) and to a lesser extent red cedar (*Thuja plicata*) and yellow cedar (*Chamaecyparis nootkatensis*). The *Tsuga*–*Picea* forest type (upland-OG) constitutes most of the closed-canopy forests in the region (Alaback 1982). Upland-OG stands are highly productive forests that support high volumes (>400 m³/ha) of timber with a closed canopy of tall (>60 m), large (≤2.5 m diameter) trees, and a mostly herbaceous understory (Harris and Farr 1974, Alaback 1982, DeMeo et al. 1992). It is spatially heterogeneous at a scale of <1 ha (Schoen et al. 1984) and usually occurs on low elevation, well-drained sites, frequently as a mosaic with muskegs (Neiland 1971).

Overstory dominants include Sitka spruce and western hemlock. Dense patches of blueberry (*Vaccinium* spp.) typically dominate the understory. These sites have an uneven-aged, multi-layered overstory, dominant trees generally >300 years old, and extensive structurally diverse understories (Ver Hoef et al. 1988, Hanley and Brady 1997).

Peatland-MC habitat differs markedly from upland-OG in many ways, not the least of which is the patchiness of dense forest canopy cover, which is a consequence of highly varied soil composition and moisture gradient (Neiland 1971). It is additionally 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 better drained, mineral soil (Neiland 1971, DeMeo et al. 1992). Conifer vegetation includes yellow cedar, red cedar, western hemlock, mountain hemlock (*Tsuga mertensiana*), and shore 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 (*Lysichitum americanum*), and Labrador tea (*Ledum glandulosum*); blueberry dominates areas with well-developed overstories.

These forest habitats overlapped appreciably in plant composition and structural features, but differed substantially in intermediate scale (<100 m) spatial heterogeneity, especially with respect to amount and distribution of large live and dead trees, coarse woody debris, woody shrubs, and canopy closure. We chose these habitats because they represent end points of a natural continuum of forest cover and productivity, and reflect the range of conditions in temperate rain forest of southeastern Alaska.

Sampling flying squirrels and habitat variables

A more thorough description of our study sites on Prince of Wales Island, southeastern Alaska, and trapping protocols can be found in Smith and Nichols (2003). Each habitat replicate was a 13-ha grid with a 10 × 10 array of trap stations spaced at 40-m intervals. Two live traps were placed at each of 100 stations: one was attached at a height of 1.5 m to the bole of the largest tree within 5 m of the grid station, and a second was placed on or near the ground (e.g., on a log) within 2 m of the tree supporting the other trap. We trapped each site once during early spring (March–April) and once during early autumn (September–October) during 1998–2000 because we wanted density estimates from periods during the year when populations were expected to be at their lowest (i.e., immediately following winter) and when population levels were expected to be at their highest (i.e., weaning has occurred but juveniles had not dispersed; Carey 1991, Villa et al. 1999). During a trapping session, grids usually were operated for 14 days, an initial 6-day marking period,

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

Habitat variable	Description
Vacc1	percent cover of <i>Vaccinium</i> ≤ 0.3 m tall
Vacc4.5	percent cover of <i>Vaccinium</i> between 0.3 m and 1.5 m tall
Decid1	percent cover of deciduous shrubs (except <i>Vaccinium</i>) ≤ 0.3 m tall
Decid4.5	percent cover of deciduous shrubs (except <i>Vaccinium</i>) between 0.3 m and 1.5 m tall
Conifer1	percent cover of conifer seedlings ≤ 0.3 m tall
Conifer4.5	percent cover of conifer saplings between 0.3 m and 1.5 m tall
Moss	percent cover of moss
Herb	percent cover of herbaceous vegetation ≤ 1.5 m tall
Wood	percent cover of downed wood ≥ 1 m long and < 25 cm midpoint diameter
Water	percent cover of surface water
Decay I	volume (m^3/m^2) of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class I†
Decay II	volume (m^3/m^2) of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class II†
Decay III	volume (m^3/m^2) of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class III†
Decay IV	volume (m^3/m^2) of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class IV†
Decay V	volume (m^3/m^2) of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class V†
Stumps	density of stumps
Tree74	density of trees > 1.5 m tall and > 74 cm dbh
Tree50–74	density of trees > 1.5 m tall and 50–74 cm dbh
Tree10–49	density of trees > 1.5 m tall and 10–49 cm dbh
Tree5–10	density of trees > 1.5 m tall and 5–10 cm dbh
Soft snag74	density of snags > 1.5 m tall and > 74 cm dbh with $< 2\%$ of limbs ≥ 30 cm remaining
Soft snag50–74	density of snags > 1.5 m tall and 50–74 cm dbh with $< 2\%$ of limbs ≥ 30 cm remaining
Soft snag10–49	density of snags > 1.5 m tall and 10–49 cm dbh with $< 2\%$ of limbs ≥ 30 cm remaining
Hard snag74	density of snags > 1.5 m tall and > 74 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining
Hard snag50–74	density of snags > 1.5 m tall and 50–74 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining
Hard snag10–49	density of snags > 1.5 m tall and 10–49 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining

Notes: Stumps are defined as the bases of topped-off dead trees between 0.3 m and 5 m tall; snags are standing dead trees > 1.5 m tall.

