SPATIAL VARIATION IN POPULATION DYNAMICS OF SITKA MICE IN FLOODPLAIN FORESTS

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Population dynamics and demography of the Sitka mouse, *Peromyscus keeni sitkensis,* were studied by mark-recapture live-trapping over a 4-year period in four floodplain and upland forest habitats: old-growth Sitka spruce *(Picea sitchensis)* floodplain; red alder *(Alnus rubra)* floodplain; beaver-pond floodplain; and nearby old-growth Sitka spruce-western hemlock *(Tsuga heterophylla)* upland forest. We did not find the expected source-sink population dynamics resulting from flood disturbance or between-habitat variation in food resources. We found significant between-year differences ($P < 0.05$) in population densities, age and sex ratios, survival rates, growth rates, and movements. Within-year differences in all demographic variables were consistently greater between replicate trapping grids within habitat types than between habitat types, and there was no year-to-year consistency in any demographic difference between replicates or habitat types. We conclude that floodplain forests, per se, do not provide unique habitat for Sitka mice in either a strongly positive or negative sense compared with upland old-growth forests.

Key words: *Peromyscus keeni sitkensis, Peromyscus sitkensis,* riparian forest, habitat heterogeneity, temporal variation

Riparian forests are among the most species rich, productive, and ecologically dynamic habitats in landscapes (Naiman and DéCamps, 1997), but little is known about population processes of their mammalian fauna. Small mammals may be year-round residents of riparian floodplain forest and may be influenced strongly by periodic flooding and unique structure and composition of those forests.

Studies of small mammals of riparian forests mostly have been short-term, community studies and have indicated speciesspecific affinities for riparian versus upland habitats (Andersen, 1994; Anthony et al., 1987; Doyle, 1990; McComb et al., 1993; Varty, 1990). Whereas such studies of animal abundance can provide a preliminary view of variation in spatial pattern, their insights are greatly weakened without longer term, demographic data (Van Home, 1983). Batzli (1977) studied the demography of *Peromyscus leucopus* on one 6.4-ha floodplain grid and one 4.0-ha upland grid over a 3-year period in mixed hardwood forest in Illinois. He concluded that although the floodplain was a more "severe" environment (subject to flooding) than the upland, it was more productive in autumn and served as a minor source of recruits for the upland.

The idea of one habitat providing recruits for another habitat has become widely accepted in ecology (Krohne, 1997). Theory predicts that in spatially complex landscapes, such as riparian forests, animal populations should react to the habitat heterogeneity by differential use of habitat patches, dispersal between patches, and apparent differential population dynamics between patches (i.e., source-sink population dynamics-Pulliam, 1988; Pulliam and Danielson, 1991; Watkinson and Sutherland, 1995).

We tested the hypothesis that floodplain and upland habitats would differ in source sink population dynamics for a common species of small mammal that inhabits for-

ests of our region. The Sitka mouse, *Peromyscus keeni sitkensis* (formerly *P. sitkens*is-Hogan et al., 1993) occurs on the outer-coast islands of the Alexander Archipelago of southeastern Alaska (Nagorsen, 1990). The species *P. keeni* includes the more widespread, former *P. maniculatus* of the other islands and mainland of southeastern Alaska and coastal British Columbia (Hogan et al., 1993), but *P. k. sitkensis* is the largest subspecies. Very few ecological studies of *P. keeni* have been conducted and almost none of *P. k. sitkensis* because of its remote range.

Differences in forest vegetation of southeastern Alaska are most pronounced between uplands and floodplains (Hanley and Brady, 1997; Hanley and Hoel, 1996). We compared populations of *P. keeni sitkensis* in upland and floodplain habitats and expected some habitats to be population sources and others to be population sinks, as found by Van Home (1981) for *P. maniculatus* in different seral stages of forests in southeastern Alaska.

MATERIALS AND METHODS

Study area.—Our study was conducted during 4 summer field seasons, 1992-1995, in the Kadashan River drainage (57°42’N, 135°13’W) of Chichagof Island, Alaska. Chichagof Island encompasses 5,450 km^2, and Kadashan River is a fourth-order stream draining a watershed of ca. 140 km^2. Average bankfull width of the river was ca. 25 m in the lower elevation (<50 m above mean sea level) areas we studied. The floodplain extended ca. 150 m on both sides of the river and was subject to periodic flooding throughout the year, but most commonly in October-November (Pollock, 1995). Climate of the study area was maritime with cool summer temperatures (mean ca. 15 ± 5°C), mild winter temperatures (mean ca. 0 ± 5°C), and much precipitation (ca. 1,500-3,500 mm/yr) year-around (Farr and Hard, 1987). The Kadashan River cycled between frozen and thawed periods throughout each winter, and snow persisted throughout the study area for most of the winter each year.

Forests were old-growth Sitka spruce-western hemlock (*Picea sitchensis-Tsuga heterophylla*), with Sitka spruce dominant in the floodplains and codominant with western hemlock in the uplands. Red alder (*Alnus rubra*) was dominant in a 14-ha part of the floodplain that was logged in 1953.

The study area was accessible only by boat or floatplane and was inaccessible for study between October through April. Our research effort varied between years. We were able to study only four trapping grids for 2.5 months in 1992 and 1993; we were able to study seven trapping grids (replicating each of three forest types) for 5 months in 1994 and 1995.

Habitat classification and trapping grids.—We recognized four major types of habitat in the study area: 1) floodplain, old-growth, Sitka spruce-dominated forest; 2) floodplain even-aged forest dominated by red alder; 3) floodplain, beaver (*Castor canadensis*) pond, which previously had been old-growth forest of Sitka spruce; and 4) upland old-growth forest of Sitka spruce-western hemlock. Two stands of each of the three types of forest were selected so that all six forest stands and the beaver pond were relatively close to one another (<2.0 km). The second spruce and second alder floodplain stands were on opposite sides of the river from all other stands and were considered independent of their replicate. The entire floodplain virtually was the same elevation above base flow of the river. Microsite variation in elevation (above base flow) within floodplain forest stands was substantial but was similar among stands (*CV* = 25.9, 26.3, 23.7, and 40.0% for spruce 1, spruce 2, alder 1, and alder 2, respectively). Flood regime of the beaver pond, however, differed from that of the forests, because the beaver pond was affected by side streams and beaver dams (Pollock, 1995). Upland forest stands were 3-6 m above the floodplain and never were subject to flooding.

