UNIVERSITY OF CALIFORNIA, SANTA CRUZ

Dietary Niche Partitioning by Sympatric *Peromyscus boylii and P. californicus* in Mixed Evergreen Forest

A Senior Thesis submitted in partial satisfaction
of the requirements for the degree of

BACHELOR OF ARTS

In

ENVIRONMENTAL STUDIES/BIOLOGY

by

Eli Nathan Greenwald

June 2011

ADVISOR(S): Christopher Wilmers, Environmental Studies

Abstract

We used stable isotope analysis to compare the diets of two sympatric species of wild mice, Peromyscus californicus and P. boylii. The ability for these two Peromyscus species to coexist is thought to be the result of niche partitioning at the canopy level, as well as dietary niche partitioning. We used analysis of carbon and nitrogen isotopes to determine the trophic level at which each species is feeding and to compare dietary preference. We used stable isotope mixing models to partition possible dietary contribution. P. californicus clearly feeds at a higher trophic level than P. boylii. P. californicus is omnivorous, but specializes mainly on arthropods. P. boylii is omnivorous as well, but specializes mainly on seeds and vegetative matter. These findings coupled with other studies on habitat niche partitioning present a clearer picture of how these two sympatric species can co-exist.

Key words: niche partitioning, *Peromyscus boylii, Peromyscus californicus,* forest ecology research plot, resource partitioning, stable isotopes, trophic level

Introduction

The competitive exclusion principle simply states that "complete competitors cannot coexist" (Hardin 1960). In other words, when two very similar species are limited by the same resource, competition should exclude one from the community unless the two species use resources in a different way. Ecological niche partitioning can be separated into three principal dimensions, space, time, and food (Kalcounis-Rüppel *et al*. 2002, Pianka 1973, Shoener 1974).

In the University of California Santa Cruz (UCSC) Forest Ecology Research Plot (FERP) the small mammal team, a group of undergraduate and graduate researchers at UCSC, has been studying two similar species of wild mice, *Peromyscus californicus* (California Mouse) and *Peromyscus boylii* (Brush Mouse) to determine how they co-exist in the same habitat. *P. californicus* is the largest of the *Peromyscus* genus and is found south of the San Francisco Bay down to Baja California (Meritt 1974). It is a dietary specialist, using its two large front teeth to crack open seeds that other species of the genus cannot, such as those from the California bay laurel (Meritt 1974). *P. boylii* is thought to be a dietary generalist, feeding primarily on acorns, but also consuming a wide variety of insects, worms, fruits and seeds (Jameson 1952, Luensmann 2005, Smartt 1978). *P. boylii* prefers dense brush habitats (Luensmann 2005, Shakeri 2010) with lots of cover.

Since both species are nocturnal, temporal partitioning seems unlikely (Kalcounis-Rüppel *et al*. 2002, Luensmann 2005, Merrit 1974). However, both Kalcounis-Rüppel *et al*. (2002) and Shakeri (2010) observed partitioning at the canopy level between *P. californicus* and *P. boylii* and some form of dietary partitioning was

found by Kalcounis-Rüppel *et al*. (2002) using food choice experiments. Dietary partitioning between the two species was therefore inferred by both Kalcounis-Rüppel *et al*. (2002) and Shakeri (2010), but not confirmed. This study aims to be the most complete and accurate study to date of dietary partitioning between *P. boylii* and *P. californicus* by using stable isotope analysis of hair collected in the field from these mice.

Stable isotope ratios have been commonly used in ecology to identify sources (e.g. pollution), infer processes (e.g. heterotrophic nitrification), estimate rates (e.g. soil C turnover), determine proportional inputs (e.g. % contribution of a particular prey item to a predator's diet), and confirm, reject, or constrain models using other processes (Sulzman 2008). Isotopes are atoms of an element (therefore with a characteristic number of protons) that differ in their number of neutrons. Stable isotopes, unlike radioactive isotopes, do not undergo decay. The chemical properties of different isotopes of an element are the same (e.g. ^{18}O and ^{16}O both readily bond with two H atoms to form water). However slight differences in their mass will lead to differences in reaction rates for the same processes. As a consequence, different processes produce natural isotopic variations, which can serve as natural "labels" of earth materials (plants, soils, water, etc.) that can be detected and studied.

This study will focus on stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$, respectively) values and their utility as dietary proxies. Because they are sourced from diet, $\delta^{13}C$ values in organic tissues (e.g. hair) can be used to determine whether an animal is primarily consuming C3, C4, or CAM plants. This is because in terrestrial systems, the greatest variation in $\delta^{13}C$ values is determined by the photosynthetic pathway of plants (Kelly 2000, O'Leary 1988). An animal feeding on C3 plants will therefore have a

relatively low $\delta^{13}C$ value, while an animal feeding on C4 and/or CAM plants will have a relatively higher $\delta^{13}C$ value (O'Leary 1988). There is potential for considerable variation in $\delta^{13}C$ values of plant sources in natural systems due to genetic and environmental (eg water stress) factors (Tieszen 1991). The range for C3 plants is -22 to -38%, C4 plants -9 to -21, and CAM plants -10 to -20 (O'Leary 1988, Tieszen 1991). Coastal California is dominated by C3 plants; very high $\delta^{13}C$ values in this system are thus likely reflective of an anthropogenic food source, as human foods tend to contain corn (a C4 plant). Nitrogen isotope ratios in organic tissues can be used to determine the trophic level of an animal, as nitrogen is largely sourced from dietary protein and a predictable increase in $\delta^{15}N$ value of between 2‰ to 4‰ has been observed with each increase in each trophic level (Bowen *et al*. 2010, Kelly 2000, Schoeninger and DeNiro 1984). Organisms at higher trophic levels or with higher amounts of protein in their diets will therefore have a higher $\delta^{15}N$ value.

Methods

Study Site

The UCSC FERPs a 6-ha (~15 acre) mapped forest plot in Mediterranean-climate, mixed-evergreen coastal forest in the Santa Cruz Mountains, along the Central California Coast (Figure 1). It is classified as temperate, with a dry, warm summer and mild, wet winter. Of the 776 mm annual rainfall, 96% falls during the rainy season from October to April (NOAA 2008). The average temperature of the hottest and coldest months are 17.1 and 9.7°C, respectively and precipitation in the driest summer and wettest winter months is 1.2 and 142.7 mm, respectively (Gilbert *et al*. 2010).