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

a two-day period when traps were closed to allow animals to recover from trap-related stress, and another six-day recapture period.

We measured 26 vegetative and structural variables at trap stations where squirrels were captured and at every third trap station without a capture (Rosenberg and Anthony 1992, Carey et al. 1999, Smith et al. 2004). Variables included understory vegetation, mid-story and overstory composition and structure, and volume and decay class (Fogel et al. 1973, Sollins 1982) of downed wood (See Table 1 for a description of variables and acronyms). Understory variables were estimated (percentage cover) in 1×1 m subplots placed at trap stations and at distances of 4 and 7 m from trap stations in the four cardinal directions (nine subplots per station). Mean values of the nine subplots were used to describe the understory at each trap station.

Statistical analysis and habitat modeling

Previously (Smith et al. 2004), we used stepwise logistic regression (SLR) to develop explanatory models to relate individual habitat variables to flying squirrel captures among 600 trap stations (six 10×10 grids, i.e., three replicates each of upland–OG and peatland–MC habitats). Trap stations were categorized as either having captured a squirrel (realized habitat) or not (un-

realized habitat; Carey et al. 1999). A dichotomous response was used because of anticipated problems with model convergence when the likelihood of capturing an animal is greatly skewed toward a single response level (e.g., zero captures; Stokes et al. 1995); and because there was little ecological justification for delineating distinct categories for multiple captures, especially differentiating between microsites with one vs. two captures (Smith et al. 2004).

SLR models of habitat variables allowed us to examine correlates of habitat use relative to individual vegetative and structural characteristics. Here we expand on that analysis by comparing those results with SLR models of habitat “factors,” which are independent linear combinations of individual habitat variables generated from factor analysis. We used factor analysis to generate multivariate habitat factors (Carey et al. 1999) from the 26 measured vegetative and structural variables (Table 1). Factor analysis uses predictive data (i.e., 26 variables) and creates “factors” using correlation matrices. The first factor accounts for a certain amount of the variance in the original variables, whereas the second is created based on the highest correlation to the original variables after accounting for variation explained by the first factor, and so on. We used VARIMAX rotation within PROC FACTOR (SAS Institute

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

Model	Variable	Chi-square test (<i>P</i>)	Parameter estimate (1 SE)	Odds ratio† (95% CI)	Model goodness of fit‡ (<i>P</i>)
Spring					
Peatland–MC	Vacc4.5	0.001	0.035 (0.01)	1.4 (1.1–1.8)	0.23
	Tree74	0.007	0.098 (0.04)	2.7 (1.3–6.8)	
Upland–OG	Water	0.005	–0.087 (0.04)	0.4 (0.2–0.8)	0.60
Autumn					
Peatland–MC	Tree74	0.003	0.283 (0.12)	16.9 (2.8–615.5)	0.85
	Vacc1	0.029	0.064 (0.03)	1.9 (1.1–3.5)	
Upland–OG	Herb	0.013	–0.040 (0.02)	0.7 (0.5–1.0)	0.30
	Soft10–49	0.034	0.017 (0.01)	1.2 (1.1–1.4)	
	Tree10–49	0.014	–0.003 (0.01)	1.0 (0.9–1.0)	
	Hard50–74	0.045	0.083 (0.04)	2.3 (1.1–5.7)	

Notes: Data are from Smith et al. (2004). See Table 1 for a description of habitat variables.

† Effect of a 10-unit increase in the value of the variable (e.g., percent cover) on the probability of capture (SAS Institute 2000).

‡ Results of Hosmer and Lemeshow test (SAS Institute 2000), reported as the probability (*P*) that the model will be improved by an additional habitat variable.

2000) to rotate factors to obtain new uncorrelated (orthogonal) variables, and visual inspection of “scree plots” to identify factors used in subsequent modeling efforts (Cody and Smith 1997:257). Factor loadings (correlation of a factor with the 26 variables) provided insights into ecological interpretation of orthogonal habitat factors. Coefficients from a correlation matrix were used to determine the extent to which habitat variables were potentially redundant in explaining variation in the response variable because of multicollinearity among habitat variables (i.e., highly correlated; Zar 1999). This information was used to develop models through an evaluation of variable selection in SLR and an interpretation of factor loadings following factor analysis.

SLR models of microhabitat use were developed for both habitats during two seasons from individual variables and from multivariate habitat factors. Individual variables or factors were entered into a model if the $P \leq 0.25$, but were retained only if $P \leq 0.05$. For each correlate in the final logistic regression models, we computed confidence intervals on the odds ratios, which were based on the profile likelihood (Stokes et al. 1995, SAS Institute 2000). Thus, odds-ratio estimates were interpreted as the odds of capturing a flying squirrel given a specified unit increase or decrease in the habitat parameter (e.g., density of trees per ha) after being adjusted for the effects of other habitat elements in the model.

If the life history of northern flying squirrels is complex and linked to multiple old forest features (and thus a suitable management indicator species), we expected the SLR models with multivariate factors to perform better in predicting microhabitat use than models with individual habitat variables. To compare the efficacy of models developed from individual variables vs. mul-

tivariate factors, we quantified their performance in predicting captures among trap stations. We used prior probabilities (i.e., proportion of traps that captured squirrels) for each habitat \times season combination to generate classification tables within PROC LOGISTIC. We compared the success rate of variable vs. factor-based models in correctly predicting capture sites, non-capture sites, and all trap stations. We used the Hosmer and Lemeshow test to evaluate the suitability of models derived using variables vs. factors, and examined several measures of goodness-of-fit (e.g., *C* statistic, R^2) to evaluate the association of predicted probabilities and observed responses (SAS Institute 2000).

