Northern California Redwood Forests Provide Important Seasonal Habitat for Migrant Bats

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Abstract

Bats are known to roost in redwood forests year-round, but their activities outside the summer season are poorly understood. To improve understanding of the use of redwoods by resident and migrant bats, we conducted 74 mist net surveys between February 2008 and October 2010. Captures were dominated by Yuma myotis (*M. yumanensis*) in the summer and silver-haired bats (*Lasionycteris noctivagans*) in the winter. During November-February, silver-haired bats, accounted for 78 percent of 23 captures and male:female sex ratio was (9:9). By contrast, during June-August, silver-haired bats accounted for 13.8 percent of 269 captures and sex ratios were highly male skewed (34:3). In combination with other regional information, this indicates that female silver-haired bats migrate to redwood forests. To infer summer locations of bats captured in redwood forests, we analyzed stable isotopes of hydrogen, carbon, nitrogen, and sulfur in their fur. Despite spatial segregation between male and female silver-haired bats during presumed molt period, we did not find differences between the sexes in range of isotope values in their fur. Nor were their values different from Yuma myotis. Our findings highlight some of the challenges in using stable istotope analysis to infer migratory pathways in bats.

Key words: bats, *Lasionycteris noctivagans*, *Lasiurus cinereus*, *Myotis yumanensis*, redwoods, stable isotopes, migration, winter

Introduction

Studies of bats in redwood forests have focused largely on their roosting ecology, in particular their use of basal hollows (Fellers and Pierson 2002, Gellman and Zielinski 1996, Rainey et al. 1992, Zielinski and Gellman 1999, Zielinski et al. 2007). A novel result of two of these studies was documentation of bat activity during winter (Gellman and Zielinski 1996, Zielinski and Gellman 1999). Autumn–spring is the period when temperate-zone bats engage in important activities that critically affect their annual energy balance such as migration, mating, and hibernation (Weller et al. 2009).

The silver-haired bat (*Lasionycteris noctivagans*, hereinafter LANO) is a tree-roosting species that is thought to undertake seasonal migrations between its summer and winter habitat (Cryan 2003). Male and female LANO are geographically segregated during the summer months throughout much of North America (Cryan 2003). In Douglas fir forests of northwestern California (hereinafter NWCAL) LANO was one of the most frequently captured species during summer; but captures were > 95 percent males (TJW unpublished data). The limited capture work in

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NWCAL from October-March, suggested that female LANO were more abundant during this time period (Zielinski and Gellman 1999). However, sample sizes were too low to accurately estimate sex ratios by season. Therefore, an important objective of this study was to verify whether the proportion of female LANO increased during autumn–spring in redwood forests of NWCAL. If so, it would suggest that female LANO move to the redwoods for the purposes of wintering, and presumably, mating.

We investigated the use of stable isotopes to help determine movement patterns and infer the summer range of LANO individuals that used NWCAL during winter. Hydrogen isotopes (δD) are commonly employed to infer migratory movements of vertebrates by exploiting characteristic latitudinal and elevational structure in the isotopic composition of precipitation (Bowen et al. 2005, Hobson and Wassenaar 1997). Because tissues such as hair and feathers are metabolically inert, stable isotope ratios reflect the geographic areas where they were synthesized rather than where they are collected (Hobson and Wassenaar 1997). Bats generally molt their fur once per year during late-summer (Constantine 1957) and δD analysis has been used to estimate minimum distances traveled between the summer range and location at time of fur collection (Cryan et al. 2004).

We explored the use of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) isotopes to provide additional information and potentially improve the accuracy of geographic inference (Rubenstein et al. 2002, Wunder et al. 2005). We were particularly interested in evaluating the efficacy of $\delta^{34}S$ because of the proximity of our study area to the Pacific Ocean (Zazzo et al. 2011). The ocean represents a uniform reservoir of sulfate with a sulfur isotopic composition of about 21‰. Due to sea spray effects, we expected bats that grew their fur in redwood forests to have higher values of $\delta^{34}S$ than individuals that grew their fur further from the ocean.