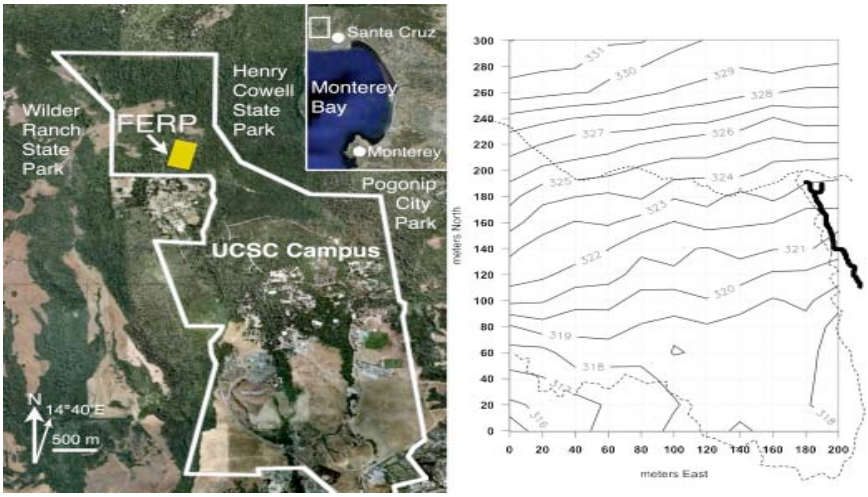

Figure 1. Map of the FERP. Source: (Gilbert et al. 2010)

Mouse Trapping

On the FERP 126 Sherman mouse traps were placed 20 m apart as part of a grid. Trapping sessions were conducted once during each season, with each trapping session lasting 3 nights. Each trap was placed strictly according to the grid, although slight care was taken to ensure the trap was set logically (not on top of a rock, for example). The traps were baited with a mixture of peanut butter and oatmeal. We also placed a small handful of polyester in each trap to provide insulation for the mice. When a mouse was caught for the first time, a small amount of hair (~5-10 hair strands) was collected using scissors. Repeated collection of hair was not possible because peanut butter was used as bait, and peanut butter is most often made with corn syrup which could bias the $\delta^{13}C$ data, as corn is a C4 plant. Mice were identified based on weight, hind foot length, and tail bicoloration. In all, a total of 64 mice were caught and analyzed, 42 *P. boylii*, and 22 *P. californicus*.

Pitfall Traps

Three pitfall traps were set to trap arthropods at four different locations on the FERP for one night during each season in 2010. We chose each location according to dominant vegetation type, as well as proximity to other trap locations and location within the FERP itself, getting four slightly different micro-habitats in the FERP per trapping session. Traps were set at the same location each trapping session. The location of each individual trap was chosen based on basic suitability (not under water, not on a steep incline, etc.) on the canopy floor. Each individual trap was no more than 15 m away from the other two traps in that location, so that different micro-habitats were not being sampled at the same trap location. Each trap was made from a medium-sized, red plastic Solo cup. A hole was dug in the ground deep enough so that when the cup was placed in the hole, the top of the cup was directly at ground level. After the cup was placed in the hole, the hole was filled in completely so that the body of the cup was completely submerged with the top just barely exposed. The cup was filled ~1/3 with water, and 2-3 drops of unscented soap were added to break the surface tension of the water. Each trap was prepared at dusk and then collected at dawn on the following morning. The arthropods collected were classified by order. In all, 372 Coleoptera (Beetles), 34 Orthoptera (Grasshoppers), 2 Arachnida (Spiders), 10 Diplopoda (Millipedes), and 1 Lepidoptera (moths and butterflies) were collected.

Seed Traps

Leaf litter traps had been placed around the FERP for a previous study conducted by Gilbert *et al*. (2010), and sample seeds were supplied to this study during the spring, summer, fall, and winter months. We analyzed seeds from *Pseudotsuga menziesii* (Douglas-fir), *Arbutus menziesii* (Madrone), *Sequoia sempvirens* (Coast redwood), *Quercus agrifolia* (Coast live oak), and *Quercus parvula* (Shreve oak).

Sample Preparation and Isotopic Analysis

Carbon and nitrogen isotope and elemental composition were determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer. Analyses were conducted at the University of California, Santa Cruz Stable Isotope Laboratory. Isotopic values are reported relative to an internationally accepted standard and expressed in parts per thousand deviation from that standard by: $\delta(‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R is the ratio of the heavy-to-light isotope (Sulzman 2007). The international standards are PeeDee Belemnite Limestone (PDB) and air for carbon and nitrogen respectively. Analytical precision on in-house standards is 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. The in-house standards used were Acetanilide and PUGEL for the arthropods and mouse hair analysis, and Acetanilide, PUGEL, and Oak standard made from oak leaves collected in Santa Cruz County. Sample isotopic values are corrected for size, drift and source stretching effects.

Arthropods were stored frozen at -20°C prior to preparation for analysis. They were then freeze dried, sonicated in MilliQ (four times for 15 minutes) and rinsed with

MilliQ in between sonications. Seeds were placed in an oven at 60ºC for 48 hours to dry before undergoing the same cleaning procedure. Both sample types were then crushed using a agate mortar and pestle and weighed for analysis. Arthropods were weighed to 700 ± 50 µg into Sn capsules for analysis. Since the seeds exhibited high variation in weight % C and N, isotopic analysis of the seeds was conducted in three parts: an initial test run to determine %C and %N, C isotope analysis, and finally N isotope analysis. For carbon, seeds were weighed according to the following formula: (X_{sample}) x %C x 0.01 = 180 µg where X_{sample} is the weight of the sample required for analysis, and %C is the value obtained for the % carbon by weight from the test analysis. For nitrogen, we used the following formula: (Y_{sample}) x %N x 0.01 = 60 µg where Y_{sample} is the weight of the sample required and %N is the value obtained for the % nitrogen by weight from the test analysis.

Mouse hair samples were rinsed and sonicated with both MilliQ and petroleum ether to remove surface contaminants and oils. They were then weighed whole to 700 ± 50 µg into Sn capsules for analysis.

Statistical Analyses

All statistical analyses except ANOVA were performed in R (version 2.10.1). Unpaired t-tests were considered significant at $p = 0.05$. One way ANOVA was conducted for each species for each variable, $\delta^{13}C$ and $\delta^{15}N$, using a free online one way ANOVA calculator at http://www.danielsoper.com/statcalc/calc43.aspx. Results from the one way ANOVA were considered significant at $p = 0.05$.

Isotopic Mixing Model

Numerous isotopic mixing models have been developed (Moore and Semmens 2008, Parnell *et al*. 2010, Schwarcz 1991). We chose to use Parnell *et al.*'s model, Stable Isotope Analysis in R (SIAR), because it is capable of accounting for concentration dependence (variation in elemental concentrations of nitrogen and carbon in the mouse food sources), which can bias model outputs if ignored (Phillips and Koch 2002).

We ran the mixing model four times for each species. The dietary sources considered were Coleoptera, Orthoptera, Arachnida, Diplopoda, *Quercus parvula*, and other seeds. Data labeled "seeds" refers to a combination of *Pseudotsuga menziesii*, *Arbutus menziesii*, *Sequoia sempvirens*, and *Quercus agrifolia* seeds; these values were lumped in the mixing model because they all have very similar isotopic signatures. *Quercus parvula*, however, was entered into the model as a separate value, as it occupies a significantly different isotopic space. The first mixing model run included isotopic data from mouse hair collected in summer, spring, and winter (fall excluded), and data from all possible dietary sources collected with the exclusion of *Quercus parvula*, which is only available in the fall. The second run was identical to the first, but excluded Arachnida in the case of *P. californicus* and Diplopoda in the case of *P. boylii*. The third run included only data from mouse hair collected in the fall and data from all possible dietary sources. Finally, the fourth run was identical to the third with Arachnida in the case of *P. californicus* and Diplopoda in the case of *P. boylii* again excluded. It should be noted that the SIAR mixing model makes a critical assumption in that it assumes all dietary sources input into the model represent the entirety of diet. In other words, all of the dietary proportions estimated by the model will always add up to 100%, even if a real

dietary source is missing. The decision to exclude Diplopoda and Arachnida from the SIAR mixing model was made as a way to evaluate the model's sensitivity to a particular source. We assumed that one or more sources could be missing, causing the model to choose a source similar in isotopic composition yet not actually eaten by the species.

