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Dietary niche partitioning by sympatric *Peromyscus boylii* and *P. californicus* in a mixed evergreen forest

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We used carbon and nitrogen isotopes measured in hair to compare the diets of 2 sympatric species of wild mice, *Peromyscus californicus* and *P. boylii*, in Santa Cruz County, California. The ability of these 2 *Peromyscus* species to coexist is thought to be the result of spatial partitioning through canopy plant associations as well as possible dietary niche partitioning. We used stable isotope analysis to determine the trophic level at which each species is feeding and stable isotope mixing models to estimate dietary contributions of various arthropod and plant-derived food sources. We found *P. californicus* to be omnivorous, specializing mainly on arthropods and consistently feeding at a higher trophic level than *P. boylii*. *P. boylii* is omnivorous as well, but specializes mainly on tanoak (*Notholithocarpus densiflorus*) acorns. Dietary niche partitioning appears to be seasonal; in the fall, partitioning breaks down to some degree, likely because food is so abundantly available, and both species consume a larger, overlapping array of acorns and arthropods. These findings coupled with other studies on habitat niche partitioning present a clearer picture of how these 2 sympatric species can coexist.

Key words: coexistence, diet, forest ecology research plot, niche partitioning, *Peromyscus* sp., resource partitioning, stable isotopes, trophic level

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According to the competitive exclusion principle, when 2 similar species are limited by the same resource, competition will eventually exclude 1 from the community unless they are able to use resources differently (Hardin 1960). Variation in resource use can generally be separated along any of 3 axes that serve to define ecological niches of coexisting animals: space, time, and food (e.g., Pianka 1973; Schoener 1974). Deer mice (Rodentia: Cricetidae: *Peromyscus*) are the most populous native mammalian genus in North America (Kaufman and Kaufman 1989), and 2 or even 3 species of *Peromyscus* often co-occur. Niche partitioning by *Peromyscus* species within a community, particularly by *Peromyscus leucopus* and *P. maniculatus*, has been investigated extensively (see review by Kaufman and Kaufman 1989). Numerous studies have demonstrated some variation in spatial resource use by congeneric species (Holbrook 1979; Wolff and Hurlbutt 1982; Harney and Dueser 1987; Etheredge et al. 1989; Barry et al. 1990; Garman et al. 1994; Dooley and Dueser 1996; Kalcounis-Rüppell and Millar 2002; and citations in Kaufman and Kaufman 1989) and a few have identified some amount of dietary partitioning (Smartt 1978; Kalcounis-Rüppell and Millar 2002).

The University of California Santa Cruz (UCSC) Forest Ecology Research Plot (FERP), a 6-ha plot of mixed-evergreen forest on the UCSC campus (Santa Cruz County), supports populations of 2 sympatric congeners of wild deer mice: *Peromyscus californicus* (California mouse) and *Peromyscus boylii* (brush mouse). *P. californicus* is the largest species in the genus *Peromyscus* and is found in coastal California south of San Francisco Bay down to Baja California, Mexico (Merritt 1974). *P. californicus* is thought to be a dietary specialist, focusing on shrub fruits, seeds, and flowers (Meserve 1976), or using its 2 large front teeth to crack open seeds that other species of the genus cannot, such as those from the California bay-laurel (*Umbellularia californica*—Merritt 1974) and possibly California buckeye (*Aesculus californica*—Kalcounis-Rüppell and Millar 2002). *P. boylii* is thought to be a

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dietary generalist, feeding primarily on acorns, but also consuming a wide variety of insects, worms, fruits, and seeds (Jameson 1952; Smartt 1978). *P. boylii* has an affinity for oak–scrub oak woodland or brushy chaparral (Kalcounis-Rüppell and Spoon 2009) and *P. californicus* is largely found in dense chaparral and mixed woodland (Merritt 1974, 1978) and may be spatially limited by the availability of existing nest burrows or *U. californica* (Merritt 1974).

The coexistence of *P. boylii* and *P. californicus* in the FERP suggests that some form of resource partitioning is taking place between these 2 congeneric species. Both species are nocturnal and Kalcounis-Rüppell and Millar (2002) found no temporal partitioning between *P. boylii* and *P. californicus* in a radiotelemetry study at Hastings Reserve in Monterey County, California. Kalcounis-Rüppell and Millar (2002) did, however, document species-specific canopy tree associations by *P. boylii* and *P. californicus* and they hypothesized that some amount of dietary partitioning also occurs based on a food-choice experiment. In this study, we aim to more thoroughly evaluate the possibility of dietary niche partitioning between *P. boylii* and *P. californicus* by comparing the stable carbon (C) and nitrogen (N) isotope compositions ($\delta^{13}C$ and $\delta^{15}N$, respectively) of their hair. We also estimate the proportional contributions of different dietary components with a Bayesian stable isotope mixing model. Stable isotope ratios are now commonly used in ecology to characterize dietary composition (Kelly 2000; Ben-David and Flaherty 2012). The $\delta^{13}C$ and $\delta^{15}N$ values of animal tissues reflect the isotopic composition of an animal's diet, offset by a characteristic trophic increase in both ^{13}C and ^{15}N, although the increase in ^{15}N is more pronounced (Schoeninger and DeNiro 1984; Kelly 2000; Koch 2007). In terrestrial ecosystems, $\delta^{13}C$ values at the base of the food web vary primarily with the photosynthetic physiology of plants (C3 versus C4, although coastal California is dominated by C3 plants). $\delta^{15}N$ values in primary producers are determined by environmental factors (e.g., N fixation and effects of aridity on soil N) and are indicative of trophic level in consumers (Schoeninger and DeNiro 1984; Kelly 2000; Koch 2007).

