

HABITAT STRUCTURE AND DEMOGRAPHIC VARIABILITY OF A HABITAT SPECIALIST: THE ROCK MOUSE (*Peromyscus difficilis*)

CARLOS GALINDO-LEAL¹ AND CHARLES J. KREBS²

¹Center for Conservation Biology, Department of Biological Sciences, Stanford University, California, 94305-5020. E.U.A.

²Center for Biodiversity Research, Department of Zoology, University of British Columbia, Vancouver, Canada, V6T-2A9.CANADA.

Abstract. We used a gradient of habitats in manzanita-oak shrubland in Durango, Mexico, to analyze demographic variability and microhabitat use patterns of the rock mouse (*Peromyscus difficilis*). We tested two hypotheses: First, demographic parameters of habitat specialists should be closely associated with habitat structure. Second, populations with higher breeding densities should have higher adult survival, less recruitment and more stable densities. In addition, we analyzed the habitat structure correlates of demographic stability. Demographic characteristics were more dissimilar in those grids with the greatest differences in vegetation characteristics. The areas with highest breeding densities had low juvenile and subadult recruitment in the breeding season. Most populations were relatively stable during the first year of study, but one declined to extinction during the second year. There were differences in microhabitat use among sexes and ages, as well as among resident and transient individuals, particularly in the breeding season.

Resumen. Utilizamos un gradiente de hábitats en el matorral de manzanita y encino en Durango, México, para analizar la variabilidad demográfica del ratón de las rocas (*Peromyscus difficilis*). Examinamos dos hipótesis. Primera, los parámetros demográficos de los especialistas de hábitat deben de estar muy relacionados con la estructura del hábitat. Segunda, las poblaciones con densidades altas de individuos reproductores deben tener mejor sobrevivencia de adultos, menor reclutamiento y mayor estabilidad. Además, analizamos la correlación entre la estructura del hábitat y la estabilidad demográfica. Las características demográficas fueron menos similares en aquellas áreas en donde existieron mayores diferencias en las características de la vegetación. Las áreas con densidades más altas de individuos reproductores tuvieron un bajo reclutamiento de individuos jóvenes y subadultos durante la época reproductiva. La mayoría de las poblaciones estuvieron relativamente estables durante el primer año de estudio, sin embargo, durante el segundo año, una población disminuyó hasta extinguirse.

Key Words: *Peromyscus difficilis*, demography, habitat structure, habitat specialists, Durango, Michilia Biosphere Reserve.

INTRODUCTION

Habitat structure may influence habitat suitability both directly and indirectly, through its effects on microclimate, food abundance, the availability and spatial distribution of nest sites, and the architecture of protective cover (Bell *et al.*, 1990; Cody, 1985). Consequently, animal distribution and abundance are often associated with structural features of the habitat such as the amount of cover, foliage height diversity, depth of perennial grasses, and dense woody understory (Brown and Lieberman, 1973; Holbrook, 1978; Kaufman and Kaufman, 1989; M'Closkey, 1975; Rosenzweig, 1973; Thompson, 1982; Verner *et al.*, 1986; Wilson, 1968). Spatial differences in habitat structure should be expected to affect the distribution of individuals, demographic parameters, population abundance and ultimately, species distribution.

Optimal habitats and distributional boundaries represent the extremes of demographic variability for populations. Between these limits, habitats vary widely in their capacity to sustain populations. Several models distinguish two extreme types of populations in contrasting habitats: Populations in primary, central, survival, or source habitats are characterized by higher stability, higher survival rates, higher reproductive rates, more stable age distributions, and lower extinction rates. Populations in secondary, marginal, colonizing, or sink habitats have lower survival rates, lower reproductive rates, less stable age distributions, and higher extinction rates (Anderson, 1970; Pulliam, 1988; Soulé, 1973). Thus, habitat suitability is best characterized by high reproduction and survival rates which often result in greater population stability (Van Horne, 1981; 1986). Therefore, to characterize demographic parameters and investigate population regulation it is necessary to closely examine the relation between habitat and demography (Halama and Dueser, 1994; Pulliam, 1988; Van Horne, 1986).

The demographic characteristics of some populations of small mammals are related to habitat structure (Bondrup-Nielsen, 1987; Hansson, 1994; Krohne and Baccus, 1985; Ostfeld and Klosterman, 1986; Ostfeld *et al.*, 1985; Van Horne, 1981), yet others exhibit very similar demographic patterns in different habitats (Adler and Wilson, 1987; Parmenter and MacMahon, 1983; Petticrew and Sadleir, 1974; Sadleir, 1974; Sullivan, 1979). Most studies on the effect of habitat characteristics on demography of small mammals have compared generalist species in highly contrasting habitats. Generalists are often selected because their wide distribution and relatively high abundance make them easy to study. However, generalists can withstand a wide variety of conditions by definition, and their individual distribution and demographic responses may not strongly reflect habitat characteristics. In contrast, the demography of habitat specialists should be more closely associated to habitat structure since their abundance often declines sharply outside suitable habitats (Adler and Wilson, 1987).