RESULTS

Logistic regression: habitat variables

Four (i.e., two habitats \times two seasons) significant logistic regression models of microhabitat use were produced from individual variables (Table 2). The models varied between habitats, and between seasons within habitats, in number and type of habitat variables. Density of large (>74 cm dbh) live trees was a significant variable in both spring and autumn models of peatland–mixed conifer (MC). The ecological impact of varying density of large trees on habitat use was substantial, especially during autumn when increasing the mean value of the predictor variable by 10 trees/ha (from a mean of 2 trees/ha to 12 trees/ha in peatland–MC) increased the odds of capturing a squirrel by a factor of 17. In upland–old-growth (OG), water was the only significant variable during spring and it was inversely related to the likelihood of capturing a squirrel. According to the odds ratio, an increase in mean percent surface water of 10% reduced the odds of capturing a squirrel by a factor of 2.5 (1.0/0.4). The autumn

TABLE 3. Multivariate factors and factor loadings (≥ 0.40) generated with factor analysis (SAS 2000) from 26 habitat variables measured in peatland-scrub/mixed-conifer (peatland-MC) and old-growth western hemlock/Sitka spruce rain forest (upland-OG) during 1999–2000, Prince of Wales Island.

Factor	Peatland-scrub/ mixed conifer		Old-growth western hemlock/Sitka spruce	
	Variable	Loading	Variable	Loading
1	Vacc4.5	0.761	Tree5–10	0.675
	Herb	-0.744	Tree10–49	0.664
	Tree10–49	0.645	Hard10–49	0.411
	Water	-0.615	Soft10–49	0.410
	Soft10–49	0.581		
	Vacc1	0.573		
	Stump	0.534		
	Moss	0.524		
	Decid4.5	-0.468		
	Hard10–49	-0.417		
2	Decay V	0.622	Wood	0.687
	Tree74	0.607	Moss	-0.602
	Decid1	-0.574	Vacc4.5	-0.503
	Tree50–74	0.567		
	Soft50–74	0.523		
	Hard74	0.445		
	Conif1	-0.416		
3			Herb	-0.507
			Vacc1	0.499
			Water	-0.480
			Decid4.5	-0.416
			Vacc4.5	0.409

Note: See Table 1 for a description of habitat variables.

upland-OG model included four habitat variables, but only density of hard snags 50–74 cm dbh and herb cover had notable ecological effects on microhabitat use. Squirrel captures were positively correlated with density of hard snags, whereas the odds of capturing a squirrel decreased with increasing herb cover (Table 2).

Logistic regression: multivariate habitat factors

Factor analysis produced two factors for peatland-MC and three factors for upland-OG (Table 3). Three

significant SLR models were obtained with multivariate habitat factors; there was no significant model for upland-OG during spring (Table 4). Factor 2 was correlated with habitat use in peatland-MC during both seasons, whereas factor 3 was a correlate of autumn squirrel captures in upland-OG. Factor 2 represented habitat space with more large trees and snags and decayed down wood, but less shrub and seedling cover. A unit increase in factor 2 increased the odds of capturing flying squirrels during spring and autumn by a multiple of 1.6 and 1.5, respectively. Factor 3 captured variation in habitat space associated with more *Vaccinium* cover and less deciduous shrub cover, herb cover, and free water. A unit increase in factor 3 increased the odds of capturing a flying squirrel by a multiple of 2.1.

Model performance: habitat variables vs. multivariate factors

The percentage of sites correctly predicted varied seasonally and between habitats for both types of models (Table 5). For variable-based models, the percentage of microsites classified correctly ranged from 62.1% to 85.0%. Sensitivity (percentage of capture sites correctly classified) and specificity (percentage of non-capture sites correctly classified) ranged between 61.4% and 100%, and 0% and 62.7%, respectively. With the exception of upland-OG model during autumn, which performed best in predicting sites that captured flying squirrels, about one-third of the trap stations were incorrectly classified as capture sites. Neither autumn model misclassified a capture site (i.e., sensitivity = 100%); however, a relatively large number of capture sites were misclassified (false negatives) with spring models (Table 5). The percentage of microsites that were correctly classified with factor-based models was 49.9–69.5%. Sensitivity and specificity

TABLE 4. Stepwise logistic regression models of multivariate habitat factors correlated with flying squirrel microhabitat use in peatland-scrub/mixed-conifer (peatland-MC) and old-growth western hemlock/Sitka spruce rain forest (upland-OG) during spring and autumn 1998–2000, Prince of Wales Island.

Model	Factor†	Chi-square test (<i>P</i>)	Parameter estimate (1 SE)	Odds ratio‡ (95% CI)	Model goodness of fit§ (<i>P</i>)
Spring					
Peatland-MC	2	0.0023	0.480 (0.16)	1.6 (1.2–2.3)	0.78
Upland-OG	N/A				
Autumn					
Peatland-MC	2	0.0212	0.426 (0.19)	1.5 (1.1–2.3)	0.26
Upland-OG	3	<0.0001	0.726 (0.20)	2.1 (1.4–3.1)	0.98

Note: N/A denotes no significant model.

