

DEMOGRAPHY OF THE PRINCE OF WALES FLYING SQUIRREL, AN ENDEMIC OF SOUTHEASTERN ALASKA TEMPERATE RAIN FOREST

WINSTON P. SMITH* AND JEFFREY V. NICHOLS

United States Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory,
2770 Sherwood Lane–Suite 2A, Juneau, AK 99801-8545, USA

We studied the Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) in temperate rain forest of southeastern Alaska to provide the 1st quantitative estimates of demography from southeastern Alaska and test predictions of the hypothesis that Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forest is primary habitat for *G. sabrinus* in southeastern Alaska. We expected that abundance, body condition, productivity, and summer and overwinter survival of *G. sabrinus* would be higher in spruce–hemlock forest (which typically are the old-growth forests of upland sites [upland-OG]) than in peatland-scrub–mixed-conifer (peatland-MC) forest. Mean values of minimum number of animals known alive and density during autumn were higher in upland-OG than in peatland-MC, and both were about 2 times higher than corresponding spring values. Age and sex composition of the population was similar among years, between seasons, and between habitats. Males comprised a larger portion of the population in upland-OG than in peatland-MC forest. Mean body mass was similar between habitats. Minimum summer survival varied among years and between habitats. Overwinter survival was less varied and similar among years and between habitats. Reproductive females were more abundant in upland-OG than in peatland-MC, but percentage of reproductive females during spring and percentage of juveniles during autumn were similar between habitats. These results support the conclusion that upland-OG forests of southeastern Alaska are primary habitat for northern flying squirrels. Still, squirrel densities in peatland-MC were higher than those reported for several managed and unmanaged forest types in the Pacific Northwest, and some demographic parameters were similar between upland-OG and peatland-MC. In southeastern Alaska, peatland-MC habitat likely contributes to breeding populations of *G. sabrinus* and reduces risk of viability in managed landscapes.

Key words: demography, *Glaucomys sabrinus griseifrons*, northern flying squirrel, old-growth forest, southeastern Alaska, temperate rain forest

Southeastern Alaska has numerous naturally fragmented landscapes, a dynamic geological history (MacDonald and Cook 1996), and coastal temperate rain forest (Alaback 1982; Harris and Farr 1974). The rain forest is distributed among islands of the Alexander Archipelago or isolated from the narrow mainland by mountains and ice fields. Topography, geology, climate, and

other environmental features create a variety of isolated habitats; spatial and temporal heterogeneity occur in a manner rarely found elsewhere. Consequently, the potential for endemism is high, and many indigenous taxa have restricted ranges. Mammals alone are represented by 24 endemic taxa (MacDonald and Cook 1996).

Southeastern Alaska has experienced extensive clear-cut logging since 1954 (50%

* Correspondent: winston_smith@fs.fed.us

of productive old-growth forest on some islands—W. P. Smith, in litt.); yet, little information is available on its natural history, biota, and ecological values and processes (Cook and MacDonald 2001; Cook et al. 2001). Arboreal rodents represent a unique guild of habitat specialists (Carey 1991, 2001; Smith et al. 2003) that influence the dynamics of temperate coniferous forests because of their functional roles, including dissemination of fungal spores (Maser and Maser 1988; Maser et al. 1978) and their importance as prey for owls and small carnivores (Carey et al. 1992; Forsman et al. 1984, 2001; Hamer et al. 2001; Martin 1994). Several aspects of the life history of arboreal rodents are linked to various elements of forest structure or ecological processes (Carey 1991; Maser and Maser 1988; Maser et al. 1978). Abundance and diversity of the arboreal rodent community often is viewed as a correlate of ecological productivity and structural complexity and as an indication of forest function (Carey 1991; Carey et al. 1999).

The northern flying squirrel (*Glaucomys sabrinus*) was implicated as a keystone species of coniferous forest ecosystems of the Pacific Northwest (Maser et al. 1978) because much of its life history is linked to attributes of old forest (Carey 1989, 1995; Carey et al. 1992; Waters and Zabel 1995; Witt 1992) and because of its close association with hypogeous mycorrhizal fungi (Carey et al. 1999; Maser and Maser 1988; Maser et al. 1978, 1986, 1985; McKeever 1960). The Prince of Wales flying squirrel (*G. s. griseifrons*) is an endemic subspecies of southeastern Alaska (MacDonald and Cook 1996), which is listed as in danger of extinction in the report of the recent status survey of North American rodents by International Union for Conservation of Nature (Demboski et al. 1998a). Until recently, it was known only from Prince of Wales Island (Howell 1934). Today, the known range of *G. s. griseifrons* includes several additional nearby islands west of Prince of Wales Island (Bidlack and Cook 2001).

However, much about distribution, natural history, and ecology of *G. sabrinus* in southeastern Alaska remains unknown (MacDonald and Cook 1996).

Of particular interest is the expected sensitivity of this endemic subspecies to cumulative impacts of clear-cut logging. Elsewhere, *G. sabrinus* is sensitive to broad-scale forest management (Carey 1991, 1995; Carey et al. 1992, 1999). In the Pacific Northwest, this species is more abundant in late-seral and complex young forests than in conventionally managed stands (Carey 1995; Carey et al. 1992; Waters and Zabel 1995; Witt 1992). Generally, flying squirrels (i.e., *Pteromys*, *Glaucomys*) are sensitive to catastrophic disturbance or repeated stand-level disturbances that cumulatively eliminate mature forest habitat across the landscape (Hanski et al. 2000; Hokkanen et al. 1982). Disturbances that reduce habitat often increase fragmentation and alter connectivity of the landscape (Hanski et al. 2000). Such disturbances often contribute to loss of local populations (Andren 1994; Hokkanen et al. 1982) and, if unchecked, may ultimately lead to extirpation of species from an entire region (Hokkanen et al. 1982). Cumulative impacts of habitat disturbance are especially problematic in archipelago systems, where habitat is naturally fragmented, average population size is often smaller than in nearby mainland habitat (MacArthur and Wilson 1967; Soulé and Wilcox 1980), and “source” populations are already isolated (Burkey 1995). Extinction rates are higher in archipelago systems (Burkey 1995), especially for endemic taxa (Frankham 1998).