The rock mouse (*Peromyscus difficilis*) is a habitat specialist of montane conifer forests (Hoffmeister, 1986). It is a relatively large, semi-arboreal species distributed along the western and eastern Sierra Madre in Mexico and southwestern U.S.A. It inhabits rocky outcrops in pinyon pine, juniper and oak forests (Holbrook, 1978; Wilson, 1968). Like other species of *Peromyscus* in xeric areas, it is also highly specific in microhabitat use. Rock mice are highly restricted to habitats with particular structural features such as protective cover, characteristic plant species composition and rocky outcrops (Hoffmeister, 1986; Holbrook, 1978; Wilson, 1968). In fact, this species has the most restricted habitat distribution among eight *Peromyscus* species in Arizona (Hoffmeister, 1986). Little is known of the demography and other aspects of the ecology of this species (Galindo-Leal, 1991, 1996, 1997).

Rock mouse populations have a relatively even sex ratio (Galindo-Leal, 1991). Adults are similar in size (males 27.5 g, s.e. = 0.21, n = 297; females 27.6 g, s.e. = 0.26, n = 240), and both sexes apparently have exclusive and non-overlapping home ranges in the breeding season. This is in contrast to most reports of *Peromyscus* where sex ratios are male-biased and male home ranges overlap with those of females (Kaufman and Kaufman, 1989; Wolff, 1989; Galindo and Krebs, 1987). Exclusive use of space by males and females is exhibited by mammals which make food caches, such as red squirrels, kangaroo rats, pikas and pack rats (Smith and Reichman, 1984). Several other species of *Peromyscus*, particularly those living in semi-arid areas, cache seeds (Barry, 1976). Rock mice cache acorns, but the extent to which they rely on them is unknown (Alvarez and Polaco, 1984).

In this study we describe the population dynamics of the rock mouse in relation to habitat characteristics. We tested two hypotheses: first, demographic parameters of habitat specialists should be closely associated with habitat structure. Second, populations with higher breeding densities should have higher adult survival, less recruitment and more stable densities. In addition, we analyzed the habitat structure correlates of demographic stability.

STUDY AREA AND METHODS

The study was conducted on the eastern slopes of the western Sierra Madre (23° 25' N; 104° 15' W) in southern Durango, Mexico (Fig. 1), from February 1986 to July 1988 (Galindo-Leal, 1991, 1996, 1997). Annual precipitation averaged from 50 to 70 cm and was concentrated in five months between June and October. Mean monthly temperatures fluctuated from 17.4° to 20.4° C. The study area was located in a dry-temperate oak-pine forest at 2,400 m altitude. Dominant tree species included several species of oaks (*Quercus durifolia*, *Q. sideroxyla*, *Q. eduardii*, *Q. chihuahuensis*, *Q. convalata*, *Q. potosina*, *Q. rugosa*), and pines (*Pinus arizonica*, *P. chihuahuana*, *P.*

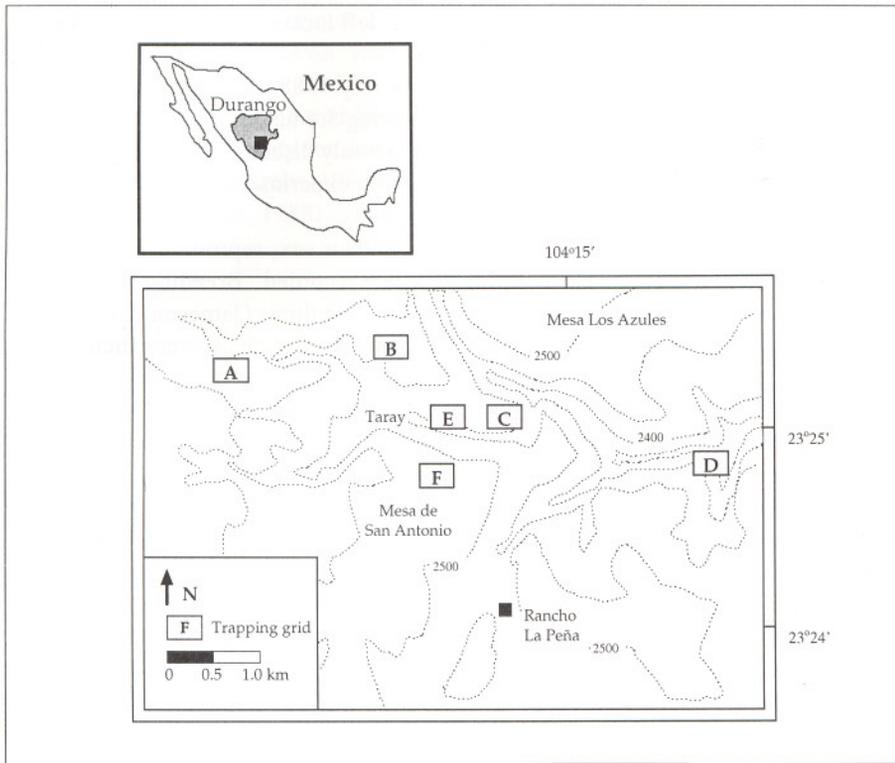


Figure 1. Map of the study area in southwestern Durango, Mexico.

engelmani, *P. leiophylla*, *P. teocote*). Point-leaf manzanita (*Arctostaphylos pungens*) and guazapol (*Ceanothus buxifolius*) were the main shrubs. The study area was within the buffer zone of the Michilia Biosphere Reserve (MAB-UNESCO; Galindo-Leal, 1991, 1996).