Our use of stable isotopes to infer seasonal movements of bats focused on quantifying the range of values for each isotope within the local population and comparing it against expectations of their movements. We speculated that fur samples from female LANO would have a wider range of isotope values than for males because they are largely absent from NWCAL during summer. However whether male LANO were year-round residents of NWCAL is uncertain. Therefore, we attempted to constrain inference by quantifying baseline levels of isotopic variation in a summer resident species, Yuma myotis (*Myotis yumanensis*, hereafter MYYU), while remaining cognizant of inter-species differences (Britzke et al. 2009). The seasonal movements of MYYU are largely unknown (Verts and Carraway 1998) but based on size and ecomorphology, MYYU is not expected to travel long distances between summer and winter habitat. Accordingly, we expected narrower ranges of isotopic values in year-round resident MYYU than female LANO. If male LANO were summer residents of NWCAL, we expected their range of isotopic values to be similar to MYYU. If instead, the range of isotopic values in male and female LANO were similar to each other but different from MYYU, this might indicate that both sexes are moving to the redwoods from summer habitat elsewhere.

Our study had three interrelated goals: 1) characterize year-round bat activity in redwood forests of NWCAL; 2) determine whether female LANO use redwood forests as wintering habitat; 3) evaluate the use of stable isotopes to infer summer locations of LANO and MYYU in NWCAL.

Study area

Our study was conducted in redwood forests of Mendocino, Humboldt, and Del Norte Counties in NWCAL (*fig. 1*). We selected 18 sites in or adjacent to redwood forests based on ease-of-access and the potential to provide conditions conducive to bat capture during all seasons of the year. All sites were stream reaches ≤ 300 m long that generally retained surface flow throughout summer and early autumn, yet were still wadeable during high flows in winter. Capture sites were located on public (California State Parks, Redwood National Park) and private lands at distances of 1.4 to 31.4 km from the Pacific Ocean (*fig. 1*).

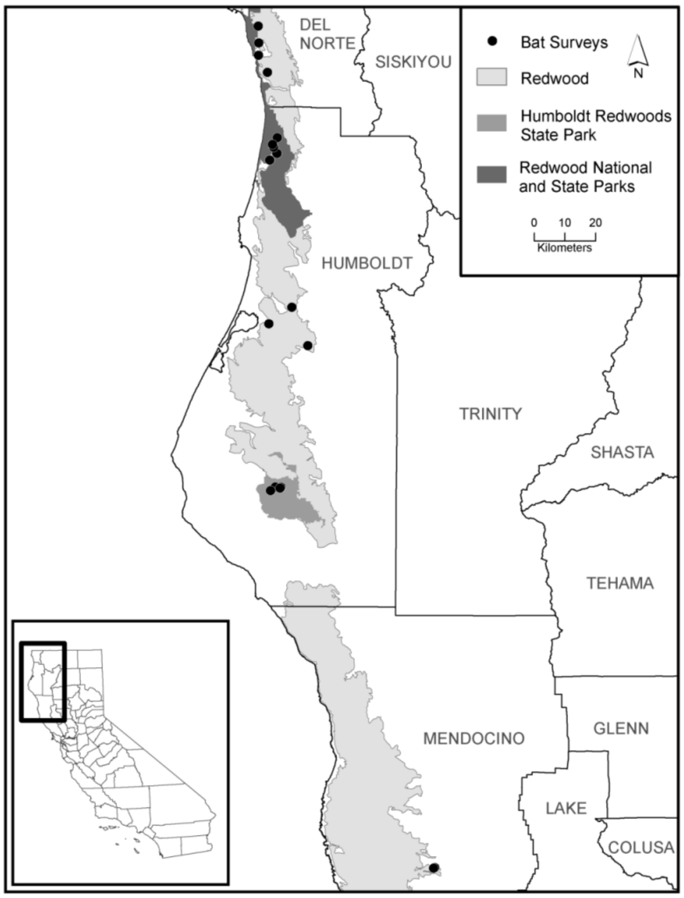


Figure 1—Location of bat captures sites relative to redwood forest habitat in northwest California.