Materials and Methods

Study area.—We conducted small mammal trapping in the UCSC FERP, a 200 × 300-m mapped plot located in a mixed-evergreen Mediterranean climate forest, Santa Cruz, California. Gilbert et al. (2010) established the FERP within the UCSC Campus Natural Reserve as a resource for teaching and research, beginning by mapping all woody stems larger than 1-cm diameter and creating a permanent grid (20 × 20-m quadrats). The plot contains 31 different woody plant species, the most common of which are Douglas-fir (*Pseudotsuga menziesii*) and 3 Fagaceae species: coast live oak (*Quercus agrifolia*), Shreve oak (*Quercus parvula* var. *shrevei*), and tanoak (*Notholithocarpus densiflorus*—Gilbert et al. 2010). The climate in Santa Cruz is Mediterranean, in that it is temperate with a dry, warm summer and mild, wet winter. Precipitation is highly seasonal; 95% of the 745-mm average annual rainfall falls during the rainy season from October to April (National Oceanic and Atmospheric Administration 2013). The average temperature of the hottest and coldest month is 17.1°C and 9.7°C, respectively (Gilbert et al. 2010).

Small mammal trapping.—We conducted quarterly 3-night small mammal trapping sessions during each season in 2010 (January, May, August, and November). We placed 126 Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) on a 9 × 14 grid in the FERP for a total of 378 trap nights for each 3-night trapping session. We placed each trap within 1 m of a flag that identified that individual trapping station. We excluded the outside perimeter of the forest plot from the experiment because plant data have not been recorded beyond the plot. The exclusion of the outer perimeter also reduced possible edge effects, especially in areas near roads and trails. Traps were set in the early evening, checked in early morning, and left closed during the day to prevent capture of diurnal, nontarget taxa. We baited the traps with a mixture of peanut butter and oatmeal and placed a small handful of polyester fluff in each trap to provide insulation for the mice. Upon capture, mice were tagged (self-piercing ear tags model 1005-1; National Band and Tag Company, Newport, Kentucky) and a small amount of hair was collected from the dorsal posterior using scissors. Hair was snipped close to the skin of the mouse so as to obtain nearly whole dorsal guard hairs for isotopic analysis. We chose not to collect and analyze hair from recaptured individuals because we were concerned that their consumption of the peanut butter bait might introduce bias into their hair $\delta^{13}C$ values. In a separate small mammal study in which mice were baited with just oats, we observed isotopic variation within individuals across multiple seasons, suggesting seasonal dietary shifts (see Supporting Information S1, DOI: 10.1644/13-MAMM-A-104.S1). Thus, we expect that any isotopic dissimilarities measured in individuals captured during different seasons reflect true seasonal variation. Mice were identified to species based on body mass, hind-foot length, ear length, ratio of tail length to body length, and tail bicoloration. Our trapping procedures were in accordance with the most recent guidelines of the American Society of Mammalogists (Sikes et al. 2011) and conducted with the approval of the UCSC Institutional Animal Care and Use Committee.

Arthropod trapping.—We sampled arthropods in the FERP with pitfall traps set out at 4 locations for 1 night apiece during each season in 2010 (except winter). We set 3 traps at each location and placed them in the same position for each subsequent trapping session. The 4 trap locations were chosen to be at least 50 m apart. The 3 individual pitfall traps within a location were set within 15 m of each other to ensure that they sampled the same microhabitat. Each trap was made with a 16-ounce plastic cup placed in the ground such that the top of the cup was flush with the ground surface. We filled the cups approximately one-third full with water and added 2 or 3 drops of unscented dish soap to break the surface tension of the water. Each trap was prepared at dusk and then collected at

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dawn on the following morning. We identified the arthropods collected to class (Diplopoda) and to order, including orders Coleoptera, Orthoptera, Araneae, Diptera, Haplotaxida, and Lepidoptera.

Seed collection.—Leaf litter traps were placed in the FERP as part of ongoing research and monitoring (Gilbert et al. 2010). Traps are checked biweekly and the seeds, flowers, fruits, and leaves that have accumulated are identified and counted (data are available at http://ferp.ucsc.edu). Seed samples were supplied to this study from the FERP traps during the spring, summer, fall, and winter months. We analyzed seeds and fruits from the 4 most common tree species in the plot—*P. menziesii*, *Q. agrifolia*, *Q. parvula* var. *shrevei*, and *N. densiflorus*—as well as from madrone (*Arbutus menziesii*) and coast redwood (*Sequoia sempervirens*). We additionally sampled fruits from coffeeberry (*Rhamnus californica*) and brittleleaf manzanita (*Arctostaphylos tomentosa*), both of which also are found in the FERP.

Sample preparation and isotopic analyses.—We stored arthropod samples in the freezer at –20°C prior to preparation for analysis. The samples were then freeze-dried and repeatedly rinsed and sonicated in MilliQ (EMD Millipore Corp., Billerica, Massachusetts) water (4 times for 15 min). Seed and berry samples were cleaned following the same procedure. After cleaning, we dried the samples in a 60°C oven for ~48 h and then crushed them with an agate mortar and pestle. We weighed arthropod samples out to ~700 μg into tin capsules for analysis. Seed and berry samples were weighed out separately for C and N isotope analysis and the exact mass depended on the C:N ratio of the sample type, which we determined in an initial test run. Mouse hair samples were repeatedly rinsed and sonicated in both MilliQ water and petroleum ether to remove surface contaminants and oils. The samples were then weighed out whole to ~700 μg into tin capsules for analysis. Some amount of sample is lost during the cleaning procedure and we did not always have enough material remaining for isotopic analysis.