Six grids (A-F) were established in oak-manzanita shrubland in March, 1986. Distances between grids ranged from 500 m to 4 km (Fig. 1). Each grid consisted of 64 Longworth traps (8 x 8 array) that were set at 20 m intervals covering an area of 2.6 ha. Traps were baited with whole oats. Traps were placed on the ground initially, but most were moved later to 1-2 m on the closest tree to avoid disturbance by grey foxes (*Urocyon cinereoargenteus*) and peccaries (*Tayassu tajacu*). Trapping sessions lasted two nights at four week intervals. Traps were opened in the afternoon, checked

for the next two consecutive mornings and were left locked open between trapping sessions (Galindo-Leal, 1991, 1996, 1997).

Trapping took place from March 1986 to July 1988. In May 1987 two grids (C, F) were enlarged to 8 x 17 trap stations covering 5.4 ha. These large grids were trapped until July 1988. For this second period, we only discuss here the demography of the population on grid F, since grid C was used for experimental manipulations and is discussed elsewhere (Galindo-Leal, 1991, 1996).

Trapped individuals were ear-tagged, and their sex, reproductive condition, weight (nearest gram) and location of capture were recorded. Breeding condition in males was determined by recording visible cauda epididymis (Jameson, 1950). Size of nipples was scored as large, medium or small and evident pregnancies were recorded. Individuals were assigned to one of three age categories: adults (sexual maturity or > 22 g), subadults (molting, brown pelage and/or >19 and < 23 g) and juveniles (grey pelage and < 20 g).

We used the complete enumeration method (Galindo-Leal, 1990) to estimate population size, since Jolly-Seber inflates estimates when immigration is high relative to number of residents (Adler and Wilson, 1987). Furthermore, both methods provide similar results when densities are low, as in this case (Galindo-Leal, 1990). There were no consistent differences in trappability between males and females on any grids (Galindo-Leal, 1991). Individuals trapped during two or more sessions were considered residents; others were considered transients. We used contingency tables and log-likelihood tests (G tests) to compare differences in the recruitment of resident and transient individuals as well as temporal patterns of recruitment. Because sample sizes were small, we made no distinction between age classes in comparing residence time, and grouped seasons into two periods: spring-summer when most individuals were overwintered adults, and fall-winter, when most individuals were new recruits.

Habitat sampling was conducted during September 1986. Density and cover of perennial vegetation was estimated in each trapping grid using 10 x 10 m (100 m²) quadrats centered on each trap station (64 quadrats per grid). Thus sampling units covered 40% of each grid. Oaks, pines, junipers and madrones were pooled into generic categories, and plants were assigned to overstory (> 1.50 m tall) or understory (< 1.50 m tall). Percentage cover was recorded in 25% increments using two parallel lines 5 m apart in every quadrat. Because cover and density were highly correlated for all plant taxa (Galindo-Leal, 1991), only cover was used in the analyses. Herbaceous plants were almost absent from this habitat, as is common in other chaparral shrub communities (Swank and Oechel, 1991), and hence, were not included in the analysis.

To test for differences in total plant cover between grids we used an analysis of variance (ANOVA) on arcsin-transformed data (Zar, 1984). We used multiple

contrasts (Scheffes test), to determine differences between grids or groups of grids when the results of ANOVA were significant (Wilkinson, 1988). The level of significance was set at $p < 0.05$. When sample sizes were unequal we used weighted mean analysis. We compared habitat composition between grids using Morisita-Horn's Index of Similarity for cover, which ranges from 0 (no similarity) to about 1 (complete similarity; Krebs, 1989). Grids were then classified using average linkage clustering (Wilkinson, 1988).

RESULTS

Habitat structure

Grids differed in overstory cover (ANOVA $F = 8.63$, $df = 1,378$, $p < 0.001$), and could be separated into three groups. The moderate cover grids were A, C, D, and F (Multiple contrasts, $p > 0.05$). Grid B had the highest cover and grid E the lowest (Multiple contrasts, $p < 0.05$). Oak cover was very similar between grids, ranging from 39% to 51%, whereas manzanita cover varied substantially from 32% to 66%. Pine cover reached 35% on grid F, but was negligible in the rest ranging from 3 to 8% (Fig. 2). Understory cover was significantly higher only on grid F (ANOVA $F = 2.89$, $df = 5,378$, $p < 0.05$; Multiple contrasts, $p < 0.05$). In the other five grids, the density of understory was very low (Multiple contrasts, all $p > 0.05$). The differences were mostly due to the higher pine density in the understory of grid F (Fig. 2). In summary, four grids were particularly similar (A-D; Morisita-Horn indices above 0.99). Grids E and F were each in their own group, but the former was closer to the other four grids (Fig. 3).

Demography

Density and population trends

Rock mouse populations on all grids were low and relatively stable throughout the study. Densities fluctuated seasonally from 1.6 to 13.3 individuals per hectare. Population numbers declined or were already low in the spring of 1986 and continued this way during the first half of the wet season (June-Aug.), then slowly increased through the rest of the wet season (Sept.-Oct.) and the first half of the dry season (Nov.-Jan.). Populations either declined at the end of the dry season (Apr-Jun) or remained stable. There was a sharp pulse of recruitment on 4 grids during April or May. On average, the minimum number of individuals per grid was 8.0 ($s.e. = 1.1$, $n = 6$) and the maximum was 29.3 ($s.e. = 2.3$, $n = 6$; Fig.4).