Trapping grids were chosen within each stand on the basis of relative uniformity of the vegetation and minimization of edge effect from neighboring habitats. Effective trapped area of each grid was within the grid’s habitat type, with the exception of the beaver pond and upland 1, which were 36 m apart. The beaver pond was problematic, because there was only one such pond within reasonable proximity to other grids (so no replication) and trapping and vegetation sampling were restricted to “island” parts of the pond, which limited number of traps and their configuration.

Trapping grids in the forest stands were 70 by 70 m with trap stations spaced at 7-m intervals (121 stations/grid) in 1992 (spruce floodplain 1, alder floodplain 1, and upland 1). Those grids subsequently were deemed too small in relation to population density and were enlarged to 70 by 147 m with trap stations spaced at 10-m intervals (121 stations/grid) in 1993-1995. Spruce floodplain 2, alder floodplain 2, and upland 2 were established in 1993 (but not trapped until 1994) at the larger 70- by 147-m size. The beaver-pond grid consisted of 67 trapping stations in 1992-1993 and 84 stations in 1994-1995, spaced at 7-m intervals throughout.

Overstory and understory vegetation of the six forest grids were studied in detail in 1993 (Hanley and Hoel, 1996). Of particular interest was the understory biomass, which was measured in July and August. Twenty-four sampling points were evenly spaced at 20-m intervals throughout each grid. At each sampling point, all above-ground shrub biomass in a 1.0-m^2 quadrat was clipped, sorted by species and leaves versus stems, and weighed. Representative samples of each were oven-dried (100°C) for dry-weight correction. Within the first 20 of the 24 sampling points, all other vascular plants were clipped at ground level, sorted by species, oven-dried, and weighed (Hanley and Hoel, 1996).

Understory biomass data, including similar data for the beaver pond (Pollock, 1995), were subjected to an agglomerative cluster analysis (Goldsmith and Harrison, 1976) based on proportional similarity matrices (Pielou, 1977). That classification procedure quantified vegetation similarity between grids and between habitat types.

Population demography.—Live-trapping was conducted with Longworth live traps, one per trap station, during each of the 4 years: 23 June-1 September 1992; 17 June-25 August 1993; 1 May-18 September 1994; and 4 May-24 September 1995. Each grid was trapped at 3-week intervals throughout the trapping season, and all mice captured were marked with both numbered ear-tags (fingerling fish tags) and individually coded electronic transponder PIT-tags. Trapping was conducted on spruce floodplain 1, alder floodplain 1, upland 1, and beaver pond in 1992 and 1993; it was extended to spruce floodplain 2, alder floodplain 2, and upland 2 in 1994 and 1995. This trapping effort resulted in 56,489 trap-nights, 9,357 captures, and marking of 1,460 Sitka mice. All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993).

Each Longworth trap was covered (tented) with a folded sheet of aluminum to provide protection from rain, and a piece of polyester batting was enclosed for thermal protection. Traps were baited with rolled oats and were set for 5 consecutive days at a time, being checked each morning and evening. Three days of prebaiting preceded the trapping of each grid for its first time each season. Animals were marked and weighed to the nearest 0.5 g with a Pesola spring balance. Trap number, animal number, sex, age (based on coloration and body weight; gray pelage and <27 g for juveniles), and reproductive condition (enlarged testes in males; pregnant deterniined by palpation or lactating determined by swollen or milky nipples for females-Gurnell and Flowerdew, 1990) were recorded. All traps remained on site and were locked open between trapping periods.

Population size on each grid at each sampling period was estimated by direct enumeration of the minimum number of animals known to be alive (MNA-Hilborn et al., 1976). We estimated population sizes also with the closed-population estimators of Program CAPTURE (White et al., 1982). Estimated population sizes were converted to estimates of population density (number of animals per ha) by calculating the effective area trapped on each grid. Effective area trapped was determined by trapping assessment lines that ran perpendicular to each side of each grid for an extra 10 trap stations (70 m, or to encounter with a water barrier such as river or pond) once (5 days) in the middle of each trapping season. Animals captured on assessment lines were not marked or included in any analysis other than that for effective area trapped. A regression equation was calculated for the ratio of marked to total animals captured (including unmarked animals) as a function of distance from edge of trapping grid. The distance yielding a ratio of 50% was the distance at which animals off the trapping grid stood an equal probability of occurring on or off the grid. That provided a measure of the effect of edge of the grid and was converted to effective area trapped (analogous to the method used by Van Home, 1982*b*).

Statistical analyses.—Trappability was the probability of capturing any animal known to be on a grid during any 5-day trapping period. It was estimated as maximum trappability (Krebs, 1966) and minimum trappability (Hilbom et al., 1976), thereby establishing upper and lower limits around the probable true trappability (Krebs and Boonstra, 1984). Population density was estimated as minimum number alive (Hilbom et al., 1976) divided by effective trapped area (Van Home, 1982*b*) per grid and also with closed-population estimators of Program CAPTURE (White et al., 1982). Minimum survival rate was the probability of recapturing any given animal in the next 5-day trapping period within the same year (standardized to a 21-day interval) or first trapping period of subsequent year (overwinter survival rate-Krebs, 1989). Growth rate was defined as change in mean live body weight of any given juvenile mouse captured in the next 5-day trapping period within the same year (Van Home, 1981).

Means of population densities, body weights of adult males, within-year and overwinter survival rates, and minimum-dispersal distance (Appendix I) were tested for statistical significance with single-factor analysis of variance followed by Student-Newman-Keuls' multiplecomparisons test (Zar, 1974). Between-year differences in 21-day survival rates were tested in a randomized block analysis of variance with years as blocks and sex as treatments, followed by Bonferroni multiple comparisons test (Wilkinson et al., 1992). Means of trappabilities, sex ratios, and proportion of transients were tested for statistical significance with the log-likelihood test for homogeneity in contingency tables (Zar, 1974). Differences in growth rates were tested with analysis of covariance (Wilkinson et al., 1992) with weight at time t the independent variable, weight at time $t + 1$ the dependent variable, and trapping grid the covariate. Statistical significance was set at $P \le 0.05$.

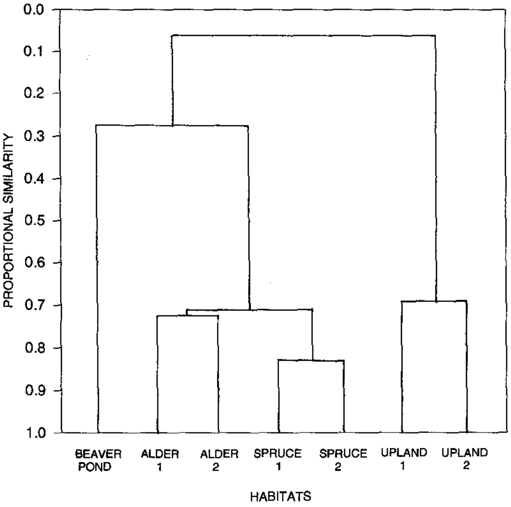

FIG. 1.-Dendrogram of cluster analysis of understory biomass from each of the six forest habitats (Hanley and Hoel, 1996) and the beaver-pond habitat (Pollock, 1995).