Tissue-to-diet discrimination factors were applied to the mouse hair isotope values. 1 ± 0.7 ‰ was subtracted from the $\delta^{13}C$ values and 3 ± 0.1 ‰ was subtracted from the $\delta^{15}N$ values (DeMots *et al*. 2010, Miller *et al*. 2008).

Fecal Analysis

Fecal pellets were removed from 6 *P. boylii*'s and 1 *P. californicus* and placed in an oven at 100°C for 48 hours to dry. They were then viewed under a microscope, along with samples of arthropod parts for comparison, including Diplopoda legs, Arachnida legs, Coleoptera legs, and a Coleoptera antennae. Each type of arthropod had a noticeably different color, providing a basis for cursory identification in the fecal samples.

Results

The mean $\delta^{13}C$ values for *P. boylii* (-23.9 ± 1.1‰, n = 42) and *P. californicus* (24.5 ± 1.3‰, n = 22) are not significantly different ($p = 0.0932$) (Figure 2).

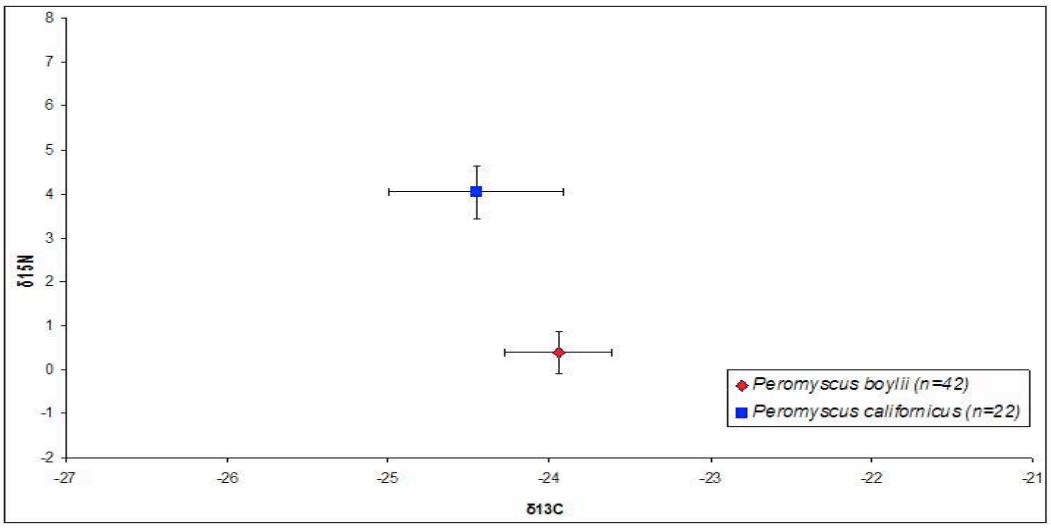

Figure 2. Mean $\delta^{13}C$ and $\delta^{15}N$ values of *Peromyscus boylii* and *Peromyscus californicus* hair for 2010. Error bars represent 2 SE's.

The mean $\delta^{15}N$ values of the two species are significantly different from one another however ($p < 0.0001$); the mean $\delta^{15}N$ for *P. boylii* is 0.4 ± 1.5‰ and the mean $\delta^{15}N$ value for *P. californicus* is 4.0 ± 1.4‰.

No significant difference was found in the $\delta^{13}C$ or the $\delta^{15}N$ values between males and females in either species (Figure 3).

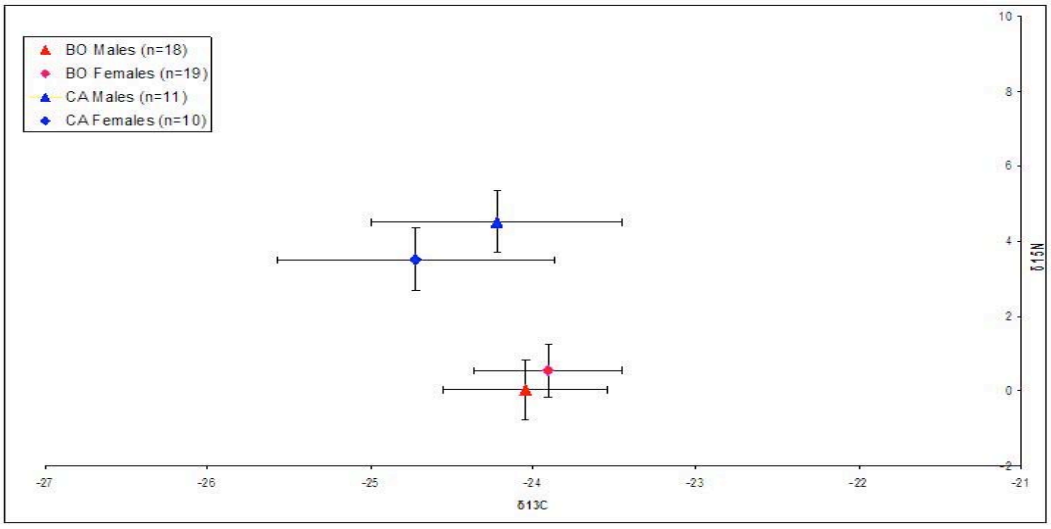

Figure 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values of male vs. female *P. boylii* and *P. californicus*. Error bars represent 2 SE's.

Seasonal patterns in $\delta^{13}C$ and $\delta^{15}N$ values for *P. californicus* and *P. boylii* are plotted in Figure 4.