Populations on grids A, B, and C had low spring, summer and fall density (minima of 4-9/grid) and high winter density (A, B, C; maxima of 27-34/grid). They

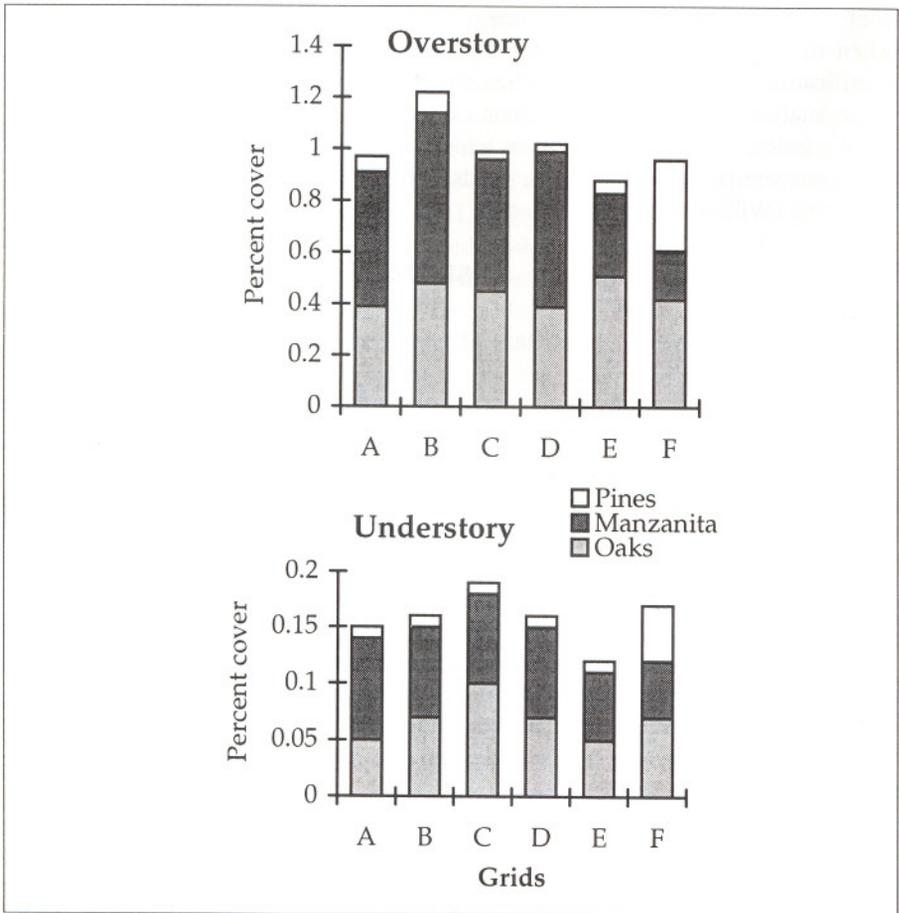


Figure 2. Overstorey and understory cover characteristics of the six grids. Grids were very similar with the exception of grid F which had higher pine cover and lower manzanita cover. Grid E had lower total cover than the other 5 grids.

increased from 3 to 8.3-fold. Populations on grids D, and F had higher summer densities (minima of 11-13/grid), and lower winter densities (maxima 23-25/grid). They increased from 1.9 to 2.1-fold. However, the population on grid D went extinct in the spring of 1987. Finally, the population on grid E had both lower summer (8 individuals) and winter densities (19 individuals) than the other types. This population increased 1.9-fold.

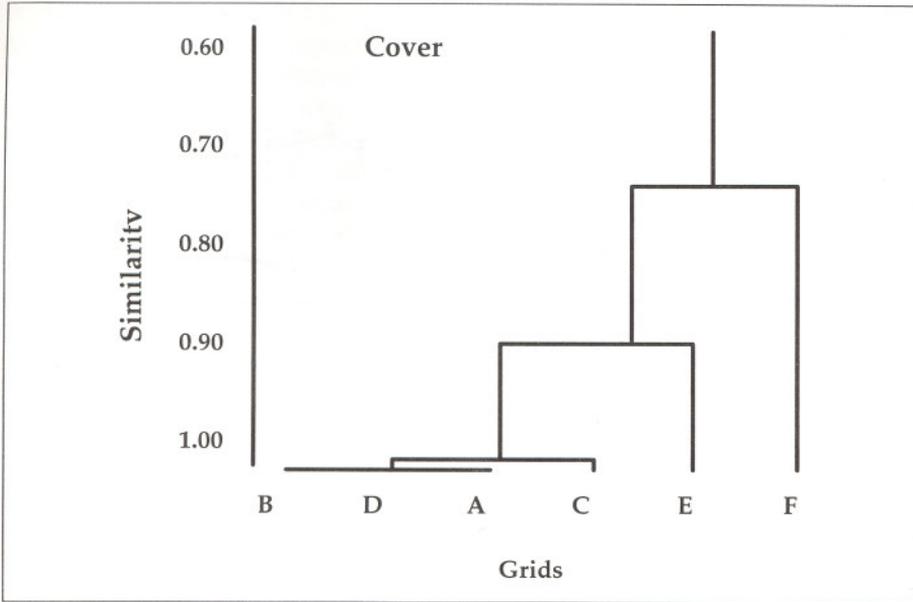


Figure 3. Classification of grids using relative composition of both under and overstory cover of perennial plants, using Morisita's Similarity Index and average linking clustering.

