

DEMOGRAPHY OF TWO ENDEMIC FOREST-FLOOR MAMMALS OF SOUTHEASTERN ALASKAN TEMPERATE RAIN FOREST

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We studied demography of the Keen's mouse (*Peromyscus keeni macrorhinus*) and the Wrangell Island red-backed vole (*Clethrionomys gapperi wrangeli*) in the Alexander Archipelago during 1998–2000 because of concerns over population viability from extensive clear-cut logging of temperate rain forest in the region. We trapped 1-ha grids and assessment lines with live traps during spring and autumn to compare populations among gap-phase old-growth, multicohort old-growth, peatland mixed-conifer, and thinned young-growth (23-year-old) forests. Generally, gap-phase old growth and peatland mixed conifer supported the highest and lowest populations of voles, respectively. One notable exception was during autumn 1998, when vole population levels were highest and density was higher ($P < 0.02$) in young growth than gap-phase old growth. Mean body mass, minimum summer and overwinter survival, age and sex composition, and percentage reproductive females did not differ among habitats. For Keen's mouse, density was highest in 1998; overall, populations were highest in young growth and lowest in peatland mixed conifer. Mean body mass and minimum summer and overwinter survival did not differ among habitats, but fewer reproductive females were recorded in multicohort than in gap-phase old growth, peatland mixed conifer, or young growth. Our results suggest that *C. gapperi* populations in southeastern Alaska are not as sensitive to canopy removal as has been indicated elsewhere in western coniferous forests and that *P. keeni* populations in southeastern Alaska flourish in a variety of habitats. If the results of our study can be generalized across southeastern Alaska, peatland mixed conifer likely contributes little to breeding populations of *C. gapperi* and thus is unlikely to mitigate any effects of broad-scale clear-cut logging of old-growth forests.

Key words: abundance, *Clethrionomys gapperi wrangeli*, demography, endemic populations, Keen's mouse, old-growth forest, *Peromyscus keeni*, southeastern Alaska, southern red-backed vole, temperate rain forest

Southeastern Alaska has naturally fragmented habitats and a dynamic geological history (MacDonald and Cook 1996; Runck 2001). The Tongass National Forest comprises about 81% of the region and includes the largest remaining northern temperate rain forest (6.9×10^6 ha) in the world (USDA Forest Service 1997). This region has experienced extensive commercial logging since 1954, yet there exists limited knowledge about its natural history, biota, and ecological value. Despite contributions of forest-floor small mammals to temperate forest communities (Buckner 1966; Elkinton et al. 1996; Maser et al. 1978; Sirotnak and Huntley 2000; Sullivan et al. 1999), the small mammal fauna of southeastern Alaska has been poorly studied (MacDonald and Cook 1996).

Two common forest-floor small mammals of southeastern Alaska rain forest are the southern red-backed vole (*Clethrionomys gapperi*) and Keen's mouse (*Peromyscus keeni*—MacDonald and Cook 1996; Smith et al. 2001). *Peromyscus keeni* is a recently revised taxon, composed of subspecies of *P. maniculatus*, *P. sitkensis*, and *P. oreas* (Hogan et al. 1993). The range of *P. keeni* is “west of the Cascade and Coastal mountains and north of the Columbia River to southern Alaska” (Hogan et al. 1993:825). In Alaska, *P. keeni* is distributed across the Alexander Archipelago and on the mainland portion of southeastern Alaska east and south of Glacier Bay (MacDonald and Cook 1996), where apparently it is a common inhabitant of old-growth riparian and upland forests (Hanley and Barnard 1999). *Clethrionomys gapperi* ranges across much of northern North America (Hall 1981) and is a common resident of mature, mesic forest habitats in the Hudsonian and Canadian life zones (Merritt 1981).

Little is known about the natural history, habitat relations, or population ecology of *C. gapperi* in southeastern Alaska (Runck 2001; Smith et al. 2001). Of particular interest is the

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reputed association of this species with old-growth coniferous forest, which apparently is optimal habitat for *C. gapperi* in the Pacific Northwest (Jerry 1984; Nordyke and Buskirk 1988; but see Taylor 1999). Densities of *C. gapperi* in old-growth forests were twice that observed in younger (55–75-year-old) 2nd-growth stands (Aubry et al. 1991) and about 4–5 times more abundant in old-growth forest than in young (17-year-old) growth (Sullivan et al. 2000) or recent (3–9-year-old) clear-cuts (Sullivan et al. 1999). Conversely, Taylor (1999) reported that *C. gapperi* populations were equally abundant among 5 successional stages of coastal temperate coniferous forest, ranging from recent clear-cut to old growth. However, *C. gapperi* populations of western coniferous forests show acute sensitivity to canopy removal (Aubry et al. 1991; Pearson 1994; Sullivan et al. 1999, 2000) and habitat fragmentation (Bayne and Hobson 1998; Bowman et al. 2001a; Mech and Hallett 2001), although their response to clear-cutting may vary, depending on the size and distribution of canopy gaps (Hayward et al. 1999).

Peromyscus keeni flourishes in a variety of habitats (Hanley and Barnard 1999), including a broad range of forest seral stages (Hanley 1996; Taylor 1999; Van Horne 1982b). However, information regarding its habitat relations, particularly the response of populations to clear-cut logging, has been limited and inconsistent. Hanley (1996) reported similar densities of *P. keeni* between old growth and even-aged 2nd growth in southeastern Alaska. On the Olympic Peninsula, *P. keeni* clearly was more abundant in old growth (Songer et al. 1997; Taylor 1999) than in younger seral stages. Highest densities occurred in continuous forests, with lower populations in fragmented landscapes (Songer et al. 1997).

Portions of the Tongass have been intensively logged over the past 50 years with a bias toward the most productive forests, particularly at lower elevations (Shephard et al. 1999). Many islands in the Alexander Archipelago have experienced substantial clear-cut logging, with some islands converting nearly 50% of old-growth forests below 400 m elevation to early seral stages (USDA Forest Service 1997). Although annual timber harvests often represent a relatively small percentage of the entire national forest, cumulative disturbance from clear-cut logging can modify a significant proportion of the range of island endemic mammals. The potential impact of broad-scale habitat disturbance on wildlife populations is exacerbated by the naturally fragmented nature of the region. Forest habitat is fragmented among islands of the Alexander Archipelago or isolated along a narrow strip of the mainland by mountains and ice fields. Moreover, geology, climate, topography, and other environmental features contribute spatial and temporal heterogeneity.

Knowledge of population dynamics is fundamental to understanding and projecting population responses to habitat modification (Van Horne 1981). The purpose of this paper was to evaluate demography of *C. gapperi wrangeli* (hereafter, voles) and *P. keeni macrorhinus* (hereafter, mice) among 4 habitats in southeastern Alaska. Specific objectives were to contrast seasonal abundance and age and sex composition, physical and reproductive condition, and summer and over-

winter survival rates among habitats. Because *C. gapperi* is a reputed associate of old-growth coniferous forests, we predicted that density, recruitment, and survivorship would be highest in old-growth coniferous forests. For *P. keeni*, an apparent habitat generalist in southeastern Alaska, we predicted that demography would be similar among habitats.