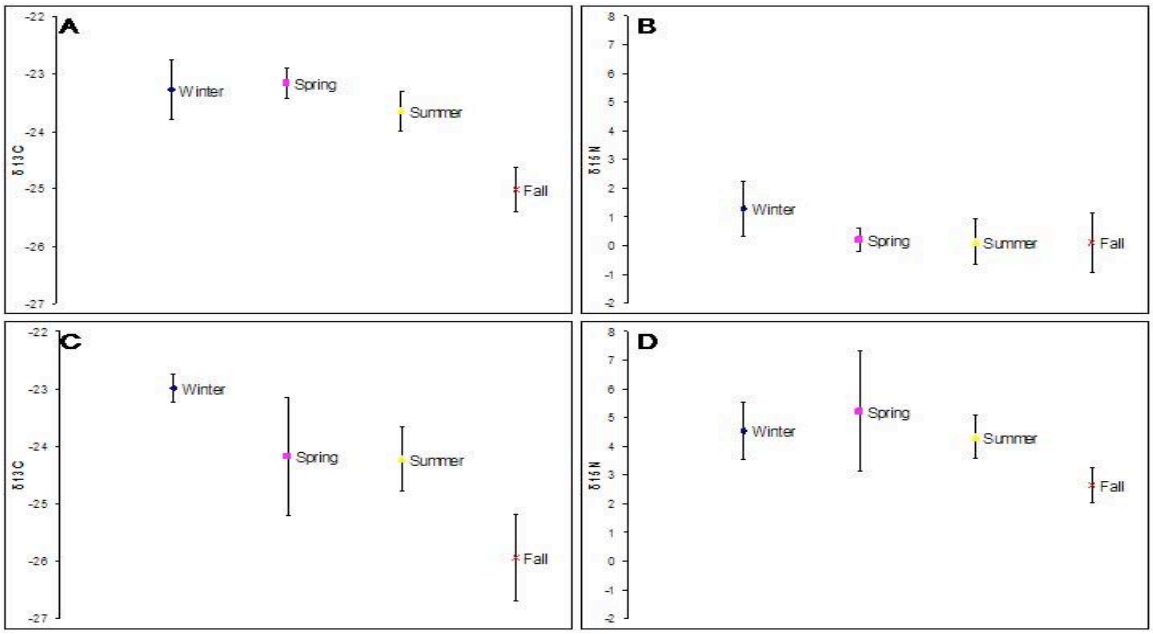

Figure 4. Seasonal variation of $\delta^{13}C$ and $\delta^{15}N$ in *P. boylii* and *P. californicus*: (A) seasonal variation of $\delta^{13}C$ in *P. boylii*; (B) seasonal variation of $\delta^{15}N$ in *P. boylii*; (C) seasonal variation of $\delta^{13}C$ in *P. californicus*; and (D) seasonal variation of $\delta^{15}N$ in *P. californicus*. Error bars represent 2 SE's.

There is significant seasonal variation ($p = 0.00$) in the $\delta^{13}C$ values for *P. boylii*, however there is no significant seasonal variation ($p = 0.28$) in the $\delta^{15}N$ values. For *P. californicus*, there is significant seasonal variation in both the $\delta^{13}C$ ($p = 0.00$) and $\delta^{15}N$ ($p = 0.015$) values.

Data from the SIAR mixing model for *P. boylii* and *P. californicus* are presented in Figures 5, 6, and 7. In the first run for *P. boylii*, which examined dietary sources during the winter, spring, and summer, the SIAR model estimates that Diplopoda constitute 87% of diet, Coleoptera make up 2%, Orthoptera 3%, Arachnida 3% and seeds 5%. When Diplopoda are excluded, the SIAR mixing model for *P. boylii* estimates that seeds make up 93% of diet, while Coleoptera, Orthoptera, and Arachnida constitute 1%, 5%, and 1% respectively. The third run of the SIAR mixing model for *P. boylii* (fall only) estimates that Diplopoda constitute 44% of diet, Coleoptera 5%, Orthoptera 16%, Arachnida 4%, seeds 24%, and *Quercus parvula* 7%. The fourth run of the SIAR mixing model, in which only fall is considered and Diplopoda are excluded, estimates that seeds comprise 69% of diet, Coleoptera 3%, Orthoptera 19%, Arachnida 3%, and *Quercus parvula* 5%.

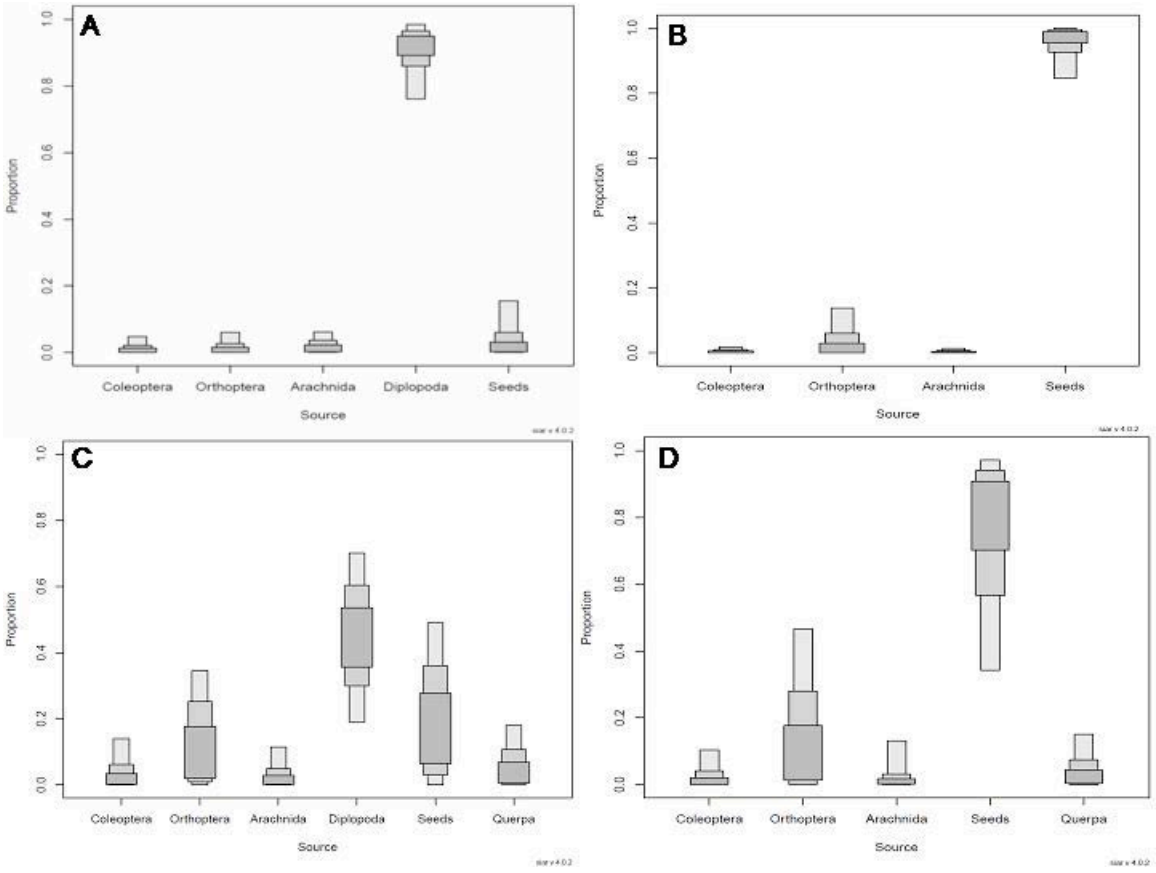

Figure 5. Results of the SIAR Mixing Model for *P. boylii*. (A) winter, spring, and summer mouse hair with all dietary sources except *Quercus parvula* (Querpa); (B) winter, spring, and summer mouse hair with all dietary sources except *Quercus parvula* and Diplopoda; (C) fall mouse hair with all dietary sources (including *Quercus parvula*); and (D) fall mouse hair with all dietary sources (including *Quercus parvula*) except Diplopoda.

The first run of the SIAR mixing model for *P. californicus* finds Arachnida to constitute 40% of diet, Coleoptera 14%, Orthoptera 5%, Diplopoda 27%, and seeds 13%. When Arachnida are excluded, the SIAR mixing model estimates that Coleoptera comprise 60% of diet, Orthoptera 4%, Diplopoda 12%, and seeds 24%. The fall only run of the SIAR mixing model for *P. californicus* indicates that *P. californicus* is eating a much more balanced diet, in which *Quercus parvula* seeds make up 19.97% of their diet, Coleoptera 16%, Orthoptera 19%, Arachnida 10%, Diplopoda 18%, and other seeds 17%.

Finally, the fourth run of the SIAR mixing model, in which Arachnida are excluded, estimates that Coleoptera constitute 25% of diet, Orthoptera 18%, Diplopoda 17%, *Quercus parvula* 21%, and other seeds 20%.