Seasonality of reproduction

Breeding activity was strongly synchronized with rainfall and was therefore highly seasonal, lasting from 6 to 7 months. Most females were in breeding condition from June to December each year, but there was some variability between years and among grids. Breeding females were recorded from late May to December in 1986, from February to December in 1987, and again in June and July in 1988. Earlier breeding in 1987 was likely due to an unusually heavy snowfall in February 1987. In 1986, most males in reproductive condition were caught from June to October (86%) but a few were caught in May (5%; D, E) and in November and early December (9%; C, D). During July and August most grids had 50% or more breeding males.

Among a total of 56 females that were recorded as evidently pregnant, 39 (70%) were overwintered adults. The rest, 17 (30%) were young of the same year. Overwintered adults had one (51%), two (31%) or three (18%) pregnancies during the breeding season. Most young of the year were pregnant only once during that year (94%), but one was pregnant twice (6%).

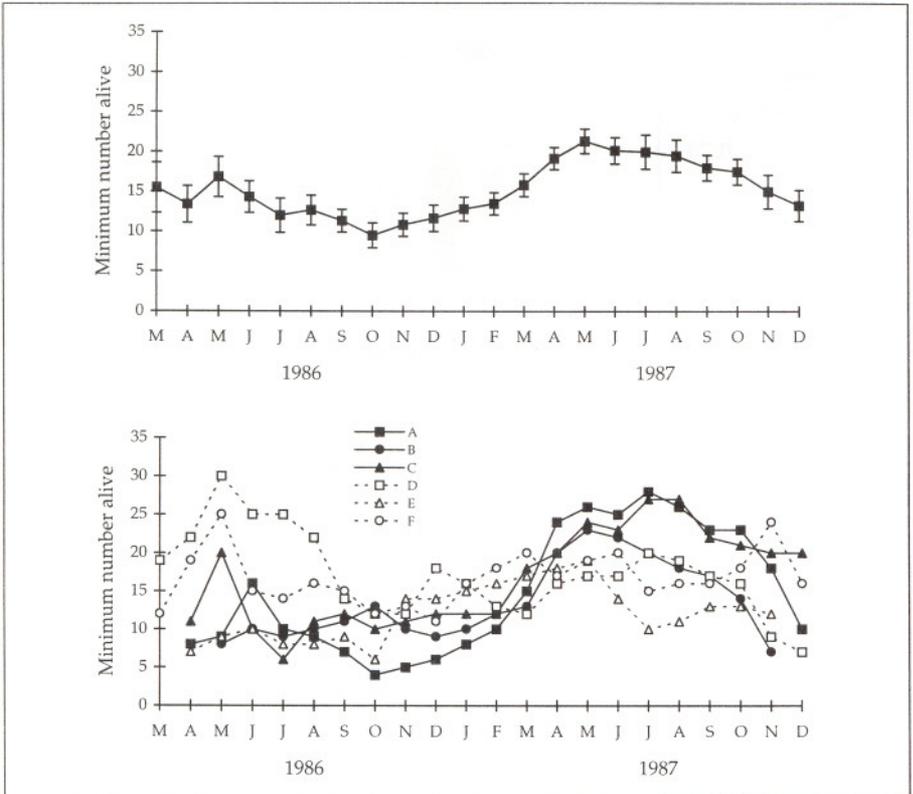


Figure 4. Changes in abundance in the six grids throughout 1986 and 1987. Grids A, B, C had low density during summer, fall and winter and increased throughout winter and spring. Grid E had a lower density throughout while populations on grids D, F were higher in the spring and declined through summer. They did not reach higher abundance as grids A, B, and C did.

Excluding evident pregnancies, breeding females ($x = 33.4$, $s.e. = 1.29$) were significantly heavier than non-breeding adult females ($x = 26.8$, $s.e. = 0.2$; Weighted means analysis $F = 53.5$, $d.f. = 1,132$ $p < 0.001$). No female less than 25 g showed signs of breeding. Breeding males ($x = 30.9$, $s.e. = 0.85$) were also significantly heavier than non-breeding adult males ($x = 27.19$, $s.e. = 0.27$; Weighted means analysis $F = 17.7$, $d.f. = 1,165$ $p < 0.001$). No male under 27 g showed signs of breeding.

Differences in recruitment

There were substantial differences in total recruitment between grids. Recruitment varied from low (E), and moderate (A, B) to high (C, D, F; Galindo-Leal, 1991). The age composition of recruits differed significantly between grids ($G = 30.34$, $d.f. = 10$, $p < 0.001$). Largest contributions to total G values were due to the low proportion of subadult recruits on grid F. Differences between grids other than F were not significant ($G = 13.92$, $d.f. = 8$, $p > 0.05$; Fig. 5). The ratio of adult to subadult and juvenile recruits was similar in all grids except grid E. The proportions of juveniles and subadult recruits also varied between grids. Two grids had mostly subadult recruits (A, C), two grids had even numbers (E, D), and two grids had mostly juvenile recruits (B, F), particularly grid F (Fig. 5).