Methods

Field

We captured bats by setting two to four (mean= 3.6 SD=0.55) 2.6 m high mist nets over the creek at each site. We selected the number and length (6 to 12 m) of mist nets to best suit the physical characteristics of each site. Mist nets were opened at sunset for a minimum of 2 hours or until at least 1 hour had passed since the last capture. Individuals were identified to species based on examination and measurement of external morphological features; MYYU was identified using the methods of Weller et al (2007). Sex was determined via external inspection (Racey 2009). We clipped 0.3 to 6 mg of fur from the dorsum of LANO and MYYU individuals for subsequent stable isotope analyses. All bats were released on site the same night.

Stable isotope analyses

Fur samples were triple-washed in a 2:1 chloroform/methanol solution, air dried, and weighed into silver (δD) and tin capsules (δ^{34}S and δ^{13}C/ δ^{15}N). Samples were allowed to air equilibrate to ambient laboratory conditions for ≥ 2 weeks prior to δD analyses (Wassenaar and Hobson 2003). All isotopic measurements were made by continuous flow isotope ratio mass spectrometry, with results reported in delta (δ) notation, expressed as parts per thousand (‰) relative to internationally accepted scales; δD data are specific to non-exchangeable hydrogen. Mean differences between duplicate samples from the same individual were ± 4.1‰ for δD (n = 29), ±0.2‰ for δ^{13}C (n=6), ± 0.1 ‰ for δ^{15}N (n=6), and ± 0.3‰ for δ^{34}S (n=11); quality control and assurance was verified by repeated analyses of an in-house keratin standard, as well as primary standards analyzed as unknowns.

Data analyses

We tested whether monthly sex ratios of LANO or MYYU differed from 50:50 using the conditional test (Przyborowski and Wilenski 1940). The conditional test assumed that the observed count followed a Poisson distribution for both sexes and months with counts for sexes within a month being independent. We used a 2-factor Analysis of Variance (ANOVA) with species and sex as fixed effects to evaluate differences in isotope values. The ANOVA assumed separate variances for each species and residuals for each isotope and sex-species combination were normally distributed. We evaluated differences in least-square means using a t-test with Tukey-Kramer adjustment of p-values; all tests performed were 2-tailed.

Results

Seasonal activity patterns

Between February 2008 and October 2010 we conducted 73 mist net surveys and captured a total of 476 bats, with a mean of 6.5 (SE = 0.78) per survey. Overall we captured 10 species of bats including *Eptesicus fuscus* (*n* = 15), *Lasiurus blossevillii* (*n* =2), *L. cinereus* (*n* = 36), LANO (*n*=116), *Myotis californicus* (*n* = 27), *M. evotis* (*n*=2), *M. lucifugus* (*n*=22), *M. thysanodes* (*n*= 7) *M. volans* (*n* =7), and MYYU (*n* = 129). An additional 113 individuals were identified only as either *M. lucifugus* or MYYU. Bats were captured in every month surveyed though overall capture rates were higher during May-July (*fig. 2*). MYYU, or individuals identified as either MYYU or *M. lucifugus,* comprised 65 percent of 269 bats captured during June-August. From May-September. females composed 36 to 63 percent of monthly captures of MYYU (*fig. 3*), and sex ratios did not differ significantly from 50:50 in any month (range: p=0.092 in Oct to p>0.999 in May). LANO was the second most frequently captured species and capture rates were relatively consistent throughout the year (*fig.* 3). LANO comprised 79% of 34 bats captured during November–March. Sex ratios of LANO were male-biased in March-July (all $p \leq 0.031$) and to a lesser extent in August (p=0.065). Sex ratios of LANO were not different than 50:50

