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STABLE HYDROGEN ISOTOPE ANALYSIS OF BAT HAIR AS EVIDENCE FOR SEASONAL MOLT AND LONG-DISTANCE MIGRATION

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Although hoary bats (*Lasiurus cinereus*) are presumed to be migratory and capable of long-distance dispersal, traditional marking techniques have failed to provide direct evidence of migratory movements by individuals. We measured the stable hydrogen isotope ratios of bat hair (δD_h) and determined how these values relate to stable hydrogen isotope ratios of precipitation (δD_p). Our results indicate that the major assumptions of stable isotope migration studies hold true for hoary bats and that the methodology provides a viable means of determining their migratory movements. We present evidence that a single annual molt occurs in *L. cinereus* prior to migration and that there is a strong relationship between δD_h and δD_p during the molt period. This presumably reflects the incorporation of local δD_p into newly grown hair. Furthermore, we present evidence that individual hoary bats are capable of traveling distances in excess of 2,000 km and that hair is grown at a wide range of latitudes and elevations. Stable hydrogen isotope analysis offers a promising new tool for the study of bat migration.

Key words: deuterium, hoary bat, hydrogen, *Lasiurus cinereus*, migration, molt, stable isotopes

Hoary bats (*Lasiurus cinereus*) are one of the most widely distributed New World bat species, with populations ranging from southern Argentina and Chile to northern Canada (Shump and Shump 1982). Although circumstantial evidence of migration in this species is plentiful (Cryan 2003), there have been no successful efforts to track long-distance movements (>100 km) of individuals. In North America, seasonal differences in the distribution of occurrence records indicate that *L. cinereus* moves within the continent, winters primarily in California and Mexico, and disperses north and east during spring and summer (Cryan 2003; Findley and Jones 1964). Occurrence records also show that the sexes segregate across the continent during summer and that females potentially migrate farther than males. However, traditional methods of tracking long-distance movements by bats are inefficient and often fail to provide satisfactory information; thus, such distribution patterns have remained largely unconfirmed. Although information from banded bats offers direct evidence

of movement, recaptures of marked individuals are very rare, particularly for solitary species such as *L. cinereus* (Griffin 1970). Eventually, the use of miniaturized radio or satellite transmitters may help resolve questions of migratory pathways in bats, but radiotransmitters that are suitable for most North American bat species (e.g., <1 g) do not have sufficient range (i.e., >10 km) or battery life for tracking bats over long distances. Furthermore, banding and tracking are costly, time consuming, and require considerable effort relative to the amount of information gathered.

In recent years, animal ecologists have been analyzing stable isotope ratios of biogenic materials (e.g., feathers, whale baleen, butterfly wings) to track long-distance movements of migratory animals (Hobson 1999). Hydrogen has proven particularly useful for such studies. The mean annual stable-hydrogen isotope ratio (δD) of local precipitation and groundwater changes with latitude and elevation (Dansgaard 1964; Sheppard et al. 1969; Taylor 1974). After an initial change in isotope ratios between precipitation and primary producers (Ziegler 1988), δD is generally conserved among trophic levels (Estep and Dabrowski 1980). Thus, body tissues of primary consumers (e.g., insects) and their predators (e.g., birds) incorporate similar δD values, which typically correlate with hydrogen isotope ratios of local precipitation

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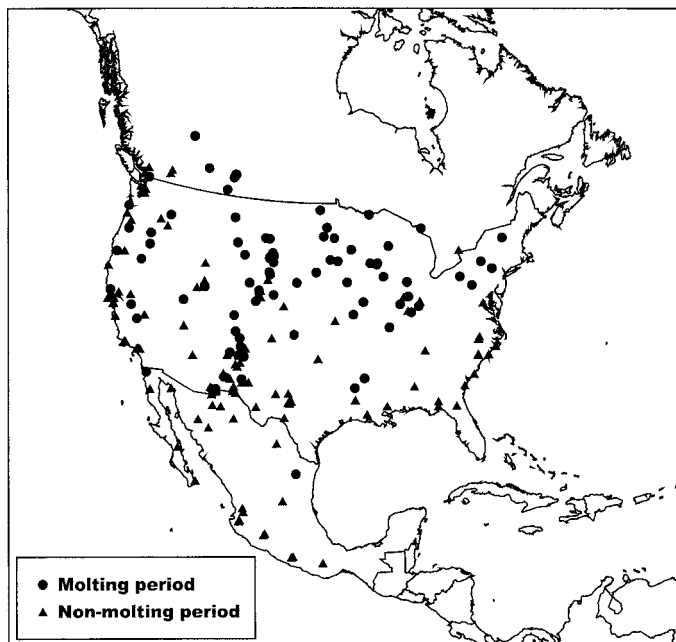


FIG. 1.—Localities where hair samples from *Lasiurus cinereus* analyzed during this study were collected. Circles represent those bats captured during the molting period (between 20 June and 23 August, determined herein), which were then used to determine the relationship between stable hydrogen isotope ratios of local precipitation (δD_p) and hair (δD_h). Triangles represent all other bats.