MATERIALS AND METHODS

Study area.—The study was conducted on Wrangell Island (56°30'N, 132°17'W; Fig. 1), a nearshore island encompassing ~500 km² with an elevation that ranges from sea level to 853 m. Across the Tongass National Forest, rain forest dominates the landscape from shoreline to about 600 m elevation, with about 90% of commercial forest in old-growth forests of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*); remaining areas are alpine, muskeg (wet, sparsely forested peatland), or riparian (Harris and Farr 1974; Hutchinson and LaBau 1974). The *Tsuga*–*Picea* forest type constitutes the majority of closed-canopy forests (Alaback 1982). This forest type is heterogeneous at a fine scale (i.e., <1 ha—Schoen et al. 1984) and typically occurs on low-elevation, well-drained sites, frequently as a mosaic with muskegs (Neiland 1971). These forests are characterized by a multicohort, multilayered overstory, dominant trees that are generally >300 years old (Alaback 1982), and structurally diverse understories (Hanley and Brady 1997; Ver Hoef et al. 1988). Forests vary in structure from scrub (low volume) communities of short (<10 m), small (<0.5-m bole diameter) trees with open canopies and dense, shrubby understories on poorly drained sites (Neiland 1971) to highly productive sites that support high-volume stands with a closed canopy, tall (>60 m), large (>3-m bole diameter) trees (Alaback 1982), and a predominantly herbaceous understory (Hanley and Brady 1997; Ver Hoef et al. 1988).

About 50% of Wrangell Island was productive forestland, of which about 11% was logged during the past 4 decades. We studied small mammals in 4 habitats selected according to type and frequency of disturbance, overstory cover, and management history: gap-phase old growth, multicohort old growth, peatland mixed conifer, thinned young (23-year-old) growth. The 2 old-growth habitat types were stands with contrasting disturbance regimes that produce notable differences in forest canopy, understory, and stand structure (Nowacki and Kramer 1998). Gap-phase old growth usually occurs on northerly slopes (sheltered from prevailing windstorms) and experiences frequent, less intense disturbance that results in blowdowns of 1 to a few trees. This habitat is relatively homogeneous at the macrohabitat scale with fine-scale spatial heterogeneity resulting from canopy gaps and trees typically >400 years old. In contrast, multicohort old growth typically has a southerly exposure and experiences infrequent (100–200 years), catastrophic disturbance from windstorms that usually blow down 10–100 ha of forest (Nowacki and Kramer 1998; Kramer et al. 2001). This habitat is spatially heterogeneous at the macrohabitat scale with patches of uniform diameter trees (typically 100–200 years old) distributed within the stand.

The overstory of old-growth forests comprised mostly Sitka spruce and western hemlock. Wetter sites included a larger component of western redcedar (*Thuja plicata*) or yellow-cedar (*Chamaecyparis nootkatensis*) in the canopy. Large trees (>75-cm diameter), downed and decaying wood, snags, and heterogeneous substrates were key components of these habitats. The understory was dominated by blueberry (*Vaccinium*), especially in canopy gaps (Hanley and Brady 1997; Ver Hoef et al. 1988). Because of a more uniformly dense canopy, multicohort old growth usually had sparser understory vegetation than gap-phase old growth. In contrast, peatland mixed-conifer sites were

typified by poor drainage and shallow and organic soils with patches of more productive mixed-conifer forests that occurred on elevated sites of deeper mineral soils. Conifer vegetation ranged from mostly lodgepole pine (*Pinus contorta*), which occurs as an open-canopy, scrub forest in muskegs to more productive mixed-conifer forest of lodgepole pine, yellow-cedar, redcedar, western hemlock, and mountain hemlock (*T. mertensiana*). Understory vegetation in open areas was dominated by a mixture of sedges (*Carex*), grasses (Poaceae), skunk cabbage (*Lysichiton americanum*), and Labrador tea (*Ledum glandulosum*). Blueberry dominated the understory of sites with well-developed overstories (Pawuk and Kissinger 1989).

We established 6 grids (2 replicates of gap-phase old growth, multicohort old growth, and peatland mixed conifer), each of 1 ha (100 × 100 m), in largely unmanaged landscapes. Two additional 1-ha grids were installed in young-growth stands in an intensively managed watershed; 47% of the productive old-growth forest had been harvested during the preceding 30-year period (USDA Forest Service, unpublished data on file with Wrangell Ranger District). Both managed sites were 23 years old and were thinned to 5.5 m ($\pm 25\%$) spacing during spring 1998. All study sites (i.e., grids) were established in ≥ 9 -ha blocks of continuous habitat. Replicates were located in the same watershed to minimize geographical variation but ≥ 800 m apart to achieve independence. Each grid was an 11 × 11 array of trap stations at 10-m intervals. In addition, each grid had 8 assessment lines (Swift and Steinhorst 1976) that began at the center of the grid and extended 90 m beyond the perimeter with 15 trap stations at 10-m intervals (i.e., 120 stations). The grid was used to obtain a marked sample of the population, whereas the assessment lines were used to estimate the effective area trapped (Van Horne 1982a).

Livetrapping animals.—Trapping, handling, and marking of study animals followed Merritt (1982) and adhered to guidelines of the American Society of Mammalogists (ASM Animal Care and Use Committee 1998). We placed 2 Sherman traps (7.6 × 8.9 × 22.9 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida; use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service) with synthetic nesting material at each trap station. During 1999–2000, we covered each trap with a folded piece of aluminum (40 × 40 cm) to afford additional protection from solar radiation and precipitation (Van Horne 1981). Trap stations were prebaited 1 day before trapping began. On the 1st morning of a trapping session, traps were baited with black sunflower seeds, raisins, and grapes. Generally, each grid was trapped for 4 consecutive days and nights (marking period). We weighed and uniquely marked (i.e., toe-clipped) all captures for identification. We recorded date, trap grid and station, age, sex, reproductive condition (Krebs et al. 1969), and identification number of recaptured mice and voles. On the 5th morning, grid traps were closed and moved to assessment line stations and prebaited. On the 6th morning, assessment traps were opened, and we followed the grid protocol except that we did not mark newly captured animals (recapture period).

During 1998–2000, we trapped small mammals in 5 seasonal periods. In each seasonal period there were 2 consecutive trapping sessions, within which we typically included 1 replicate of each habitat. The total time to trap all grids per season was <3 weeks. In September 1998, we trapped 2 replicates each of gap-phase old growth, multicohort old growth, and young growth. In early spring 1999, we added 2 grids in peatland mixed-conifer forest, and during 1999–2000 all grids were trapped once during spring (April–May) and once during autumn (August–September). During spring 1999, both replicates of gap-phase old-growth and young-growth grids were trapped in the same session because snow limited access to other grids.