† Orthogonal, multivariate factors from factor analysis of habitat variables. For peatland-MC, factor 2 is density of large trees and snags; for upland-OG, factor 3 is understory composition and structure (mostly *Vaccinium* cover).

‡ Effect of a one-unit increase in the value of the variable (e.g., percent cover) on the probability of capture (SAS Institute 2000).

§ Results of Hosmer and Lemeshow test (SAS Institute 2000), reported as the probability (*P*) that the model will be improved by an additional habitat variable.

TABLE 5. Performance of logistic regression models of habitat variables ("Variable" columns) and multivariate factors ("Factor" columns) in predicting flying squirrel microhabitat use in peatland-scrub/mixed-conifer (peatland-MC) and old-growth western hemlock/Sitka spruce rain forest (upland-OG) spring and autumn 1998–2000, Prince of Wales Island.

Model	Probability level (%)	Correct (%)		Sensitivity (%)		Specificity (%)		False positive (%)		False negative (%)	
		Variable	Factor	Variable	Factor	Variable	Factor	Variable	Factor	Variable	Factor
Spring											
Peatland-MC	51	62.1	54.9	61.4	40.4	62.7	70.0	36.8	41.7	39.0	47.0
Upland-OG†	64	65.6		99.4		5.6		34.8		16.8	
Autumn											
Peatland-MC	70	70.0	49.9	100	41.0	0	70.6	30.0	23.5	‡	66.1
Upland-OG	85	85.0	69.5	100	72.2	0	54.1	15.0	10.1	‡	74.5

Notes: "Probability level" is the expected probability of a capture, which is based on the observed or prior probability. (For consistency within this paper, these values are reported as percentages instead of proportions.) "Correct" is the fraction of trap stations that were correctly classified. "Sensitivity" is the fraction of capture sites that were correctly classified. "Specificity" is the fraction of noncapture sites that were correctly classified. "False positive" is the fraction of trap stations predicted to capture an animal that were incorrectly classified as a capture site. "False negative" is the fraction of trap stations predicted to not be a capture site that were incorrectly classified as a noncapture site.

† There was no significant ($P > 0.05$) model of multivariate factors for upland-OG during spring.

‡ Rate was not computable.

were 40.4–72.2% and 54.1–70.6%, respectively. The autumn upland-OG model performed best in predicting the percentage of sites that captured a squirrel and the percentage of capture sites classified correctly.

DISCUSSION

Models of microhabitat use

The overall performance of single habitat variables in predicting microhabitat use was better than habitat models constructed with multivariate factors. The percentage of trap stations correctly classified was consistently higher with variable-based models than models developed from multivariate factors, which, except for upland-old-growth (upland-OG) during autumn, did not depart appreciably from 50%. These results differ markedly from patterns of habitat use reported for flying squirrel populations in the Pacific Northwest (Carey et al. 1999), which can vary considerably across geographic areas (Smith et al. 2003).

Carey et al. (1999) quantified habitat use at two scales: microhabitat use within, and density among, 19 natural and managed forest stands that represented three seral stages and spanned the range of variation in closed canopy forests in the Coast Range of southwestern Oregon. From their analyses within individual stands, they observed that only multivariate habitat factors consistently explained variation in flying squirrel captures among microhabitats. Four multivariate factors correctly classified 60% of points (i.e., trap stations) according to flying squirrel use. Additionally, multivariate factors such as decadence, habitat breadth, and moisture-temperature gradient values (MGV) explained substantially more variation in squirrel carrying capacity (i.e., maximum density) across stands than individual variables (Carey et al. 1999). That they also observed a significant relationship between flying

squirrel density and habitat factors among stands demonstrated that multivariate factors explained habitat use at multiple spatial scales (microhabitat and stand level) across a relatively broad range of forest conditions. Drawing also on the findings of studies conducted elsewhere in Oregon and in Washington (Carey 1989, 1991, 1995), they concluded that flying squirrel habitat in the Pacific Northwest is an emergent property of old-growth forest.

We tested their hypothesis by examining whether there was evidence from modeling flying squirrel captures among microhabitats that the habitat of flying squirrels in southeastern Alaska was multifactorial. That our study differed from Carey et al. (1999) in number and types of habitats investigated does not limit the value of comparing correlates of microhabitat use within old-growth stands between regions. Indeed, the causal mechanisms underlying variation in the abundance of flying squirrels among forest habitats likely is linked to resource availability at the scale of individual home ranges (Morris 1984, 1987). Number of quality macrohabitats (i.e., home ranges) determines the carrying capacity of larger habitat patches (forest stands). Still, the fact that we did not include managed stands in our analysis likely diminished our ability to identify specific limiting habitat features of younger, less complex forests, particularly those that emerge as significant correlates of density among managed and unmanaged habitats. But, this should not have hindered our ability to identify emergent factors of old growth forests, particularly with the inclusion and replication of peatland-mixed-conifer (MC) habitats, as we used similar procedures to ask similar questions in similar habitats. Upland-OG and peatland-MC are near opposite ends of a wide range of variation in canopy cover, plant species composition, and vertical and horizontal structure (Harris and Farr 1974, Neiland 1971).