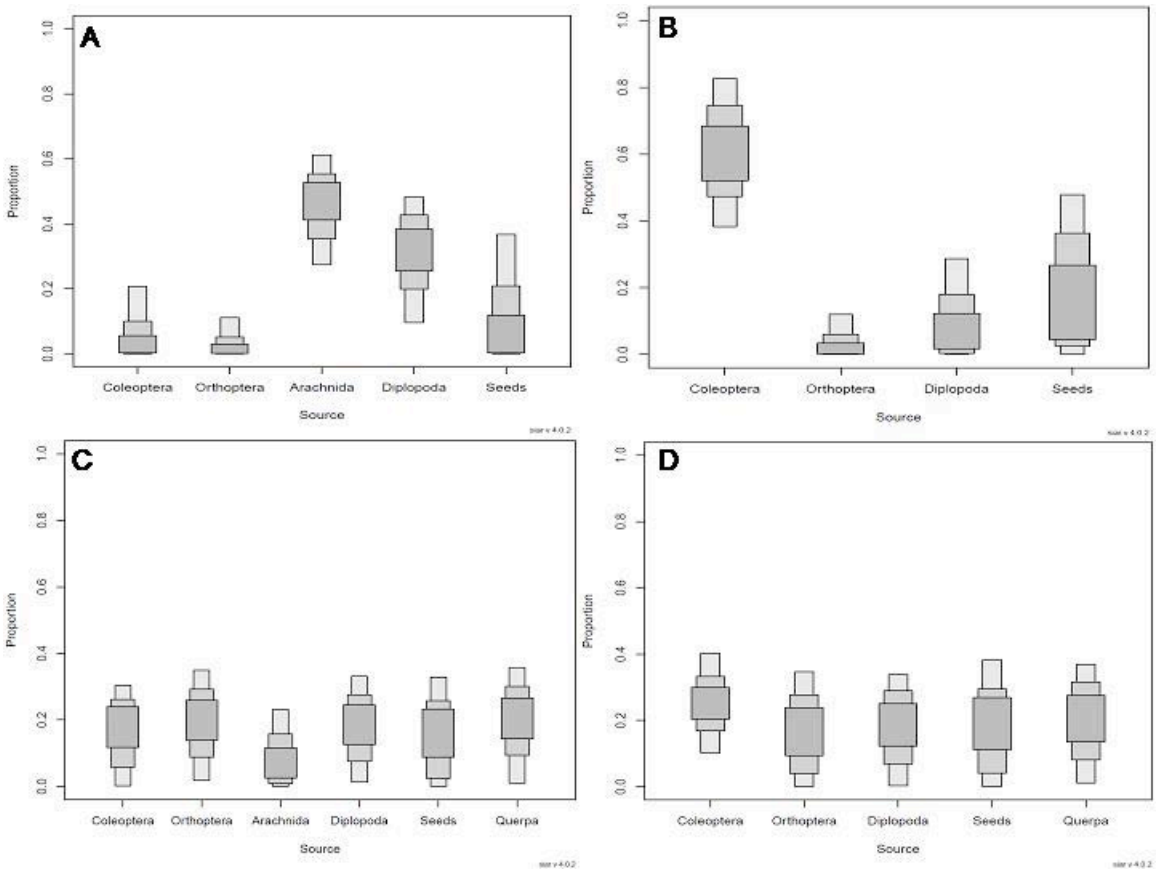

Figure 6. Results of the SIAR Mixing Model for *P. californicus*. (A) winter, spring, and summer mouse hair with all dietary sources except *Quercus parvula* (Querpa); (B) winter, spring, and summer mouse hair with all dietary sources except *Quercus parvula* and Arachnida; (C) fall mouse hair with all dietary sources (including *Quercus parvula*); and (D) fall mouse hair with all dietary sources (including *Quercus parvula*) except Arachnida

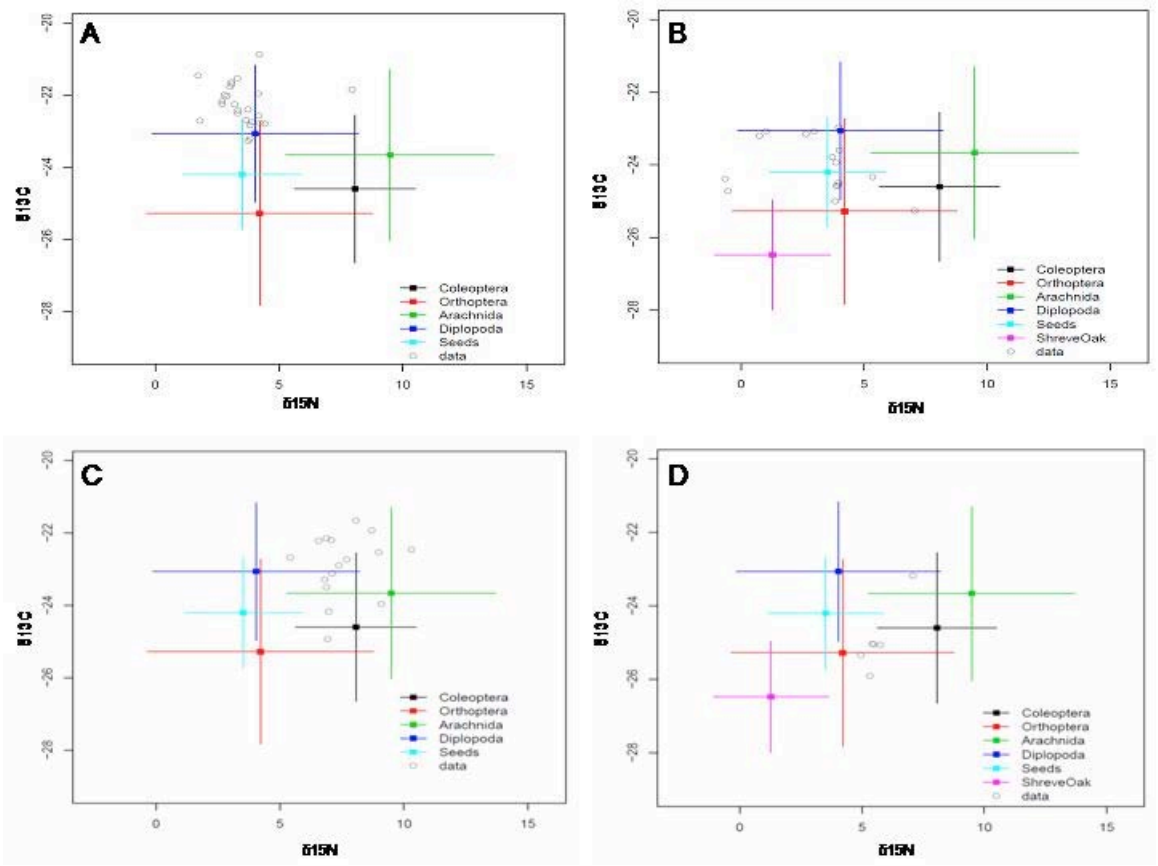

Figure 7. Isotopic values of possible dietary contributions by source: (A) *P. boylii* hair from winter, spring, and summer (labeled "data") and possible dietary sources; (B) *P. boylii* hair from fall (labeled "data") and possible dietary sources; (C) *P. californicus* hair from winter, spring, and summer (labeled "data) and possible dietary sources; (D) *P. californicus* hair from fall (labeled "data") and possible dietary sources.