(δD_p —Hobson and Wassenaar 1997). This relationship between δD_p and the δD values of animal tissues has enabled researchers to infer the geographic origins of migratory birds by analyzing feather tissue collected on the wintering grounds or during migration (Chamberlain et al. 1997; Hobson and Wassenaar 1997, 2001; Meehan et al. 2001). Many species of birds grow feathers before autumn migration; the isotopic signatures of those feathers thus reflect δD_p values of the breeding rather than the wintering area.

Like bird feathers, mammal hair is comprised mainly of keratin, so feathers and hair may incorporate hydrogen in a similar manner during growth. Bats typically molt into new pelage just once per year (Quay 1970), so it is reasonable to assume that the stable hydrogen isotope ratio of bat hair (δD_h) will reflect δD_p of the locale where the hair was grown. Therefore, as with feathers, movements from areas where hair was grown should be discernible using stable isotope analysis.

The potentially long distances traveled by *L. cinereus* make it an excellent candidate for studying migratory movements using δD analysis. The species appears to be capable of movements in excess of 2,000 km, as evinced by its occasional appearance at locations far outside of its normal range (e.g., Bermuda, Newfoundland, Northwest Territories, Iceland, and the Orkney Islands) as well as its colonization of the Hawaiian Islands (Shump and Shump 1982). The objectives of this study were to confirm that *L. cinereus* exhibits a single annual molt prior to autumn migration, determine if a relationship exists between δD_h and δD_p where the hair is grown, and measure the minimum distances potentially traveled by *L. cinereus* from

areas where molt occurred, thus establishing whether long-distance migration occurs.

MATERIALS AND METHODS

We analyzed hair samples from 265 *L. cinereus* captured throughout North America between 1894 and 2002 (Fig. 1; Appendix I). These hair samples were taken from live bats and museum specimens. Protocols for capturing and handling live bats followed guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by the University of New Mexico Animal Care and Use Committee. The pelage of *L. cinereus* is distinct and easily discernible from all other bat species in North America. This distinct pelage makes species misidentification unlikely, which is important when dealing with samples contributed by numerous collaborators. Hair (1–2 mg) was cut from the scapular region of each bat and stored in plastic centrifuge tubes. Prior to isotope analysis, hair was cleaned of surface oils using a 2:1 chloroform:methanol solution, weighed (0.25–0.35 mg), and placed into silver foil capsules. All sample analyses were performed at the United States Geological Survey's Stable Isotope Laboratory located in Denver, Colorado. Samples were pyrolyzed in a thermal combustion elemental analyzer (Finnigan MAT, Thermo Finnigan, San Jose, California) prior to analysis by continuous-flow isotope ratio mass spectrometry (Delta^{Plus} XL, Thermo Finnigan). All values are reported in δ notation as parts per thousand (‰) units relative to Vienna Standard Mean Ocean Water (VSMOW). Measured analysis error was $\pm 5\%$. Because about 20% of the hydrogen in keratinous tissue exchanges freely with hydrogen in ambient water vapor (Wassenaar and Hobson 2000b) and because such proportions had not been quantified for mammal hair, preliminary experiments were carried out to determine the amount of free-exchangeable hydrogen in the hair of *L. cinereus* using the steam-equilibration method described by Wassenaar and Hobson (2000b). We determined that 17% of the hydrogen in the hair of *L. cinereus* could exchange with the environment; this value is similar to proportions of exchangeable hydrogen reported for other vertebrate tissues (about 16%–22%—Wassenaar and Hobson 2000b).

The free-exchangeable hydrogen in organic samples presents a problem for stable isotope analyses because temporal or spatial differences in the isotopic composition of ambient moisture can influence analytical results (Wassenaar and Hobson 2003). Thus, the total hydrogen isotope ratio (δD_t) must be corrected for exchangeable proportions if results are to be comparable among studies and laboratories. This requires a calibrated laboratory standard to correct for variation in the isotopic composition of ambient moisture among laboratories and among analyses done over long periods of time. In the absence of widely available laboratory standards for organic samples, we developed our own from hair of a black bear (*Ursus americanus*) collected in Alaska and a male *L. cinereus* collected in New Mexico. Comparative equilibration methods (Wassenaar and Hobson 2000b) yielded nonexchangeable hydrogen isotope ratios (δD_n) for the bear and bat standards of $-164 \pm 2\%$ and $-57 \pm 2\%$, respectively. These standards were included in each batch of samples analyzed and known δD_n of standards was plotted against measured δD_t values to develop a regression equation that was used to calculate δD_n of all other samples in a batch (Wassenaar and Hobson 2003).