Within peatland–MC alone, there is substantial variation in the density and distribution of forest canopy, in the size (height and diameter) and density of live trees and snags, and in the amount and distribution of downed woody material (Smith et al. 2004). We believe that habitats in our study overlapped much of the range of forest conditions in southwestern Oregon, including managed stands. More importantly, the differences in habitat use we report between studies were apparent within individual stands across a range of forest conditions. That we did not observe ecologically significant variation in habitat use correlated with multivariate factors suggest that the habitat of *Glaucomys sabrinus* in southeastern Alaska is not an emergent property of old growth.

An alternative explanation for the differences we report is that northern flying squirrels in southeastern Alaska may differ ecologically in important ways from populations across the Pacific Northwest. One marked difference in habitat relations between regions was the significance of decadence (especially coarse woody debris), which was the single most important factor explaining flying squirrel habitat use and density in the Pacific Northwest (Carey et al. 1999). The association of flying squirrel populations in Oregon with decadence largely may be a function of their dependence on truffles, i.e., hypogeous ectomycorrhizal fungi (Carey et al. 1999). Many truffle species are directly correlated with old forest attributes, such as coarse woody debris and decayed, downed wood (Amaranthus et al. 1994, Smith et al. 2000, 2002). Furthermore, the most consistent predictor of flying squirrel density across the Pacific Northwest has been frequency or abundance of hypogeous sporocarps (i.e., truffles; Waters and Zabel 1995, Carey et al. 1999, Pyare and Longland 2002).

Equally striking was the significance of habitat breadth and moisture–temperature gradient values (MGV) in southwestern Oregon, which together with decadence, explained 70% of the variation in flying squirrel carrying capacity (Carey et al. 1999). Habitat breadth and MGV apparently reflect ecologically significant gradients and variability within and among stands that influence arboreal rodent communities, including the abundance of northern flying squirrel populations (Carey 1991, 1995, 1996, Carey et al. 1999). In turn, the composition and diversity of arboreal rodent communities likely has shaped the habitat relations of flying squirrel populations in western coniferous forests (Carey 1989, 1991, 1996, Carey et al. 1999, Smith et al. 2003). Within arboreal rodent communities of the Pacific Northwest, interactions among resources and among species sharing resources may have created an ecological environment where populations frequently are not limited by a single factor and their life histories are linked to multiple resources (Carey 1989, 1991, 1996, Carey et al. 1999). That flying squirrel microhabitat use and relative abundance among habitats in the Pacific Northwest are linked to

a suite of old forest features may have as much to do with the composition of small mammal communities as the specific life history traits of local populations (Carey et al. 1999).

In temperate rain forests of southeast Alaska, the community structure of arboreal rodents, and the diet of northern flying squirrels (although not mutually exclusive), may be sufficiently different to facilitate a more general lifestyle. In southeast Alaska, northern flying squirrels rely less on truffles, and their diet includes a greater diversity of food items than populations in California, Oregon, or Idaho (Maser et al. 1986, Rosentreter et al. 1997, Carey et al. 1999, Waters et al. 2000, Pyare et al. 2002). The less specialized diet may reflect greater opportunities to use a broader range of rain forest habitats because of less interspecific competition (Carey 1991, 1996, 2000a, 2001, Carey et al. 1999). Several investigators have noted the significance of diet in influencing the habitat relations of flying squirrels (Waters and Zabel 1995, Rosentreter et al. 1997, Carey et al. 1999, Pyare and Longland 2002), or their role in forest communities (Maser et al. 1978, 1986, Maser and Maser 1988, Waters et al. 2000). Diet and competitive release were proposed as factors contributing to differences in population density between the Pacific Northwest and southeastern Alaska (Smith and Nichols 2003).

Flying squirrels as a management indicator species (MIS)

The assumption that the northern flying squirrel is a good MIS of north temperate rain forest was not supported by our study. *Glaucomys sabrinus* was proposed as an MIS of the Tongass National Forest (USDA Forest Service 1997), the largest contiguous temperate rain forest in the northern hemisphere, because its populations were thought to indicate conditions of late-seral coniferous forests. This assumption was based on the notion that the ecology of *G. sabrinus* in southeastern Alaska is similar to populations in the Pacific Northwest (Suring 1993), which ostensibly have a complex life history that is linked to a suite of old forest characteristics (Carey et al. 1999, Carey 2000a). North temperate rain forests have many attributes that parallel mesic coniferous forests in the Pacific Northwest and the expectation is that habitat relations of flying squirrel populations in southeastern Alaska are similar to populations in the Pacific Northwest (Suring 1993).

We found little empirical support for the hypothesis that the habitat of *Glaucomys sabrinus* in southeastern Alaska is an emergent property of old-growth forest. Rather, variation in microhabitat use largely was explained by a few individual habitat variables and multivariate habitat factors contributed essentially no unique ecological information. This conclusion is supported further by the findings of Smith et al. (2004) that variation in flying squirrel density among forest stands (spring and autumn) was attributable to indi-

vidual habitat variables, some of which (e.g., large trees) were key correlates of microhabitat use in our study. Furthermore, we believe there are ecological differences between regions, particularly in diet and interspecific relations (Pyare et al. 2002, Smith and Nichols 2003, Smith et al. 2004) that are sufficient to explain why the habitat of flying squirrels in temperate rain forest is not multifactorial.