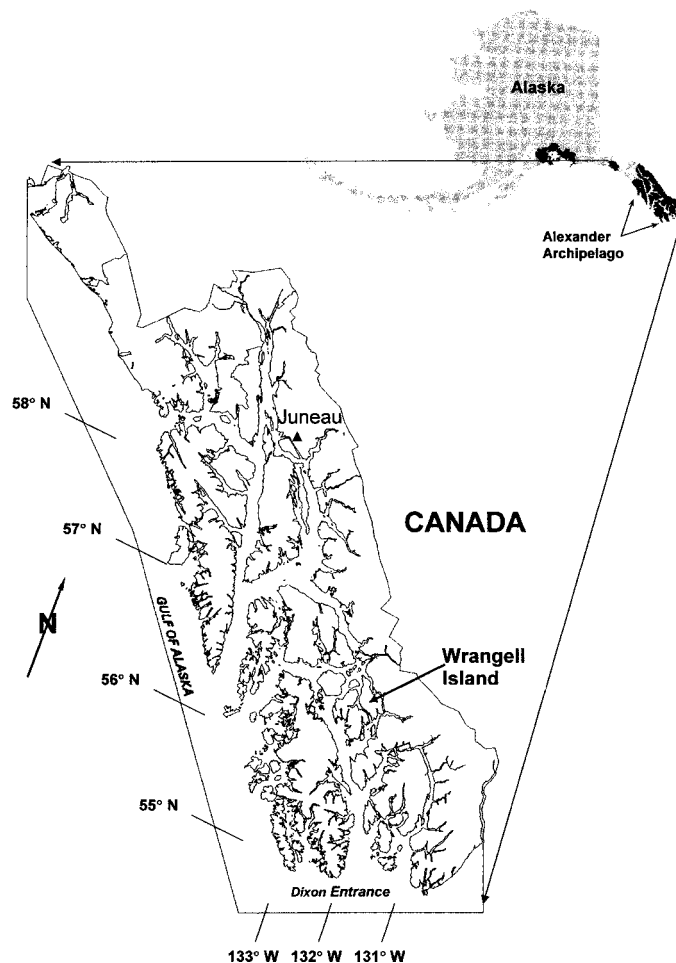


FIG. 1.—Location of the study area, Wrangell Island, in the Alexander Archipelago, southeastern Alaska. Shaded areas in the insert are the Tongass National Forest (southeastern Alaska) and the Chugach National Forest (south-central Alaska).

Demographic analysis.—We computed density with Chapman's unbiased adaptation of the Lincoln–Petersen estimate (Seber 1982) and effective area sampled (Swift and Steinhorst 1976; Van Horne 1982a). The Lincoln–Petersen estimator of population size is appropriate when there are 2 sampling periods and the interval between sampling occasions is relatively short (Menkens and Anderson 1988; Williams et al. 2002). Population size was estimated from the ratio of marked to unmarked individuals captured on the grid during the recapture period. Effective area sampled was estimated as the x-intercept of a simple linear regression (Swift and Steinhorst 1976). We regressed the ratio of marked to total number of animals captured in assessment traps within successive concentric bands against corresponding cumulative area, which becomes larger as distance from grid center increases. We pooled these ratios across grids, seasons, and years to improve the fit of the regression model (Hanley and Barnard 1999). The radius of the circle encompassing the bands of assessment traps estimates distance from grid center beyond which the probability of capturing a marked animal approaches zero. The area of this circle is the effective area sampled (Swift and Steinhorst 1976; Van Horne 1982a).

Minimum summer (mid-May–August) survival was estimated as number of recaptured animals during autumn expressed as a proportion of animals known to be alive in the preceding spring trapping period.

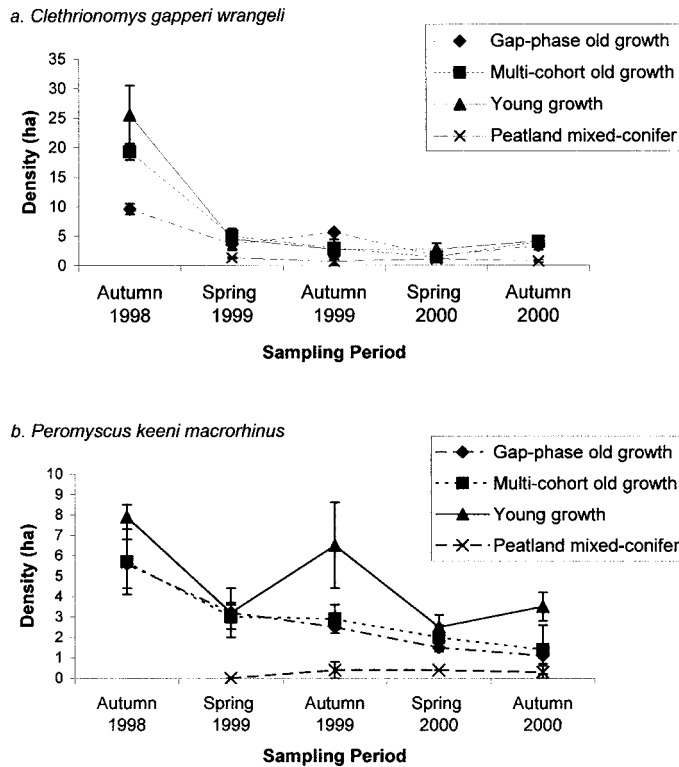


FIG. 2.—Seasonal population density among gap-phase old-growth forest, multicohort old-growth forest, peatland mixed-conifer, and precommercially thinned young-growth (23-year-old) habitats during 5 sampling periods 1998–2000 for a) southern red-backed vole, *Clethrionomys gapperi wrangeli*, and b) Keen's mouse, *Peromyscus keenii macrorhinus*, populations on Wrangell Island, Alexander Archipelago, southeastern Alaska. Densities presented as means \pm SE.

Minimum overwinter (mid-September–April) survival was number of recaptures in the spring expressed as a proportion of animals known to be alive in the previous autumn trapping period (Hanley and Barnard 1999). We chose to estimate survival directly with minimum number of animals known alive during consecutive trapping periods rather than use a program model (e.g., MARK—White and Burnham 1999) because of an untenable assumption of equal recapture probability and the lack of reliable closed capture–recapture models that accommodate individual heterogeneity (White and Burnham 1999), especially with small samples (Menkens and Anderson 1988). Because we used toe-clipping to uniquely mark individuals, we may have influenced survival of marked animals (Pavone and Boonstra 1985). However, we assumed no interaction between habitat and survival with respect to this effect. Mean body mass was used to index body condition, and reproductive performance was estimated as the proportion of adult females on a grid with evidence of reproductive activity (Sullivan et al. 1999). We used contingency-table analysis and log-likelihood ratios to examine variation in age and sex composition, survival, and reproductive performance between seasons and among years or habitats within species (Zar 1999). For multidimensional contingency tables (≥ 3 variables), we used log-linear models to test for mutual independence. When significant interactions occurred, we used log-linear models to test for partial independence. A probability of <0.05 was accepted as indicating statistical significance.

