

## PARTITIONING OF SPACE, FOOD, AND TIME BY SYNTOPIC *PEROMYSCUS BOYLI* AND *P. CALIFORNICUS*

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We used trap associations, nest-site preferences, a food selection experiment, and measurements of nightly activity to describe resource partitioning by syntopic *Peromyscus californicus* and *P. boylii* in Monterey County, California. *P. californicus* and *P. boylii* were active over the same range of time during the night. *P. boylii* was caught frequently near *Quercus agrifolia*, nested under canopies with high densities of *Q. agrifolia*, and consumed more *Q. agrifolia* acorns than *P. californicus*. Relative to *P. boylii*, *P. californicus* was a habitat generalist that did not discriminate among canopy plants for nest sites and had a broad diet. At high densities of *P. californicus*, the 2 species were negatively numerically associated. Both interspecific interactions and habitat partitioning (canopy level), via the specialization of *P. boylii* on *Q. agrifolia*, appear to facilitate the coexistence of *P. boylii* and *P. californicus*.

**Key words:** coexistence, diet, habitat, nest sites, *Peromyscus californicus*, *P. boylii*, resource partitioning, scale, time of activity

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Ecological niches of coexisting animals may be separated in 3 principal dimensions, time, space, and food (Pianka 1973; Schoener 1974). In general, studies of resource partitioning within vertebrate guilds attempt to determine mechanisms underlying community structure by quantifying niche dimensions and overlap of component species (e.g., reptiles—Pianka 1973; mammals—Grant 1972; birds—Cody 1985).

Related sympatric species are especially valuable in studies of resource partitioning because they are the most likely to be current or past competitors. Several studies of *Peromyscus* have quantified variation in resource use between and among congeneric and confamilial species within a community (reviewed in Kaufman and Kaufman 1989). Although some studies have failed to find partitioning of resources among species

(Graves et al. 1988; Knuth and Barrett 1984; Newton et al. 1980; Wolff et al. 1985), the majority have demonstrated that *Peromyscus* species partition resources among each other or with other small mammals in the community along axes of food (Smartt 1978; Wolff and Dueser 1986) and space (Barry et al. 1990; Dooley and Dueser 1996; Dueser and Hallett 1980; Etheredge et al. 1989; Frank and Layne 1992; Galindo and Krebs 1985; Garman et al. 1994; Hallett et al. 1983; Harney and Dueser 1987; Holbrook 1979; Morris 1983, 1984; Wolff and Dueser 1986; Wolff and Hurlbutt 1982; and those cited in Kaufman and Kaufman 1989).

Resource partitioning can be mediated by interspecific competition or differential habitat preference resulting from evolved preferences or results of past competitive exclusions. Studies that include *Peromyscus* have shown evidence of both of these pro-

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cesses. Because of the extensive overlap of the wide ranging *P. leucopus* and *P. maniculatus*, the majority of studies on coexistence within small mammal assemblages that include *Peromyscus* have involved 1 or both of these species (Etheredge et al. 1989; Frank and Layne 1992; Holbrook 1979). This pattern is also evident in studies of the behavioral ecology of *Peromyscus* (Wolff 1989). The large number of studies involving *P. leucopus* and *P. maniculatus* provide long-term data upon which to formulate testable hypotheses (see studies by Wolff or Dueser [or both]). However, concentration on a few species of *Peromyscus* provides only a limited understanding of ecological variation in the genus (Wolff 1989).

The Hastings Natural History Reserve (Monterey County, California, 36°22'N, 121°33'W) has populations of the brush mouse (*Peromyscus boylii*) and California mouse (*P. californicus*) distributed along canyon bottoms of north-facing slopes dominated by live oak (*Quercus agrifolia*), California bay-laurel (*Umbellularia californica*), and California buckeye (*Aesculus californica*; Griffin 1977; Heske et al. 1997; Ribble 1992; Ribble and Salvioni 1990). *P. californicus* is the largest species of *Peromyscus* and is restricted to coastal California and associated with woodland habitat (Merritt 1974). *P. boylii* is a medium sized *Peromyscus* species that ranges over much of the southwestern United States and Mexico. It is associated with dense, shrubby vegetation in canyon bottoms and other riparian habitat (Findley et al. 1975), and in New Mexico, it is thought to be limited by the distribution of live oak (*Q. agrifolia*) woodland, oakbrush, and nest sites (Armstrong 1979; Findley 1987; Findley et al. 1975). *P. californicus* weighs 33.2–54.4 g, and the smaller *P. boylii* weighs 22–36 g (Wilson and Ruff 1999).

Seeds of California bay-laurel (*U. californica*—Merritt 1974), and fruits, seeds and flowers of shrubs (Meserve 1976) were reported as a major food source for *P. californicus*. Two factors limiting distribution

of *P. californicus* may be the need for relatively large existing nest burrows and availability of California bay-laurels (Merritt 1974). The relatively large size of *P. californicus* may enable it to feed on the large fruits of buckeyes. In California, *P. boylii* feeds primarily on acorns in winter and insects in spring (Jameson 1952).