RESULTS

Habitats.—Total understory biomass did not differ between forest habitat types, but species-specific biomasses did differ ($P < 0.05$-Hanley and Hoel, 1996). Understory of the upland forest was dominated by blueberry (*V. ovalifolium* and *V. alaskensis*), but that of the spruce floodplain and alder floodplain forests was dominated by devilsclub (*Oplopanax horridum*-Hanley and Hoel, 1996). Other species-specific differences occurred in less abundant forbs and mosses (Hanley and Hoel, 1996). The beaver-pond habitat was dominated by devilsclub, salmonberry (*Rubus spectabilis*), and a wide variety of forbs (Pollock, 1995); it was by far the most species-rich habitat (Hanley and Barnard, 1999).

Cluster analysis of the understory-biomass data indicated that each of the replicate forest stands was more similar to the other stand of its respective habitat type than to other habitat types (Fig. 1). Spruce and alder floodplain forests were most similar among habitat types, and the beaver pond was more similar to the floodplain forests than to the upland forest.

Population densities.—Trappability was high for all grids and did not differ between sexes or grids. Maximum trappability did not differ between years, averaging 0.99 ± 0.01 (*SE*) throughout. Minimum trappability, however, did differ between years: 1.00

± 0.00 in 1992, 0.77 ± 0.03 in 1994, and 0.92 ± 0.02 in 1995; sample sizes were too small for estimating minimum trappability in 1993. Those results were similar to Krebs and Boonstra's (1984) findings for voles and indicate high trappability throughout. The live-trapping data, therefore, provide reliable estimates of the trappable population of mice on each grid at each sampling time.

Assessment-line data, relating the ratio of marked mice: total mice as a function of distance from edge of grid, was highly variable for individual grids in individual years, and correlation coefficients were low. The combined data set for all grids and years, however, provided a strong linear relation (ratio = 0.637-0.0051 distance, m, $r = 0.861$, $P = 0.001$), which when solved for ratio = 0.50, yielded an effective trapping distance of 27.0 m beyond the grid edge. That distance, adjusted for any water boundaries (river or pond), provided estimates of effective trapped area of each grid, necessary to convert population estimates (minimum number alive, MNA) to density estimates (MNA/ha).

Densities estimated by program CAPTURE yielded virtually identical patterns to those of MNA estimates, although values were ca. 21 % greater on average (CAPTURE = 0.21 + 1.21 MNA, $r = 0.946$, $P < 0.001$). We feel more confident in our MNA estimates than the others, because the assumptions behind MNA are minimal and those of the various CAPTURE models are substantial. Furthermore, CAPTURE estimates were impossible to make in several instances, especially those involving low densities. Therefore, we limited our analysis to the estimates of MNA.

Total densities varied from zero to 95.9 mice/ha and varied greatly between years and trapping grids (Fig. 2). Densities on replicate trapping grids varied as much within habitat types as between habitat types (Table 1). Overall, highest densities were achieved in the beaver pond for adults and juveniles. The most important pattern, however, was that despite large grid-to-grid variation and variation within grids from year-to-year, densities on all grids responded similarly to overall year-to-year variation. Densities were low in 1992 and declined in 1993; they peaked in 1994 and declined in 1995 (but still greater than 1992-Fig. 2).

Juveniles outnumbered adults in the low population years of 1992 and 1993, but adults outnumbered juveniles in the high-population years of 1994 and 1995. In all years, densities were lowest in early summer, peaked in late summer, and often declined in September (Fig. 2).

Breeding seasons.—Trapping seasons in 1992 and 1993 were short, and animal densities were low, with small sample sizes. Our data indicated that all adult males were already in breeding condition when first captured (mid-June) and still were in breeding condition when last captured (late August) in both years. Adult females appeared to enter breeding condition later (3 of 6 in late June and 7 of 8 in early July 1992; 1 of 5 in June 1993) than did males. Most of the few adult females captured in late August were in breeding condition (4 of 5 in 1992; none captured in 1993). The trapping seasons in 1994 and 1995 covered most of the breeding season on all grids. More than 70% of adult males already were in breeding condition when first captured in early May of both years. The proportion in breeding condition declined steadily through both summers.

Adult females entered breeding condition later than males. The breeding season in 1994 began early, however, with ≥40% of adult females already in breeding condition when first captured in May in all grids except alder floodplains 1 and 2, which had no individuals in breeding condition. Breeding began a few weeks later in 1995, with only upland 1 and beaver pond having 30-40% of adult females in breeding condition in early May; all other sites were near zero then. More than 95% of adult females were in breeding condition on all grids by