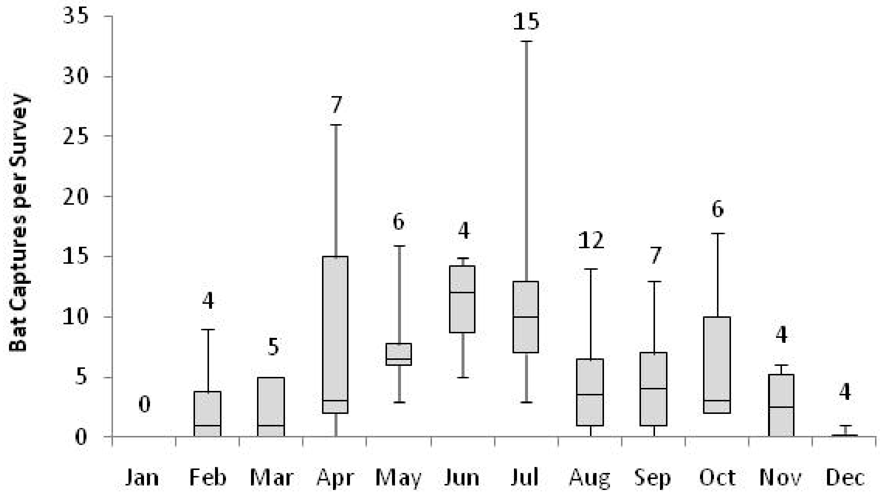
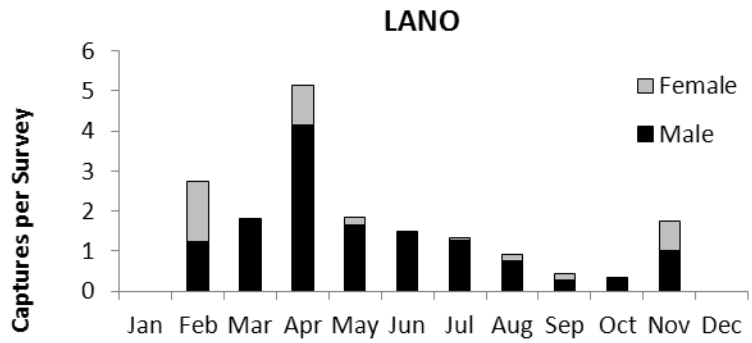


Figure 2—Number of bat captures per survey (all species combined) by month in redwood forests of northwestern California 2008 – 2010. Boxes represent 1st and 3rd quartiles, horizontal line is median, and whiskers represent maximum and minimum captures per survey. Number above whiskers is total number of surveys conducted in each month.

in any other month (all p≥0.500). Capture rates for male LANO were lowest (0.29 – 0.77 captures/survey) during August-October, however they comprised 67 to 100% of LANO captures during these months (fig. 3). Though not a primary focus of this study, 36 hoary bats were captured (6 from 11 April-16 May and 27 from 25 September-5 October); all but two hoary bats were males.

Stable isotopes

We analyzed stable isotope content in fur samples collected from bats during 2008 and 2009. We found no difference in δD values between male and female LANO (t_{65}= -0.57, p = 0.571, *table* 1). Although MYYU fur samples averaged 5 ± 3‰ higher than LANO (*table* 1), the difference was not significant ($F_{1,114}$= 2.98, p = 0.087). The range of δD values in LANO fur from Jun-Aug (-94 to -52‰), when male:female sex ratio of samples were 13:3, was not substantively different from Nov-Feb (-103 to -55‰) when sex ratios of samples were 8:8. Further, neither differed from the range of values for MYYU during June-August (-111 to -49‰), or throughout their April-November activity period (-111 to -41‰).



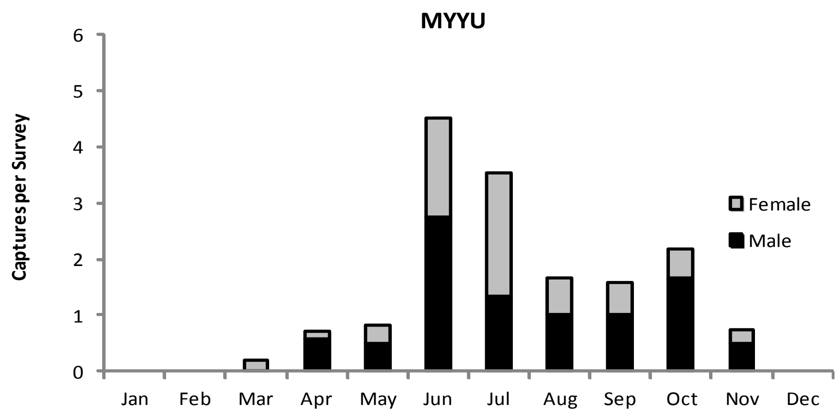


Figure 3—Mean monthly number of captures per survey and sex ratios for Yuma Myotis (MYYU) and silver-haired bats (LANO) captured during 74 mist net surveys in redwood forests of northwestern California 2008 to 2010.