Coexistence of *P. californicus* and *P. boylii* may be explained by differences in energetics (Knuth and Barrett 1984), behavior (Perri and Randall 1999), and time of activity (Bruseo and Barry 1995; Haim and Rozenfeld 1993; Kotler et al. 1993) between species. However, given the difference in body size and feeding behavior, some segregation of *P. californicus* and *P. boylii* along space and food niche axes may also occur.

The purpose of this study was to quantify partitioning of space, food, and time by *P. californicus* and *P. boylii*. We tested the prediction that interspecific interactions and habitat partitioning facilitate the coexistence of *P. boylii* and *P. californicus*. Our 4 approaches were to describe the numerical associations of *P. californicus* and *P. boylii* with each other and with canopy features, describe nest-site preferences of *P. californicus* and *P. boylii* at both understory and canopy scales, use a food selection experiment to compare the diets of *P. californicus* and *P. boylii*, and compare the time of nightly activity of *P. californicus* and *P. boylii*.

#### MATERIALS AND METHODS

*Study grids and trapping.*—We conducted the study on 3 live trapping grids along Robertson Creek and in Madrone Canyon (along Big Creek) within the Hastings Reserve (Monterey County, California) during the winter (December to April) of 1997 and 1998 (Fig. 1). Live trapping occurred from 25 December 1996 to 25 March 1997 (13 weeks) and 24 December 1997 to 3 April 1998 (14 weeks). Lower Robertson Creek grid (Grid LRC) and Upper Robertson Creek grid (Grid URC) were contiguous. Grid LRC consisted of a 4-by-34 configuration of trap stations encompassing 1.36 ha (134 trap sta-

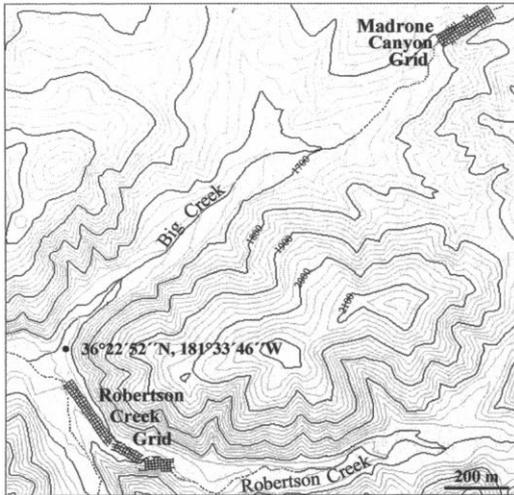


FIG. 1.—Topographic map of study area showing layout of Madrone Canyon and Robertson Creek grids at the Hastings Reserve, Monterey County, California. Topographic lines show elevation in feet (1,600 feet is about 490 m; 1,800 feet about 550 m).

tions). Grid URC consisted of a 6-by-13 trap configuration and encompassed 0.78 ha (54 trap stations). One Sherman trap and one Longworth trap were used at each trap station on grids LRC and URC. The grids were trapped separately because their topography and relief differed (Fig. 1), but despite these differences, some mice were trapped on both grids. Therefore, these 2 grids were treated as a single Robertson Creek grid in some analyses. The Madrone Canyon grid (Grid MC) consisted of a 7-by-20 configuration of trap stations encompassing 1.40 ha (100 trap stations). One Sherman trap was used at each trap station on Grid MC. Thus, we had 3 study grids, 2 along Robertson Creek and 1 in Madrone Canyon along Big Creek.

All grid configurations had 10 m spacing, although not every grid intersection was dry enough for a trap. Traps were baited with rolled oats and set at least weekly during the study to collect demographic and population data using standard individual mark and recapture techniques. We sampled some grids twice weekly and occasionally trapped small portions of grids to recapture specific individuals for other studies (Table 1; Kalcounis-Rüppell 2000). Because Grid RC was large, it was often trapped over 2

consecutive nights (half the grid sampled on each night).

We defined residents as individuals caught more than once with at least 7 days between 1st and last capture. We expressed density as the total number of residents during the trapping period divided by the area of the trapping grid. Trap saturation was the number of mice caught divided by the number of traps set on any given night.

Normality assumptions of parametric statistics were tested for all variables using the Kolmogorov–Smirnov test for normality (Zar 1984) and Levene’s test for homogeneity of variance (StatSoft, Inc. 1995). For all statistical analyses we used Statistica\* 1998 edition software (StatSoft, Inc. 1995). Differences between groups were considered to be statistically significant at  $P < 0.05$  unless otherwise specified.