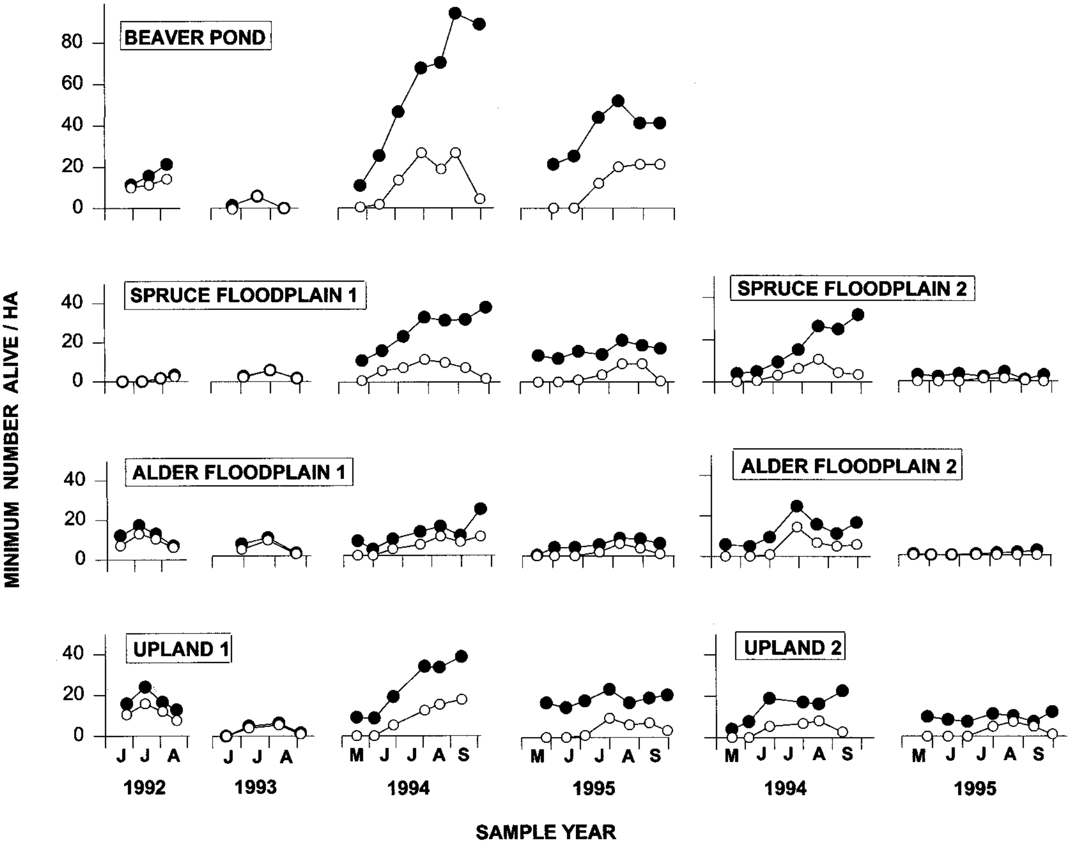

FIG. 2.—Density (minimum number alive per hectare) of Sitka mice on each trapping grid throughout the study; total animals (closed circles) and juveniles (open circles).

early June 1995. Breeding peaked in early June, declined as the summer progressed, and was finished in September of both years. Unlike the low-population years in 1992 and 1993, however, proportion of adult females in breeding condition already had declined to low levels (<20%) by late August in the high-population years in 1994 and 1995.

Survivorship.—Survival rates (probability of recapture in next trapping period) were a function of mortality and dispersal. Minimum survival rates per 21 days during the trapping season varied substantially during our study but did not differ between trapping grids within any year. Overall, adult survival rates were lower for males (0.34) than females (0.50); juvenile survival rates did not differ between sexes (0.39). Adult survival rates were lower in 1993 (0.13, but sample sizes were small) than the other 3 years (0.50); juvenile survival rates were lower in 1993 and 1994 (0.19) than 1992 and 1995 (0.60).

Overwinter survival rates of marked animals averaged 0.27 ± 0.08/260-day interval (Table 2). However, when expressed on a 21-day interval (comparable to trapping season intervals), rates were higher, averaging 0.80 ± 0.06 overall. Mortality or dispersal, therefore, was greater during the trapping (and breeding) season than during winter.

When overwinter survival rates were estimated on the basis of total animals (including new, unmarked animals) rather than marked (only) animals, however, an unusual pattern was evident in the 1993-1994

TABLE *1. Average population density (MNAlha) and range of densities during the trapping season, 1992-1995.*[a]

Year and trapping grid	N[b]	Total		Adult		Juvenile	
		Mean	Range	Mean	Range	Mean	Range
1992							
Spruce floodplain 1	4	1.2a	0.0-3.3	0.la	0.0-0.4	1.0a	0.0-2.5
Alder floodplain 1	4	12.4b	7.0-17.4	3.3b	0.9-5.2	9.3b	6.1-13.0
Upland 1	4	17.3b	12.8-24.1	5.8b	4.5-8.3	11.5b	7.5-15.8
Beaver pond	3	16.2b	11.4-21.4	4.3b	1.4-7.1	11.9b	10.0-14.3
1993							
Spruce floodplain 1	3	2.1	0.5-4.5	0.2	0.0-0.5	2.0	0.0-2.5
Alder floodplain 1	3	5.7	0.5-6.2	1.6	0.5-2.9	4.1	1.0-8.1
Upland 1	4	3.1	0.0-6.2	0.6	0.0-1.0	2.5	0.0-5.3
Beaver pond	3	3.8	1.4-7.1	1.0	0.0-2.9	2.9	0.0-7.1
1994							
Spruce floodplain 1	7	24.9ab	10.0-36.3	19.5ab	10.0-35.3	5.5	0.0-10.5
Spruce floodplain 2	7	16.7ab	4.0-31.8	12.6ab	4.0-28.2	4.1	0.0-10.8
Alder floodplain 1	7	11.7a	3.3-24.3	6.5a	3.3-14.3	5.2	0.0-7.1
Alder floodplain 2	7	12.7a	5.0-24.8	8.0a	5.0-10.8	4.7	0.0-14.4
Upland 1	6	23.8ab	8.6-38.8	15.4ab	8.6-21.5	8.5	0.0-17.7
Upland 2	6	14.4ab	4.1-22.5	10.6ab	4.1-19.8	3.8	0.0-8.1
Beaver pond	7	58.7b	10.8-95.9	45.6b	10.8-86.5	13.1	0.0-27.0
1995							
Spruce floodplain 1	7	15.4bcd	11.4-20.4	12.1bcd	9.0-15.9	3.3ab	0.0-9.0
Spruce floodplain 2	7	2.8ab	0.9-4.5	2.4ab	0.5-3.6	0.5ab	0.0-1.4
Alder floodplain 1	7	5.5abc	0.5-9.1	3.7abc	0.5-5.2	1.8ab	0.0-6.2
Alder floodplain 2	7	0.8a	0.0-2.3	0.8a	0.0-2.3	0.0a	0.0
Upland 1	7	18.9cd	14.8-23.9	15.0cd	11.0-17.7	3.9ab	0.0-9.6
Upland 2	7	8.8abcd	9.0-11.3	6.4abcd	2.7-10.4	2.4ab	0.0-6.8
Beaver pond	6	38.1e	21.6-52.7	25.4e	20.3-32.4	12.6b	0.0-21.6

[a] Means with different letters within the same column and same year differ at the 0.05 level (samples from successive trapping periods frequently involved the same individual mice in ≥ 2 periods and, therefore, were not strictly independent; statistical validity should be interpreted with caution).

[b] N = number of 5-day trapping periods.

winter; many more adults were captured in spring 1994 than had occurred (even as juveniles) in autumn 1993 (Table 2); that pattern occurred on all grids. Few animals were present in the study area by August 1993, but 5-20 times more were present by spring 1994 (Fig. 2).