Carbon and nitrogen isotope and elemental composition were determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer (Carlo Erba, Milan, Italy) coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Waltham, Massachusetts) at the UCSC Stable Isotope Laboratory. Isotopic values are reported relative to an internationally accepted standard (Vienna Pee Dee Belemnite and air for C and N, respectively) and expressed in parts per thousand deviation from that standard by: $\delta(‰) = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, where R is the ratio of the heavy isotope to light isotope (e.g., Sulzman 2007). We corrected sample isotopic values for size, drift, and source stretching effects with in-house standards. The standard deviations for replicates of both an in-house gelatin standard and powdered oak leaf standard were $< 0.2‰$ for both $\delta^{13}C$ and $\delta^{15}N$.

We tested the normality of the mouse isotope data with the generalized Shapiro–Wilk test for multivariate normality proposed by Villasenor Alva and González Estrada (2009) and tested the homogeneity of variance with the Bartlett test. We used Hotelling's T^2-test, the multivariate analogue to the univariate *t*-test, to evaluate whether *P. boylii* and *P. californicus* have statistically different multivariate means. To assess whether mouse diets varied significantly by season, we used a multivariate analysis of variance (Wilks lambda test statistic) carried out independently on each mouse species. When statistically significant differences between seasons were observed, we performed 1-way analysis of variance followed by the post hoc Tukey test to determine which of the 4 seasons contributed to the differences. Means are reported ± standard deviation (*SD*) and we tested significance at the $P = 0.05$ level. All statistical analyses were performed in R (version 2.15.2—R Development Core Team 2012).

Isotopic mixing model.—A number of isotopic mixing models have been developed, many of which can now handle numerous dietary sources and incorporate uncertainty from various sources (e.g., Phillips and Gregg 2003; Moore and Semmens 2008; Parnell et al. 2010; see also review by Phillips 2012). We chose the Bayesian stable isotope mixing model of Parnell et al. (2010), Stable Isotope Analysis in R (SIAR), because it is capable of accounting for concentration dependence (variation in elemental concentrations of N and C in the mouse food sources), which can bias model outputs if ignored (Phillips and Koch 2002). This is particularly important for our data, as the possible dietary sources for the mice span a wide range of C:N ratios.

We ran the mixing model 3 times for each species; we 1st incorporated all of the mouse hair and possible dietary source data over the course of an entire year, and then separated the analysis by season (fall versus winter, spring, and summer). We considered 10 possible dietary sources, including 4 types of arthropods (Coleoptera, Orthoptera, Araneae, and Diplopoda) and 6 plant-derived sources (*Q. parvula*, *Q. agrifolia*, *R. californica*, *A. tomentosa*, *N. densiflorus*, and a combined "seeds" source that includes *P. menziesii*, *A. menziesii*, and *S. sempvirens*, which all had statistically similar isotopic values). The 1st model contains all possible data, including isotopic data from mouse hair collected throughout the year and averages of all possible sources. The fall mixing model includes isotopic data from mouse hair collected in the fall and data from all possible dietary sources also collected in the fall and finally, the winter–spring–summer model includes only data from mouse hair collected in those seasons (fall excluded) and data from possible dietary sources also sampled during those seasons. Given that these mouse species are known to cache acorns (e.g., Kalcounis-Rüppell and Millar 2002), we also included some fall fruits in the winter–spring–summer model, because we anticipated that these foods would remain in the mouse diets well beyond the fall.

An assumption behind mixing models, including SIAR, is that the dietary sources input into the model represent the entirety of diet. There is a very real possibility that we are missing a dietary source—fungi have been identified as periodically important food sources for *P. californicus* and *P. boylii* (Meserve 1976; Kalcounis-Rüppell and Spoon 2009), as