The dearth of information from southeastern Alaska adds uncertainty to planning efforts to maintain well-distributed and viable populations of *G. sabrinus* (Everest et al. 1997; Shaw 1999). Knowledge of demography is fundamental for understanding and projecting population responses to habitat modification (Van Horne 1981). The purpose of this study was to provide the 1st quantitative estimates of abundance and de-

mography of populations of *G. sabrinus* in southeastern Alaska. Specific objectives were to test predictions of the hypothesis that Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forest is primary habitat for *G. sabrinus*. Based on the results of numerous studies from the Pacific Northwest (Carey 1995, 1989; Carey et al. 1992; Waters and Zabel 1995; Witt 1992), we expected that abundance, body condition, productivity, and summer and overwinter survival of *G. sabrinus* would be higher in spruce–hemlock forest than in peatland–scrub–mixed-conifer (peatland–MC) forest.

MATERIALS AND METHODS

Study area.—Southeastern Alaska has glaciated mountain ranges and fjords and 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). About 4 million ha (60%) is forestland (United States Department of Agriculture Forest Service 1997), of which 2.2 million ha is productive forests (Julin and Caouette 1997). Coniferous rain forest dominates the landscape from shoreline to about 600-m elevation, with about 90% of commercial forest in Sitka spruce–western hemlock forests, which typically are the old-growth forests of upland sites (upland-OG); remaining areas are alpine, muskeg, or riparian (Hutchinson and LaBau 1974). Unmanaged forests have a multilayered overstory of uneven-aged trees, dominant trees that generally are >300 years old, and extensive, structurally diverse understories (Hanley and Brady 1997; Ver Hoef et al. 1988). These forests vary in structure from “scrub” or low-volume communities of short (<10 m), small (<0.5-m diameter) trees with open canopies and dense, shrubby understories on poorly drained sites (peatland) to high-volume stands with a closed canopy, tall (>60 m), large (>3-m diameter) trees, and a predominantly herbaceous understory on highly productive sites (Alaback 1982; Harris and Farr 1974). The *Tsuga–Picea* forest type constitutes most of the closed-canopy forests in the region (Alaback 1982). It is spatially heterogeneous at a fine scale—<1 ha (Schoen et al. 1984)—and typically occurs on low-elevation, well-drained sites,

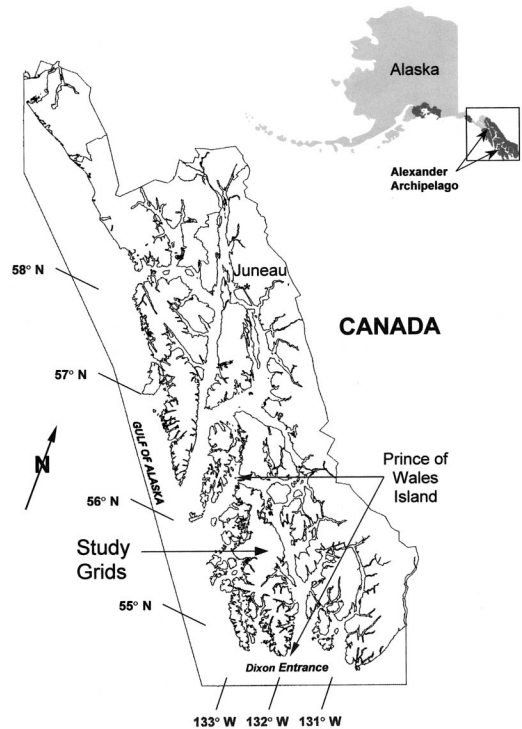


FIG. 1.—Location of study grids for northern flying squirrel (*Glaucomys sabrinus griseifrons*) during 1998–2000, north-central Prince of Wales Island, Alexander Archipelago, southeastern Alaska. Inset map illustrates relative location of southeastern Alaska (box) and Tongass National Forest (darker region). (The darker region in southcentral Alaska is the Chugach National Forest.)

frequently as a mosaic with muskegs (Neiland 1971).

Study sites were selected in north-central Prince of Wales Island, Alaska (55°42′–55°48′N, 132°47′–132°52′W; Fig. 1). The island has experienced the most extensive logging in southeastern Alaska, with about 25% of old-growth forests clear-cut since 1954, mostly at low (<300 m) elevations (United States Department of Agriculture Forest Service 1997). We established study grids (Carey et al. 1991) in largely unmanaged landscapes: 3 replicates each of old-growth Sitka spruce–western hemlock (upland-OG) forest (Julin and Caouette 1997) and peatland–MC forest (Neiland 1971). These 2 habitats were selected because they represent endpoints of a continuum of forested cover types in south-

eastern Alaska. Because peatland-MC forest has a limited distribution in North America, few studies of its indigenous wildlife have been conducted (Smith et al. 2001). Therefore, its capability to support breeding populations of *G. sabrinus* was unknown.

Livetrapping, handling, and marking of animals.—Our livetrapping protocol closely followed that of Carey et al. (1991). Each grid encompassed about 13 ha and consisted of a 10-by-10 array of 100 trap stations at 40-m intervals (360 by 360 m). Two Tomahawk No. 201 (13 by 13 by 41 cm) live traps (Tomahawk Live Trap, Tomahawk, Wisconsin; the use of trade or firm names in this publication is for reader information and does not imply endorsement by United States Department of Agriculture of any product or service) were placed at each station. 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 the other was placed on or near the ground (e.g., on a downed log) within 2 m of the tree supporting the other trap. Two traps were placed on or near the ground within 5 m of the trap station when suitable trees were unavailable. Each trap was covered with a box (4-liter waxed carton) for insulation and to reduce exposure to precipitation. Traps on the tree bole were aligned, with the entrance tilted slightly downward to encourage runoff and reduce accumulation of water. A nesting box, consisting of a waxed carton cut in half and polyester batting, was placed in the rear of each trap to provide refuge against cold and precipitation. Traps were baited with a mixture of peanut butter, whole oats, and molasses (Carey et al. 1991).

We trapped each site twice per year. We selected early spring (March–April) and early autumn (September–October) because we wanted estimates of abundance immediately after winter and during the period when most reproduction and weaning has occurred but juveniles likely have not dispersed (Carey et al. 1991; Villa et al. 1999). During trapping sessions, 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. Trap sites were baited at least 1 day before traps were opened. Traps were opened and baited during early morning of the 1st day. Beginning shortly after sunrise on each day thereafter, all traps were visited and replenished with bait.