Recruitment also varied seasonally. In 1986 many adults recruited during spring. Mean monthly recruitment for these months was 9 individuals per grid ($s.e. = 1.8$, $n = 18$). From June 1986 to May 1987, monthly recruitment averaged only 2.1 ($s.e. = 0.2$, $n = 72$). Pooled results from all age classes indicate that most recruitment occurred in spring, autumn and winter. Recruitment was very low (7-11%) on all grids in summer, and also low in the spring of 1987 (3-7%). Grids differed significantly in seasonal patterns of recruitment ($G = 40.0$, $d.f. = 20$, $p < 0.005$). The greatest differences were due to high recruitment during winter on grid B and during autumn on grids A and E.

Populations differed by as much as two months in the date of first juvenile recruitment. Juvenile recruitment was highest in September and late November and December (E, F), in December (B, C) or was relatively constant (A, D). Juveniles and subadults mostly recruited in fall and winter. Recruitment was highly seasonal in some areas with 83 to 94% of all juveniles and 74 to 86% of all subadults recruited in this period (A, B, C, E). In other areas it was more prolonged with 67 to 71% of all juveniles and 53 to 57% of all subadults recruited in fall and winter (F and D). Very few juveniles recruited in summer or spring. Pooling juveniles and subadults, the mean monthly recruitment was 5.3 individuals ($s.e. = 0.7$, $n = 30$) in fall and winter. Outside this period, monthly recruitment averaged only 0.98 individuals ($s.e. = 0.2$, $n = 51$). Recruitment was even among sexes both for juveniles and subadults.

Transient individuals constituted between 29 and 33% of all the recruits in most grids (A, C, D, E), but grids B and F had higher proportions (40 and 42 % respectively). The age composition of transients was similar between grids ($G = 13.81$, $d.f. = 10$, $p > 0.05$; Fig. 5). Most transients were also adult individuals, but the percentages varied widely. Grid E had the fewest adult transients (Fig. 5). Juvenile transients outnumbered subadults in all grids except grid A. On grid E, 50% of all transients were juveniles. Transients followed a similar temporal pattern to that of recruits. In 1986, they were most abundant in the spring, autumn and winter and

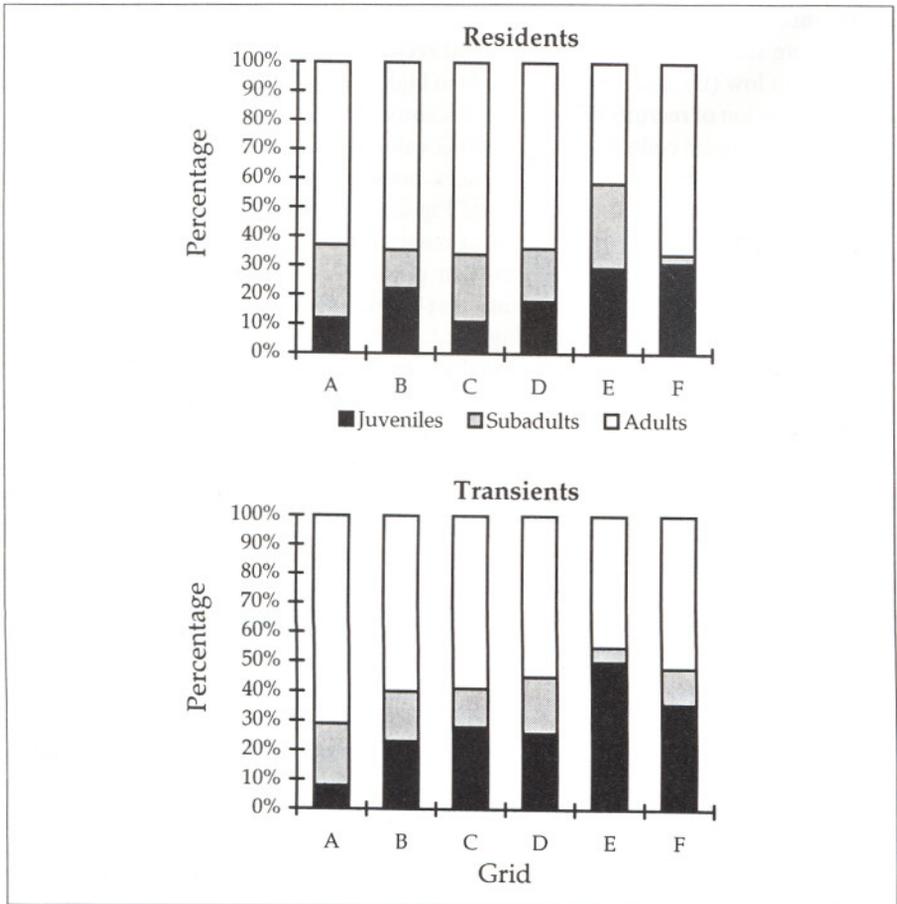


Figure 5. Percentage of age classes for residents and transients in each grid. Grid E had a lower percentage of adult residents while grid F had almost no subadult residents. Transient juveniles were almost absent in grid A and were more common in grids E and F.

less abundant in the summer. In 1987 they were less abundant in spring. Seasonal differences between grids were not significant (Fig. 6).