To determine species associations we used a Spearman rank correlation ( $r$ ) to correlate the number of captures of *P. californicus* and *P. boylii* at each trapping station (Barry et al. 1990) for each grid to test the null hypothesis that the presence of one species does not affect the presence of the other. We also used trap captures to test for canopy-level habitat associations. We mapped and identified every canopy plant that reached >75% of canopy height (about 20 m) within the trapping grids. We determined the canopy plant closest to each trap site. We used a contingency analysis (with a Bonferroni-corrected  $\alpha = 0.008$ ) to test the null hypothesis that the number of captures of *P. californicus* and *P. boylii* was not contingent on the species of canopy plant nearest to the trap station. The expected number of captures for the analysis (null distribution) was the relative frequency of *P. californicus* to *P. boylii* captures on a given grid in a given year (i.e., grid-level population frequency).

*Locating and measuring nest sites.*—We located nest sites using radio telemetry on resident mice that were outfitted with a 1.15-g radiocollar (MD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). We attempted to locate nest sites within 3 days of attaching radiocollars. In 1997 we outfitted 19 *P. boylii* (13 females, 6 males) and 11 *P. californicus* (7 females, 4 males). In 1998 we outfitted 29 *P. boylii* (18 females, 11 males) and 24 *P. californicus* (16 females, 8 males). If a radiocollared mouse nested at >1 site, we considered these nests to be independent nest selec-

tion events. In addition to nest sites found in 1997 and 1998, we included all known *P. californicus* nest sites recorded by Gubernick and Teferi (2000) in 1996.

It was impossible to determine exact locations of the below-ground nests and exact type of nest these species used without disturbing the site. Therefore, nest sites were recorded as the surface point directly above the radiocollared mouse. Nest sites located and marked during 1996, 1997, and 1998 were measured from 15 March to 7 April 1998 to minimize variation caused by vegetation phenology and variation in eye calibration estimates of understory characteristics. We measured nest characteristics at 2 spatial scales, 1 of structure and cover, 1 m<sup>3</sup> around the nest site (understory), and 1 of tree species and tree density, 12 m<sup>2</sup> around the nest site (canopy).

We placed a 1-m<sup>2</sup> quadrat, divided into 4 equal quadrants, on top of each nest site with the nest site in the center of the quadrat. In each quadrant, we estimated (to the nearest 5%) the percentage ground cover of leaf litter, branch litter, rock, roots, dirt, sand, live vegetation, and the amount of physical cover 1 m above the nest site. Percentages were estimated by eye calibration by the senior author. We also identified live plant species. The total number of plant species constituted species richness (S) for each site. At each nest site, we also determined the distance (m) to water and to the nearest tree of canopy height (about 20 m). Means of the 4 quadrants were used for all analyses involving understory variables.

For all grids, we mapped every canopy plant and nest site. We used this map to count the number and types of trees within 12 m<sup>2</sup> of each nest site.

To test the prediction that mice select nest habitat, a random site, defined as any piece of ground potentially suitable for a mouse nest, within the defined trapping grid was selected for every nest site measured. A random site was identified as the nearest available site from a given nest site at a distance (0–50 m) and direction (0–360°) dictated from a table of random numbers. We measured characteristics of random sites in the same way as we measured nest-site characteristics.

We used multivariate analysis of variance (MANOVA; Wilks'  $\lambda$  test statistic) to test for differences between nest and random sites and

canonical discriminant analysis to describe differences in habitat characteristics between nest and random sites of the mice (Green 1971; Kachigan 1991). Both canopy and understory variables were included in the canonical discriminant analysis. Because sample size is important for ensuring stability of the canonical discriminant analysis axes and we had relatively few *P. californicus* sites, we minimized the number of variables included in the canonical discriminant analysis (Williams and Titus 1988) by including only those variables that had the highest overall variation within and between groups. To illustrate patterns of habitat characteristics for each group, 95% confidence ellipses were drawn around each group's mean on the first 2 canonical variates (Krzanowski 1989). Mahalanobis distance between each pair of groups in canonical variate space was used to illustrate differences in average habitat characteristics between the groups.

*Food selection behavior.*—To investigate food selection patterns between *P. californicus* and *P. boylii* we conducted a food selection experiment (Knuth and Barrett 1984; Reese et al. 1997). Ten *P. californicus* and 12 *P. boylii* individuals were involved in three to eight 5-day ( $\bar{X} \pm 1 SD = 5.5 \pm 1.4$ ) trials during March–April 1998. The analyses were conducted on the mean trial values for each individual. The experiment took place in an outdoor enclosure at the study site using subjects and food collected from the study grids. Mice were housed individually in plastic cages (12.5 by 17.0 by 28.0 cm) with hard-chip bedding, cotton, and water ad lib. Food reflected food types found cached in or around the openings of nest sites. Fruits of *Q. agrifolia*, *A. californica*, *Heteromeles arbutifolia*, and various mushroom species were found in or around *P. californicus* nest sites, whereas only fruits of *Q. agrifolia* were found in caches of *P. boylii* nests. No evidence of fruits of *U. californica* was found in or around *P. californicus* nest sites or on the study grids. Thus, we presented mice with an excess of fruits of *Q. agrifolia* (about 60 g), *A. californica* (about 60 g), and *H. arbutifolia* (about 10 g) that we collected daily from the study grids. In addition, we presented mice with leaves of *Ribes speciosum* (about 20 leaves), commercially available mushrooms (*Agaricus*, about 10 g), and as a source of protein, cat food (AvoCat® Irwindale, California, about 10 g).