The trapping schedule was adjusted when repeated recaptures (≥ 3) of individuals occurred during a 6-day period. Traps were closed for a 2- to 3-day period before we resumed trapping (Carey et al. 1991). Handling and marking of captured squirrels followed Carey et al. (1991). Flying squirrels were weighed to the nearest 1 g with a 300-g spring scale. Body mass, age class, and sex were recorded for initial captures, which were uniquely ear-tagged. The identity (i.e., ear-tag number) of recaptures, date, grid station number, and trap location were recorded. After processing, flying squirrels were released near the capture site.

Demography.—We computed 2 estimates of abundance to increase opportunities for comparing our results with other studies (e.g., Carey 1995). We recorded minimum number known alive (MNA—Krebs 1966), an index commonly used as a measure of relative abundance for comparative purposes (Slade and Blair 2000). The 2nd estimate, the Lincoln–Petersen index, is an unbiased estimator of population size that was selected because it affords relatively precise estimates, with low biases but without many assumptions or other constraints of program models (Menkens and Anderson 1988). Also, the Lincoln–Petersen index performs well over many different conditions and may be the best estimate of small-mammal population size (Menkens and Anderson 1988). Furthermore, we limited sampling periods to ≤ 14 days so that a closed population model could be used to estimate the abundance of flying squirrels (Carey et al. 1991). As recommended by previous investigators (Otis et al. 1978; White et al. 1982), we evaluated individual behaviors and capture probabilities (Menkens and Anderson 1988). We estimated trapability (i.e., recapture probability) using the procedure of Hilborn et al. (1976) because it is the most conservative estimate among common, acceptable measures in the literature (Krebs and Boonstra 1984). Because capture probabilities were not extremely low (< 0.1) and were relatively uniform, we used Chapman's unbiased version (Seber 1982) of the Lincoln–Petersen estimator, which generally performs better than software programs (e.g., CAPTURE—Otis et al. 1978) when sample sizes are small ($n \leq 100$ —Menkens and Anderson 1988).

To obtain density, we used the procedures of Wilson and Anderson (1985a) to estimate “edge effect” and effective area sampled. Mean max-

imum distance moved was estimated seasonally for each grid by averaging maximum straight-line distance between recaptures of all individuals with ≥ 2 captures. A strip equal to one-half mean maximum distance moved was added as a border width to the grid to compute total area trapped (Wilson and Anderson 1985a). The strip represents the expected maximum distance beyond the grid that animals are drawn to live traps. Mean maximum distance moved may be biased because it may vary with number of captures (Wilson and Anderson 1985a), spacing of traps, or subsequent behavior of previously trapped animals (Carey 2000a; Carey et al. 1991). Carey et al. (1991) reported that home ranges of flying squirrels determined from telemetry locations were similar to estimates obtained with mean maximum distance moved, but mean maximum distance moved likely underestimates the movements of flying squirrels (Carey 2000a) and ultimately the effective area trapped. Consequently, density estimates may have a positive bias, but the bias is relatively small, especially with larger grids (Carey 2000a; Carey et al. 1991). Moreover, this approach seems to be the preferred method (Carey et al. 1991; Rosenberg and Anthony 1992; Waters and Zabel 1995; Witt 1992) because of practical considerations (Carey et al. 1991; Wilson and Anderson 1985b) and the difficulty in meeting assumptions of or obtaining sufficient number of captures required by other methods (Carey et al. 1991; White et al. 1982).

Minimum summer (March–mid-September) survival was estimated from the number of recaptured animals during autumn, expressed as a proportion of animals known to be alive in the preceding spring trapping period. Minimum overwinter (November–March) survival was the number of recaptures in spring, expressed as a proportion of animals known to be alive in the previous autumn trapping period (Villa et al. 1999). We tested hypotheses regarding age and sex composition with the log-likelihood ratio, i.e., G -statistic (Zar 1999). Mean body weight was used as an index of body condition. We evaluated productivity by enumerating adult females during spring with evidence of recent reproductive activity, by computing the relative abundance of reproductive females expressed as a percentage of total adult females (Villa et al. 1999), and by comparing recruitment rates of juveniles into the autumn population.

We chose repeated-measures analysis with habitat as the “among-subject” factor or treatment, with seasonal and annual estimates as multiple measurements of each site (i.e., grid) nested within habitat treatment (Zar 1999). We used a mixed linear model in general linear model (GLM—SAS 2000) to reveal an effect of season or year (random effects) or of site or habitat (fixed effects) on demographic parameters of flying squirrels. Thus, during exploratory analysis, grids were treated as subunits of habitat similar to a split-plot analysis of variance (ANCOVA), whereas trapping sessions were viewed as repeated measures of individual grids (Littell et al. 1996; Ramsey and Schafer 1997). Comparison-wise experiment rates were ≤ 0.05 ; maximum experiment-wise error rate was set at 0.10 to reduce the risk of a type II error (Zar 1999). When significance was indicated, we used the Waller–Duncan K -ratio t -test to determine which means differed based on a minimum significant difference with pairwise t -tests (SAS 2000). We took several measures to control experiment-wise error rates, including use of the Waller–Duncan K -ratio, limiting multiple comparisons with significant GLM and testing only hypotheses identified a priori during the development of our study. The Waller–Duncan K -ratio t -test controls for type I error without ignoring consequences for type II error (SAS 2000; Waller and Duncan 1969). Nevertheless, we conducted several ANOVAs and performed numerous paired comparisons. Therefore, to reduce the likelihood of spurious conclusions, we limited inferences to patterns or relationships that were supported by multiple lines of evidence.

RESULTS

Abundance and age and sex composition.—During early spring and autumn of 1998–2000, we captured 163 and 237 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. Average probability of capture (i.e., number captured/estimated number present) was relatively high across habitats, seasons, and years (range, 0.51–0.78). Capture probability was higher ($G = 17.7$, $d.f. = 1$, $P = 0.00002$) in spring ($\bar{X} = 0.72$, $SE = 0.04$) than during autumn ($\bar{X} = 0.58$, $SE = 0.03$).

TABLE 1.—Mean maximum distance moved (MMDM) by and 2 abundance estimates of northern flying squirrels (*Glaucomys sabrinus griseifrons*) during spring and autumn in unmanaged peatland-scrub-mixed-conifer (peatland-MC) and Sitka spruce-western hemlock (upland old-growth [OG]) forests, Prince of Wales Island, southeastern Alaska, 1998–2000. (Some values are not available for spring 1998.)