The results of the fecal analysis were subjective and unclear. Although the fecal pellets were quite processed, and sources were difficult to distinguish definitively, differences between fecal pellets of *P. boylii* and *P. californicus* were observed. In both species' fecal pellets, there seemed to be light brown, almost amber colored fragments that looked similar in color and consistency to the arthropod samples, although slightly different in color. These were assumed to be arthropod chitin fragments. The amber fragments in *P. californicus* fecal pellets were noticeably darker in color than the

fragments found in *P. boylii* fecal pellets and, consequently, *P. californicus* fecal pellets were overall darker than *P. boylii*. No further conclusions were able to be drawn from the fecal analysis.

Discussion

The significant difference in the $\delta^{15}N$ values between *P. boylii* and *P. californicus* suggests that *P. californicus* is eating at a higher trophic level than *P. boylii*. There is roughly a 3‰ increase in $\delta^{15}N$ values with each increase in trophic level (Sponheimer *et al*. 2003). The 3.6‰ difference in mean $\delta^{15}N$ values between the two species therefore suggests that *P. californicus* is feeding one trophic level higher than *P. boylii*. This is consistent with the implications of Shakeri (2010), who inferred dietary partitioning between the two species, as well as with the implications of Kalcounis-Rüppel *et al*. (2002), who found that *P. californicus* ate more cat food than *P. boylii* when given a choice of multiple food sources.

In the first run of the SIAR model for *P. boylii*, Diplopoda is estimated to contribute more than 87% to their diet, while seeds account for less than 5%. This was perceived as highly unlikely because the mixing model results for *P. californicus* indicate that seeds contribute greater than 13% to their diet in all runs, and from comparing the $\delta^{15}N$ values for both *P. boylii* and *P. californicus*, we can argue that *P. californicus* is likely eating more animal protein than *P. boylii*. The removal of Diplopoda as a dietary source for *P. boylii* presents a more accurate representation of possible dietary sources. It is therefore most likely that *P. boylii* feeds primarily on vegetation, but will consume

insects during times of low food availability. This is consistent with the findings of Jameson (1952), Smartt (1978), and Kalcounis-Rüppel *et al*. (2002).

Because Coleoptera were the most abundant insects in the plot, we were initially surprised by the mixing model result that indicates that Arachnida contribute ~40% to the diet of *P. californicus* during all seasons except fall, and that Coleoptera constitute only ~14%. When Arachnida are removed, Coleoptera are estimated to contribute ~60% of *P. californicus's* diet. However, both Arachnida and the dominant family of Coleoptera recovered in the traps, Carabidae (ground beetle), are predators, and their relative population size should be about the same. It is also likely that Arachnida are more capable of avoiding the pitfall traps than Coleoptera, and are therefore under-represented in our sample. Further, studies have shown some species of *Peromyscus* actually prefer arachnids (Bellocq and Smith 1994). Therefore, without a good ecological reason to exclude Arachnida from the mixing models other than the pitfall trap data, their inclusion most likely represents the most accurate description of *P. californicus*'s diet. Based on these stable isotope data, it is most likely that *P. californicus* eats mostly arthropods, specifically Arachnida and Diplopoda and some seeds depending on availability, and then shifts to a more broad diet including *Quercus parvula* during the fall. Our data do not suggest that *P. californicus* becomes completely herbivorous, nor that seeds makes up the majority of its diet at any time, though they remain at least a small dietary component during all seasons. This is consistent with the implications of Shakeri (2010), who concluded that compared to *P. boylii*, *P. californicus* should be more of a generalist. This is also consistent with the findings of Kalcounis-Rüppel *et al*. (2002), who inferred that *P. californicus* is relatively more carnivorous than *P. boylii*. These results are not,

however, consistent with the findings of Merritt (1974), who found that *P. californicus* specialized on *Umbellularia* (California bay laurel) seeds and that arthropods made up only a small percentage of its diet. This discrepancy may be due to the fact that there are no *Umbellularia* trees that drop seeds on the FERP (Gilbert n.d.). Finally, differences between the results of this study and those of Meserve (1977), who found *P. californicus* to specialize on vegetation and proposed that *P. californicus* does not actively hunt arthropods, may stem from broad differences in community structure and interactions with other *Peromyscus* species, as Meserve's study was conducted in Irvine, California.

However one possibility cannot be discounted; it could still be possible for *P. boylii* to be consuming Diplopods and *P. californicus* to be consuming Arachnids, as suggested when they are both included in the SIAR mixing model. If each species of mouse was feeding on similar proportions of seeds and arthropods, then the difference in $\delta^{15}N$ values between the two species can be explained by the difference in $\delta^{15}N$ values between Arachnids and Diplopods. Given the results of all the mixing models together, this does not seem likely, however it cannot be discounted until further data is collected on other possible dietary sources (e.g. Manzanita berries).

The lack of a significant difference found in the $\delta^{13}C$ and $\delta^{15}N$ values between males and females in each species suggests that no dietary partitioning exists between the sexes within either population of *P. boylii* and *P. californicus*.

The diets of both *P. boylii* and *P. californicus* vary seasonally. It is important to note when considering seasonal change in the diets of these mice that they molt twice a year, once in the spring and then again in the fall (Brown 1963). *P. boylii* seems to shift its vegetative preference during the fall months, as indicated by a significant shift in the

$\delta^{13}C$ value of hair collected during the fall season (Figure 4). Shakeri (2010) found that during the fall months, *P. boylii* is spatially correlated with *Lithocarpus densiflorus* (Tan oak). One possible explanation for the dietary shift of *P. boylii* in the fall months is that they are eating more *Lithocarpus densiflorus* acorns; however none were obtained and analyzed in this study, and the majority of *Lithocarpus densiflorus* acorns fall in late July/early August (Gilbert n.d.). *P. boylii* feeds at a higher trophic level in the winter months, as indicated by the shift in $\delta^{15}N$ value of the winter season. This could be due to a rise in the consumption of Diplopoda or Orthoptera as indicated by the mixing model, and would be consistent with the presumption that *P. boylii* is primarily herbivorous, but will feed on arthropods during times of low food availability (Jameson 1952, Smartt 1978, Kalcounis-Rüppel *et al*. 2002). However, it should be noted that of the 9 *P. boylii* caught in the winter season of this study, all but one had $\delta^{15}N$ values below 1.5‰, and mouse #341 had a $\delta^{15}N$ value of 4.9‰. This could be a possible misidentification; mouse #341 was identified as a *P. boylii* female weighing 18 g, however it's possible that mouse #341 is in fact a young *P. californicus*, as this weight is in the range in which they overlap. Other than the $\delta^{15}N$ values, no further information is available to suggest that mouse #341 was misidentified, so it was included in our analysis as originally presented, as a *P. boylii* with an unusually high $\delta^{15}N$ value.

P. californicus also seems to switch its vegetative consumption seasonally. *P. californicus* caught in the fall and winter seasons have $\delta^{13}C$ values different from the spring and summer seasons (Figure 4). The difference in the fall $\delta^{13}C$ values may be explained by the noticeable dietary shift by *P. californicus* in the fall, which may be due to the dropping of oak acorns, as is indicated by the mixing model (Figure 6). There is

also considerable, steady seasonal variation in the $\delta^{15}N$ values of *P. californicus*. This is consistent with the implications made by Shakeri (2010), who inferred *P. californicus* to be a dietary generalist. It is likely that *P. californicus* feeds primarily on available insects and will eat certain seeds or fruits when available.