Growth.—Growth rates did not differ between years or trapping grids with the exception of one; growth rates were significantly lower on spruce floodplain 2 in 1994 than on any other grid in any other year. Body weights of adults (breeding males) did not differ between grids or years in any of the 4 years of study; mean body weight was 33.9 g ± 0.2 (*SE*) overall. Body weights of adult females varied in relation to reproductive status, so they could not serve as accurate indicators of adult body mass.

Sex ratios.—Sex ratios (proportion of males) of adults differed between years, with 1994 (0.62) being greater than that of the other 3 years (0.55). Adult sex ratios in 1992 and 1993 did not differ from 0.50, but those in 1994 (0.62) and 1995 (0.57) did. Sex ratios of adults differed between grids in 1992 and 1994: There were significantly more males than females in spruce floodplain 1 and upland 1 than alder floodplain 1 in 1992, and beaver pond than spruce floodplain 2, alder floodplain 2, and upland

TABLE 2.-Overwinter survival rates of mice in all trapping grids.[a]

		Marked animals[c]		Total animals[d]	
Year and trapping grid	N[b]	260-day interval	21-day interval	260-day interval	21-day interval
1992-1993					
Spruce floodplain 1	4	0.30	0.91	0.30	0.91
Alder floodplain 1	8	0.78	0.98	0.78	0.98
Upland 1	17	0.09	0.82	0.16	0.86
Beaver pond	15	0.10	0.83	0.17	0.87
1993-1994					
Spruce floodplain 1	1	1.00	1.00	18.69	1.27
Alder floodplain 1	3	0.66	0.97	5.20	1.14
Upland 1	3	0.32	0.91	6.57	1.16
Beaver pond	1	0.00	0.00	6.90	1.17
1994-1995					
Spruce floodplain 1	73	0.17	0.87	0.32	0.91
Spruce floodplain 2	71	0.01	0.68	0.09	0.81
Alder floodplain 1	51	0.01	0.71	0.01	0.71
Alder floodplain 2	37	0.02	0.73	0.02	0.73
Upland 1	81	0.32	0.91	0.44	0.94
Upland 2	50	0.18	0.87	0.40	0.93
Beaver pond	67	0.09	0.83	0.24	0.89

[a] Number of adults captured in first trapping period of one year expressed as a proportion of the total number of animals captured in the last trapping period of the preceding year, standardized to a 260-day interval (close to actual) and a 21-day interval (comparable to trapping-season interval-Krebs, 1989).

[b] N = number of animals captured in last trapping period of preceding year (all were marked).

[c] Based on number of marked animals (only) captured in first trapping period of subsequent year.

[d] Based on total number of adults captured in first trapping period of subsequent year (including new, unmarked animals).

2 in 1994. Differences that occurred in 1994 when habitat types were replicated were at least as great between replicates of habitat types as they were between habitat types. Sex ratios of juveniles did not differ between trapping grids in any year or between years (0.47, overall) and did not differ from 0.50 in any year.

Transients.—A high proportion of the animals we captured were transients (captured in only one trapping period, although that also might have included animals that were trap-shy after one capture). Proportion of adults that were transients differed between years, with 1992 (0.30) being lower than the other 3 years (0.57). The proportion of adults that were transients differed between trapping grids in 1994 and 1995; transients were most common in upland 1 (0.72) and least common in alder floodplain 1 (0.27) in 1994; they were most common in spruce floodplain 2 (0.78) and least common in alder floodplain 2 (0.55) in 1995. Variation between replicates within habitat types, however, was at least as great as between habitat types in both years.

Proportion of juveniles that were transients differed between all years: 1993 (0.87) > 1994 (0.73) > 1995 (0.62) > 1992 (0.25). It also differed between trapping grids in 1994; transients were greater in beaver pond (0.90) and upland 2 (0.87) than all other habitats (0.68). Similar to adults, however, variation between replicates within habitat types was at least as great as between habitat types in both years when replicates were available.

Dispersal and home range.—Incidental observations and our data on sex ratios, survival rates, locations of repeated captures, and effective area trapped provided insights into dispersal and home range. There was substantial evidence for considerable movement throughout the study, especially summer. Probability of recapturing any given individual in the next 5-day trapping period (21 days later) averaged only 0.43 throughout trapping seasons when populations increased. That was lower than comparable rates in winter when populations decreased (averaging 0.83, excluding the 1993-1994 winter; Table 2). Thus, a large part of the low survival rates in summer must have been related to movement. Similarly, lower survival rates of males than females with simultaneously higher male sex ratios were indicative of greater movement, not simply greater mortality.

A total of 168 individuals that had been marked on one trapping grid was subsequently captured on another grid. Known emigrants (marked on one grid and captured on another), as a proportion of the total number of animals marked on a given grid, were greatest in beaver pond (0.24 ± 0.09) and upland 1 (0.22 ± 0.02), intermediate in alder floodplain 1 (0.11 ± 0.03), and least in the other sites (0.04 ± 0.01, combined). Known immigrants also were greatest in beaver pond (0.44 ± 0.11), intermediate in upland 1 (0.09 ± 0.02), and least in the other sites (0.03 ± 0.01). Those data indicated a high degree of movement between beaver pond and nearby upland 1 but a relatively low degree of intermixing of populations among other grids. Data also provided an estimate of minimum-dispersal distance (Appendix I). Mean minimum-dispersal distances were significantly lower in the low-population years of 1992 and 1993 (248 ± 10 m) than in the high-population years of 1994 and 1995 (381 ± 6 m). The Kadashan River apparently did not present a significant barrier to dispersal, as emigrants and immigrants in spruce floodplain 2 and alder floodplain 2 (both on the opposite side of the river from all other grids) were at least as likely to go to (and come from) grids on the opposite side of the river as from the same side of the river.

Two independent sources of information provided estimates of average home-range size. First, the decreasing ratio of marked mice:total mice captured on assessment lines for effective area trapped indicated an effect of edge of 27.0 m beyond the trapping grid. If that were taken as the radius of an average-sized circular home range, the corresponding home range would have been 2,290 m^2. Second, we calculated sizes of minimum convex polygons (MCP) for all data from all animals that were captured in at least four separate 5-day trapping periods during 1 season on any of the six forest grids. There were 69 such animals over the course of the study, and there were no significant differences in mean MCP by years, sex-age classes, or habitat types. Mean MCP overall was 1,275 ± 116 m^2, but the effective areas trapped were 2.10 ± 0.03 times greater than areas of the trapping grids alone. Thus, average home-range size was most likely 2.1 X 1,275 m^2 = 2,678 m^2. Our overall estimate of average homerange size, therefore, is ca. 0.25 ha.