For each 5-day trial, all food types were dried at room temperature for 5 days, weighed, mixed, and placed in a petri dish in the cage. At the end of each trial, food was removed, dried for 5 days at room temperature, and weighed. During each trial, 1–3 dishes of food were set in cages without mice to determine loss of mass because of evaporation. Mice were weighed at the beginning and end of the experiment, and initial and final weights were compared with a paired *t*-test (Zar 1984). After correcting for mass loss due to evaporation, we calculated mass-specific daily intake by dividing the average total dry matter intake of each individual by body mass (Reese et al. 1997). We also calculated diet breadth (B—Levins 1968), diversity ( $H'$ —Shannon and Weaver 1949), evenness ( $J'$ —Pielou 1966), and preference ( $I$ —Ivlev 1961) for each individual on uncorrected values of dry matter intake. Non-normal data and all indices were transformed with square-root (B,  $H'$ ,  $J'$ ) and arcsine ( $I$ ) transformations. Differences between species for all indices were tested with a single-factor analysis of variance (ANOVA), and differences between mass-corrected consumption of food types between species were tested with a 2-factor ANOVA. Although the assumption of independence of observations is violated in food preference experiments (Lockwood 1998), we used ANOVA to facilitate between species comparison.

*Time of nightly activity.*—Time of nightly activity was determined for *P. californicus* and *P. boylii* using radio telemetry. In 1997 nightly activity of 10 *P. boylii* (7 female, 3 male) and 9 *P. californicus* (5 female, 4 male) was measured. In 1998 nightly activity of 23 (12 female, 11 male) *P. boylii* and 15 *P. californicus* (9 female, 6 male) was measured. We used departure time (the time when a mouse first left the nest in the evening), return time (the last time when the mouse returned to the nest in the morning), and activity range (total time elapsed from departure to return time on a given night) to define time of nightly activity. To record these parameters, we documented when the mice were present or absent at the nest by automated reception of radio-transmitter signals. We used 3 Lotek SRX-400 telemetry receivers with Event Log Version 3.6x W14 or W21 firmware and an ASP antenna switcher (Lotek Wireless, Newmarket, Ontario, Canada). We placed a 5-element Yagi antenna on each nest site and set the lowest possible gain that received the transmitter signal to ensure that

signals would be recorded only when the mouse was in the nest. We attempted to record a minimum of 3 consecutive nights for each individual. Receivers were set in the early afternoon before the 1st night of recording, and at mid-morning after the last night of recording logged data were downloaded to a laptop computer using Host e3 software (Lotek Engineering Inc.).

We standardized departure and return times to time after sunset because the activity of nocturnal mammals is correlated with nautical twilight (Bruseo and Barry 1995; Harland and Millar 1980), and absolute times change with sunset time over the period of study. All data were corrected to minutes after sunset for each day of the study with sunset times for the village of Carmel Valley, California (36°29'N, 121°44'W), obtained from the United States Naval Observatory Department of Astronomical Applications. All data referring to absolute times are presented as minutes after sunset. We used ANOVA to test for differences between *P. californicus* and *P. boylii* in time of nightly activity. Protocols were approved by the Animal Care and Use Committee of the University of Western Ontario.

## RESULTS

We captured *P. boylii* 940 and 1,651 times and *P. californicus* 784 and 704 times in 1997 and 1998, respectively. The difference in the number of captures between years can be attributed to differences in the number of resident *P. boylii* between years, 42 versus 89 individuals/ha in 1997 and 1998, respectively. The number of resident *P. californicus* was 30 individuals/ha in 1997 and 29 individuals/ha in 1998. With the removal of those captures that were not part of a grid census, the total number of captures was 3,884 over 17,308 trap nights (Table 1). Overall, the pattern of trap saturation was similar in both years (Table 1). Differences in trap saturation between years, especially on Grid LRC, can be attributed to the difference in the number of resident *P. boylii*.

*Associations from trap captures.*—The mean proportion of resident mice that were *P. boylii* on Grids LRC, URC, and MC were 0.80, 0.56, and 0.55, respectively.

TABLE 1.—*Peromyscus* trapping details, by grid, during 1997 and 1998 at the Hastings Reserve (Monterey County, California). Percent saturation reflects the mean percent saturation over all nights that the grid was trapped. Nights when only small portions of the grid were trapped are excluded.