Conclusion

This study aimed to answer two main questions. First, is there dietary partitioning between *P. boylii* and *P. californicus*? Second, what, specifically do members of each species primarily eat? Based on significant differences in the stable nitrogen isotope values of their hair, we conclude that there is dietary partitioning between *P. boylii* and *P. californicus* and that *P. californicus* feeds one trophic level higher than *P. boylii*. This can best be explained by considering *P. californicus* to primarily be a secondary consumer, but that it will become more omnivorous, depending on the availability of specific plant sources. These results are in contrast to the findings of Merritt (1974) and Meserve (1977), but support the implications of Kalcounis-Rüppel *et al.* (2002) and Shakeri (2010). The results of this study also indicate, in support of the findings of Jameson (1952), Smartt (1978), and Kalcounis-Rüppel *et al*. (2002), that *P. boylii* is primarily a primary consumer, but will supplement its diet with arthropods, depending on food availability. Since there is no significant difference between the $\delta^{13}C$ or $\delta^{15}N$ values between the sexes of the two species, the hypothesis of dietary partitioning existing between the sexes of each species was rejected.

This study was unable to definitively estimate the specific proportions of dietary sources for either species because of the inherent limitations of working with wild

populations. Although SIAR includes an error term to account for unquantified variation (e.g. unmeasured food sources), like all mixing models, it is biased toward the dietary sources that are initially input into the model. And, although it seems likely that one or more sources missing, as can be seen in Figure 7, we are at least able to suggest some probable dietary sources. *P. californicus* is most likely feeding primarily on Arachnida, Diplopoda, Coleoptera, and various seed sources. During winter, spring, and summer, they consume relatively more Arachnida than any other arthropod, however during the fall, *P. californicus* switches to feed on a variety of plants and arthropods, and consumes less Arachnida compared to other arthropod sources. *P. boylii* feeds primarily on various seed sources and will occasionally feed on insects, most likely due to low availability of other sources.

Acknowledgements

I would like to thank Gregory Gilbert and Stevenson College for contributing funding necessary to carry out this study. I would also like to thank Rachel Brown for mentoring me through the entire process, from proposing the original idea and conducting a preliminary study to spending countless hours instructing me, answering questions, and giving me advice. I would also like to thank Yiwei Wang, Christopher Wilmers, Paul Koch, and Dyke Andreasen for advising me on research, data analysis, and the construction of my paper. Finally, I would like to thank everyone who came out to help during trapping seasons, especially Kathlyn Del Franco, Yasaman Shakeri, Graham Redman, and Brendan Lehman.

WORKS CITED

Bellocq, I., and Smith, S.M. (1994). Arthropods preferred as food by sorex cinereus (masked shrew) and peromyscus maniculatus (deer mouse)-an experimental approach. *Mammalia*, 58(3): 391-396.

Bowen, G. J., Cerling, T.E., Chesson, L.A., Ehleringer, J. R., Podlesak, D. W., & Thompson, A. H. (2010). Stable isotope analysis of modern human hair collected from asia (china, india, mongolia, and pakistan). *American Journal of Physical Anthropology*, 141: 440-451.

Brown, L.N. (1963). Maturational molts and seasonal molts in peromyscus boylii. *American Midland Naturalist*, 70(2): 466-469.

Craig, H. (1957). Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta*. 12: 133-149.

DeMots, R.L., Novak, J.M., Gaines, K.F., Gregor, A.J., Romanek, C.S., and Soluk, D.A. (2010). Tissue-diet discrimination factors and turnover of stable carbon and nitrogen isotopes in white-footed mice (peromyscus leucopus). *Canadian Journal of Zoology*, 88: 961-967.

Gilbert, G.S., Howard, E., Ayala-Orozco, B., Bonilla-Moheno, M., Cummings, J., Langridge, S., Parker, I.M., Pasari, J., Schweizer, D., and Swope, S. (2010). Beyond the tropics: forest structure in a temperate forest mapped plot. *Journal of Vegetation Science*, 21: 388-405.

Gilbert, G.S. (n.d.) University of California Santa Cruz - Forest Ecology Research Plot. Retrieved from: http://learnlab.webfactional.com/

Hardin, Garret. (1960). The competitive exclusion principle. *Science*, 131 (3409): 1292-1297.

Jameson, E. (1952). Food of deer mice, peromyscus maniculatus and p. boylei, in the northern sierra nevada, california. *Journal of Mammalogy*, 33: 50-60.

Kalcounis-Rüppel, Matina C. and Millar, John S. (2002). Partitioning of space, food, and time by syntopic peromyscus boylii and p. californicus. *Journal of Mammalogy*, 83(2): 614-625.

Kelly, J.F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78: 1-27.

Luensmann, Peggy S. (2005). Peromyscus boylii. in: fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2010, May 21]

Merritt, J. (1974). Factors influencing the local distribution of peromyscus californicus in northern california. *Journal of Mammalogy*, 55: 102-113.

Meserve, P. (1977). Three-dimensional home ranges of cricetid rodents. *Journal of Mammalogy*, 58: 549-558.

Miller, J.F., Millar, J.S., and Longstaffe, F.J. (2008). Carbon and nitrogen isotope tissue–diet discrimination and turnover rates in deer mice, Peromyscus maniculatus. *Canadian Journal of Zoology*, 86(7): 685–691.

Moore, J.W., and Semmens, B.X. (2008). Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters*, 11:470-480.

NOAA. (2008). NOAA National Weather Service Cooperative Observer Network Program. Western Regional Climate Center, Santa Cruz Station 047916. Retrieved from: http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca7916. Accessed 16 July 2008.

O'Leary, Marion H. (1988). Carbon isotopes in photosynthesis. *Bioscience*, 38(5): 328-335.

Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L. (2010). Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, 5(3): e9672

Phillips, D.L., and Koch, P.L. (2002). Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, 130: 114-125.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53-74.

Schoener,T. W. (1974). Resource partitioning in ecological communities. *Science*, 185: 164-168.

Schwarcz, H.P. (1991). Some theoretical aspects of isotope paleodiet studies. *Journal of Archaeological Science*, 18: 261–276

Shakeri, Y. (2010). Niche partitioning by peromyscus californicus and peromyscus boylii in mixed evergreen forest. Senior Thesis, University of California Santa Cruz.

Smartt, R. (1978). A comparison of ecological and morphological overlap in a Peromyscus community. *Ecology*, 59: 216-220.

Sponheimer, M. Robinson, T. Ayliffe, L. Roeder, B. Hammer, J. Passey, B. West, A. Cerling, T. Dearing, D. and Ehleringer, J. (2003). Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}N$ values from a controlled feeding study. *International Journal of Osteoarcheology*, 13: 80-87.

Sulzman, E. W. (2008). Stable isotope chemistry and measurement: a primer. *Stable Isotopes in Ecology and Environmental Science (Second Edition)*, 1-21.

Tieszen, L. L. (1991). Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *Journal of Archeological Science*, 18: 227-248.