Survival and residence time

Survival was relatively high and similar for both adult males and females throughout the seasons. Sexes did not differ in residence time (Three-way ANOVA, $F = 0.754$,

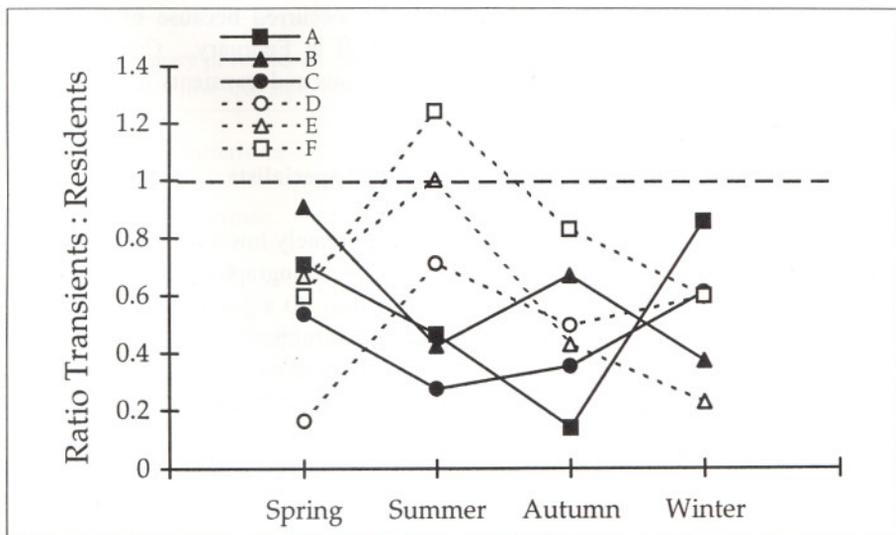


Figure 6. The number of transients increased in grids D, E, and F, during the summer and then decreased, whereas the opposite pattern occurred in grids A, B and C.

$d.f. = 1,281, p > 0.05$). There was a significant interaction between grid and season (Three-way ANOVA, $F = 2.70, d.f. = 5,281, p < 0.05$). Residence time was longer in the fall-winter period on grids A and C, whereas the opposite occurred on grid B. There were no differences among the other grids.

DISCUSSION

Unlike herbivorous rodents that reach densities of 100 to 800 individuals per hectare with amplitudes of numerical change over 10-fold (Taitt and Krebs, 1985), insectivorous and granivorous rodents usually range from 5 to 50 individuals per hectare, and increase less than 5-fold in their annual fluctuations. In this study, rock mice fluctuated annually in density, similar to northern species of *Peromyscus* (Montgomery, 1989). In general, numbers were lowest during the summer, increased in the fall and winter, and declined in the spring. Densities were relatively low and the amplitudes of population fluctuation were small (from 2 to 8-fold) as in other *Peromyscus* species living in lower latitudes (*P. eremicus*, *P. boylii*, *P. californicus*, *P. polionotus*, *P. gossypinus*; Kaufman and Kaufman, 1989, Montgomery, 1989). Reproduction was usually restricted to the wet season from June to November or

December. Earlier breeding in 1987 may have occurred because of increased humidity caused by an unusually heavy snowfall in February. Consequently, demographic parameters, like low numbers of recruits and transients during spring 1987, resembled those of the previous summer.

Habitat structure and habitat specialists

By definition, habitat specialists are absent or in extremely low abundances in other than their preferred habitat. Thus, comparison of demographic characteristics is limited to smaller variations in habitat characteristics. At a gross scale, all grids in this study have the same habitat: oak-manzanita shrubland. Nevertheless, rock mouse distribution was sensitive to slight modifications of habitat structure, and their demographic characteristics were more extreme on grids with greatest differences in vegetation characteristics (E, F; Figs. 2 and 3). The results support the hypothesis that demographic parameters of habitat specialists are closely associated with habitat structure.

Grid F had the highest heterogeneity, highest understory cover, highest pine density and highly clumped manzanita (Galindo-Leal, 1991), and also differed demographically from the other grids. The population in this grid had a consistently female-biased sex ratio, breeding densities were higher, stability was higher and the breeding season was shorter (Galindo-Leal, 1991). Recruitment was higher than in other grids in the spring of 1986, but was lower in the fall (Table 1). That this grid had lower juvenile and subadult recruitment in fall and winter and more transients may indicate a higher turnover due to immigration. Grid D shared several of the demographic characteristics of grid F (Table 1), but there were also differences. Grid D had few transients, moderate subadult recruitment and a longer breeding season. In spite of high breeding densities during summer and relative stability during fall and winter 1986, the population on grid D went extinct during the spring of 1987. Habitat structure in this grid was most similar to that on grids A, B, and C.