We used a mixed-linear model within GLM software (SAS Institute Inc. 2000) to test the null hypothesis that there was no effect of season or

year (random effects) or site or habitat (fixed effects) on demographic parameters of voles or mice. Grids were subunits of habitat similar to a split-plot analysis of variance (ANOVA), whereas seasonal trapping sessions were viewed as repeated measures of individual grids (Littell et al. 1996; Ramsey and Schafer 1997). The maximum experiment-wise error rate was 0.10; comparison-wise experiment rates were ≤ 0.05 . When significant variation occurred, we used the Waller–Duncan K -ratio t -test to determine which means differed according to a minimum significant difference (SAS Institute Inc. 2000) or computed pairwise t -tests. The Waller–Duncan t -test is a Bayesian approach to multiple comparisons that minimizes the Bayes risk under additive loss rather than controlling Type I error rates. The loss for the joint decision (i.e., Type I and Type II errors) of all pairs of means is the sum of the loss for each individual decision and thus includes consideration of the experiment-wise error rate (SAS Institute Inc. 2000). For pairwise t -tests, we limited the number of hypotheses examined by ranking means and comparing only values that fell outside the range of means that were not significantly different (Zar 1999).

RESULTS

During September 1998 and spring (April–May) and autumn (August–September) 1999–2000, we caught 682 voles and 540 mice (unique individuals). Total captures were 1,743 voles and 1,221 mice, with 72,845 trap nights of effort. Standardized effort (Nelson and Clark 1973) for voles within gap-phase old growth, multicohort old growth, peatland mixed conifer, and young growth were 18,593, 18,231, 14,932, and 18,586 trap nights, respectively. Corresponding values for mice were 18,511, 18,162, 14,912, and 18,493 trap nights. Effective area sampled for voles varied ($F = 7.05$, $d.f. = 3, 20$, $P < 0.01$) among habitats. For gap-phase old-growth forest, effective area sampled was 11.8 ha, larger (mean significant difference = 2.70) than for multicohort old growth (8.0 ha), young growth (7.7 ha), or peatland mixed conifer (7.4 ha). Effective areas in the latter 3 habitats were similar ($\bar{X} = 7.7$ ha). For mice, effective area sampled was similar ($F = 0.05$, $d.f. = 2, 4$, $P = 0.96$) among habitats, averaging 10.8 ha (range 10.3–11.2 ha).

Density.—We obtained density estimates for voles and mice in all habitats during spring and autumn 1999 and 2000 and for gap-phase old growth, multicohort old growth, and young growth during autumn 1998 (Fig. 2a). Vole density in autumn varied by a year \times habitat interaction (Table 1). Vole densities were lower in young growth and multicohort old growth during autumn 1999 and 2000 than in autumn 1998, when young growth had the highest density of all habitats (Table 2). During the 2 years we obtained spring and autumn estimates, there was a year \times season interaction (Table 1). In 2000, vole density during autumn ($\bar{X} = 3.03$ /ha) was higher ($t = 2.95$, $P = 0.018$) than during spring ($\bar{X} = 1.70$ /ha). Also, there was habitat variation within this period (Table 1). Average population density in 1999 (3.29 voles/ha) was higher than in 2000 (2.36 voles/ha), with variation among habitats during both seasons attributable to differences between peatland mixed conifer and the remaining habitats (Table 2). For both species, there was a trend of decreasing density over the period of study (Figs. 2a and 2b) with annual variation in autumn population density for voles ($F = 70.24$, $d.f. = 2, 6$, $P = 0.01$) and mice ($F = 10.70$, $d.f. = 2, 6$, $P = 0.010$). Density was higher in 1998 than

TABLE 1.—Analysis of variance summary from analyses of density^a (GLM procedure, SAS 2000) of red-backed voles (*Clethrionomys gapperi wrangeli*) and Keen’s mouse (*Peromyscus keeni macrorhinus*) among thinned young-growth, gap-phase old-growth, multicohort old-growth, and peatland mixed-conifer forests in southeastern Alaska during autumn 1998–2000 and spring and autumn 1999–2000. *d.f.* given for the numerator (num) and denominator (denom) of the *F*-statistic.

Model and source of variation	<i>d.f.</i>		Type III mean square ^b	<i>F</i>	<i>P</i> > <i>F</i>
	num	denom			
Red-backed vole					
Autumn 1998–2000					
Habitat ^c	2	3	31.981	3.41	0.169
Year	2	6	414.267	70.24	<0.001
Habitat × year	4	6	50.890	8.63	0.012
Grid (habitat)	3		9.378		
Error	6		5.898		
Spring and autumn 1999–2000					
Habitat ^c	3	4	12.615	26.29	0.004
Year ^d	1	4	6.892	1.83	0.247
Habitat × year ^d	3	4	1.867	0.50	0.704
Season	1	8	0.986	1.25	0.297
Habitat × season	3	8	2.094	2.65	0.121
Year × season	1	8	7.685	9.71	0.014
Spring and autumn 1999–2000					
Habitat × year × season	3	8	2.756	3.48	0.070
Grid (habitat)	4		0.480		
Grid × year (habitat)	4		3.760		
Error	8		0.791		
Keen’s mouse					
Autumn 1998–2000					
Habitat ^c	2	3	15.398	7.78	0.065
Year	2	6	29.176	10.70	0.010
Habitat × year	4	6	0.561	0.21	0.926
Grid (habitat)	3		1.979		
Error	6		2.728		
Spring and autumn 1999–2000					
Habitat ^c	3	4	17.876	33.85	0.003
Year ^d	1	4	10.251	14.55	0.019
Habitat × year ^d	3	4	1.589	2.26	0.224
Season	1	8	0.988	0.52	0.491
Habitat × season	3	8	3.087	1.62	0.259
Spring and autumn 1999–2000					
Year × season	1	8	1.209	0.64	0.448
Habitat × year × season	3	8	0.606	0.32	0.812
Grid (habitat)	4		0.528		
Grid × year (habitat)	4		0.704		
Error	8		1.900		

^a Lincoln-Petersen estimate of abundance divided by effective area sampled in hectares (Swift and Steinhorst 1976).

^b Unless otherwise noted, the denominator mean square and *d.f.* used to compute an *F*-statistic for a test of Type III hypotheses were values from the error term in the summary table (C error term—Zar 1999).

^c Denominator mean square and *d.f.* used to compute *F*-statistic was grid (habitat, A error term—Zar 1999).

^d Denominator mean square and *d.f.* used to compute *F*-statistic was grid × year (habitat, B error term—Zar 1999).

TABLE 2.—Statistically significant pairwise comparisons with individual *t*-statistics and probabilities (*P*) of factors influencing density^a of red-backed voles (*Clethrionomys gapperi wrangeli*) and Keen’s mouse (*Peromyscus keeni macrorhinus*) during autumn 1998–2000 in 23-year-old precommercially thinned young-growth, gap-phase old-growth, multicohort old-growth, and peatland mixed-conifer forests, southeastern Alaska.