		Peatland-MC						Upland-OG					
		MNA ^a		MMDM ^b (m)		Density ^c (no./ha)		MNA ^a		MMDM ^b (m)		Density ^c (no./ha)	
		\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
1998	Spring	2	1					4	1	142	38		
	Autumn	18	3	89	8	1.9	0.4	22	2	76	6	2.2	0.2
1999	Spring	13	2	109	11	1.0	0.5	19	2	78	11	1.6	0.2
	Autumn	17	4	104	10	1.5	0.8	33	4	93	5	4.0	0.8
2000	Spring	17	1	96	13	1.3	0.1	20	2	88	10	2.0	0.4
	Autumn	19	5	106	10	1.9	0.7	30	6	93	7	3.4	0.6

^a Minimum number known alive on a grid from current and previously marked individuals.

^b Wilson and Anderson (1985a).

^c Chapman's unbiased Lincoln-Petersen estimate of abundance (Seber 1982) divided by effective area sampled as estimated with MMDM (Wilson and Anderson 1985a).

In addition, seasonal variation in capture probability was not independent of habitat ($G = 8.07$, $d.f. = 3$, $P = 0.045$); upland-OG (0.66–0.53) had smaller seasonal differences than peatland-MC (0.77–0.61). Recapture probability averaged 0.33 ($SE = 0.04$) and ranged 0.30–0.39.

Minimum number known alive ranged among grids from 1, recorded during spring 1998 on 1 upland-OG and 2 peatland-MC grids, to 35 during autumn 1999 on an upland-OG grid (Table 1). Overall, mean MNA was 50% higher ($F = 5.26$, $d.f. = 1$, 4 , $P = 0.08$) in upland-OG (21, $SE = 3$) than in peatland-MC (14, $SE = 3$), but it varied among years ($F = 18.62$, $d.f. = 1$, 8 , $P = 0.0010$). Average MNA was lower in 1998 (11, $SE = 2$) than in 1999 (20, $SE = 3$; $t = 4.68$, $d.f. = 35$, $P = 0.0005$) or 2000 (21, $SE = 4$; $t = 5.15$, $d.f. = 35$, $P = 0.0002$), which did not differ ($t = 0.47$, $d.f. = 35$, $P = 0.6453$). In addition, on average, MNA during autumn (23) was 2 times greater than during spring (12; $F = 4.47$, $d.f. = 2$, 12 , $P = 0.0355$), except in 1998 when value in autumn (20) was an order of magnitude greater than that in spring (3).

Mean maximum distance moved ranged from 75 to 142 m (Table 1) but was similar

between habitats ($F = 1.35$, $d.f. = 1$, 4 , $P = 0.31$) and seasons ($F = 0.27$, $d.f. = 1$, 387 , $P = 0.60$), averaging 92 m ($SE = 9.12$). However, significant annual variation occurred in autumn ($F = 3.93$, $d.f. = 2$, 362 , $P = 0.0206$), with squirrels averaging smaller mean maximum distance moved in 1998 (81 m) than in 1999 (100 m; $t = 2.51$, $d.f. = 371$, $P = 0.0126$) or 2000 (98 m; $t = 2.20$, $d.f. = 371$, $P = 0.0281$). Effective area sampled averaged 16.5 ha ($SE = 0.08$), and mean density ranged from 1.0 to 4.0 squirrels/ha (Table 1). Overall, mean densities in upland-OG and peatland-MC forest did not differ significantly ($F = 3.91$, $d.f. = 1$, 4 , $P = 0.1191$). However, we found a significant habitat-by-season interaction ($F = 5.03$, $d.f. = 1$, 8 , $P = 0.0552$), with mean squirrel density during autumn higher in upland-OG forest (3.7/ha) than in peatland-MC (1.7/ha; $t = 4.58$, $d.f. = 23$, $P = 0.0018$). Also, mean autumn density varied annually ($F = 3.55$, $d.f. = 2$, 8 , $P = 0.0789$), with squirrel density in 1998 (2.1/ha) lower than in 1999 (2.8/ha; $t = 2.48$, $d.f. = 17$, $P = 0.0381$); density in 2000 (2.6/ha) did not differ significantly from 1998 ($t = 2.08$, $d.f. = 17$, $P = 0.0709$) or 1999 ($t = 0.40$, $d.f. = 17$, $P = 0.7012$).

TABLE 2.—Seasonal age and sex composition and productivity (i.e., percentage of reproductive females) of the Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) in unmanaged peatland-scrub-mixed-conifer (peatland-MC) and Sitka spruce-western hemlock (upland old-growth [OG]) forests of southeastern Alaska, 1998–2000.

	Spring						Autumn					
	Males			Females			Males			Females		
	<i>n</i> ^a	Juv ^b	Ad ^c	Juv ^b	Ad ^c	% reproductive ^d	<i>n</i> ^a	Juv ^b	Ad ^c	Juv ^b	Ad ^c	% reproductive ^d
1998												
Peatland-MC	6	0	3	0	3	100	52	5	24	3	20	8
Upland-OG	11	0	6	0	5	80	65	8	25	7	25	8
1999												
Peatland-MC	38	0	24	0	14	78	50	5	26	6	13	0
Upland-OG	57	0	28	0	29	75	100	10	47	6	37	0
2000												
Peatland-MC	50	0	32	0	18	71	57	7	29	2	19	5
Upland-OG	60	0	36	0	24	75	89	8	35	10	36	0

^a Total number of animals for which age and sex were recorded, which was \leq minimum number known alive.

^b Young of the year (i.e., age class I) according to Villa et al. (1999).

^c Individuals that showed pelage or rostrum features of adults (Villa et al. 1999), regardless of evidence of reproductive maturity.

^d Percentage of females exhibiting evidence of reproductive activity (i.e., in estrus, pregnant, lactating). Because data were not obtained for all adult females, sample size is \leq number of adult females recorded.

We observed no significant annual variation in age and sex composition ($G = 0.165$, $d.f. = 2$, $P = 0.92$); therefore, we pooled observations across years to compare seasonal age and sex ratios between habitats. Relatively more adult and juvenile males were observed in peatland-MC than in upland-OG (Table 2), but age and sex composition was independent of habitat during spring ($G = 1.46$, $d.f. = 1$, $P = 0.24$) and autumn ($G = 2.75$, $d.f. = 3$, $P = 0.44$). When data were pooled across seasons, however, proportionally more ($G = 4.10$, $d.f. = 1$, $P = 0.045$) male squirrels were captured in peatland-MC (1.6 male:1 female) than in upland-OG (1.1 male:1 female).