Grid	Times trapped	Trap nights	Total captures	Percent saturation			Percent saturation with <i>P. boylii</i>			Percent saturation with <i>P. californicus</i>		
				$\bar{X}$	<i>SD</i>	Range	$\bar{X}$	<i>SD</i>	Range	$\bar{X}$	<i>SD</i>	Range
1997												
MC	18	1,800	457	25.4	10.0	11–40	5.9	3.8	0–12	19.8	8.2	5–32
LRC	18.5	5,044	935	20.7	9.2	4–48	14.5	7.0	3–33	6.2	3.7	1–15
URC	14	1,456	249	17.1	5.6	7–30	8.4	3.2	5–14	8.7	3.8	1–13
1998												
MC	19	1,900	493	25.9	13.4	11–55	11.1	8.0	1–25	14.9	6.8	1–30
LRC	19.5	5,236	1,394	27.6	11.2	10–60	23.2	9.6	8–53	4.3	2.4	0–9
URC	18	1,872	356	19.0	5.2	11–34	10.5	3.9	4–23	8.5	7.7	2–18

Mean ( $\pm 1$  *SD*) times of residence on grids for *P. boylii*, the species more likely to exhibit population turnover, were  $39.4 \pm 25.0$  days in 1997 and  $47.0 \pm 25.5$  days in 1998. In addition, 78.1% in 1997 and 75.1% in 1998 of all new adult recaptures occurred in the 1st one-third of the field season. These values suggest a low rate of population turnover.

Patterns of association were similar between years for each grid. A negative correlation was found in both years between species on Grid MC ( $r_{1997} = -0.42$ , *d.f.* = 90,  $P < 0.001$ ;  $r_{1998} = -0.51$ , *d.f.* = 95,  $P < 0.001$ ) and Grid URC ( $r_{1997} = -0.40$ , *d.f.* = 52,  $P < 0.005$ ;  $r_{1998} = -0.46$ , *d.f.* = 52,  $P < 0.001$ ), but no association existed in either year between *P. californicus* and *P. boylii* on Grid LRC ( $r_{1997} = -0.06$ , *d.f.* = 124,  $P > 0.05$ ;  $r_{1998} = -0.001$ , *d.f.* = 126,  $P > 0.05$ ).

The proportion of *P. boylii* and *P. californicus* captured at each trap station was contingent on the nearest tree species to the trap station on all 3 grids during both years, although patterns differed among grids and between years (Fig. 2). In general, the capture of *P. boylii* was contingent on nearness to *Quercus* species, especially *Q. agrifolia*, whereas the capture of *P. californicus* was contingent on nearness to a relatively large range of tree species.

*Nest sites.*—Of the 61 *P. boylii* nest sites

(belonging to 43 individuals), 59 were located on Grid RC and 2 on Grid MC. Of the 32 *P. californicus* nest sites (belonging to 32 pairs of individuals) 14 were located on Grid RC and 18 on Grid MC. Because only 2 *P. boylii* nest sites were found on Grid MC, we only tested for differences between *P. californicus* nest sites and random sites.

Nest sites of the 2 species on Grid RC were different (Wilks'  $\lambda = 0.32$ ,  $P < 0.0001$ ). The first 2 canonical variates accounted for 96% of the among-group variation (Table 2). The magnitude-of-structure coefficients on canonical variate 1 and canonical variate 2 suggest that canonical variate 1 is an axis that describes understory characteristics, whereas canonical variate 2 describes canopy characteristics (Table 2; Fig. 3). We found no difference between the centroids of random sites of *P. boylii* and *P. californicus* (squared Mahalanobis distance = 1.52,  $F = 1.51$ , *d.f.* = 10, 133,  $P > 0.05$ ). Random sites of *P. boylii* and *P. californicus* overlapped in canonical habitat space, had a relatively open understory with little vegetation or ground cover by branches and moss, and a canopy of relatively low density of *Q. agrifolia* (Fig. 3). Relative to random sites, *P. californicus* nest sites had high vegetation and ground cover by branches and moss (squared Mahalanobis distance = 7.31,  $F = 12.48$ , *d.f.* = 10, 133,