Fur of LANO was higher than MYYU in $\delta^{13}C$ ($F_{1,49.2}$= 5.86, p = 0.019; *table* 1) though mean difference between species was small (0.8 ± 0.3‰). We found no difference in $\delta^{15}N$ between LANO and MYYU ($F_{1,70.9}$= 2.77, p = 0.101). On average LANO fur was 1.9 ± 0.7‰ higher for $\delta^{34}S$ than MYYU ($F_{1,91.1}$= 6.60, p = 0.012, *table* 1) and patterns differed between the species according to site where fur was collected. MYYU exhibited a visual trend toward lower $\delta^{34}S$ with increasing distance from the Pacific Ocean, but LANO did not (*fig. 4*). Neither sex (all $p \geq 0.240$), nor the interaction of species and sex (all $p \geq 0.092$), explained significant portions of the variation for any of the four isotopes.

Discussion

Seasonal activity patterns

Our study confirmed that bats are active year-round in redwood forests of NWCAL but that the species responsible for this activity differ markedly on a seasonal basis. MYYU was the most frequently captured species and followed a

Table 1—*Mean stable isotope values (‰) in fur by sex, for Yuma myotis (MYYU) and silver-haired bats (LANO) captured during all seasons of the year in redwood forests of northwestern California 2008–2009.*

Element	Species	Sex	*n*	Mean	Range
Hydrogen (δD)	LANO	M	51	-75	-113 to -39
		F	16	-78	-94 to -53
	MYYU	M	34	-75	-111 to -53
		F	22	-67	-105 to -41
Sulfur ($\delta^{34}S$)	LANO	M	42	6.6	-3.5 to 12.9
		F	15	6.2	1.6 to 9.2
	MYYU	M	32	3.5	-4.1 to 12.7
		F	21	5.6	-0.8 to 10.7
Carbon ($\delta^{13}C$)	LANO	M	31	-23.0	-25.0 to -21.5
		F	11	-23.1	-24.8 to -21.9
	MYYU	M	24	-23.9	-29.6 to -21.5
		F	12	-23.8	-26.2 to -21.2
Nitrogen ($\delta^{15}N$)	LANO	M	31	6.4	4.9 to 7.8
		F	11	6.8	4.2 to 9.1
	MYYU	M	24	7.0	5.0 to 10.4
		F	12	7.1	5.6 to 8.6

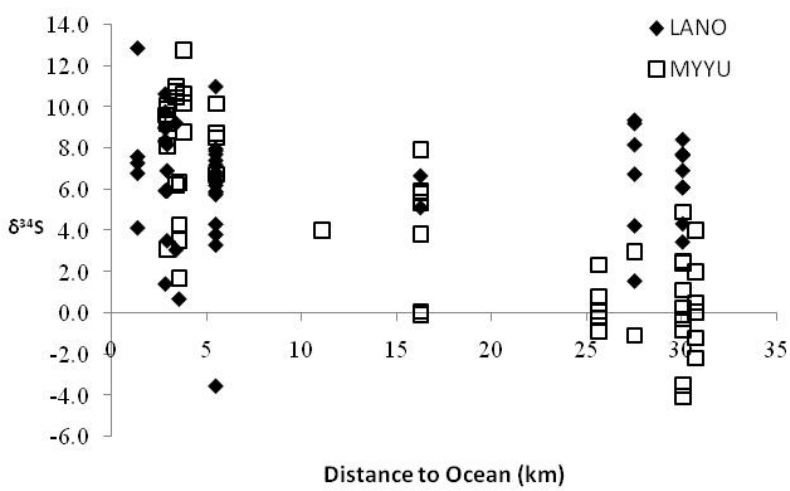


Figure 4—Sulfur isotope ratios ($\delta^{34}S$) in fur of silver-haired bats (LANO) and Yuma myotis (MYYU) versus distance of sample site from the Pacific Ocean during surveys in redwood forests of northwest California 2008 to 2009.