What remain unclear are implications of apparent ecological differences to questions about the suitability of northern flying squirrels as an MIS in temperate rain forest. If the habitat of *G. sabrinus* in southeastern Alaska is not multifactorial, does that limit its utility as an MIS? Or, might there be other aspects of its life history or ecology that renders it an effective MIS? Evidence from our study demonstrated that large standing live and dead trees were ecologically significant correlates of flying squirrel habitat use and density. Large trees and snags also may be crucial or limiting resources for a multitude of species in temperate rain forest, particularly cavity nesters (Hughes 1985, Zarnowitz and Manuwal 1985, Joy 2000) or species whose food resources are more abundant with larger trees (e.g., tree squirrels; Smith et al. 2003). But if this were true, large trees and snags likely would be more useful indicators of rain forest communities because they are easier to measure than flying squirrels. Still, land managers may choose to monitor flying squirrels in southeastern Alaska because their populations are correlated with large trees and snags and because of concerns over the viability of endemic populations (Smith and Nichols 2003). Threatened, endangered, or sensitive status increases the impetus and value of monitoring MIS populations (Simberloff 1998).

There are ecological attributes other than multifactorial habitat that render species suitable as indicators of biological diversity or ecosystem health (Landres et al. 1988, Simberloff 1998, Carey 2000a). Flying squirrels may have a keystone role in rain forests of southeastern Alaska. In the Pacific Northwest, flying squirrels are important prey for old-growth-associated predators (Carey et al. 1992, 1999), including small carnivores (e.g., American marten, *Martes americana*) and raptors, and are the primary prey of the northern spotted owl (*Strix occidentalis occidentalis*). In turn, flying squirrels eat sporocarps and disseminate spores of ectomycorrhizal fungi (Maser et al. 1978, 1985, 1986, Forsman et al. 1984, Maser and Maser 1988, Carey 1995, Carey et al. 1999), which are essential symbionts of dominant conifers (e.g., Douglas-fir, *Pseudotsuga menziesii*). However, *G. sabrinus* in southeastern Alaska depends much less on truffles than populations in the Pacific Northwest (Pyare et al. 2002) and there are no known predators that rely on flying squirrels as prey (e.g., Flynn and Schumacher 2001, Lewis 2001). Still, the low diversity of small mammals in southeastern Alaska (MacDonald and Cook 1996) may increase the importance of flying squirrels as prey for raptors or

small carnivores, or as disseminators of fungal spores or other reproductive propagules (Bruner et al. 2001).

Alternatively, flying squirrels may be good indicators of processes that are important for conservation planning. A fundamental assumption of the wildlife conservation strategy for the Tongass National Forest is that populations of old-growth reserves will be able to freely interact through dispersal. Thus, widely distributed breeding populations of flying squirrels across the planning area may be a good indicator of landscape permeability (sensu Singleton et al. 2002) in intensively managed landscapes, where successful dispersal of arboreal rodents with limited vagility likely serve as a good benchmark of functional connectivity (Selonen and Hanski 2003).

Perhaps the more important question is whether the expectation of using single species to reflect the health or integrity of an ecosystem is realistic (Simberloff 1998). Although the concept of an indicator species has been around for nearly a century and in common use by researchers and land managers for at least three decades, rigorous analyses of this concept have produced few positive examples of its utility (Lawler et al. 2003). More often than not, investigations have failed to support the underlying assumption of a correlation between the indicator species and the organisms, habitat or, processes it represents (Mannan et al. 1984, Szaro 1986, Niemi et al. 1997, Rolstad et al. 2002). A fundamental issue is that frequently there is little agreement over what the indicator is supposed to indicate (Simberloff 1998), or that the goals and objectives are poorly defined (Landres et al. 1988). Even then, selecting the best indicator species often is not intuitive or well founded in science or knowledge of natural history. More importantly, there is the recognition that managing for one species almost always conflicts with management of other species (Landres et al. 1988, Simberloff 1998).

Several alternatives to MIS have been proposed (e.g., flagship, umbrella, or keystone species), all of which have unique nuances. Of these, keystone species seems to have the most promise (Simberloff 1998). However, identifying keystone species and associated mechanisms that have wide-ranging impacts on communities and ecosystems is no small task. Furthermore, even when good species are identified, using keystone species in conservation planning (like MIS) is not exempt from the shortcomings of relying on a single species to represent the response of entire biological communities to perturbation (Simberloff 1998).

Alternatively, some investigators have proposed more comprehensive approaches including the use of multiple species to monitor communities at the ecoregional scale (Manley et al. 2004), or combining the monitoring of habitat and multiple species across broad scales (Niemi et al. 1997). Regardless, a critical feature of an effective monitoring program is ensuring that the measures of future desirable condition correlate with

the ecological indicators that have been selected. For MIS, this means knowing the biology of the species (Landres et al. 1988, Simberloff 1998) and requires quantitative documentation of habitat associations (Jorgensen 2002, Morris 2003). Simply assuming that a species will be a suitable indicator of desired ecological conditions because it reputedly functions in that role in a similar ecosystem elsewhere can be misleading, counterproductive, and costly.