Body condition, survival, and reproductive success.—Overall, mean body weight of squirrels was similar ($F = 0.41$, $d.f. = 1, 4$, $P = 0.56$) between habitats and averaged 122 g (Table 3). Juvenile body weight varied among years ($F = 6.94$, $d.f. = 2, 9$, $P = 0.0150$); in both habitats, juveniles were smaller during 1998 ($\bar{X} = 93$ g) than during 1999 ($\bar{X} = 117$ g; $t = 16.02$,

$d.f. = 32$, $P = 0.00001$) and 2000 ($\bar{X} = 112$ g; $t = 15.45$, $d.f. = 32$, $P = 0.00001$), which also differed ($t = 4.48$, $d.f. = 32$, $P = 0.0001$).

Minimum summer (mid-April to mid-September) survival ranged from 16.7% (1/6) during 1998 in peatland-MC to 65.7% (46/70) during 2000 in upland-OG forest. Minimum summer survival in peatland-MC during 1999 and 2000 was 57.8% (26/45) and 38.0% (19/50), respectively. In upland-OG forests, minimum summer survivorship was 20.0% (2/10) and 47.6% (30/63) in 1998 and 1999, respectively. Minimum winter (November–February) survival varied from 43.9% (25/57) in peatland-MC during 1999–2000 to 60.4% (32/53) in peatland-MC in the previous winter. Corresponding values for upland-OG forests were 49.0% (50/102) and 49.2% (32/65). We compared minimum survival rates between habitats and among years with a log-likelihood ratio and found that minimum summer survival, year, and habitat were not mutually independent ($G = 17.99$, $d.f. = 7$, $P = 0.013$). Moreover, neither year ($G =$

TABLE 3.—Seasonal body weights (g) of juvenile and adult northern flying squirrel (*Glaucomys sabrinus griseifrons*) in peatland-scrub-mixed-conifer (peatland-MC) and Sitka spruce-western hemlock (upland old-growth [OG]) forests, Prince of Wales Island, southeastern Alaska, 1998–2000.

Year and habitat	Adult												Juvenile ^a					
	Male						Female						Male Autumn		Female Autumn			
	Spring		Autumn		Spring		Autumn		Spring		Autumn		Autumn		Autumn			
	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>		
1998																		
Peatland-MC	131	2	3	121	2	22	139	1	2	128	2	18	89	8	4	103	11	3
Upland-OG	130	4	6	119	2	23	129	13	3	123	3	23	86	7	8	100	1	7
1999																		
Peatland-MC	135	3	12	117	2	10	127	4	6	116	2	6	108	6	4	116	11	5
Upland-OG	125	2	17	124	1	35	124	3	16	123	2	19	119	3	10	117	3	6
2000																		
Peatland-MC	130	3	12	127	2	11	118	3	8	128	4	11	108	4	7	110	1	2
Upland-OG	138	2	15	124	3	12	126	3	11	121	2	36	114	3	7	114	3	9
Overall	132	3	65	122	2	113	125	4	46	123	3	113	106	5	40	111	6	32

^a Age-class I (i.e., young of the year—Villa et al. 1999).

16.06, $d.f. = 6$, $P = 0.015$) nor habitat ($G = 10.33$, $d.f. = 5$, $P = 0.070$) was independent of flying squirrel survival rate ($G = 17.88$, $d.f. = 5$, $P = 0.004$) with summer survival overall higher in upland-OG (55%) than in peatland-MC (46%). Minimum summer survival increased during the period of the study, with substantially lower rates in 1998 (3/16) than in 1999 (56/108) or 2000 (65/120). In contrast, winter survival was independent of year and habitat ($G = 5.53$, $d.f. = 4$, $P = 0.24$). Survival over extended periods (i.e., 12, 18, and 24 months) was independent of habitat ($G = 4.55$, $d.f. = 5$, $P = 0.48$). Longevity in both habitats was 30 months, which was the maximum value that could be obtained in this study.

The number of reproductive females was higher ($F = 6.89$, $d.f. = 1, 4$, $P = 0.0585$) in upland-OG (3.9/grid) than in peatland-MC (2.1/grid) but varied significantly ($F = 4.84$, $d.f. = 2, 12$, $P = 0.0419$) among years, with more reproductive females during 2000 (4.4/grid) than during 1998 (1.7/grid; $t = 3.49$, $d.f. = 35$, $P = 0.0045$); values in 1999 (2.8/grid) did not differ significantly from those in 2000 ($t = 2.01$, $d.f. = 35$, $P = 0.0674$) or 1998 ($t = 1.48$, $d.f. = 35$, $P = 0.1643$). However, percentage of reproductive females in peatland-MC (75.9%) did not differ ($G = 0.002$, $d.f. = 1$, $P = 0.97$) from upland-OG (75.5%). Moreover, juvenile recruitment rates did not differ ($G = 0.183$, $d.f. = 1$, $P = 0.69$) between upland-OG (19.3%) and peatland-MC (17.6%).

DISCUSSION

This study provides the 1st quantitative estimate of flying squirrel abundance and demography in temperate rain forest of southeastern Alaska. Despite significant seasonal and annual variation, patterns existed that provide valuable insights regarding habitat distribution and abundance of squirrels. As predicted, flying squirrels were consistently more abundant in upland-OG than peatland-MC forests. Old-growth

Sitka spruce–western hemlock forests are dense-canopied, structurally complex forests that occur on the most productive sites in southeastern Alaska (Alaback 1982; Julin and Caouette 1997). In addition, these forests apparently contain many vegetative and structural habitat features (DeMeo et al. 1992) important to the life history of *G. sabrinus* among coastal coniferous forests of the Pacific Northwest (Carey 1995, 2000b; Carey et al. 1999). Nevertheless, flying squirrels were relatively abundant in peatland-MC, and documenting breeding populations in these largely noncommercial forests was a unique finding that was somewhat unexpected (L. A. Suring, in litt.). The habitat capability model developed for *G. sabrinus* in southeastern Alaska assumed that peatland-MC was unsuitable for sustaining breeding populations. Peatland-MC sites in our study were spatially heterogeneous, with a diversity of conditions ranging from poorly drained mixed-conifer forests to a mosaic of less-productive open-canopied scrub forest (shore pine) and boggy, open muskegs (DeMeo et al. 1992). On better-drained sites were patches of closed-canopied forests, which were of marginal value commercially but with structural complexity and understory composition that approach upland-OG (DeMeo et al. 1992; Julin and Caouette 1997). In interior Alaska, populations of *G. sabrinus* apparently thrive in open-canopied white spruce (*Picea glauca*) forests (Mowrey and Zasada 1984) that seem similar in stand structure (albeit less diverse compositionally) to sites in peatland-MC forests of southeastern Alaska.