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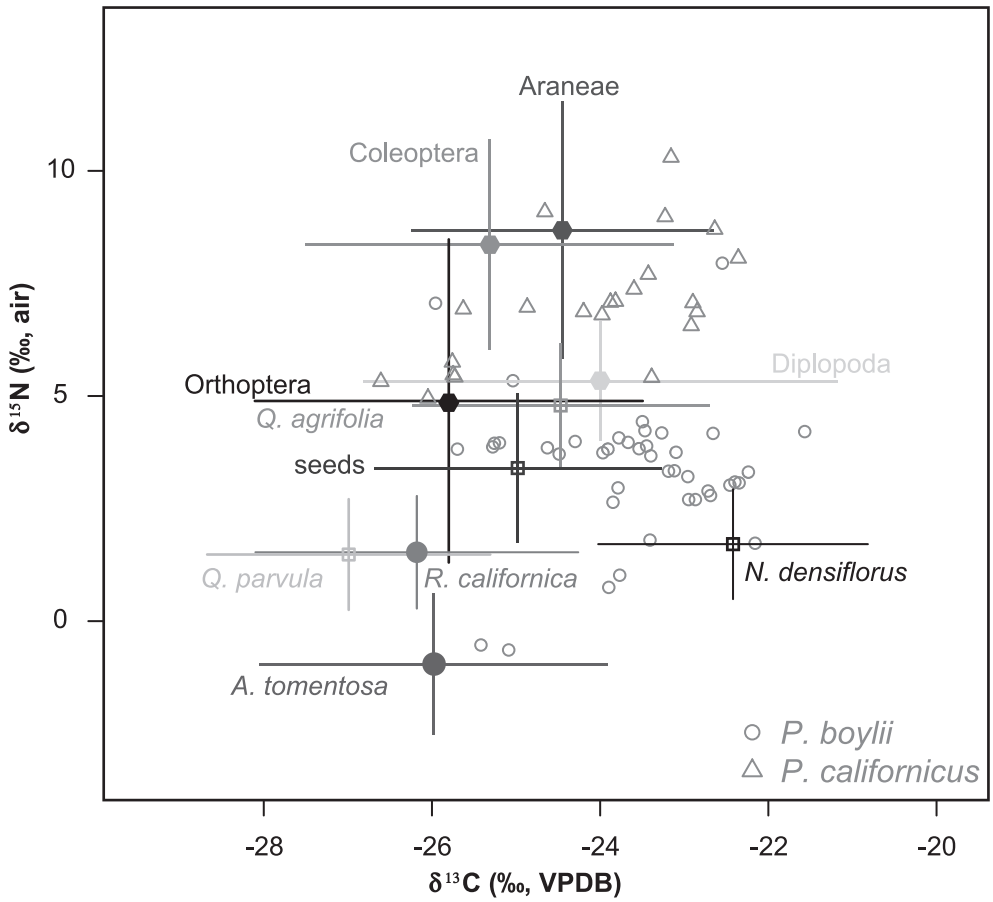


Fig. 1.—Carbon and nitrogen stable isotope values for all analyzed food sources averaged across all seasons and plotted +/- 2 *SD*. Possible dietary source data are corrected to mouse diet space (+1‰ ± 0.8‰ $\delta^{13}C$, +3.3‰ ± 0.6‰ $\delta^{15}N$). Arthropods are represented by hexagons, seeds by squares, and berries by circles. Isotopic values for individual *Peromyscus californicus* (triangles) and *P. boylii* (small circles) also are plotted.

are some leaves (e.g., *Ceanothus*—Jameson 1952), both of which are lacking from our analysis. Another assumption of mixing models is that, prior to the synthesis of new tissues, the nutrients an animal consumes are well mixed (Martínez del Rio and Carleton 2012; Phillips 2012). Animals, however, incorporate the isotopic values of the resources they consume at different rates, which can vary between individuals and tissue types (Martínez del Rio and Carleton 2012). Here we are comparing isotope values measured in hair from *P. boylii* to those in hair from *P. californicus*. Both species undergo 2 annual molts, once in fall and once in early summer (Brown 1963; Merritt 1978; Kalcounis-Rüppell and Spoon 2009), and we can thus be fairly confident that their hair integrates diet over similar amounts of time. Miller et al. (2008) observed in their study of *P. maniculatus* that hair growth during molting begins at the sides, progresses up the dorsum and finishes in the caudal area. Hair growth is likely concentrated during periods of molting; however, Tabacaru et al. (2011) observed in *P. maniculatus* from the Rocky Mountains that some continuous molting occurs throughout the year. Collins (1923) also observed some amount of continuous molting in *P. maniculatus* in California. Given the close relation of these species, it is reasonable to assume that hair growth for *P. boylii* and *P. californicus* also continues between concentrated molting periods. Another potentially important factor influencing the isotopic composition of mouse tissues are their C and N isotope turnover rates (Martínez del Rio and Carleton 2012). Turnover rates for tissues other than hair have been experimentally determined in a few small mammal species (e.g., Arneson and MacAvoy 2005; MacAvoy et al. 2005; Arneson et al. 2006; Miller et al. 2008; DeMots et al. 2010), but only 1 study targeted turnover rates in hair specifically as hair is a largely inert tissue. Tieszen et al. (1983) determined a half-life of 47.5 days for C isotopes in gerbil (i.e., Mongolian jird [*Meriones unguiculatus*]) hair, suggesting that our sampling interval of ~90 days is sufficiently long.

Finally, the choice of a diet–tissue discrimination factor, which can be highly species and tissue specific, can significantly impact mixing model results. Although neither *P. boylii* nor *P. californicus* have been the subject of a diet–tissue fractionation study, 2 other *Peromyscus* species have: *P. maniculatus* and *P. leucopus*. DeMots et al. (2010) calculated hair–diet discrimination factors of −1.1‰ ± 0.7‰ for $\delta^{13}C$ and 2.9‰ ± 0.1‰ for $\delta^{15}N$ in *P. leucopus*, and Miller et al. (2008) calculated hair–diet