Comparison ^b	Red-backed vole		Keen’s mouse	
	<i>t</i> -statistic	<i>P</i>	<i>t</i> -statistic	<i>P</i>
Young growth 1998 versus young growth 1999	9.38	<0.001		
Young growth 1998 versus young growth 2000			2.61	0.040
Young growth 1998 versus young growth 2000	8.81	<0.001		
Young growth 1998 versus gap phase 1998	6.54	0.001		
Young growth 1998 versus multicohort 1998	8.21	0.044		
Young growth 1998 versus mixed conifer 1999	4.11	0.003	4.77	0.001
Gap phase 1998 versus gap phase 2000			2.76	0.033
Gap phase 1999 versus mixed conifer 1999			2.70	0.027
Gap phase 1999 versus mixed conifer 1999	5.72	<0.001		
Multicohort 1998 versus multicohort 2000			2.62	0.039
Multicohort 1999 versus mixed conifer 1999	4.69	0.002	2.84	0.022
Young growth 2000 versus mixed conifer 2000	4.02	0.004	2.72	0.026
Gap phase 2000 versus mixed conifer 2000	2.52	0.036		
Multicohort 2000 versus mixed conifer 2000	2.82	0.023		

^a Lincoln-Petersen estimate of abundance divided by effective area sampled in hectares (Swift and Steinhorst 1976).

^b Values of habitat-year combinations on the left side of contrast statement are greater than values on the right side.

in 1999 (voles: *t* = 10.29, *P* < 0.001; mice: *t* = 2.53, *P* = 0.045) and 2000 (voles: *t* = 10.24, *P* < 0.001; mice: *t* = 4.62, *P* = 0.004).

Population density of mice varied among habitats during autumn 1998 (Fig. 2b) and during both seasons in 1999 and 2000 (Table 1). Most variation was attributable to differences with peatland mixed conifer (Table 2), which had the lowest density (0.30/ha). Mean density in young growth (3.95/ha) was higher (mean significant difference = 1.59) than multicohort old growth (2.34/ha) and gap-phase old growth (2.07/ha). Population density during 1999–2000 was similar between seasons but varied (*F* = 14.55, *d.f.* = 1, 4, *P* = 0.02) between years. Mouse density in 1999 (2.73 mice/ha) was higher (*t* = 2.32, *P* < 0.05) than in 2000 (1.60 mice/ha; Fig. 2b).

Age and sex composition and reproductive performance.—Sex ratios of voles consistently favored males in all habitats except peatland mixed conifer (Table 3), but proportions of

TABLE 3.—Seasonal age and sex composition and reproductive performance (%) of red-backed voles (*Clethrionomys gapperi wrangeli*) and Keen's mouse (*Peromyscus keeni macrorhinus*) among gap-phase old-growth forest, multicohort old-growth forest, peatland mixed-conifer and precommercially thinned young (23-year-old) growth habitats, Wrangell Island, Alexander Archipelago, southeastern Alaska, 1998–2000 (n/a = not available).

Year and habitat	Red-backed vole						Keen's mouse					
	N ^a	Males		Females		% ^d	N ^a	Males		Females		% ^d
		Juvenile ^b	Adult ^c	Juvenile ^b	Adult ^c			Juvenile ^b	Adult ^c			
Spring												
1999												
Gap phase	34	0	26	0	8	0	45	0	29	0	16	6.7
Multicohort	32	0	20	0	12	0	34	0	24	0	10	0
Mixed conifer	11	0	6	0	5	0	0	0	0	0	0	0
Young growth	26	0	15	0	11	0	29	0	14	0	15	6.7
2000												
Gap phase	15	0	9	0	6	0	20	0	12	0	8	0
Multicohort	9	0	2	0	7	0	23	0	17	0	6	33.3
Mixed conifer	9	0	3	0	6	25.0	4	0	0	0	4	0
Young growth	16	0	12	0	4	0	23	0	9	0	14	7.1
Autumn												
1998												
Gap phase	92	1	53	2	36	60.0	78	2	38	5	33	9.7
Multicohort	120	3	77	2	38	15.8	61	4	36	3	18	0
Mixed conifer	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Young growth	137	0	93	0	44	11.2	68	0	38	1	29	0
Autumn												
1999												
Gap phase	55	11	28	3	13	31.2	31	2	16	4	9	55.6
Multicohort	20	2	9	2	7	14.3	33	6	17	1	9	33.3
Mixed conifer	6	1	1	0	4	66.6	4	1	1	0	2	100.0
Young growth	14	1	6	0	7	28.6	57	7	21	2	27	40.7
2000												
Gap phase	34	1	23	0	10	60.0	14	0	4	0	10	75.0
Multicohort	24	1	15	1	7	42.9	16	2	5	5	4	25.0
Mixed conifer	6	0	3	0	3	33.3	3	0	0	0	3	66.6
Young growth	24	6	6	5	7	20.0	31	8	10	3	10	90.0

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

^b Juvenile, which included individuals that showed juvenile pelage (Merritt 1981).

^c Adult, which included individuals that showed adult pelage regardless of whether there was evidence of reproductive maturity.

^d Because reproductive condition was not obtained for all adult females, sample size for reproductive performance is \leq number of adult females recorded.

adult and juvenile male or female voles were independent ($G = 12.53$, $df. = 10$, $P > 0.25$) of habitat. Initial analyses indicated an annual trend in age composition of vole populations in some habitats. Subsequent tests of specific hypotheses indicated that the age composition of young-growth populations was not independent of year ($G = 36.7$, $df. = 2$, $P < 0.0001$) with a relatively larger fraction of juvenile males and females in autumn 1999 and 2000 populations than in 1998.

Habitat, age, and sex distribution of mice ($G = 27.0$, $df. = 10$, $P < 0.005$) were not mutually independent (Table 3). Subsequent tests of partial independence revealed that habitats varied ($G = 27.0$, $df. = 11$, $P < 0.005$) in composition of male and female juveniles and adults and that habitat influenced age ($G = 17.7$, $df. = 7$, $P < 0.025$) and sex ($G = 29.3$, $df. = 7$, $P < 0.001$) of mice captured across grids. The sex ratio of mice favored males in all habitats except peatland mixed conifer and

young growth, and juveniles appeared to be underrepresented in gap-phase old growth. Also, age composition during autumn varied ($G = 19.7$, $df. = 2$, $P < 0.001$) among years, with juveniles (especially males) composing a smaller proportion of the population in 1998 (7.2%) than in 1999 (18.4%) or 2000 (28.1%).

Percentage of reproductive female voles appeared to differ among habitats (Table 3), but the variation was not significant ($G = 6.00$, $df. = 3$, $P = 0.120$). However, the pattern in our data suggested that unmanaged forests (gap-phase old growth, multicohort old growth, peatland mixed conifer) had higher percentages of reproductive females than young growth, which seemed to increase over the period of the study. Therefore, we compared the percentage of females in unmanaged forests that were reproductive each year to corresponding percentages in young growth and confirmed that the percentage of reproductive females in the vole population was not mutu-

ally independent of year and habitat ($G = 12.82$, $d.f. = 7$, $P = 0.080$). The fraction of female voles that were reproductive was smaller ($G = 3.53$, $d.f. = 1$, $P = 0.065$) in young-growth (14.8%) than in unmanaged forests (25.4%), but annual percentages in young growth were independent of year ($G = 0.69$, $d.f. = 2$, $P > 0.50$). For mice, percentage of reproductive females differed among years ($G = 25.3$, $d.f. = 2$, $P < 0.001$), with lower values during 1998 (9.7%) than 1999 (44.7%) or 2000 (72.0%). Unlike voles, reproductive performance of mice did not differ between unmanaged forests and young growth and was similar among habitats during spring ($G = 2.78$, $d.f. = 2$, $P > 0.25$) and autumn ($G = 5.14$, $d.f. = 3$, $P > 0.25$), averaging 11.1% and 54.2%, respectively.