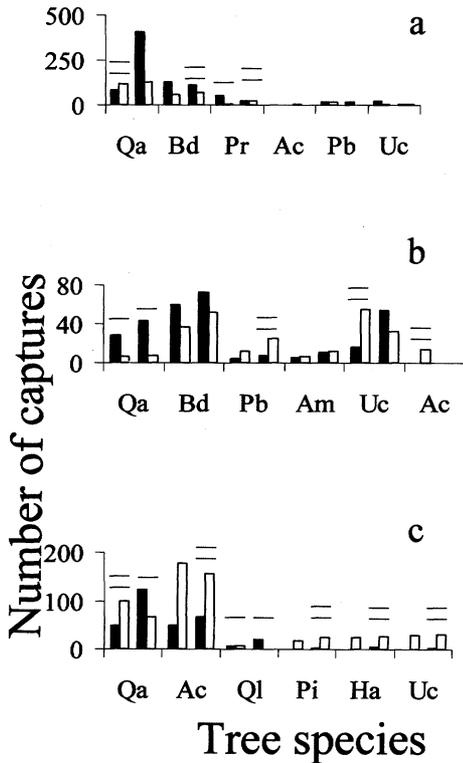


FIG. 2.—Number of captures of *Peromyscus boylii* (black) and *P. californicus* (white) on a) Lower Robertson Creek, b) Upper Robertson Creek, and c) Madrone Canyon grids relative to the tree species nearest the trap stations at the Hastings Reserve, Monterey County, California. The 1st pair of bars for a tree species refers to 1997 and the 2nd pair to 1998. A single line above a bar indicates significant bias toward *P. boylii* and a double line significant bias toward *P. californicus*. *Qa* = *Quercus agrifolia*, *Bd* = *Baccaris douglasii*, *Pr* = *Platanus racemosa*, *Ac* = *Aesculus californica*, *Pb* = *Populus balsamifera*, *Uc* = *Umbellularia californica*, *Am* = *Arbutus menziesii*, *Ql* = *Q. lobata*, *Pi* = *Prunus ilicifolia*, *Ha* = *Heteromeles arbutifolia*.

$P < 0.001$ ; Fig. 3). *P. boylii* nest sites were found under canopies with relatively high densities of *Q. agrifolia* (squared Mahalanobis distance = 2.85,  $F = 7.73$ ,  $d.f. = 10, 133$ ,  $P < 0.001$ ; Fig. 3). Centroids of nest sites differed between the species (squared Mahalanobis distance = 9.36,  $F = 9.31$ ,  $d.f. = 10, 133$ ,  $P < 0.001$ ). In canonical habitat space, *P. californicus* nests were

TABLE 2.—Pooled within-class structure coefficients for ecological variables from canonical discriminant analysis of nest and random sites for *P. boylii* and *P. californicus* on Grid RC (Monterey County, California). Relatively large coefficients are italicized. Relatively large negative structure coefficients on canonical variate 1 corresponded to sites that had relatively high vegetation and ground cover by branches and moss (*S. bigelovii*). Positive structure coefficients on canonical variate 2 corresponded to sites with relatively high densities of *Q. agrifolia*.

Variable	Canonical variate 1	Canonical variate 2
Cover	-0.36	0.43
Leaves	0.26	0.27
Branches	-0.38	0.27
Rock	0.05	0.00
Sand	0.26	-0.32
Water	-0.17	0.09
Tree	0.23	-0.25
<i>Selaginella bigelovii</i>	-0.44	-0.01
<i>Rubus ursinus</i>	0.10	0.15
<i>Quercus agrifolia</i>	0.13	0.85
Eigenvalue	0.986	0.514
Proportion of variance	0.637	0.332

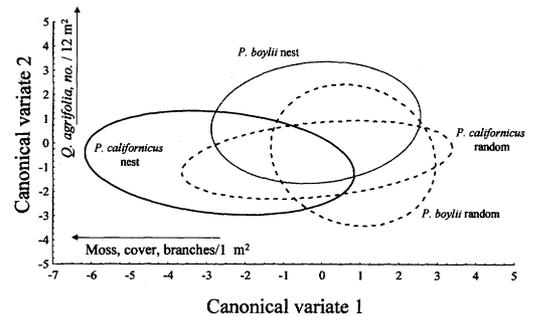


FIG. 3.—Plot of the first 2 canonical variate axes for *Peromyscus boylii* and *P. californicus* nest sites (solid lines) and random sites (dotted lines) on Robertson Creek, Hastings Reserve, Monterey County, California. Ellipses represent the 95% confidence ellipses for the group's mean in canonical habitat space. The proportion of among-group variance explained by each axis is 63% for canonical variate 1 and 33% for canonical variate 2 (Table 2). The ecological variables with relatively large structure coefficients (Table 2) are labeled on each axis with an arrow indicating the direction along the axis that they increase.

TABLE 3.—Pooled within-class structure coefficients for 7 habitat variables from canonical discriminant analysis of nest and random sites for *P. californicus* on Grid MC (Monterey County, California). Relatively large coefficients are italicized.

Variable	Canonical variate 1
Cover	-0.26
Leaves	0.40
Branches	-0.46
Rock	0.37
Dirt	0.20
<i>Selaginella bigelovii</i>	-0.54
<i>Symphoricarpos albus</i>	-0.09
Eigenvalue	0.843
Proportion of variance	1.000

associated with canopies of relatively low *Q. agrifolia* density and had an understory with more vegetation and ground cover by branches and moss than *P. boylii* nests (Fig. 3).

We used the same variables in the Grid MC canonical discriminant analysis as in Grid RC, (Table 2), except for the exclusion of the uncommon sand and *Rubus ursinus* variables. We found no significant difference on Grid MC between nest and random sites of *P. californicus* (Wilks'  $\lambda = 0.59, P > 0.05$ ). However, we observed a significant difference between nest and random sites of *P. californicus* (Wilks'  $\lambda = 0.54, P < 0.01$ ) when we included only variables that had relatively high overall variation within and between random and nest sites (Table 3). Negative scores on canonical variate 1 corresponded to sites that had relatively high vegetation and ground cover by branches and moss (*Selaginella bigelovii*). The means of the canonical variables for random and nest sites were 0.89 and -0.89, respectively, suggesting that *P. californicus* on Grid MC, like *P. californicus* on Grid RC, had nest sites with high vegetation and ground cover by branches and moss.