In the Pacific Northwest, squirrel densities varied considerably (0.1–3.5 squirrels/ha), depending on forest type, seral stage, and management history (Carey 1995; Carey et al. 1992, 1999; Rosenberg and Anthony 1992; Waters and Zabel 1995; Witt 1992). Highest mean density (3.3 squirrels/ha) was reported from old-growth fir (*Abies*) forest of northeastern California during summer (Waters and Zabel 1995),

which was comparable with our autumn estimate in upland-OG (3.7 squirrels/ha). Lowest density (0.1 squirrels/ha) occurred in 2nd-growth Douglas-fir (*Pseudotsuga menziesii*) forest of southwestern Oregon (Witt 1992). Low densities (0.2–0.5 squirrels/ha) also were reported in the Puget Trough, Olympic Peninsula, and Northern Cascades of Washington (Carey et al. 1992). In eastern North America, demographic studies of *G. sabrinus* are relatively few and lack comparable estimates of population density (Reynolds et al. 1999; Weigl et al. 1992).

The range of variation among forest types and locations raises questions about factors that influence squirrel density. Carey (1995) reported latitudinal variation in abundance, with densities in the southern Coast Ranges and Central Western Cascades of Oregon notably higher than on the Olympic Peninsula or in the North Cascades of Washington. In old-growth forests of the Olympic National Forest of Washington, he found that abundance was associated with the presence of ericaceous shrubs and large snags. Flying squirrels of the Douglas fir–western hemlock zone in Oregon selected habitats with higher decadence and more complex forest canopies (Carey et al. 1999).

Many of the vegetative and structural features correlated with higher squirrel densities in the Pacific Northwest (Carey 1995; Carey et al. 1999) are common to forests of southeastern Alaska (Alaback 1982; DeMeo et al. 1992), and therefore it is unlikely that habitat alone explains the variation in squirrel density between the 2 regions.

Despite many ecological similarities among regional populations, several aspects of the natural history of *G. sabrinus* may vary geographically (Carey 1995; Carey et al. 1999). Phylogeography of *G. sabrinus* in northwestern North America is highly variable, and flying squirrel populations in southeastern Alaska apparently were not established by immigrants from the Pacific

Northwest (Arbogast 1999; Demboski et al. 1998b). Flying squirrels in the Pacific Northwest are substantially different genetically from flying squirrels in southeastern Alaska, which are more closely related to populations in eastern North America. Flying squirrels in southeastern Alaska are as genetically distinct from populations in the Pacific Northwest as each is from the southern flying squirrel (*G. volans*—Arbogast 1999; Demboski et al. 1998b).

The diet of *G. sabrinus* in southeastern Alaska also differs substantially from the diet of squirrels in the Pacific Northwest (Pyare et al. 2002). Studies of food habits in the Pacific Northwest consistently documented a predominance of truffles in the diet (Carey 1995; Hall 1991; Maser and Maser 1988; Maser et al. 1986; McKeever 1960; Pyare and Longland 2001; Rosentreter et al. 1997; Waters and Zabel 1995). Flying squirrels from southeastern Alaska ate fewer taxa of truffles, consumed truffles less frequently, and consumed vascular vegetation, lichens, and epigeous fungi (i.e., mushrooms) more frequently. Diet and food habits have been implicated as a factor influencing squirrel abundance in the Pacific Northwest (Carey et al. 1999; Pyare and Longland 2002). However, evidence linking diet to quality and capability of habitats to support flying squirrel populations is limited (Claridge et al. 1999).

Alternatively, variation in the composition of ecological communities, especially interspecific interactions, may contribute to geographic variation in habitat distribution and abundance of flying squirrel populations (Carey 1991, 1995; Carey et al. 1999). Predation may be an important ecological factor distinguishing southeastern Alaska from the Pacific Northwest. Southeastern Alaska has few (if any) predators that specialize on *G. sabrinus*, and predation rates on flying squirrels may be relatively low. In the Pacific Northwest, *G. sabrinus* is the primary prey of the northern spotted owl, *Strix occidentalis occidentalis* (Forsman et al. 1984, 2001; Hamer et al. 2001), and pre-

dition rates are presumably much higher than in southeastern Alaska. In addition, competitive release from interspecific competition may further distinguish populations of flying squirrels in southeastern Alaska from those in the Pacific Northwest. Coastal coniferous forests of Washington and Oregon support several arboreal and forest-floor squirrels (i.e., Sciuridae) and other small mammals (Carey 1995; Verts and Carraway 1998), many of which are mycophagous (Maser et al. 1978) or use other food or habitat resources (e.g., dens) important to flying squirrels (Carey 1995; Carey et al. 1991, 1999). Conversely, small-mammal communities of southeastern Alaskan rain forest are relatively depauperate (MacDonald and Cook 1996), much less diverse than forest communities of the Pacific Northwest (Carey 1991, 1995; Verts and Carraway 1998). Although red squirrels (*Tamiasciurus hudsonicus*) and flying squirrels are sympatric over a large portion of the range of *G. sabrinus*, red squirrels are absent from Prince of Wales Island (MacDonald and Cook 1996). The Prince of Wales flying squirrel has almost exclusive access to many resources important to its life cycle.

Previous investigators of flying squirrels in the Pacific Northwest (Carey 1995; Rosenberg and Anthony 1992; Villa et al. 1999) generally observed 1:1 sex ratios or ratios slightly favoring females (e.g., Carey 1995) during autumn with one notable exception: Rosenberg and Anthony (1992) reported male-biased juvenile sex ratios in 1 year of a 3-year study. Also, Villa et al. (1999) reported seasonal variation, with males comprising a larger proportion of spring sample. We recorded similar spring and autumn sex ratios (within habitats), which consistently favored males. Villa et al. (1999) suggested that the sex ratio favoring males in spring was likely a result of a difference in capture probability rather than demography. In our study, capture probability was higher in spring than during autumn, but this variation could be related

to seasonal differences in density. Also, upland-OG had smaller seasonal differences in capture probability than peatland-MC, which also had a higher male:female ratio. Therefore, some variation in sex ratios between habitats may have been related to differences in the number or behavior of males seeking estrous females (Villa et al. 1999; Witt 1991).