Habitat structure was also substantially different on grid E. This grid had the least overstory and understory cover and also differed demographically from the rest of the grids in several parameters: consistently lower density, adult recruitment, numbers of adult and subadult transients and low to medium survival. The other grids (A, B, C), had similar habitat structure. Grid C had slightly lower total plant density, but very similar cover. Demographically, these grids had low to medium breeding densities, lower stability, high adult recruitment and many transient adults (Table 1).

Breeding densities and population stability

Van Horne (1981) described two general types of summer demography for *Peromyscus maniculatus* that were related to seral stages of coastal coniferous forest.

Table 1. Summary of results on demographic parameters in all grids. + indicates relatively high; - relatively low. No sign indicates moderate.

Demographic characteristics	A	B	C	D	E	F
Summer to winter increase	8.3	3.0	5.7	1.9	2.4	2.1
Proportion of females	0.48	0.45	0.53	0.43	0.56	0.57
Breeding density	-			+	-	+
Reproduction	-	-	+	+	+	-
Recruitment			+	+	-	+
Adults	+	+	+	+	-	+
Subadults/Juveniles	+	-	+			-
Transients	-	+	-	-	-	+
Adults	+	+	+	+	-	+
Subadults/Juveniles	+				-	
Residence time (1st period)	-	+				
(2nd period)	+	-	+	+	-	+

First, relatively stable and high density populations, with mostly adult individuals, were found in intermediate seral stages. These had a high perennial shrub cover and some canopy closure. Second, less stable, high density populations, with mostly juvenile individuals, were found in earlier and later seral stages with less understory cover. In our study, the population on grid F was somewhat equivalent to Van Horne's first type, because higher breeding densities were accompanied by higher stability, and juvenile and subadult recruitment were lower in the breeding season. This supports the hypothesis that populations with higher breeding densities, particularly of females, have higher survival, lower recruitment and have more stable densities.

Populations on grids D and E were also relatively stable. However, the population on grid D in spite of higher breeding density and its resemblance with that on grid F, declined to extinction during the spring of 1987. Krohne (1989) also reported that populations of *P. leucopus* with similar demography during part of the year may differ during others. The low densities and few recruits and transients of grid E with sparse overstory and understory cover suggest that its stability resulted from unsuitable habitat. The populations on grids A, B, and C were more similar to Van Horne's second type. They all had high percentage of juvenile and subadult recruits and population changes from summer to winter were more dramatic.

Habitat structure and demographic stability

Ostfeld *et al.* (1985) underscored cover as a good index of habitat quality. Their populations of California voles (*Microtus californicus*) had higher peak densities, female-biased sex ratios, higher juvenile recruitment, and longer persistence in habitats with dense cover.

In this study, high within-year stability was not related to plant cover or density *per se*, but occurred in the grid with highest heterogeneity in composition of plant cover. Heterogeneous habitats might provide a combination of protective cover with more stable food supplies, since different plant components provide alternative resources at different times. The branching configuration of manzanita shrubs offers dense, protective cover, while hollowed oaks and junipers provide nest sites. In terms of food, manzanita provides flowers and fruits during spring and summer, whereas oaks, junipers and pines provide seeds in late fall and throughout winter. Insects are consumed mostly in winter and spring (Alvarez and Polaco, 1984).

While our results support the idea that differences in demographic parameters of habitat specialists are closely related to subtle changes in habitat structure, other studies of small mammals have reported populations in very distinct habitat types to be very similar in demography (Adler and Wilson; 1987; Petticrew and Sadleir, 1974; Sadleir, 1974; Sullivan, 1979). There are at least three plausible reasons for demographic similarities in the face of habitat differences in those studies. First, most of the studied species were extreme habitat generalists with wide geographic distributions and including diverse habitats. For example, the most well-studied species of *Peromyscus* (*P. maniculatus* and *P. leucopus*) are the only ones among 42 mainland species that have distributional ranges covering more than 30° of latitude. The rest cover less than 25° (15 species) or less than 10° of latitude (25 species; Carleton, 1989). Second, many studies have been restricted to only a part of the annual cycle, usually summer and fall. Populations in different habitats might be similar demographically while they were being studied but different in winter (Krohne, 1989; this study). Third, habitat structure and demography may have been evaluated on different spatial scales. For example, Adler and Wilson (1987) reported similar summer demography of *P. leucopus* in different habitat types, but that conclusion was based on very small trapping grids (0.28 ha). Home range sizes of *Peromyscus* range from 0.02 ha to over 0.30 ha (Wolff, 1989). Therefore, while the characterization of the habitat might truly represent that area sampled, the characterization of the demography of *Peromyscus* does not; most individuals captured in that study probably lived elsewhere.

General aspects of the demography of rock mice are similar to those of northern species, but other features are very different. Most *Peromyscus* species have restricted distributional ranges (Carleton, 1989) and many are probably habitat specialists. In fact, many of the large sized species seem to have specialized nest site

requirements (*P. californicus*, *P. truei*, *P. boylii*; Merritt, 1974). However, most of our knowledge (Kirkland and Layne, 1989) comes from only 2 of the 53 recognized *Peromyscus* species (Carleton, 1989). These two have the widest geographical distribution of all and are therefore atypical (Montgomery, 1989). Further research on the other 51 little-studied species should provide fruitful insights into the relations of habitat structure, demographic variability and geographical distribution.

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