In our food selection experiment, both species of mice were maintained on the diet provided. No difference was observed be-

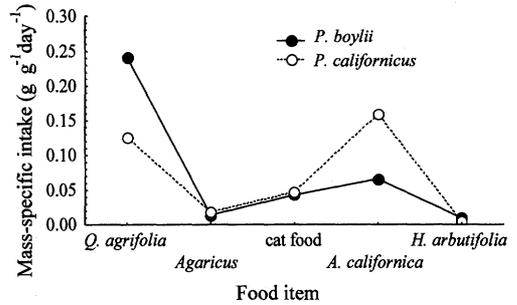


FIG. 4.—Interaction plot of mass-specific food intake (gram of food per gram of mouse per day) of all diet items for *Peromyscus boylii* and *P. californicus* at the Hastings Reserve in Monterey County, California.

tween the 1st ( $\bar{X} \pm 1 SD = 24.8 \pm 4.0$  g) and last ( $26.5 \pm 3.0$  g) weights of 10 *P. boylii* in the experiment (2 individuals escaped before being weighed at the end of the experiment;  $t = -1.24, d.f. = 9, P > 0.05$ ). Similarly, no difference was observed between the 1st ( $39.1 \pm 4.2$  g) and last ( $42.3 \pm 4.1$  g) weights of the 10 *P. californicus* ( $t = -3.28, d.f. = 9, P < 0.01$ ). Mice ate all food types presented, except the leaves of *R. speciosum*, which was not included in the diet analysis. We observed a significant interaction between species and mass-specific consumption of food type ( $F = 21.64, d.f. = 4, 100, P < 0.001$ ), with *P. boylii* consuming more *Q. agrifolia* than *P. californicus* and *P. californicus* consuming more *A. californica* than *P. boylii* (Fig. 4). *P. californicus* had a broader ( $F = 23.12, d.f. = 1, 20, P < 0.001$ ), more diverse ( $F = 12.80, d.f. = 1, 20, P < 0.005$ ), and more evenly apportioned ( $F = 12.80, d.f. = 1, 20, P < 0.005$ ) diet than did *P. boylii* (Table 4). *P. californicus* had a comparatively high preference for cat food ( $F = 18.67, d.f. = 1, 20, P < 0.001$ ) and fruit of *A. californica* ( $F = 9.83, d.f. = 1, 20, P < 0.01$ ).

In total, we recorded time of nightly activity on 237 nights from 57 radiocollared individuals (33 *P. boylii* and 24 *P. californicus*). In 1997 and 1998, time of activity was recorded on 62 and 175 nights, respec-

TABLE 4.—Differences between diet indices of *P. californicus* ( $n = 10$ ) and *P. boylii* ( $n = 12$ ) as shown by the food selection experiment at the Hastings Reserve, Monterey County, California in 1998. Mean breadth (B), diversity ( $H'$ ), evenness ( $J'$ ), and preference (I) values for each food type are shown.

Index	<i>P. boylii</i>		<i>P. californicus</i>	
	$\bar{X}$	SD	$\bar{X}$	SD
Breadth	1.63	0.30	2.41	0.47
Diversity	0.73	0.21	1.06	0.21
Evenness	0.55	0.16	0.80	0.16
Preference for <i>Q. agrifolia</i>	0.37	0.12	0.28	0.12
Preference for <i>A. californica</i>	-0.72	0.28	-0.34	0.29
Preference for <i>H. arbutifolia</i>	-0.05	0.58	-0.09	0.49
Preference for mushroom	-0.18	0.48	0.08	0.34
Preference for cat food	0.29	0.15	0.53	0.10

tively. On average ( $\pm 1$  SD),  $4.2 \pm 1.8$  nest attendance nights were recorded per individual (range 1–8). We observed no difference between *P. boylii* and *P. californicus* in the range of time spent active during the night ( $F = 0.42$ ,  $d.f. = 1, 55$ ,  $P > 0.05$ ;  $651.28 \pm 86.51$  min and  $637.58 \pm 67.51$  min, respectively) or the time after sunset that mice finally returned from being active in the morning ( $F = 0.05$ ,  $d.f. = 1, 55$ ,  $P > 0.05$ ;  $691.56 \pm 71.83$  min and  $695.52 \pm 57.99$  min, respectively). In the evening, *P. boylii* departed approximately 18 min earlier than *P. californicus* ( $F = 4.11$ ,  $d.f. = 1, 55$ ,  $P = 0.047$ ;  $40.28 \pm 27.35$  min and  $57.93 \pm 38.48$  min after sunset, respectively).