The proportion of juveniles captured in our study was much lower than that reported by Villa et al. (1999) in the Pacific Northwest. In the Oregon Coast Range and Puget Trough of Washington, they reported percentages of juveniles in autumn of about 40% and 30%, respectively. In our study, juvenile percentages averaged 19% for both males and females. Villa et al. (1999) proposed density-dependent reproduction as a mechanism to explain variation in juvenile recruitment between Puget Trough and Oregon Coast Range. They suggested that breeding is delayed in younger females and that fewer flying squirrels breed at higher densities, a consequence of which is lower juvenile recruitment rates with a smaller percentage of juveniles in the autumn population. We found higher squirrel densities than those reported for Washington and Oregon (Carey 1995; Carey et al. 1992).

Contrary to our prediction, we found no difference in body mass between upland-OG and peatland-MC habitats. Similarly, Rosenberg and Anthony (1992) did not detect differences in body mass between old-growth and 2nd-growth Douglas-fir stands in the Oregon Cascade Range. However, Villa et al. (1999) reported that mean body mass of flying squirrels varied considerably among locations in Washington and Oregon. Average body mass of adults in our study (122 g) was lower than values reported for flying squirrels in the Pacific Northwest (Carey 1995; Rosenberg and Anthony 1992; Villa et al. 1999). Conversely, juveniles in our study weighed more on average (108 g) than juveniles from the Pacific Northwest. In habitat most similar to southeastern Alaska (Olympic Trough,

Washington), Carey (1995) reported mean body weights of adults and juveniles similar to values at several locations in Oregon and Washington (Rosenberg and Anthony 1992; Villa et al. 1999). The relationship between body condition and survival is not well documented for *G. sabrinus*, but the likelihood of surviving winter (or other periods of stress) probably improves with increasing body mass, which is linked to habitat quality (Villa et al. 1999). We had predicted that survival would be higher in upland-OG than in peatland-MC, but neither body mass nor overwinter survival differed between habitats. Minimum summer survival was higher in upland-OG than in peatland-MC, which was unexpected because in the Pacific Northwest, survival of older squirrels was similar among forest types in different regions (Villa et al. 1999).

As expected, the number of reproductive females during spring was higher in upland-OG than in peatland-MC. However, relative abundance (i.e., percentage) of reproductive females in the population and juvenile recruitment into the autumn population did not differ between habitats. No detailed studies have been conducted on the reproductive ecology of flying squirrels in the Pacific Northwest or southeastern Alaska (Smith et al. 2003). Substantial variation in percentage of reproductive females exists between forest types and geographic regions, ranging from 90% in the Puget Trough to 39% in the Oregon Coast Range (Villa et al. 1999). On the Olympic Peninsula, 31% and 29% of the females in old-growth and young forests, respectively, were reproductive (Carey 1995). Variation in juvenile recruitment among geographic regions of the Pacific Northwest may be attributable to a density-dependent response of squirrel populations (Villa et al. 1999).

We found that percentage of reproductive females was similar (76%) in peatland-MC and upland-OG, which differed substantially in density of flying squirrels. Densities in southeastern Alaska are comparable with (if not higher than) those in the Oregon

Coast Range; yet, the percentage of reproductive females in our study was nearly twice that reported by Villa et al. (1999). Several factors likely contribute to variation in reproductive performance of flying squirrel populations, not the least of which is the ability of investigators to assess reproductive parameters accurately (Carey et al. 1991; Villa et al. 1999). In our study, variation in reproductive performance appeared to be linked to differences in habitat capability (i.e., density of reproductive females) rather than the consequence of a density-dependent response (i.e., percentage of reproductive females or juvenile recruitment) to winter population levels.

Our results are consistent with those from studies of several coniferous forest types in the Pacific Northwest in support of old-growth Sitka spruce–western hemlock forests of southeastern Alaska as primary habitat of northern flying squirrels. More importantly, we documented squirrel densities in peatland-MC forests that were comparable with, or greater than, densities reported for several unmanaged and managed forest types in the Pacific Northwest. Furthermore, other demographic parameters were similar between habitats. If the results of our study can be generalized across southeastern Alaska, peatland-MC forests likely contribute to breeding populations in managed landscapes and thus reduce the risk of viability for local populations of flying squirrels. However, no information exists on how habitat distribution and demography of *G. sabrinus* change as population levels vary. Additional study is needed to determine what landscape features and configurations might restrict squirrel dispersal and potentially isolate populations, further reducing opportunities for rescue and increasing the likelihood of local extinctions.

ACKNOWLEDGMENTS

We thank the personnel of Thorne Bay and Craig Ranger Districts for logistic and personnel support, especially M. McFadden. T. Wilson refined our protocol for livetrapping and handling

flying squirrels. R. Woodsmith loaned us a vehicle for fieldwork. The following volunteers endured unusually challenging conditions to contribute to this study: P. Hillman, K. Murabito, and N. Soucey. Also, the following seasonal technicians were an invaluable field crew: M. Anderman, J. DePiero, A. Eddingsaas, N. Favreau, J. Frisch, J. Heys, A. Hurst, D. Magness, B. Marston, M. McMurray, J. Moran, K. Moughamer, K. Obermeyer, S. Pyare, T. Rinaldi, A. Rinker, T. Smith, K. White, and J. Wisnowski. We thank A. B. Carey, W. Eastland, I. K. Hanski, K. Parker, and S. Pyare for reviewing an early draft of the manuscript.