APPENDIX

Table 1. Data from hair collected from P. boylii and P. californicus. "#" refers to tag number; genus is classified as "PE" for Peromyscus; "BO" refers to Boylii and "CA" refers to Californicus.

#	Genus	Species	δ13C	δ15N	Season	Sex
341	PE	BO	-21.85	7.95	Winter '10	F
344	PE	BO	22.7678	4.23	Winter '10	F
388	PE	BO	21.5389	3.31	Winter '10	F
303	PE	BO	23.2699	3.74	Winter '10	F
333	PE	BO	22.7458	3.89	Winter '10	F
312	PE	BO	21.7646	3.02	Winter '10	M
301	PE	BO	20.8723	4.21	Winter '10	?
306	PE	BO	22.8357	3.83	Winter '10	?
334	PE	BO	22.7996	4.43	Winter '10	?
245	PE	BO	-21.46	1.73	Spring '10	F
353	PE	BO	-21.99	2.79	Spring '10	F
377	PE	BO	-23.08	4.07	Spring '10	F
288	PE	BO	-22.26	3.21	Spring '10	F
233	PE	BO	-22.02	2.89	Spring '10	F
293	PE	BO	-22.42	3.34	Spring '10	F
323	PE	BO	-22.57	4.18	Spring '10	M
244	PE	BO	-22.25	2.7	Spring '10	M
192	PE	BO	-22.49	3.33	Spring '10	M
291	PE	BO	-21.7	3.09	Spring '10	M
300	PE	BO	-21.65	3.07	Spring '10	M
352	PE	BO	-21.96	4.17	Spring '10	?
55	PE	BO	-22.4	3.75	Summer '10	F
246	PE	BO	-22.7	3.67	Summer '10	F
80	PE	BO	-22.71	1.8	Summer '10	M
236	PE	BO	-23.21	3.82	Summer '10	M
87	PE	BO	-22.17	2.7	Summer '10	M
42	PE	BO	-24.39	-0.64	Fall '10	F
95	PE	BO	-24.56	3.95	Fall '10	F
6	PE	BO	-23.93	3.85	Fall '10	F

#	Genus	Species	δ13C	δ15N	Season	Sex
973	PE	BO	-24.5	3.96	Fall '10	F
71	PE	BO	-23.6	3.99	Fall '10	F
950	PE	BO	-23.79	3.71	Fall '10	F
98	PE	BO	-24.72	-0.53	Fall '10	M
39	PE	BO	-24.58	3.87	Fall '10	M
299	PE	BO	-23.15	2.64	Fall '10	M
56	PE	BO	-23.2	0.75	Fall '10	M
43	PE	BO	-23.07	1.02	Fall '10	M
974	PE	BO	-22.97	3.97	Fall '10	M
983	PE	BO	-23.09	2.96	Fall '10	M
72	PE	BO	-25.26	7.06	Fall '10	M
975	PE	BO	-24.34	5.34	Fall '10	M
89	PE	BO	-25	3.82	Fall '10	?
309	PE	CA	21.6634	8.06	Winter '10	F
343	PE	CA	22.1457	6.87	Winter '10	F
346	PE	CA	21.9399	8.70	Winter '10	M
347	PE	CA	22.2198	6.56	Winter '10	M
253	PE	CA	-22.9	7.37	Spring '10	M
243	PE	CA	-24.17	6.97	Spring '10	M
79	PE	CA	-23.96	9.09	Summer '10	F
398	PE	CA	-22.69	5.41	Summer '10	F
84	PE	CA	-23.12	7.1	Summer '10	F
54	PE	CA	-24.93	6.93	Summer '10	M
74	PE	CA	-22.73	7.7	Summer '10	M
394	PE	CA	-22.53	8.98	Summer '10	M
85	PE	CA	-23.5	6.87	Summer '10	M
77	PE	CA	-22.2	7.07	Summer '10	M
78	PE	CA	-23.28	6.8	Summer '10	?
93	PE	CA	-23.18	7.08	Fall '10	F
33	PE	CA	-25.03	5.42	Fall '10	F
297	PE	CA	-25.35	4.95	Fall '10	F
88	PE	CA	-25.06	5.75	Fall '10	F
61	PE	CA	-25.05	5.47	Fall '10	F
59	PE	CA	-25.91	5.32	Fall '10	M
75	PE	CA	-22.46	10.3	Spring '10	M

Table 2. Insect Data. "#" refers to unique identifier given to each individual insect.

#	Class	δ13C	δ15N	Season
70	Arachnida	-23.99	7.89	Fall '10
56	Arachnida	-25.34	5.08	Spring '10
67	Coleoptera	-24.79	3.93	Fall '10
68	Coleoptera	-25.50	5.94	Fall '10
74	Coleoptera	-25.00	3.62	Fall '10
76	Coleoptera	-26.19	5.13	Fall '10

#	Class	δ13C	δ15N	Season
60	Coleoptera	-26.22	5.39	Summer '10
61	Coleoptera	-26.17	3.99	Summer '10
65	Coleoptera	-25.02	4.98	Summer '10
66	Coleoptera	-26.99	4.75	Summer '10
51	Coleoptera	-25.89	5.65	Spring '10
58	Coleoptera	-25.39	5.24	Spring '10
59	Coleoptera	-24.54	7.07	Spring '10
52	Coleoptera (larvae)	-24.16	10.34	Spring '10
71	Diplopoda	-24.53	1.78	Fall '10
55	Diptera	-25.54	9.7	Spring '10
72	Haplotaxida	-23.92	3.79	Fall '10
54	Lepidoptera	-24.92	1.06	Spring '10
69	Orthoptera	-26.24	2.48	Fall '10
62	Orthoptera	-27.72	1.26	Summer '10
63	Orthoptera	-26.00	-1.85	Summer '10
53	Orthoptera	-25.16	2.96	Spring '10
57	Platydesmida	-22.30	1.6	Spring '10
77	Spirobolida	-24.34	2.53	Fall '10
78	Spirobolida	-23.33	-1.18	Fall '10

Table 3. Seed Data. Seeds were run as a collection of individual seeds according to species.

Species Name	δ13C	δ15N
Pseudotsuga menziesii	-25.13	0.43
Arbutus menziesii	-25.62	0.43
Sequoia sempvirens	-25.08	-0.55
Quercus agrifolia	-24.98	1.76
Quercus parvula	-27.48	-1.72

Table 4. Results of one way ANOVA.

Test 1: BO δ13C	Sum of Squares	Degrees of Freedom	Mean Square	Fisher F-value	Significance (p)
Between Groups	30.297	3	10.099	23.311	0
Within Groups	16.463	38	0.433		
Total	46.761	41			

Test 2: BO δ15N	Sum of Squares	Degrees of Freedom	Mean Square	Fisher F-value	Significance (p)
Between Groups	9.234	3	3.078	1.327	0.28
Within Groups	88.163	38	2.32		
Total	97.397	41			

Test 3: CA δ13C	Sum of Squares	Degrees of Freedom	Mean Square	Fisher F-value	Significance (p)
Between Groups	37.208	3	12.403	19.239	0
Within Groups	11.604	18	0.645		
Total	48.811	21			

Test 4: CA δ15N	Sum of Squares	Degrees of Freedom	Mean Square	Fisher F-value	Significance (p)
Between Groups	17.246	3	5.749	4.541	0.015
Within Groups	22.789	18	1.286		
Total	40.034	21			