#### DISCUSSION

The coexistence of *P. californicus* and *P. boylii* is not facilitated by differences along the niche axis of time, as has been demonstrated for other rodents (Haim and Rozenfeld 1993; Kotler et al. 1993). Apart from an earlier emergence by *P. boylii*, the timing of the nocturnal activity of these 2 species is remarkably similar. These similarities probably reflect biotic constraints (predation pressure, optimal foraging, and hormone-mediated activity levels) on activity that are similar for both species and likely affect the timing of activity of all *Peromyscus*.

Our results suggest that the coexistence of *P. californicus* and *P. boylii* is facilitated by differences along the niche axes of space and food. As predicted, interspecific interactions and habitat partitioning via the specialization of *P. boylii* on *Q. agrifolia* facilitate the coexistence of *P. boylii* and *P. californicus* at the Hastings Reserve. It is probable that the ability of *P. californicus* to eat the fruit of *A. californica* also facilitates the coexistence of these two *Peromyscus* species; however, this was not directly tested and deserves further investigation.

At an understory scale, *P. californicus* and *P. boylii* preferred nest sites that had relatively high vegetation and ground cover. Densities of *P. maniculatus* and *P. leucopus* have been positively correlated with cover, such as logs and stumps because these provide protection from predation and nesting sites (Bendell 1961; Crowell and Pimm 1976; Smith and Speller 1970), which translates into greater survival of both juveniles and adults (Van Horne 1982).

Despite similarity in nest requirements, *P. californicus* and *P. boylii* partition resources at the canopy level. There are 3 factors that lead us to conclude that *P. boylii* is a specialist on *Q. agrifolia*: *P. boylii* was caught most frequently in traps that were near *Q. agrifolia*; it nested under canopies with high densities of *Q. agrifolia* relative

to random sites and the nest sites of *P. californicus*; and it had a narrower diet consisting of more *Q. agrifolia* acorns than *P. californicus*. There are 3 factors that lead us to conclude that *P. californicus* is a habitat generalist: *P. californicus* was caught in traps near *U. californica*, *H. arbutifolia*, *A. californica*, *P. ilicifolia*, and *Q. agrifolia*; it did not discriminate among canopy plants with respect to its nest sites; and it had a broad, diverse and evenly apportioned diet. These results emphasize that various spatial scales need to be considered when explaining community level patterns of distribution (Kelt et al. 1999; Morris 1989).

The relatively large body size of *P. californicus* probably allows it to exploit the large fruits of *A. californica*, which are not accessible to the smaller *P. boylii*. Differences in feeding strategy based on body size have previously been demonstrated for rodents (Adler 1995; Bowers and Brown 1982). In the food selection experiment *P. californicus* consumed more *A. californica* fruit than *P. boylii* and had a comparatively high preference for the fruit. Furthermore, the lowest observed mass-specific intake of food types for *P. boylii* was that of *A. californica* fruit. No evidence of cached *A. californica* fruit was observed for either species, but partially eaten *A. californica* fruits were found around those nest sites of *P. californicus* that were under *A. californica* trees. This suggests that even for the largest *Peromyscus*, the large size of *A. californica* fruit precludes transport.

Coexistence of species is determined by how resources are partitioned (Schoener 1974; Smartt 1978), but it is impossible to determine from observation alone whether the patterns of resource use by *P. boylii* and *P. californicus* reflect evolved preferences or whether competitive interspecific interactions result in the displacement of one species to a less preferred resource area (Holbrook 1979). Our results suggest that the generalist *P. californicus* may experience a competitive advantage over the specialist *P. boylii*. When the ratio of the den-

sities of the 2 species neared equality or became less biased toward *P. boylii* (grids URC and MC) a negative correlation was observed between species. The presence of the specialist *P. boylii* in relatively high densities on Grid LRC did not influence the presence of *P. californicus*. These results do not simply reflect differences in canopy-level habitat preference because a similar pattern was evident when only traps under *Q. agrifolia* were included in the correlation analyses (M. C. Kalcounis-Rüppell, in litt.). Although these findings suggest a role for interspecific interactions in the coexistence of *P. californicus* and *P. boylii*, controlled experimental manipulations would be required for unequivocal evidence of competitive relationships.

Our results suggest that canopy-level partitioning by *P. boylii* and *P. californicus*, via the specialization of *P. boylii* on *Q. agrifolia*, precludes the necessity for understory partitioning where these two species of mice coexist. Small mammal abundance may respond to differences in resource productivity at a macrohabitat scale (Morris 1984, 1989). Furthermore, coexistence between generalists and specialists is possible if both exploit the shared environment at a large spatial scale because the generalist can exploit habitat unused or underused by the specialized species (Brown 1996). However, *P. boylii* populations are probably linked to oak trees and the mast they produce (Ostfeld et al. 1998; Drickamer 1990). Both 1997 and 1998 were slightly above average mast years for live oak (W. Koenig, in litt.). In a below average mast year a shift by *P. boylii* to a wide range of other food sources might be expected.

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