DISCUSSION

Population dynamics.—Despite between-year differences in population densities, we found few differences between trapping grids and, especially, habitat types. Few differences also were observed in other demographic factors (breeding seasons, survivorship, growth rates, sex ratios, and relative frequency of transients), and certainly none that indicated any one habitat was better than any other. The few differences that did occur between trapping grids were not repeated across years and were seldom consistent across replicate grids of any one habitat type. We, therefore, found no evidence of source-sink population dynamics occurring within our study area, at least at the level of habitat classification that we studied. Our habitat types fully included all types within the floodplain and nearby upland of our study area, so it also is unlikely that animals immigrated from, or emigrated to, other habitat types not included in our study.

This is a very different pattern of population dynamics than that observed by Van Home (1981) in her study of the response of *P. maniculatus* to different successional stages of upland forest in southeastern Alaska. Van Horne (1981) found two different types of high-density population: a largely adult population with high adult female survival, large breeding males, and high growth and survival rates of juveniles, and a largely nonbreeding population of juvenile young-of-the-year. The former occurred in her 23-25-year-old forest and was considered a source population; the latter occurred in both younger and older forests and was considered a sink population. Our greatest differences occurred between years rather than habitats. Juveniles predominated in the low-population years of 1992 and 1993, whereas adults predominated in the high-population years of 1994 and 1995; breeding seasons began earlier and ended earlier in the high-population years than in the low-population years; and dispersal distances were greater in the high-population years than in the low-population years. Most important was a large overwinter increase in number of mice between the lowest population year of 1993 and the highest population year of 1994. That increase occurred in all habitats and all grids and was not related to an influx of juveniles or adults from one habitat to another. Our results are similar to studies of P. maniculatus in coastal forests of British Columbia, where between-year differences in population densities and dynamics consistently have been greater than differences between treatments (successional stages or herbicide application-Petticrew and Sadleir, 1974; Runciman and Sullivan, 1996; Sadleir, 1974; Sullivan, 1979, 1990).

Flooding apparently had no significant effect on populations in our study area. Flooding was fairly frequent (several times per year), but durations always were very short, lasting only a few days (Pollock, 1995). We are uncertain how mice responded behaviorally to flooding, because it never occurred during our trapping seasons. Given the short duration of floods and lack of consistent differences in overwinter survival (including dispersal) between upland and fioodplain habitats, we suspect that mice reacted by temporarily seeking higher ground or climbing trees within the floodplain rather than dispersing to uplands. The situation of the beaver pond, on the other hand, was different than the other floodplain habitats. There was a high degree of movement between the beaver pond and adjacent upland (44% of the beaver-pond population were immigrants, and 24% were emigrants, on average). The beaver pond was flooded during most of each winter, and duration of flooding in spring and autumn frequently lasted several weeks (Pollock, 1995). Although population densities reached their highest levels in the beaver pond than other habitats (Fig. 2), they must have been dependent in large part on temporary refuge in adjacent upland habitat (source of most immigrants and destination of most emigrants).

Relation to food resources.—*Peromyscus* are well known for their wide variation in population densities between years and sites (Kaufman and Kaufman, 1989). That variation usually is attributable to local factors influencing recruitment rates (Batzli, 1991; Krohne et al., 1988). Recruitment in *P. maniculatus* usually is believed to be most strongly regulated by length of breeding season (Millar et al., 1979), which largely is a function of timing of initiation of breeding in spring (Sharpe and Millar, 1991), survival of adult females (Millar et al., 1992), and female aggression (Galindo and Krebs, 1987; Wolff, 1989). However, food availability strongly affects female aggression (Hansen and Batzli, 1978), social tolerance and dispersion (Fordham, 1971), juvenile survival and growth (Porter and Busch, 1978), maturation (Teferi and Millar, 1993), and, therefore, population densities and fluctuations (Taitt, 1981). Northern populations of *P. maniculatus* may reduce daily metabolic requirements and food intake by increasing periods of torpor during winter (Pierce and Vogt, 1993; Stebbins, 1977), but torpor cannot fully compensate for reduced food intake (Nestler et al., 1996). Furthermore, *P. maniculatus* neither caches food (Sullivan, 1978; Tadlock and Klein, 1979) nor stores fat seasonally (Kenagy and Barnes, 1988; Millar and Schieck, 1986). Availability of food, therefore, remains important year-around.

Mice are relatively inefficient digestors of fibrous plant materials such as leaves and stems (Foley and Cork, 1992; Justice and Smith, 1992), so high-energy, readily digestible foods such as seeds and fruit are most important and consistently preferred (Vickery, 1984; Vickery et al., 1994). Sitka mice in our study area ate a diet composed of mostly fruit and seed throughout the trapping season (Hanley and Barnard, 1999), which is consistent with results observed by Van Home (1982*a*) for *P. maniculatus* in southeastern Alaska. Use of arthropods and fungi was low (Hanley and Barnard, 1999). Tree seed has been reported widely as an especially important winter and early spring food for *P. maniculatus* (Gashwiler, 1979; Halvorson, 1982; Sullivan, 1979; Wolff, 1996), and that was evident in our data for Sitka spruce seed during May and June 1994-1995 (Hanley and Barnard, 1999).

Despite the great between-habitat differences in overstory (Hanley and Hoel, 1996) and understory species composition (Fig. 1), total food resources and mouse diets differed little between habitats (Hanley and Barnard, 1999). Lack of between-habitat differences in population demographics of Sitka mice in our study area, therefore, corresponds with lack of between-habitat differences in food resources. Importance of food resources was evident in between-year differences rather than between-habitat differences in diet composition (Hanley and Barnard, 1999) and population dynamics (Fig. 2).

Demographic differences between trapping seasons in 1993 and 1994 provided the most clear insight into processes determining population response to habitat. Lowest population densities occurred in 1993, and highest population densities occurred in 1994 (Table 1). Overwinter survival rates (Table 2) were highest in the winter of 1993-1994 of any of the 3 winters; overall 260-day survival rates for marked animals (regardless of habitat) were 0.24 for 1992-1993, 0.50 for 1993-1994, and 0.13 for 1994-1995. Breeding seasons began very early in 1994, especially for females, and more animals were present on all trapping grids in May 1994 than were present in August 1993 (Fig. 2). The winter of 19931994 had a productive seedfall of Sitka spruce, and tree seeds as a proportion of stomach contents were greatest in 1994, especially in May and June (May-June, 1994 equaled 59.1%-Hanley and Barnard, 1999). It is likely that the breeding season of 1993 lasted longer into the autumn than usual, as a consequence of low population density (and low aggression in adult females) and an abundant berry crop that year (T A. Hanley, in litt.). A highly productive spruce-seed crop that winter favored overwinter survival and an early breeding season in 1994, resulting in a major population increase. Even if this scenario is incorrect, however, it is of particular importance that the population increase was widespread across all habitats throughout the study area. Similarly, other year-to-year differences, although less than 1993 to 1994, also were widespread (Fig. 2). Variations in food resources (Hanley and Barnard, 1999) and population dynamics were greater temporally than spatially throughout our study area.