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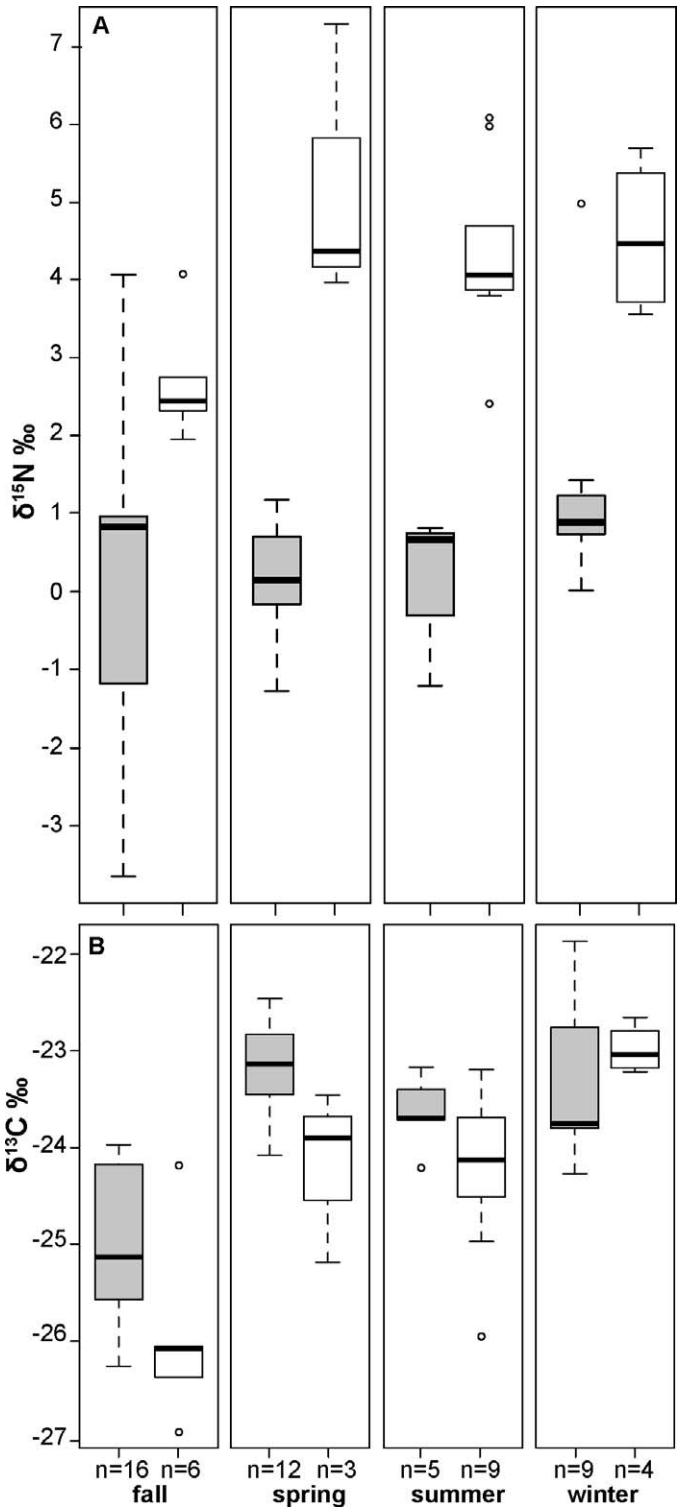


FIG. 2.—Box plots displaying the seasonal break down of A) nitrogen isotope values for hair of *Peromyscus boylii* (gray) and hair of *P. californicus* (white) as well as B) carbon isotope values for each species, respectively.

discrimination factors of 0.3‰ ± 0.8‰ for $\delta^{13}C$ and 3.3‰ ± 0.6‰ for $\delta^{15}N$ in juvenile *P. maniculatus*. A negative C isotope diet–tissue discrimination factor makes little sense with our data, because it would place the mice far outside the envelope of possible dietary source isotope values. Although it is possible that we missed a dietary source (fungi), it is highly unlikely that it would be able to resolve this issue. Indeed, a C isotope diet–tissue discrimination factor of just 0.3‰ also is not sufficient to place the mice C isotope values into the source isotope envelope. We therefore chose to apply discrimination factors of 1‰ ± 0.8‰ for C, a value that is often observed with each increasing trophic step (DeNiro and Epstein 1978; Kelly 2000) and the experimentally determined 3.3‰ ± 0.6‰ for N (Miller et al. 2008). To evaluate the impact of this choice on the mixing model output, we also ran the model using the experimentally determined 0.3‰ diet–hair discrimination factor for C and found the results to be very similar.

RESULTS

Stable isotope values.—We caught and tagged 135 individual mice over the course of 4 trapping sessions, of which 109 were *P. boylii* and 26 were *P. californicus*. Of these, we had large enough hair samples from 42 *P. boylii* and 22 *P. californicus* for isotope analysis. *P. boylii* has a mean $\delta^{13}C$ value of –23.9‰ ± 1.1‰ and mean $\delta^{15}N$ value of 0.4‰ ± 1.5‰, whereas *P. californicus* has a mean $\delta^{13}C$ value of –24.5‰ ± 1.3‰ and mean $\delta^{15}N$ value of 4.0‰ ± 1.4 ‰ (Fig. 1). The multivariate means for the 2 groups are statistically different ($F_{2,61} = 49.4$, $P = 1.75e^{-13}$). There also are significant differences in seasonal isotope values for both *P. californicus* ($F_{3,18} = 5.22$, $P < 0.001$) and *P. boylii* ($F_{3,38} = 10.0$, $P < 0.001$). In looking at the C and N isotope values separately, we see significant seasonal differences in both *P. californicus* $\delta^{13}C$ and $\delta^{15}N$ values ($F_{3,18} = 11.6$, $P < 0.001$ $F_{3,18} = 4.54$, $P = 0.015$), as well as in *P. boylii* $\delta^{13}C$ values ($F_{3,38} = 23.2$, $P < 0.001$), although not in $\delta^{15}N$ values ($F_{3,38} = 1.3$, $P = 0.28$). Results from the post hoc Tukey tests suggest that fall is the season with consistently different $\delta^{13}C$ and $\delta^{15}N$ values, whereas spring, summer, and winter isotope values are not significantly different from one another (Fig. 2).