Body mass and survival.—Mean body mass of voles was similar among habitats ($F = 0.71$, $d.f. = 3, 4$, $P = 0.549$) and among years ($F = 2.84$, $d.f. = 2, 6$, $P = 0.136$). There was no interaction of year \times habitat ($F = 0.38$, $d.f. = 4, 6$, $P = 0.817$), but when we compared mean body mass during autumn 1998 (when density was higher) to the corresponding value pooled across 1999–2000, adults in young growth weighed less ($t = 4.36$, $d.f. = 240$, $P < 0.001$) in 1998 (21.9 g, $SE = 0.4$) than during the last 2 years (26.1 g, $SE = 1.4$) of the study. Also, mean body mass of adults in young growth (22.6 g, $SE = 0.3$) was less ($t = 3.84$, $d.f. = 498$, $P < 0.001$) than the body mass of adults (24.7 g, $SE = 0.2$) pooled across unmanaged habitats. Juveniles in young growth did not differ in body mass between 1998 and 1999–2000 ($t = 1.15$, $d.f. = 48$, $P > 0.20$) or from juveniles in unmanaged habitats ($t = 1.11$, $d.f. = 48$, $P > 0.20$), averaging 18.0 g ($SE = 0.3$). During years with estimates from both seasons, adults weighed less ($t = 4.94$, $d.f. = 240$, $P < 0.001$) during spring ($\bar{X} = 23.4$ g, $SE = 0.7$) than autumn ($\bar{X} = 26.2$ g, $SE = 1.6$).

Minimum summer survival in 1999 (16.3%) was not significantly different ($G = 0.81$, $d.f. = 1$, $P > 0.25$) from 2000 (22.4%). Also, overwinter survival during 1998–1999 (16.9%) was not different ($G = 0.81$, $d.f. = 1$, $P > 0.25$) from 1999–2000 (12.4%). Therefore, we pooled years to compare survival among habitats. Minimum summer survival was 26.0%, 17.1%, 6.0%, and 11.9% in gap-phase old growth, multicohort old growth, peatland mixed conifer, and young growth, respectively. Corresponding estimates of minimum overwinter survival were 17.3%, 17.2%, 16.7%, and 13.6%. Minimum survival did not differ among habitats during summer ($G = 3.28$, $d.f. = 3$, $P > 0.25$) and winter ($G = 1.10$, $d.f. = 3$, $P > 0.75$). Also, neither summer ($G = 1.70$, $d.f. = 1$, $P > 0.20$) nor winter ($G = 1.09$, $d.f. = 1$, $P > 0.25$) survival of voles in young growth differed from corresponding values in unmanaged habitats and averaged 18.3% and 16.0%, respectively. Trap mortality rate (percentage of unique captures) in 1998 (22.6%) was twice the average of 1999 and 2000 (9.9%).

Mean body mass of mice did not differ among habitats ($F = 1.53$, $d.f. = 3, 4$, $P = 0.336$) or among years ($F = 0.43$, $d.f. = 2, 6$, $P = 0.668$). There was no interaction of age \times year \times habitat ($F = 0.88$, $d.f. = 3, 17$, $P = 0.472$), but adult mice weighed less ($t = 8.66$, $d.f. = 394$, $P < 0.001$) in 1998 (22.4 g, $SE = 0.5$), when density was higher than during 1999–2000

(25.2 g, $SE = 0.7$). Also, mean body mass of adults in young growth (23.4 g, $SE = 0.26$) was less ($t = 2.26$, $d.f. = 396$, $P = 0.026$) than the body mass of adult mice (24.5 g, $SE = 0.19$) averaged across unmanaged habitats. Juvenile mice in young growth did not differ in body mass between 1998 and 1999–2000 ($t = 0.94$, $d.f. = 61$, $P > 0.25$) or from juveniles in unmanaged habitats ($t = 0.48$, $d.f. = 61$, $P > 0.50$), averaging 16.9 g ($SE = 0.35$). Body mass of adults during 1999–2000 differed ($t = 4.40$, $d.f. = 253$, $P < 0.001$) between spring ($\bar{X} = 24.0$ g, $SE = 0.6$) and autumn ($\bar{X} = 26.3$ g, $SE = 0.7$).

Minimum summer survival of mice in 1999 (35.2%) did not differ ($G = 0.61$, $d.f. = 1$, $P > 0.25$) from 2000 (29.6%). Also, overwinter survival during 1998–1999 (30.4%) did not differ ($G = 3.11$, $d.f. = 1$, $P > 0.05$) from 1999–2000 (21.8%). Again, we pooled years to compare habitats. Minimum summer survival of mice was 25.8% in gap-phase old growth, 29.8% in multicohort old growth, 50.0% in peatland mixed conifer, and 44.2% in young growth. Corresponding estimates of minimum overwinter survival were 31.6%, 27.0%, 50.0%, and 22.5%. Minimum summer survival was independent ($G = 5.22$, $d.f. = 3$, $P > 0.10$) of habitat, averaging 33%. However, summer survival in young growth (44.2%) was higher ($G = 4.11$, $d.f. = 1$, $P < 0.05$) than among unmanaged habitats (28.3%). There was no difference among habitats ($G = 3.51$, $d.f. = 3$, $P > 0.25$) or between young-growth and unmanaged habitats ($G = 2.25$, $d.f. = 1$, $P > 0.10$) in overwinter survival, which averaged 27.1%. Like voles, the trap mortality rate in 1998 (4.0%) was twice the average of 1999 and 2000 (2.1%).

DISCUSSION

Assumptions and limitations of analyses.—Equal catchability between marked and unmarked animals is a key assumption of mark-recapture estimators (Jolly and Dickson 1983; Nichols and Pollock 1983). Fortunately, the Lincoln–Petersen estimator assumes that capture probability varies with time, and it is robust under a wide range of conditions (Menkens and Anderson 1988). Situations where it performs poorly include extreme heterogeneity in capture probabilities or extreme trap shyness, which we believe occurred rarely during our study. By pooling captures into single mark-and-recapture periods, heterogeneity of capture probabilities was reduced, and average capture probabilities likely were increased (Menkens and Anderson 1988). Still, some density estimates may be biased because of different capture probabilities between marked and unmarked animals during the recapture period. Also, we may have over- or underestimated the error of the area sampled for a specific season because effective area trapped was computed from a pooled regression (Link 1999), and we used the error term from the pooled regression as an average error across the period of study (Hanley and Barnard 1999). Consequently, precision of specific seasonal density estimates may have departed from what we report in this paper.