pattern typical for a summer-active resident bat species with captures peaking during June and July and LANO was the most frequently captured species during winter. Hoary bats made significant, if episodic, visits to redwood forests presumably as they migrated through the area.Previous studies with guano traps in basal hollows established that bats are active throughout the winter in NWCAL, though at much lower levels than during summer (Gellman and Zielinski 1996, Zielinski and Gellman 1999). However, guano traps likely index of activity by *Myotis* spp. and big brown bats because LANO are not likely to make significant use of basal hollows (Zielinski et al. 2007). Both sexes of MYYU are summer residents of redwood forests and they likely hibernate during winter, although hibernation sites are unknown throughout their range (Verts and Carraway 1998). Although winter captures of LANO have previously been recorded in redwood forests (Zielinski and Gellman 1999), our results establish that such activity is common. Further our work is in agreement with previous reports that captures of LANO in redwood forests of NWCAL are nearly all male during summer while sex ratios are roughly equal from November-March (Zielinski and Gellman 1999). This strongly indicates that female LANO migrate elsewhere for parturition and pup-rearing before returning to the northwest coast of California to overwinter.

The closest summer records of female LANO are from the upper Sacramento River Canyon (Rainey 1994), Whiskeytown National Recreation Area, and Lassen National Forest (Morrell and Duff 2005), all > 150 km inland. Whether LANO that winter in redwoods of NWCAL spend summers in these areas, or are drawn from a wider range of geographic locations, is unknown. The attractiveness of NWCAL may be explained by relatively moderate winter temperatures that are conducive to tree-roosting (Cryan 2003). Areas, such as redwood forests of NWCAL, which maintain ambient winter temperatures of 5 to 10 °C may be energetically optimal for LANO (Dunbar 2007). Further, cool summer temperatures in redwood forests may enable male LANO to maximize use of torpor (Weller et al. 2009). The presence of both male and female LANO beginning in autumn and continuing throughout winter suggests that redwood forests may be important locations for mating in this species. Hence redwood forests of NWCAL could prove a vital area for maintenance of LANO populations at regional- or, perhaps, continental-scales.

Stable isotopes

Ours is the first study to report stable isotope values in the fur of either MYYU or LANO. The range of values for all four isotopes was similar among both sexes and species. Contrary to our expectations we did not find that isotope values in female LANO differed from MYYU or male LANO. Instead, mean values were similar and LANO females exhibited the narrowest range of values for δD, $\delta^{13}C$, and $\delta^{34}S$ (*table 1*), although this group had the smallest sample size.

The 40 to 70 ‰ range in δD we observed is similar to ranges of four species in the eastern U.S. (Britzke et al. 2009) and a sedentary population of big brown bats in Colorado (Cryan et al.[3]). The wide range of δD values we observed could be associated with bats making relatively short regional movements (e.g., to Sacramento Valley) across a steep gradient in δD values from the Pacific Coast (Bowen et al. 2005). As such, the range of δD values may not differ much between male and female LANO or MYYU individuals. We observed a 70‰ range of δD values for MYYU captured over 1.4° range in latitude. This is similar to the apprximately 60‰ range of δD over a 2° range in latitude reported for little brown bats (*M. lucifugus*;

[3] Cryan, P.M.; Stricker, C.A.; Wunder, M.B. **Biologically structured isotopic variation in a sedentary population of bats.** Unpublished draft supplied by authors.

Britzke et al. 2009). This level of within-area variability in δD is troubling because it could equally have been interpreted as movements over multiple degrees of latitude (Wunder et al. 2005, Cryan et al. unpublished draft); which seems particularly unlikely for MYYU. These findings underscore the challenges inherent in using isoscapes to characterize migratory movements of animals because assignment of tissue origin requires characterization of the isoscape at multiple spatial and temporal scales (Wunder 2010).