We determined stable C and N isotope values and elemental concentrations for 10 possible dietary sources (Fig. 2). $\delta^{13}C$ values for these sources range from –22.72‰ to –27.29‰ and their $\delta^{15}N$ values range from –4.26‰ to 5.38‰. Given that we are considering both plant and animal (arthropod) material, there is a wide variety in the elemental concentrations of C and N of these sources, with values ranging from 32% to 50% for C and 0.7% to 12% for N. There is a significant amount of differentiation in C isotope values among the different Fagaceae species in particular; *N. densiflorus* has the highest $\delta^{13}C$ value (–22.72‰ ± 0.05‰, $n = 4$) and *Q. parvula* has the lowest (–27.29‰ ± 0.26‰, $n = 3$). As might be expected, N isotope values vary most considerably with trophic level; we see the highest values in Araneae (5.38‰ ± 1.3‰, $n = 5$) and lowest in *A. tomentosa* (–4.26‰ ± 0.51‰, $n = 4$).

Mixing model results.—The SIAR dietary mixing model results for *P. californicus* and *P. boylii* differ substantially when all data are considered for the entire year. The 1st model,

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in which we consider mouse hair and all possible dietary source data from the entire year, finds acorns of *N. densiflorus* to constitute a mode proportional contribution value of 51% of the diet of *P. boylii* (Fig. 3). The remaining dietary sources are more difficult for the model to determine, in part because there are trade-offs between the inclusion of one or another. For example, *R. californica* and *Q. parvula* lie very close together in isotope space, so we might expect some solutions of the model to include one or the other, but not both. Indeed, the dietary proportions of these 2 sources are weakly, negatively correlated with one another (–0.24). The model is, however, fairly certain that Araneae and Coleoptera are unimportant dietary components for *P. boylii*. The residual error term for this model has a mode value of 0.9‰ in C and 1.5‰ in N. Acorns of *N. densiflorus* also make up a major proportion of the diet of *P. californicus*, with a mode value of 16%, whereas Araneae comprise 17% and Coleoptera account for 11% of the diet. Again, the remaining dietary sources are less distinguishable and many are negatively correlated with one another. The residual error term for this model has a mode value of 1.2‰ in C and 1.2‰ in N.

When we consider the mouse hair and food sources from the winter, spring, and summer (fall excluded), the mixing model results are similar to those for the full 4-season model (Fig. 3). Acorns of *N. densiflorus* again make up the largest proportion of the diet of *P. boylii* with a mode value of 75% and the remaining dietary sources are more difficult to separate. The residual error term has a mode value of 0.1‰ in C and 1.0‰ in N. The diet of *P. californicus* appears to be split again between acorns of *N. densiflorus* (33%) and Araneae (24%) and the residual error term has a mode value of 0.9‰ in both C and in N.

The model including only data from the fall (Fig. 3) differs from the 2 previous models, in that *Q. parvula* is identified as a more important food source, with a mode value of 20% for *P. boylii* and 21% for *P. californicus*. *N. densiflorus* remains an important component of the diet of *P. boylii*, with a mode value of 25%, but drops to a mode value of just 2% for *P. californicus*. Instead, Orthoptera (mode value of 22%) and Diplopoda (mode value of 17%) gain importance for *P. californicus*. The residual error term for the model for *P. boylii* has a mode value of 0.6‰ in C and 2.5‰ in N and for the model for *P. californicus* the mode value is 0.8‰ in C and just 0.4‰ in N.

Discussion

Based on the $\delta^{15}N$ values of their hair, *P. californicus* is eating at a higher trophic level than *P. boylii* and we therefore infer that these 2 species are able to share space in part through dietary niche partitioning. The 3.6‰ difference in mean $\delta^{15}N$ values between the 2 species is on par with observations of ~3‰ increase in $\delta^{15}N$ values with trophic level in numerous other systems and food webs (e.g., DeNiro and Epstein 1981; Schoeninger and DeNiro 1984; Sponheimer et al. 2003). Kalcounis-Rüppell and Millar (2002), who investigated niche partitioning by these 2 mouse species in the Hastings Natural History Reserve (Monterey County, California), also found that *P. californicus* likely consumes more protein than does *P. boylii*. In a food selection experiment, they offered captive mice cat food and commercially available *Agaricus* mushrooms as well as a selection of foods found cached at the openings of nest sites (fruits of *Q. agrifolia*, *Aesculus californica*, and *Heteromeles arbutifolia*, and leaves of *Ribes speciosum*). When given the choice between these food sources, Kalcounis-Rüppell and Millar (2002) observed that *P. californicus* had a comparatively higher preference for cat food than did *P. boylii*.

Because Coleoptera were the most abundant arthropods in the plot during all seasons sampled, we were initially surprised by the mixing model result that indicates that Araneae comprise ~17–24% of the diet of *P. californicus* during all seasons except fall, and that Coleoptera constitute just ~3% (winter–spring–summer) to ~6% (fall). Araneae are likely more capable of avoiding the pitfall traps than Coleoptera, however, and could therefore be underrepresented in our sample. Further, Bellocq and Smith (1994) found that *P. maniculatus* actually prefers arachnids. Based on these stable isotope data and mixing model results, *P. californicus* appears to consume a large proportion of arthropods, specifically Araneae, and a steady amount of acorns of *N. densiflorus*. In the fall, these mice shift to a broader diet that includes a wider range of arthropods (Coleoptera and Orthoptera) and acorns from *Q. parvula*, which drops the greatest number of acorns on the FERP in September and October. Examination of our data shows that, although *P. californicus* has a partially carnivorous diet throughout the year, nuts and seeds comprise a significant dietary component during all seasons. These findings are consistent with those of Shakeri (2010), who concluded that, compared to *P. boylii*, *P. californicus* should be more of a generalist consumer, and with the findings of Kalcounis-Rüppell and Millar (2002), who inferred that *P. californicus* is relatively more carnivorous than *P. boylii*. These results differ from the conclusions of Merritt (1974), who found that *P. californicus* specialized on seeds of *U. californica* and that arthropods made up only a small percentage of the diet. This discrepancy may in part be due to the fact that there are only 4 individual *U. californica* in the FERP, none of which were dropping seeds during the period of our study. Differences between the results of this study and those of Meserve (1977), who proposed that *P. californicus* does not actively hunt arthropods and instead specializes on vegetation, may stem from broad differences in community structure and interactions with other *Peromyscus* species, as Meserve's (1977) study was conducted in a coastal sage scrub community in Irvine, California.