We took several measures to control experiment-wise error rates, including use of the Waller–Duncan K -ratio, limiting multiple comparisons with significant GLM models, and testing only hypotheses that were identified a priori in our

study design. Nevertheless, we conducted several ANOVAs and performed numerous paired comparisons. Therefore, to further reduce the likelihood of spurious conclusions, we focus our discussion on significant relationships that were supported by multiple lines of evidence.

Effective area sampled.—An important contribution of our study was that we documented magnitude and variation among habitats in effective area sampled, which for both species was an order of magnitude larger than the study grids. Most studies of populations of small mammals report indices of abundance (Slade and Blair 2000) or density estimates that assume area sampled is the study grid (naive estimates) or the grid plus a boundary derived from “mean maximum distance moved” (Wilson and Anderson 1985). Naive estimates (Wilson and Anderson 1985) or edge effect estimated with mean maximum distance moved (Carey 2000) may underestimate area of the sampled population, a consequence of which is an inflated population density estimate. Effective area sampled (Swift and Steinhorst 1976) has not been widely used, probably because of the substantial additional effort (about 100%) required to install and trap assessment lines. Also, unlike mean maximum distance moved, assessment lines have not been rigorously tested and shown to be unbiased under a wide range of conditions (Wilson and Anderson 1985). However, assessment lines appear to be a useful approach for estimating effective area sampled (Van Horne 1982a), especially when obtaining a realistic estimate of population density is a high priority.

Mean effective area sampled for voles was larger in gap-phase old growth than in remaining habitats. To our knowledge, these are the 1st estimates of effective area sampled for *C. gapperi* using assessment lines (Swift and Steinhorst 1976). Van Horne (1982a) used assessment lines to estimate density of *Peromyscus* populations in managed forests of southeastern Alaska and reported an average effective trapped area of 9.5 ha, which was similar to what we observed across habitats ($\bar{X} = 10.8$ ha). In contrast, Hanley and Barnard (1999) observed an effective trapping distance of 27.0 m for *P. keeni*, but this was computed according to a 50% probability of encountering a marked animal beyond the grid. When recalculated with a capture probability equal to zero, edge effect averaged 125.2 m (T. A. Hanley, pers. comm.). Our mean effective trapping distance for mice was 185.4 m for an average edge effect of about 135 m.

Habitat distribution and demography of red-backed voles.—We provide the 1st quantitative estimates of habitat distribution and demography of *C. gapperi* populations in southeastern Alaska. *Clethrionomys gapperi* is a reputed mature-forest specialist (Merritt 1981), especially in coniferous forests of western North America (Aubry et al. 1991; Bayne and Hobson 1998; Campbell and Clark 1980; Medin 1986; Pearson 1994; Ramirez and Hornocker 1981; West 1991). Vole populations attain their highest densities in continuous, late-seral, mesic coniferous forests (Aubry et al. 1991; Campbell and Clark 1980; Medin 1986; Ramirez and Hornocker 1981; Sullivan et al. 1999, 2000) with abundant understory cover (Nordyke and Buskirk 1991), but size and distribution of canopy openings apparently influence population response (Hayward et al.

1999). Only Von Trebra et al. (1998; but see Smith 1999) and Taylor (1999) did not find higher populations in mature forest than in early seral stages of recently logged stands. Regardless of forest type, voles favor mesic habitats (Merritt 1981; Ramirez and Hornocker 1981; Yahner 1992; but see West 1991) and moist micro-environments (Getz 1968; Gunderson 1959; Odum 1944), probably because of high water requirements and little resistance to drought (Getz 1962, 1968; McManus 1974). Voles prefer microsites typical of old-growth coniferous forests, including abundant stumps, downed coarse woody debris (especially rotting logs), and exposed roots within a loose forest litter (Gunderson 1959; Merritt 1981; Moses and Boutin 2001). What remains unclear, however, is whether habitat features required to sustain breeding vole populations occur only in late-seral forests.

The clearest pattern that emerged from our study was that peatland mixed conifer supported the fewest voles. Even when population levels were relatively high across other habitats, we caught only a few voles in peatland mixed-conifer forests and these exclusively in the more densely forested portions. Because this habitat is unique and has a limited distribution across western North America, there are few studies with which to compare our results. However, our findings in peatland mixed-conifer forests are not surprising, given the macro- and microhabitat preferences of voles (Merritt 1981; Nordyke and Buskirk 1991; Sekgororoane and Dilworth 1995) and the results of studies in sparsely forested habitats (Hargis 1996; Ramirez and Hornocker 1981). Muskegs and peatland-scrub forests of southeastern Alaska are relatively exposed with a sparse canopy and understory (Neiland 1971). More productive sites with mixed-conifer associations occur as patches interspersed within the more open peatland, but these patches are typically small (<5 ha) and relatively isolated from larger tracts of productive forest. Thus, it is unlikely that muskegs and associated scrub and mixed-conifer forests of southeastern Alaska perennially support breeding populations of *C. gapperi*. Similar findings were reported for subalpine basins and montane meadows (Hargis 1996; Ramirez and Hornocker 1981). However, black spruce (*Picea mariana*) peatlands of boreal forest apparently support viable populations of *C. gapperi* (Lawrence 1996).

Another clear pattern was that the density of voles during 1999 and 2000 was similar between old-growth (gap-phase, multicohort) and managed (young-growth) habitats, which was unexpected. With few exceptions (Sullivan et al. 2001), previous investigators reported few or no vole captures in older clear-cut or young, 2nd-growth coniferous forests (Ramirez and Hornocker 1981; Sullivan et al. 1999). Our findings suggest that voles in southeastern Alaska may not be as sensitive to overstory removal as has been reported elsewhere. There are 2 important circumstances that may explain why vole densities in young growth were similar to old-growth habitats. The 1st is related to management history and structural characteristics of selected young-growth sites, whereas the 2nd has more to do with the climate of southeastern Alaska. Young-growth sites were precommercially thinned in 1998, which deposited vast amounts of woody

debris on the forest floor and opened the canopy to sunlight. Although removing the forest canopy exposes the understory to drier conditions (Sullivan et al. 1999), the cool, wet climate of southeastern Alaska likely mitigates the effect of partially removing the overstory, such as when young, 2nd-growth forests are thinned. Equally important are dense patches of ground cover and development of herbs and woody plants in the understory following partial removal of the canopy (Alaback 1982). Taylor (1999) reported similar results in coniferous forests of the Olympic Peninsula, where climatic conditions and vegetation in the Pacific Northwest most resemble southeastern Alaska.