ACKNOWLEDGMENTS

We thank Thorne Bay District and Craig Ranger District, Tongass National Forest, for logistic and personnel support, especially Marla Dillman, Mike McFadden, and Amy Russell. Todd Wilson provided guidance in the development of our protocol for live-trapping and handling flying squirrels. Rick Woodsmith loaned us a vehicle for fieldwork. The following volunteers endured unusually challenging conditions to substantially contribute to this study: Paul Hillman, Kari Murabito, and Noel Soucy. Also, the following seasonal technicians were an invaluable field crew: Melinda Anderman, Jeremy DePiero, Aren Eddingsaas, Nathan Favreau, John Frisch, Jeff Heys, Aaron Hurst, Dawn Magness, Brian Marston, Mike McMurray, Jorie Moran, Kirk Moughamer, Kim Obermeyer, Sanjay Pyare, Todd Rinaldi, Aren Rinker, Tracy Smith, Kevin White, and Jamie Wisnowski. We thank Vicki Bakker, Andrew Carey, Mark Ford, Douglas Kelt, Sanjay Pyare, Peter Weigl, and an anonymous reviewer for valuable comments on an earlier draft of this paper.

LITERATURE CITED

- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* **63**:1932-1948.
- Amaranthus, M. P., D. S. Parrish, and D. A. Perry. 1994. Decaying logs as moisture reservoirs after drought and wildfire. Pages 191-194 in E. Alexander, editor. Stewardship of soil, air, and water resources: proceedings of Watershed 89. United States Department of Agriculture, Forest Service, Region 10, Juneau, Alaska, USA.
- 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.
- Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* **3**:131-136.
- Bruner, B. L., G. A. Laursen, E. Follmann, E. Rexstad, W. P. Smith, and J. Nichols. 2001. Small mammals and forest interactions; mycorrhizal fungi as model organisms for understanding natural webs. Proceedings of the Non-timber Forest Products Convention (November 2001), Anchorage, Alaska, USA.
- 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. USDA Forest Service General Technical Report PNW-GTR-276. Portland, Oregon, USA.
- 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. Pages 45-66 in R. L. Goldingay and J. S. Scheibe, editors. *Biology of gliding mammals*. 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., and R. O. Curtis. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. *Wildlife Society Bulletin* **24**:610-620.
- 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.
- Code of Federal Regulations. 1985. Title 36, Code of Federal Regulations, Chapter II. Part 219.19, subpart 64. U.S. Government Printing Office, Washington, D.C., USA.
- Cody, R. P., and J. K. Smith. 1997. Applied statistics and the SAS programming language. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- DeMeo, T., J. Martin, and R. A. West. 1992. Forest plant association guide: Ketchikan Area, Tongass National Forest. USDA Forest Service, Alaska Region R10-MB-210.
- Everest, F. H., D. N. Swanston, C. G. Shaw, III, W. P. Smith, K. R. Julin, and S. D. Allen. 1997. Evaluation of the use of scientific information in developing the 1997 Forest Plan for the Tongass National Forest. USDA Forest Service General Technical Report PNW-GTR-415, Portland, Oregon, USA.
- Flynn, R. W., and T. Schumacher. 2001. Ecology of martens in southeast Alaska. Federal Aid Research Final Report, Study 7.16. Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau, Alaska, USA.
- 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, Washington, USA.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment. United States Department of Agriculture, United States Department of Interior, and others, Portland, Oregon, USA.
- 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.
- Hall, H. H., and J. Grinnell. 1919. Life-zone indicators in California. Proceedings of the California Academy of Sciences **9**:37-67.
- 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. USDA Forest Service General Technical Report PNW-25. Portland, Oregon, USA.
- Huff, M. H., R. S. Holthausen, and K. B. Aubrey. 1992. Habitat management for red tree voles in Douglas-fir forests. Pages 1-16 in M. H. Huff, R. S. Holthausen, and K. B. Aubrey, technical coordinators. *Biology and management of old-growth forests*. USDA Forest Service General Technical Report PNW-GTR-302. Portland, Oregon, USA.