LITERATURE CITED

- ALABACK, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* 63:1932–1948.
- ANDREN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitats: a review. *Oikos* 71:355–366.
- ARBOGAST, B. S. 1999. Mitochondrial DNA phylogeography of the New World flying squirrels (*Glaucomys*): implications for Pleistocene biogeography. *Journal of Mammalogy* 80:142–155.
- BIDLACK, A. L., AND J. A. COOK. 2001. Reduced genetic variation in insular northern flying squirrels (*Glaucomys sabrinus*) along the North Pacific Coast. *Animal Conservation* 4:283–290.
- BURKEY, T. V. 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. *Conservation Biology* 9:527–541.
- 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-276:1–46.
- CAREY, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications* 5:648–661.
- 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., 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-273:1–24.
- 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.
- CLARIDGE, A. W., J. M. TRAPPE, S. J. CORK, AND D. I. CLARIDGE. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. *Journal of Comparative Physiology, B. Biochemical, Systematic, and Behavioral Physiology* 169:172–178.
- COOK, J. A., ET AL. 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska. *Biological Conservation* 97:215–227.
- COOK, J. A., AND S. O. MACDONALD. 2001. Should endemism be a focus of conservation efforts along the north Pacific coast of North America? *Biological Conservation* 97:207–213.
- DEMBOSKI, J. R., J. A. COOK, AND G. L. KIRKLAND, JR. 1998a. *Glaucomys sabrinus* (Shaw 1801): northern flying squirrel. Pp. 37–39 in *North American rodents: status survey and conservation action plan* (D. J. Hafner, E. Yensen, and G. L. Kirkland, Jr., eds.). IUCN/SSC Rodent Specialist Group, Gland, Switzerland.
- DEMBOSKI, J. R., B. K. JACOBSEN, AND J. A. COOK. 1998b. Implications of cytochrome *b* sequence variation for biogeography and conservation of the northern flying squirrels (*Glaucomys sabrinus*) of the Alexander Archipelago, Alaska. *Canadian Journal of Zoology* 76:1771–1777.
- 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-210:1–405.
- 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. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-415:1–69.
- 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.
- FORSMAN, E. D., ET AL. 2001. Spatial and temporal variation in diets of spotted owls in Washington. *Journal of Raptor Research* 35:141–150.
- FRANKHAM, R. 1998. Inbreeding and extinction: island populations. *Conservation Biology* 12:665–675.
- HALL, D. S. 1991. Diet of the northern flying squirrel at Sagehen Creek, California. *Journal of Mammalogy* 72:615–617.
- HAMER, T. E., D. L. HAYS, C. M. SENGER, AND E. D. FORSMAN. 2001. Diets of northern barred owls and northern spotted owls in an area of sympatry. *Journal of Raptor Research* 35:221–227.
- 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.
- HANSKI, I. K., M. MÖNKKÖNEN, P. REUNANEN, AND P. STEVENS. 2000. Ecology of the Eurasian flying squirrel (*Pteromys volans*) in Finland. Pp. 67–86 in *Biology of gliding mammals* (R. L. Goldingay and J. S. Scheibe, eds.). Filander Verlag, Fürth, Germany.
- 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-25:1–109.
- HILBORN, R., J. A. REDFIELD, AND C. J. KREBS. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology* 54:1019–1024.
- HOKKANEN, H., T. TORMALA, AND H. VUORINEN. 1982. Decline of the flying squirrel (*Pteromys volans* L.) populations in Finland. *Biological Conservation* 23:273–284.
- HOWELL, A. H. 1934. Description of a new race of flying squirrel from Alaska. *Journal of Mammalogy* 15:64.
- 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-34:1–57.
- JULIN, K. R., AND J. P. CAQUETTE. 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, tech. coord.). United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-392:1–58.
- KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36:239–273.
- KREBS, C. J., AND R. BOONSTRA. 1984. Trappability estimates for mark-recapture data. *Canadian Journal of Zoology* 62:2440–2444.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute Inc., Cary, North Carolina.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Monographs in Population Biology. Princeton University Press, Princeton, New Jersey.
- MACDONALD, S. O., AND J. A. COOK. 1996. The land mammal fauna of southeast Alaska. *Canadian Field-Naturalist* 110:571–598.
- MARTIN, S. K. 1994. Feeding ecology of martens and fishers. Pp. 297–315 in *Martens, sables, and fishers: biology and conservation* (S. W. Buskirk, A. S. Harstad, M. G. Raphael, and R. A. Powell, eds.). Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- 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.
- MCKEEVER, S. 1960. Food of the northern flying squirrel in northeastern California. *Journal of Mammalogy* 41:270–271.
- 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, 12–15 April 1982* (W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds.). American Institute of Fishery Research Biologists, Morehead City, North Carolina.
- NEILAND, B. J. 1971. The forest bog complex of southeast Alaska. *Vegetatio* 22:1–63.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- PYARE, S., AND W. F. LONGLAND. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. *Journal of Mammalogy* 82:681–689.
- 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* 116:98–103.
- RAMSEY, F. L., AND D. W. SCHAFER. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury and Wadsworth, Belmont, California.
- REYNOLDS, R. J., J. F. PAGELS, AND M. L. FIES. 1999. Demography of northern flying squirrels in Virginia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 53:340–349.
- 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 INSTITUTE INC. 2000. SAS/STAT user's guide. Release 8.1 ed. 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 *Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982* (W. R. Meehan, T. R. Merrell, and T. A. Hanley, eds.). American Institute of Fishery Research Biologists, Morehead City, North Carolina.
- 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, Asheville, North Carolina.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. Griffen, London, United Kingdom.
- SHAW, C. G., III. 1999. Use of risk assessment panels during revision of the Tongass Land and Resource Management Plan. United States Department of Agriculture, Forest Service, General Technical Report PNW-GTR-460:1–43.
- SLADE, N. A., AND S. M. BLAIR. 2000. An empirical test of using counts of individuals captured as indices of population size. *Journal of Mammalogy* 81: 1035–1045.
- 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., M. J. STOTTS, B. A. ANDRES, J. M. MELTON, A. GARIBALDI, AND K. BOGGS. 2001. Bird, mammal, and vegetation community surveys on Research Natural Areas in the Tongass National Forest. United States Department of Agriculture, Forest Service, Research Paper-PNW-RP-535:1–44.
- SOULÉ, M. E., AND B. A. WILCOX (EDS.). 1980. *Conservation biology*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- 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.
- VAN HORNE, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeastern Alaska. *Canadian Journal of Zoology* 59:1045–1061.
- 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.
- 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-444:1–59.
- WALLER, R. A., AND D. B. DUNCAN. 1969. A Bayes rule for the symmetric multiple comparison problem. *Journal of the American Statistical Association* 64: 1484–1499.
- 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 and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. North Carolina Wildlife Resources Commission, Raleigh.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. United States Department of Energy, Office of Health and Environmental Research, National Environmental Research Park, Los Alamos National Laboratory Publication LA-8787-NERP:1–235.
- WILSON, K. R., AND D. R. ANDERSON. 1985a. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- WILSON, K. R., AND D. R. ANDERSON. 1985b. Evaluation of a nested grid approach for estimating density. *Journal of Wildlife Management* 49:675–678.
- WITT, J. W. 1991. Fluctuations in the weight and trapping response for *Glaucomys sabrinus* in western Oregon. *Journal of Mammalogy* 72:612–615.
- 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 ed. Prentice Hall, Inc., Upper Saddle River, New Jersey.

Submitted 10 April 2002. Accepted 14 October 2002.

Associate Editor was Ronald E. Barry.