The C and N isotope values we observe for *P. boylii* are indicative of a lower trophic level diet and the consumption of a food source with slightly higher C isotope values. Indeed, all 3 SIAR models for *P. boylii* identify *N. densiflorus* (–22.72‰, Vienna Pee Dee Belemnite) as the most important dietary component for these mice. The residual error terms in

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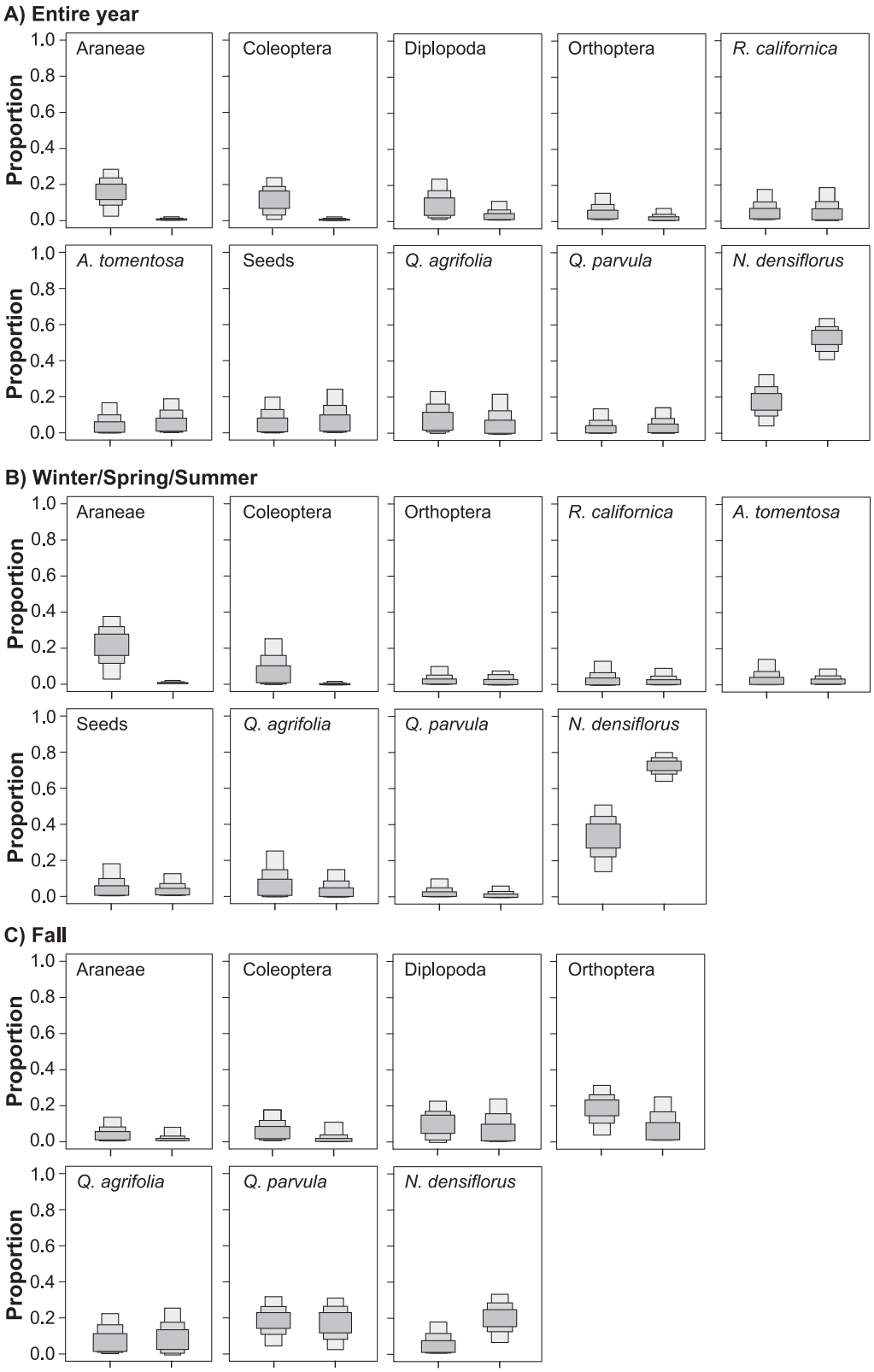


Fig. 3.—Contributions of potential food sources to diets of *Peromyscus californicus* (left) and *P. boylii* (right) as determined by A) the all-season Stable Isotope Analysis in R (SIAR) mixing models, B) by the winter–spring–summer SIAR mixing models, and C) by the fall SIAR mixing models. Boxes illustrate the relative proportions of each food source with 95% (darkest gray), 75%, 25%, and 5% (lightest gray) credibility intervals.