The range of stable isotope values present in local bat communities has only recently been the subject of study (Britzke et al. 2009, Cryan et al. [see footnote 3]), and it is possible that it may be great enough to preclude identification of all but long distance seasonal movements (e.g. > 500 km). A primary impediment to the use of stable isotopes in bat fur is poor understanding of molt (Britzke et al. 2009). A single molt in bats is expected during July and August (Constantine 1957, Cryan et al. 2004) but molt may be protracted over a month, even at a single locale (Constantine 1957). In addition, timing of molt may vary by latitude, species, or sex (Constantine 1957). The consequences of these molt characteristics are magnified if seasonal movements are concurrent with new fur growth (Britzke et al. 2009). Further impediments include poor resolution of δD baselines relative to the scale of daily or seasonal movements (Wunder and Norris, 2008), lack of controlled experiments linking diet and water to isotope values in mammalian consumers (Martinez del Rio et al. 2009), and inherent system noise.

Although used successfully in other studies (Rubenstein et al. 2002) the combination of δD with $\delta^{13}C$ and $\delta^{15}N$ did not appreciably improve our understanding of the seasonal movement patterns of LANO or MYYU. The range of values we observed were relatively similar among the four species-sex groups we evaluated and to a population of big brown bats in Colorado (Cryan et al. unpublished draft). We believe the most parsimonious explanation for the wide range in $\delta^{13}C$ and $\delta^{15}N$ for both MYYU and LANO is that they are habitat and dietary (Ober and Hayes 2008) generalists.

We conjectured that $\delta^{34}S$ may provide longitudinal inference because of our study area's proximity to the Pacific Ocean (Zazzo et al. 2011). Indeed we observed a pattern in MYYU fur with lower $\delta^{34}S$ values as distance from coast increased; a pattern not observed in LANO. Taken together these observations are consistent with the hypothesis that capture locations reflect location of fur growth for MYYU but not LANO. If confirmed, this pattern suggests that the $\delta^{34}S$ gradient is quite steep inland from the ocean and that $\delta^{34}S$ may be a useful tool for evaluating local- versus regional-scale movements of bats.

Conclusions

As a result of year-round capture activities we determined that the bat communities in redwood forests of NWCAL are dominated by MYYU in the summer, LANO in the winter, and may also provide important stopover habitat for hoary bats during fall and spring migration. Female LANO appear to migrate from the redwoods during spring and return to them during autumn. Male and female LANO are only together during autumn through spring when mating occurs, further emphasizing the importance of redwood forests of NWCAL to LANO populations at regional- and perhaps continental-scales.

Despite spatial segregation between male and female LANO during their presumed molt period, we did not find differences between the sexes in range of isotope values in their fur. Further, the range of isotope values in the presumably migrant LANO did not differ from the presumably resident MYYU. Although differences in mean values were observed between the species for $\delta^{34}S$ and $\delta^{13}C$, broad ranges in individual dietary preferences may obscure inferences about summer ranges of MYYU and LANO in our study area (Cryan et al. unpublished draft). Nevertheless, we noted a promising trend between $\delta^{34}S$ and distance to coast for MYYU which may prove useful in future work.

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References

Bowen, G.J.; Wassenaar, L.I.; Hobson, K.A. 2005. **Global application of stable hydrogen and oxygen isotopes to wildlife forensics.** Oecologia 143: 337-348.

Britzke, E.R.; Loeb, S.C.; Hobson, K.A.; Romanek, C.S.; Vonhof, M.J. 2009. **Using hydrogen isotopes to assign origins in bats in the eastern United States.** Journal of Mammalogy 90(3): 743-751.

Constantine, D.G. 1957. **Color variation and molt in *Tadarida brasiliensis* and *Myotis velifer*.** Journal of Mammalogy 38: 461-466.

Cryan, P.M. 2003. **Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America.** Journal of Mammalogy 84: 579-593.

Cryan, P.M.; Bogan, M.A.; Rye, R.O.; Landis, G.P.; Kester, C.L. 2004. **Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration.** Journal of Mammalogy 85: 995-1001.