Implications for conservation.—Floodplain forests in southeastern Alaska differ substantially from upland forests in their species composition of both overstory and understory dominants but do not differ in total understory biomass and production (Hanley and Brady, 1997; Hanley and Hoel, 1996). Our floodplain forests also did not differ from upland forests in their production of food for Sitka mice (Hanley and Barnard, 1999) or in population dynamics and demographics of Sitka mice. We found no evidence of source-sink population dynamics or any consistent between-habitat differences in habitat quality (sensu Van Home, 1983). Practical implications of our results are that floodplain forests, per se, apparently do not provide unique habitat for Sitka mice in either a strongly positive or strongly negative sense compared with upland old-growth forests. Floodplain forests protected as "buffer" forest reserves, therefore, also should be able to function as habitat reserves for mice if they are of sufficient size and productivity of understory.

A key feature of habitat patches functioning as reserves is the concept of landscape connectivity (Taylor et al., 1993). Connectivity in this sense (and its opposite, fragmentation) is in relation to the ability of the particular organism to disperse among and utilize patches across a landscape (With and Crist, 1995). Connectivity was great among habitat types in our study; the riparian landscape was not a fragmented landscape for Sitka mice.

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Literature Cited

Andersen, D. C. 1994. Demographics of small mammals using anthropogenic desert riparian habitat in Arizona. The Journal of Wildlife Managemant, 58: 445-454.

Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer, Arm S. K. Nelson. 1987. Small mammal populations in riparian zones of different-aged coniferous forests. The Murrelet, 68:94-102.

Batzli, G. O. 1977. Population dynamics of the white-footed mouse in floodplain and upland forests. The American Midland Naturalist, 97:18-32.

—. 1991. Dynamics of small mammals: a review. Pp. 831-850, *in* Wildlife 2001: Populations (D. R. McCullough and R. H. Barrett, eds.). Elsevier, New York.

Canadian Council On Animal Care. 1993. Guide to the care and use of experimental animals. Second ed. Canadian Council on Animal Care, Ottawa, Ontario, Canada, 1:1-208.

Doyle, A. T 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy, 71:14-23.

Farr, W. A., And J. S. Hard. 1987. Multivariate analysis of climate along the southern coast of Alaska: some forestry implications. United States Forest Service Research Paper, PNW-RP-372, 1-38.

Foley, W J., And S. J. Cork. 1992. Use of fibrous diets by small herbivores: how far can the rules be 'bent'? Trends in Ecology and Evolution, 7:159162.

Fordham, R. A. 1971. Field populations of deermice with supplemental food. Ecology, 52:138-146.

Galindo, C., And C. J. Krebs. 1987. Population regulation in deer mice: the role of females. The Journal of Animal Ecology, 56:11-23.

Gashwiler, J. S. 1979. Deer mouse reproduction and its relationship to the tree seed crop. The American Midland Naturalist, 102:95-104.

Goldsmith, E B., And C. M. Harrison. 1976. Description and analysis of vegetation. Pp. 85-155, *in* Methods in plant ecology (S. B. Chapman, ed.). John Wiley & Sons, New York.

Gurnell, J., AND J. R. Flowerdew. 1990. Live trapping small mammals: a practical guide. Second ed. Occasional Publication Number 3, The Mammal Society, London, United Kingdom.

Halvorson, C. H. 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. Ecology, 63:423-433.

Hanley, T A., And J. C. Barnard. 1999. Food resources and diet composition in riparian and upland habitats for Sitka mice, *Peromyscus keeni sitkensis*. The Canadian Field-Naturalist, 113:

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, 75:574580.

Hanley, T A., And T Hoel. 1996. Species composition of old-growth and riparian Sitka spruce-western hemlock forests in southeastern Alaska. Canadian Journal of Forest Research, 26:1703-1708.

Hansen, L., And G. O. Batzll 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Canadian Journal of Zoology, 56:2530-2541.

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.

Hogan, K. M., M. C. Hedin, H. S. Koh, S. K. Davis, And I. E Greenbaum. 1993. Systematic and taxonomic implications of karyotypic, electrophoretic, and mitochondrial-DNA variation in Peromyscus from the Pacific Northwest. Journal of Mammalogy, 74:819-831.

Justice, K. E., And E A. Smith. 1992. A model of dietary fiber utilization by small mammalian herbivores, with empirical results for Neotoma. The American Naturalist, 139:398-416.

KAUFMAN, D. W , AND G. A. KAUFMAN. 1989. Population biology. Pp. 233-270, in Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.

KENAGY, G. J., AND B. M. BARNES. 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. Journal of Mammalogy, 69:274-292.

KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs, 36:239-273.

—. 1989. Ecological methodology. Harper Collins, New York.

KREBS, C. J., AND R. BOONSTRA. 1984. Trappability estimates for mark-recapture data. Canadian Journal of Zoology, 62:2440-2444.

KROHNE, D. T 1997. Dynamics of metapopulations of small mammals. Journal of Mammalogy, 78:1014-1026.

KROHNE, D. T, J. F. MERRRTT, S. H. VESSEY, AND J. O. WOLFF. 1988. Comparative demography of forest *Peromyscus*. Canadian Journal of Zoology, 66: 2170-2176.

MCCOMB, W. C., K. MCGARIGAL, AND R. G. ANTHONY. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. Northwest Science, 67: 7-15.

MILLAR, J. S., AND J. O. SCHIECK. 1986. An annual lipid cycle in a montane population of *Peromyscus maniculatus*. Canadian Journal of Zoology, 64: 1981-1985.

MILLAR, J. S., E. M. DERRICKSON, AND S. T E SHARPE. 1992. Effects of reproduction on maternal survival and subsequent reproduction in northern *Peromyscus maniculatus*. Canadian Journal of Zoology, 70: 1129-1134.

MILLAR, J. S., E. B. WILLE, AND S. IVERSON. 1979. Breeding by *Peromyscus* in seasonal environments. Canadian Journal of Zoology, 57:719-727.

NAGORSEN, D. W 1990. The mammals of British Columbia: a taxonomic catalogue. Memoir Number 4. Royal British Columbia Museum, Vancouver, British Columbia, Canada.