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all 3 models are a bit high, particularly for N; however, a few outlier data points for *P. boylii* are likely responsible for inflating these terms. For example, of the 9 *P. boylii* we analyzed from the winter season, only 1 had $\delta^{15}N$ values above 1.5‰. At 4.9‰, its N isotope value is significantly different from the rest. This could be a misidentification; mouse 341 was identified as a female *P. boylii* weighing 18 g, yet this body mass is in the range in which *P. boylii* and *P. californicus* overlap. Other than the $\delta^{15}N$ values, no further information is available to suggest that mouse 341 was misidentified, so we included it in our analysis as originally presented, as a *P. boylii* with an unusually high $\delta^{15}N$ value. Regardless, *N. densiflorus* is a very important food source for *P. boylii*. *N. densiflorus* is broadly distributed in the FERP and is the 2nd most numerous species behind *P. menziesii* (Gilbert et al. 2010). Fruits of *N. densiflorus* begin to accumulate in the leaf litter traps in June, reach a peak in September, and finally disappear from the traps in late December. Shakeri (2010) observed spatial associations between *P. boylii* and *N. densiflorus* in the FERP during spring, summer, and fall, as well as an association with *Q. parvula* during spring and summer. Like *N. densiflorus*, peak accumulation of acorns of *Q. parvula* in the FERP seed traps occurs in September, and it is during the fall that *Q. parvula* and *Q. agrifolia* become important to the diet of *P. boylii*. These results differ somewhat from the findings of Kalcounis-Rüppell and Millar (2002), who found that *P. boylii* preferentially consumed fruits of *Q. agrifolia* and was captured more frequently near *Q. agrifolia*. Other Fagaceae species are less common in the Hastings Reserve, and it may be that *P. boylii* prefers Fagaceae species in general, but when multiple species are available to these mice, their preferences fall out along a gradient with *N. densiflorus* as the favorite, followed by *Q. parvula* and then *Q. agrifolia*. In the FERP it appears that *P. boylii* feeds primarily on acorns of *N. densiflorus*, but will consume other acorns when they are abundantly available and some insects opportunistically. Given the importance of acorns of *N. densiflorus* to both mouse species on the FERP but to *P. boylii* in particular, recent losses of *N. densiflorus* to sudden oak death may be of concern and could impact interactions between these 2 mouse species where these trees are dying.

Our results suggest that, during much of the year, *P. californicus* and *P. boylii* are able to coexist through dietary niche partitioning, except in the fall, when their diets converge. At that time of year, *P. californicus* has a mean $\delta^{13}C$ value of –24.92‰ ± 0.9‰ and *P. boylii* has a very similar value of –24.0‰ ± 0.8‰, although their $\delta^{15}N$ values are still divergent (3.1‰ ± 0.8‰ and 5.7‰ ± 0.7‰ for *P. boylii* and *P. californicus*, respectively). The mixing model results suggest that other acorns (e.g., *Q. parvula* and maybe even *Q. agrifolia*) gain dietary importance for both species. Interestingly, some of the spatial associations observed by Shakeri (2010) break down in the fall—there is no significant relationship between *P. boylii* and either *Q. parvula* or *Q. agrifolia*, although they are important dietary components at that time. Instead, there is an association between *P. californicus* and both of these oaks. Fagaceae species, particularly members of the genus *Quercus*, are mast seeders (Sork 1993); that is, they synchronously produce large seed crops within a community or population every 2 or more years (Janzen 1971; Waller 1979; Silvertown 1980). It may be the case that, when acorns from these trees are abundantly available, any dietary and even spatial niche partitioning between *P. boylii* and *P. californicus* breaks down; when resources are not limiting, there is no need to invoke competition. It is, however, important to note that, because these mice molt only twice a year, once in early spring and again in the fall (Merritt 1978), the seasonal hair samples are not truly independent of one another. We are likely seeing distinctly different fall isotope values because the fall trapping occurred shortly after the fall molt, such that the fall hair samples actually represent an independent sample of a short time period.

We have shown that *P. californicus* occupies a higher trophic level than does *P. boylii*. Despite some ambiguity in assigning proportional dietary contributions, particularly of some of the more minor components, our mixing model results suggest that *P. boylii* specializes on acorns of *N. densiflorus* for the majority of the year, but consumes other acorns in the fall when Fagaceae species are mast fruiting. *P. californicus* also relies heavily on acorns of *N. densiflorus*, but consumes a steady proportion of arthropods, including Araneae, Orthoptera, and Coleoptera. The latter 2 of these gain importance in the diet of *P. californicus* in the fall, as do other acorns. These dietary differences, in conjunction with spatial associations observed by Shakeri (2010), suggest that during the winter, spring, and summer, *P. californicus* and *P. boylii* are able to coexist on the FERP through a combination of dietary niche partitioning and spatial partitioning. In the fall, because food is so abundantly available, dietary niche partitioning breaks down and the diets of *P. boylii* and *P. californicus* converge to some degree. Researchers studying the diets of the predators of these mice should take note of the significant difference in their N isotope values; failure to take into account the possible degree of isotopic differentiation between these phylogenetically similar animals could unduly bias diet predictions.

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Supporting Information

Supporting Information S1.—Seasonal isotopic variation in 3 resampled individual *Peromyscus californicus*.
Found at DOI: 10.1644/13-MAMM-A-104.S1

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