Dunbar, M.B. 2007. **Thermal energetics of torpid silver-haired bats.** Acta Theriologica 52: 65-68.

Fellers, G.F.; Pierson, E.D. 2002. **Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California.** Journal of Mammalogy 83: 167-177.

Gellman, S.T.; Zielinski, W.J. 1996. **Use by bats of old-growth redwood hollows on the north coast of California.** Journal of Mammalogy 77: 255-265.

Martinez Del Rio, C.; Wolf, N.; Carleton, S.A.; Gannes, L.Z. 2009. **Isotopic ecology ten years after a call for more laboratory experiments.** Biological Reviews 84: 91-111.

Morrell, T.E.; Duff, A.A. 2005. **Distribution and relative abundance of bats in Whiskeytown National Recreation Area, Lassen Volcanic National Park, and Lassen National Forest: with emphasis on predicting bat occurrence using landscape scale characteristics.** Technical Report No. 5. Final Report 2005. Muncie, IN: Department of Biology, Ball State University.

Ober, H.K.; Hayes, J.P. 2008. **Prey selection by bats in forests of western Oregon.** Journal of Mammalogy 89: 1191-1200.

Przyborowski, J.; Wilenski, H. 1940. **Homogeneity of results in testing samples from Poisson series: with an application to testing seed clover for dodder.** Biometrika 31: 313-323.

Racey, P.A. 2009. **Reproductive assessment in bats.** In: Kunz, T.H.; Parsons, S., editors. Ecological and behavioral methods for the study of bats. Baltimore, MD: Johns Hopkins University: 249-264.

Rainey, W.E.; Pierson, E.D.; Colberg, M.; Barclay, J.H. 1992. **Bats in hollow redwoods: seasonal use and role in nutrient transfer into old-growth communities.** Bat Research News 33: 71.

Rainey, W.E.; Pierson, E.D. 1994. **Maternity roosts and geographic scale of foraging activity of *Lasionycteris noctivagans* in northern California forests.** Bat Research News 35: 111.

Rubenstein, D.R.; Chamberlain, C.P.; Holmes, R.T.; Ayres, M.P.; Waldbauer, J.R.; Graves, G.R.; Tuross, N.C. 2002. **Linking breeding and wintering ranges of a migratory songbird using stable isotopes.** Science 295: 1062-1065.

Verts, B.J.; Carraway, L.N. 1998. **Land mammals of Oregon.** Berkeley, CA: University of California Press. 668 p.

Weller, T.J.; Scott, S.A.; Rodhouse, T.J.; Ormsbee, P.C.; Zinck, J.M. 2007. **Field indentification of the cryptic vespertilionid bats, *Myotis lucifugus* and *M. yumanensis*.** Acta Chiropterologica 9: 133-147.

Wunder, M.B. 2010. **Using isoscapes to model probability surfaces for determining geographic origins.** In: West, J.B.; Bowen, G.J.; Dawson, T.E.; Tu, K.P., editors. Understanding movement, pattern, and process on Earth through isotope mapping. New York: Springer: 251-270.

Wunder, M.B.; Norris, D.R. 2008. **Improved estimates of certainty in stable-isotope-based methods for tracking migratory animals.** Ecological Applications 18: 549-559.

Wunder, M.B.; Kester, C.L.; Knopf, F.L.; Rye, R.O. 2005. **A test of geographic assignment using isotope tracers in feathers of known origin.** Oecologia 144: 607-617.

Zazzo, A.; Monahan, F.J.; Moloney, A.P.; Green, S.; Schmidt, O. 2011. **Sulphur isotopes in animal hair track distance to sea.** Rapid Communications in Mass Spectrometry 25: 2371-2378.

Zielinski, W.J.; Gellman, S.T. 1999. **Bat use of remnant old-growth redwood stands.** Conservation Biology 13: 160-167.

Zielinski, W.J.; Mazurek, M.J.; Zinck, J. 2007. **Identifying the species of bats roosting in redwood basal hollows using genetic methods.** Northwest Science 81: 155-162.