- Hughes, J. 1985. Characteristics of standing dead trees in old-growth forests on Admiralty Island, Alaska. Thesis. Washington State University, Pullman, Washington, USA.
- Jorgensen, E. E. 2002. Small mammals: consequences of stochastic data variation for modeling indicators of habitat suitability for a well-studied resource. *Ecological Indicators* **1**:313–321.
- Joy, J. B. 2000. Characteristics of nest cavities and nest trees of the red-breasted sapsucker in coastal montane forests. *Journal of Field Ornithology* **71**:525–530.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* **2**:316–328.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* **5**:79–89.
- Lawler, J. J., D. White, J. C. Sifneos, and L. L. Master. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* **17**:875–882.
- Lewis, S. B. 2001. Breeding season diet of northern goshawks in southeast Alaska with a comparison of techniques used to examine raptor diet. Thesis. Boise State University, Boise, Idaho, USA.
- Loehle, C., J. G. MacCracken, D. Runde, and L. Hicks. 2002. Forest management at landscape scales: solving the problems. *Journal of Forestry* **100**:25–33.
- Lomolino, M. V., and D. R. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* **81**:1517–1532.
- MacDonald, S. O., and J. A. Cook. 1996. The land mammal fauna of southeast Alaska. *Canadian Field Naturalist* **110**:571–598.
- Manley, P. A., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple species approach to monitoring species at the ecoregional scale. *Ecological Applications* **14**:296–310.
- Mannan, R. W., M. L. Morrison, and E. C. Meslow. 1984. Comment: the use of guilds in forest management. *Wildlife Society Bulletin* **12**:426–430.
- 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, C. E., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* **59**:799–809.
- 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.
- Morris, D. W. 1984. Patterns and scale of habitat use in two temperate-zone small mammal faunas. *Canadian Journal of Zoology* **62**:1540–1547.
- Morris, D. W. 1987. Ecological scale and habitat use. *Ecology* **68**:362–369.
- Morris, D. W. 2003. How can we apply theories of habitat selection to wildlife conservation and management? *Wildlife Research* **30**:303–319.
- Neiland, B. J. 1971. The forest bog complex of southeast Alaska. *Vegetatio* **22**:1–63.
- Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. *Journal of Wildlife Management* **61**:1240–1252.
- Patton, D. R. 1992. *Wildlife habitat relationships in forested ecosystems*. Timber Press, Portland, Oregon, USA.
- 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**: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 Forestry Research* **33**:587–596.
- Rauscher, H. M. 1999. Ecosystem management decision support for federal forests in the United States: a review. *Forest Ecology and Management* **114**:173–197.
- Rolstad, J., I. Gjerde, V. S. Gunderson, and M. Sætersdal. 2002. Use of indicator species to assess forest continuity: a critique. *Conservation Biology* **16**:253–257.
- 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.
- Rosentreter, 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 Institute. 2000. *SAS/STAT user's guide*, release 8.1 edition. Cary, North Carolina, USA.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* **155**:141–153.
- Schoen, J. W., M. D. Kirchhoff, and O. C. Wallmo. 1984. Sitka black-tailed deer/old-growth relationships in southeast Alaska: implications for management. Pages 315–319 in W. R. Meehan, T. R. Merrell, and T. A. Hanley, editors. *Proceedings of a symposium: fish and wildlife relationships in old-growth forests*. 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*. U.S. Department of Commerce, Environmental Science Service Administration, Environmental Data Service, Silver Spring, Maryland, USA.
- Selonen, V., and I. K. Hanski. 2003. Movements of the flying squirrel (*Pteromys volans*) in corridors and in matrix habitat. *Ecography* **26**:641–651.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? *Biological Conservation* **83**:247–257.
- Singleton, P. H., W. L. Gaines, and J. F. Lehmkuhl. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. *USDA Forest Service Research Paper PNW-RP-549*. Portland, Oregon, USA.
- Smith, C. C. 1981. The indivisible niche of *Tamiasciurus*: an example of nonpartitioning of resources. *Ecological Monographs* **51**:343–363.
- 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, J. E., R. Molina, M. M. P. Huso, D. L. Luoma, D. McKay, M. A. Castellano, T. Lebel, and Y. Valachovic. 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.

- 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. Pages 157–206 in C. J. Zabel and R. G. Anthony, editors. Mammal community dynamics in western coniferous forests: management and conservation. Cambridge University Press, Cambridge, UK.
- Smith, W. P., S. M. Gende, and J. V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rain forest of southeastern Alaska. *Journal of Mammalogy* **85**:663–674.
- Smith, W. P., and J. V. Nichols. 2003. Demography of the Prince of Wales flying squirrel: an endemic of Southeastern Alaska temperate rain forest. *Journal of Mammalogy* **84**:144–158.
- 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.
- Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* **17**:1238–1250.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 1995. Categorical data analysis using the SAS system. SAS Institute, Cary, North Carolina, USA.
- Suring, L. A., compiler. 1993. Habitat capability models for wildlife in southeast Alaska. USDA Forest Service, Alaska Region, Juneau, Alaska, USA.
- Szaro, R. C. 1986. Guild management: an evaluation of avian guilds as a predictive tool. *Environmental Management* **10**:681–688.
- Szaro, R. C., and D. W. Johnston, editors. 1996. Biodiversity in managed landscapes. Oxford University Press, New York, New York, USA.
- USDA Forest Service. 1997. Land and resource management plan: Tongass National Forest. United States Department of Agriculture, Forest Service R10-MB-338dd. Juneau, Alaska, USA.
- U.S. Department of Interior. 1980. Habitat evaluation procedure (HEP). Ecological Services Manual Number 102. Division of Ecological Services, U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C., USA.
- 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.
- Villa, L., A. B. Carey, T. M. Wilson, and K. E. Glos. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. USDA Forest Service General Technical Report PNW-GTR-444.
- 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. USDA Forest Service General Technical Report PSW-GTR-178, Albany, California, USA.
- 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, USA.
- Williams, S. E., H. Marsh, and J. Winter. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* **83**:1317–1329.
- Willson, M. F. 1996. Biodiversity and ecological processes. Pages 96–107 in R. C. Szaro and D. W. Johnston, editors. Biodiversity in managed landscapes. Oxford University Press, New York, New York, USA.
- Willson, M. F., S. M. Gende, and B. Marston. 1998. Fishes and the forest: expanding perspectives on fish–wildlife interactions. *BioScience* **48**:455–462.
- 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. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. *Journal of Wildlife Management* **49**:255–263.