However, the crucial issue is whether young growth can sustain breeding populations of *C. gapperi* in intensively managed landscapes. Population density alone can be misleading (Van Horne 1983), and in high population years, poorer-quality habitats can have relatively high (albeit ephemeral) population densities because animals predictably immigrate into marginal habitats as optimum habitats become saturated (Fretwell and Lucas 1970). Attributes directly related to fitness, such as body condition, survival, and reproductive success, reflect the interactions of individuals with their habitat and ultimately determine population persistence (Fuller 1977a, 1977b). Animals occupying habitats that are unable to sustain breeding populations (e.g., sink habitats—Pulliam 1988) typically are less dominant with lower survivorship and reproduction than individuals in optimum habitat (Pearson 1994). In our study, autumn vole densities in young growth showed substantially greater variability among years (coefficient of variation [CV] = 119%) than did vole densities in either of the old-growth habitats, especially gap-phase old growth (CV = 52%). The mean body mass of adult voles was lower in young-growth than in unmanaged habitats, but overwinter and summer survival did not differ. Relatively fewer females were reproductive in young-growth than in unmanaged forests, and there was little evidence of juvenile recruitment into the autumn population in young growth, especially in 1998. These results indicate that voles did not reproduce much in young growth and that young growth may not have experienced much juvenile recruitment from immigration during 1998.

The extent to which cumulative disturbance from forest management poses a threat to the persistence of endemic *C. gapperi* populations in southeastern Alaska remains unclear, but evidence from numerous studies conducted elsewhere in its geographic range is varied with implications of risk to local extirpation ranging from low to moderate. Our findings suggest that vole populations in southeastern Alaska may not be as sensitive to overstory removal as has been reported in western coniferous forests. Many managed forest types support substantially lower vole densities (Aubry et al. 1991; Bayne and Hobson 1998; Campbell and Clark 1980; Medin 1986; Ramirez and Hornocker 1981; Sullivan et al. 1999, 2000; but see Taylor 1999). In southeastern Alaska and in other regions with cool, moist climates, voles may be able to sustain breeding populations in managed forests (Taylor 1999) because desiccation is not as frequent and intense as in drier climates

or with xeric forest types. However, our study was short in duration and did not provide an opportunity to study habitat distribution or demography of voles during a prolonged period when populations may fluctuate widely (Fuller 1977a). Vole populations undergo dramatic annual fluctuations at varying time intervals, the consequence of which is poorly understood. Critical questions require further inquiry, especially the role of dispersal in determining spatial patterns of abundance within forests and across landscapes (Bowman et al. 2000, 2001b). Without detailed, longer-term studies, it is difficult to thoroughly understand and accurately predict how vole populations will respond to cumulative habitat disturbance.

Habitat distribution and demography of Keen's mouse.—Overall, mice abundance varied among years, but habitat distribution remained consistent throughout the study. Several population attributes (e.g., percentage of reproductive females) were similar among habitats. Most habitat variation was attributable to low numbers in peatland mixed conifer. Several sources of evidence suggested young growth was the highest-quality habitat for mice. Young growth consistently was the highest-ranked habitat according to density, and during 1999–2000 it had higher densities and summer survival rates than other habitats. Like voles, mice were more abundant during 1998 than 1999 or 2000. Also, demographic parameters varied between 1998 and 1999–2000 in a similar manner as voles—mean adult body mass, juvenile recruitment, and percentage reproductive females were lowest during the peak population.

Peromyscus keeni is a relatively new taxon (a subspecies that was recently elevated to species level) with a limited geographic range (Hogan et al. 1993). However, 2 detailed studies in southeastern Alaska (Hanley and Barnard 1999; Van Horne 1981) provide data from which to draw insights. Van Horne (1981) studied populations of *P. maniculatus hylaeus* (= *P. keeni hylaeus*) among 4 seral stages of temperate rain forest, the results of which we believe are directly comparable to ours because of similar protocols and average effective area trapped (9.5 ha—Van Horne 1982a). Like us, Van Horne (1981) obtained evidence from multiple sources that indicated young (23–25-year-old) 2nd growth (unthinned) was the highest-quality habitat for mice. Young growth consistently yielded the highest numbers of unique adults and total animals and frequently had the highest minimum survival rates. Young growth in her study had not been thinned, but the canopy was not completely closed, and the understory was near maximum production (Van Horne 1981).

In addition, Van Horne (1981) reported that mature (≥ 190 -year-old) forest had lower adult densities than young growth but that its numbers were similar to those in young (2–5-year) and older (5–9-year) clear-cuts. This differs from our results in old-growth forests and those of Hanley and Barnard (1999), who found that Sitka mice (i.e., *P. keeni sitkensis*) flourished in old-growth riparian and upland coniferous forests. Whereas 190-year-old coniferous forests of western North America usually attain old-growth condition, in southeastern Alaska old-growth features typically do not develop until stands are > 300 years old (Alaback 1982; Nowacki and Kramer 1998). Until then, the

canopy remains closed with little sunlight reaching the forest floor. Not surprisingly, understory production in the stands ≥ 190 years old was lower than in old-growth stands (Van Horne 1981).

In contrast, Songer et al. (1997) and Taylor (1999) reported that *P. keeni* (= *P. oreas*—Songer et al. 1997) populations were higher in old-growth forests than in managed stands on the Olympic Peninsula of Washington. Populations of *P. keeni* were >2 times more abundant in old growth than in shrub-sapling, open sapling-pole, or closed sapling-pole stands and >1.5 times more abundant than in grass-forb stands (Taylor 1999). At the landscape scale, *P. keeni* showed sensitivity to habitat fragmentation with the highest densities recorded in continuous old-growth forests or old-growth forests with corridors (Songer et al. 1997). Whereas *P. keeni* populations of the Olympic Peninsula may have become habitat specialists in sympatry with *P. maniculatus* (Songer et al. 1997), the Keen's mouse of southeastern Alaska seems to have radiated in the absence of its sibling species to flourish in a wide range of habitats (Hanley and Barnard 1999; Smith et al. 2001; Van Horne 1981, 1982b). For that reason, endemic populations of *P. keeni* in southeastern Alaska are less likely to be impacted by cumulative disturbance from clear-cut logging than *C. gapperi* populations.

The similar annual demographic pattern between mice and voles in our study during 1998–1999 was unexpected. *Peromyscus maniculatus* populations reputedly remain temporally stable through the interplay of social factors (Healey 1967). Van Horne (1981) reported similar conclusions for *P. keeni hylaeus* (= *P. maniculatus hylaeus*) in southeastern Alaska. In our study, annual fluctuation in vole numbers between 1998 and 1999 was more dramatic than for mice. However, the synchrony, similarity, and consistency of demographic variation across habitats suggest that the 2 species were responding to a common proximate factor (Morris 1996). Both species experienced trap mortality rates in 1998 that were twice that recorded in the 2 subsequent years. We believe that higher trap mortality was due to poorer body condition and other factors associated with higher densities rather than the cause of a population decline.

Regrettably, it is difficult to speculate on factors responsible for parallel changes in mice and vole demography between 1998 and 1999 because it is unclear whether 1998 was an average or peak year for each species. Two snapshots per year (i.e., early spring and early autumn) for 2.5 years are insufficient to capture natural variation or understand processes that influence demography of small mammal populations across an array of habitats. Factors that govern small mammal population processes often are complex and can vary for the same species over a small geographic area (Bowman et al. 2000; Van Horne 1981). The magnitude of population change during a 1-year period underscores the need for long-term studies to understand population dynamics and habitat relations of small mammal populations.

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