NAIMAN, R. J., AND H. DÉCAMPS. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics, 28:621-658.

NESTLER, J. R., G. P. DIETER, AND B. G. KLOKEID. 1996. Changes in total body fat during daily torpor in deer mice (*Peromyscus maniculatus*). Journal of Mammalogy, 77:147-154.

PETTICREW, B. G., AND R. M. E. S. SADLEIR. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Population dynamics. Canadian Journal of Zoology, 52:107-118.

PIELOU, E. C. 1977. Mathematical ecology. John Wiley & Sons, New York.

PIERCE, S. S., AND E. D. VOGT. 1993. Winter acclimatization in *Peromyscus maniculatus gracilis, P. leucopus noveboracensis*, and *P. 1. leucopus*. Journal of Mammalogy, 74:665-677.

POLLOCK, M. M. 1995. Patterns of plant species richness in emergent and forested wetlands of southeast Alaska. Ph.D. dissertation, University of Washington, Seattle.

PORTER, W. P, AND R. L. BUSCH. 1978. Fractional factorial analysis of growth and weaning success in Peromyscus maniculatus. Science, 202:907-909.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist, 137:S50-S66.

RUNCIMAN, J. B., AND T. P SULLIVAN. 1996. Influence of alternative conifer release treatments on habitat structure and small mammal populations in south central British Columbia. Canadian Journal of Forest Research, 26:2023-2034.

SADLEIR, R. M. E. S. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction. Canadian Journal of Zoology, 52:119-131.

SHARPE, S. T, AND J. S. MILLAR. 1991. Influence on the variation in initiation of breeding in *Peromyscus maniculatus*. Canadian Journal of Zoology, 69:698-705.

STEBBINS, L. L. 1977. Some aspects of overwintering in Peromyscus maniculatus. Canadian Journal of Zoology, 56:386-390.

SULLIVAN, T. P. 1978. Lack of caching of direct-seeded Douglas fir seeds by deer mice. Canadian Journal of Zoology, 56:1214-1216.

—. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Canadian Journal of Zoology, 57:1636-1648.

—. 1990. Demographic responses of small mammal populations to a herbicide application in coastal coniferous forest: population density and resiliency. Canadian Journal of Zoology, 68:874-883.

TADLOCK, C. G., AND H. G. KLEIN. 1979. Nesting and food-storage behavior of *Peromyscus maniculatus gracilis* and *P. leucopus noveboracensis*. The Canadian Field-Naturalist, 93:239-242.

TAITT, M. J. 1981. The effect of extra food on small rodent populations: 1. Deermice (*Peromyscus maniculatus*). The Journal of Animal Ecology, 50:111124.

TAYLOR, P. D., L. FAHRIG, K. HENEIN, AND G, MERRIAM. 1993. Connectivity is a vital element of landscape structure. Oikos, 68:571-573.

TEFERL T., AND J. S. MILLAR. 1993. Early maturation of northern Peromyscus maniculatus. Canadian Journal of Zoology, 71:1743-1747.

VAN HORNE, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology, 59:1045-1061.

—. 1982*a*. Niches of adult and juvenile deer mice (Peromyscus maniculatus) in seral stages of coniferous forest. Ecology, 63:992-1003.

—. 1982*b*. Effective trapped area for live-trap grids. Journal of Mammalogy, 63:155-157.

—. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management, 47:893-901.

VARTY, N. 1990. Ecology of the small mammals in the riverine forests of the Jubba Valley, southern Somalia. Journal of Tropical Ecology, 6:179-189.

Vickery, W L. 1984. Optimal diet models and rodent food consumption. Animal Behaviour, 32:340-348.

Vickery, W. L., J. -L. Daoust, A. El Wartiti, And J. Peltier. 1994. The effect of energy and protein content on food choice by deer mice, *Peromyscus maniculatus* (Rodentia). Animal Behaviour, 47:55-64.

Watkinson, A. R., And W. J. Sutherland. 1995. Sources, sinks, and pseudo-sinks. The Journal of Animal Ecology, 64:126-130.

White, G. C., D. R. Anderson, K. P Burnham, And D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico, Publication LA-8787-NERP, 1-235.

Wilkinson, L., M. Hill, J. P. Welna, And G. K. Birkenbeuel. 1992. SYSTAT for Windows: Statistics, Version 5. SYSTAT, Evanston, Illinois.

With, K. A., And T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology, 76:2446-2459.

Wolff, J. O. 1989. Social behavior. Pp. 271-291, *in* Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock.

—. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy, 77:850-856.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

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Appendix I

Calculation of Minimum-dispersal Distance

A total of 168 individuals that were marked on one trapping grid was subsequently captured on another grid: 14 in 1992, 10 in 1993, 89 in 1994, and 55 in 1995. Those animals provided a basis for estimating minimum-dispersal distances. For simplification, each trapping grid was considered a circle of 10,290 m^2 (114.5-m diameter), which was the same area as the actual 70- by 147-m rectangular grids. Distances between centers of all pairs of grids were measured on a map; those were considered distances moved between grids for any animal captured on both grids. They were minimum-dispersal distances because we knew only that the animal moved at least that far.

Probability of an animal encountering a new grid (Grid *j*) decreased with increasing distance from point of origin (Grid *i*). We adjusted our actual number of recaptured animals (N_{ij}) that travelled distance *ij* by estimating a distance-adjusted number (N'_{ij}) for each distance *ij*. Probability of an animal encountering a given grid when travelling a given distance *ij* was the area of the grid (10,290 m^2) expressed as a proportion of the area of a 114.5-m-wide ring with midradius of distance *ij*. N_{ij} divided by probability of encounter provided the estimate of the total number of animals (N'_{ij}) that travelled at least as far as distance *ij*:

$$N'_{ij} = \{[(\text{area of circle with radius } ij+57.25) - (\text{area of circle with radius } ij - 57.25)]^{-1} (10{,}290 \text{ m}^2) \}^{-1} N_{ij}$$

Those totals for each distance ij provided data for calculating mean (and variance) distance traveled.

For example, distance from the center of alder 1 to the center of upland 1 was 285 m. The area of a 114.5-m-wide ring with mid-radius of 285 m is 205,036 m^2. The proportion of that ring occupied by the upland 1 grid (10,290 m^2) was 0.050, which was the probability of capture of any individual wandering 285 m in any direction from alder 1. If 10 individuals from alder 1 were subsequently captured on upland 1, our estimate of total number of animals travelling at least that far in any direction (N'_{ij}) was 10/0.050 or 200.