To investigate the relationship between δD_p and δD_h , we derived δD_p values for locations where hair samples were collected in the following manner. Localities where bats occurred were assigned latitude and longitude coordinates (Cryan 2003) and incorporated into a geographic information system (GIS; ArcGIS 8.2, Environmental

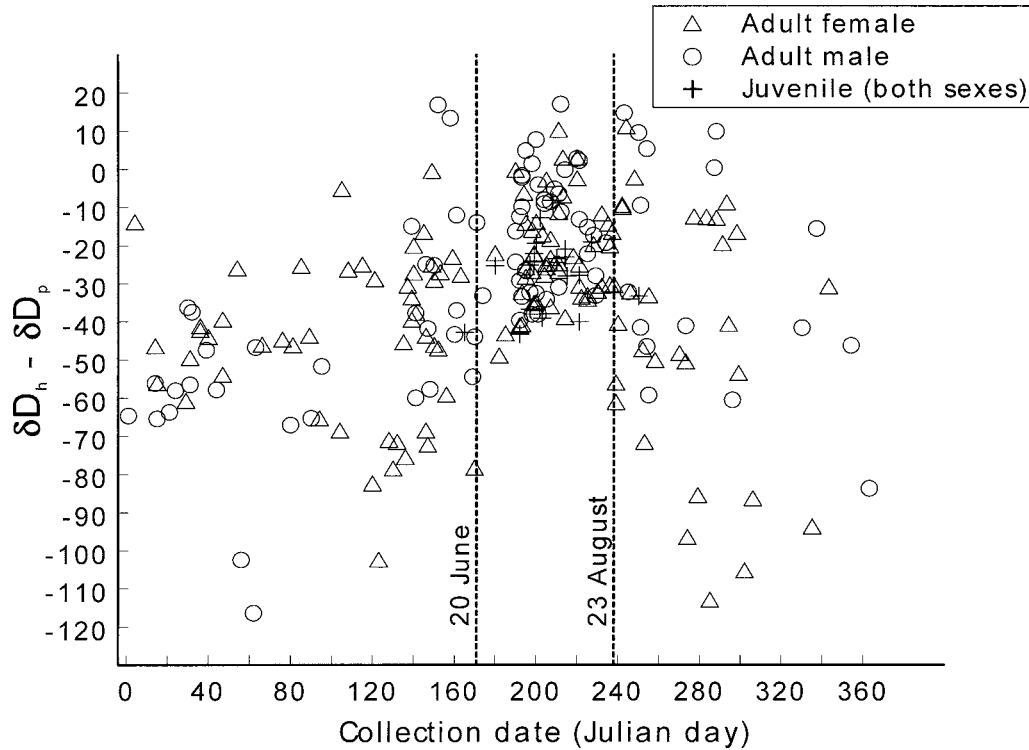


FIG. 2.—Differences between the stable hydrogen isotope ratios of bat hair samples (δD_h) and altitude-corrected mean growing-season precipitation (δD_p), as a function of collection date (Julian day). Vertical dashed lines surround the presumed molt period, determined herein. Isotope ratios are in ‰ relative to Vienna Standard Mean Ocean Water (see text).

Systems Research Institute, Redlands, California). Then, δD_p values were determined for each locality where a bat occurred by spatially relating that locality to the nearest grid cell on an adjacent digital map (cell resolution = 1 km²) of elevation-corrected growing season δD_p for North America (Meehan et al., in press). Because precipitation data spanned a shorter time period (~40 years—Meehan et al., in press) than the hair samples collected for this study (97 years), a major assumption of our analysis was that annual variation in local δD_p did not change in a systematic way over the past century. The δD_p map did not include Mexico, so records from that region were excluded from analyses.

The period during which molt occurred, for the species as a whole, was defined by visually estimating the range of Julian dates during which the difference between isotope ratios of bat hair and collection-locality precipitation ($\Delta\delta D_{hp}$) was closest to the typical offset for keratin-based tissues (approximately -25‰—Wassenaar and Hobson 2001). Relative timing of molt between males, females, and juveniles (both sexes) was investigated by fitting piecewise regression models to the $\Delta\delta D_{hp}$ data for each group and using the breakpoint between the 2 phases of the regression to determine the date during which $\Delta\delta D_{hp}$ among each group was minimized.

We used a 2-step process to estimate the minimum distance traveled by each bat from its capture locality to the nearest area of potential hair growth. First, we quantified the relationship between δD_h and δD_p for samples collected within the defined molt period by fitting a regression slope using the least squares method. This regression model was then used to predict δD_p for the site of hair growth from δD_h values ($\delta D_p = \delta D_h + b_0/b_1$), where b_0 and b_1 represent the intercept and slope of the regression, respectively. Next, we measured the distance from the point where each bat was collected to the nearest locality with the predicted δD_p value, using the elevation-corrected growing season

δD_p map (resolution = 1 km²—Meehan et al., in press). The distance from a bat collection site (km) to the nearest locality with the δD_p value of predicted growth was measured using GIS (estimated error = ±15 km).

Statistical analyses were carried out using NCSS 2000 (Number Crunching Statistical Software, Kaysville, Utah) and SPLUS 2000 (Insightful Corp., Seattle, Washington) for Windows. Tests for differences between sample means were made using *t*-tests. We used 2-way analysis of variance (ANOVA) to investigate the effects of sex and season (winter = December–February; spring = March–May; summer = June–August; autumn = September–November) on the mean minimum distance traveled. Distance data exhibited right-skewed distributions and were normalized using a log 10 transformation prior to analysis. Statistical significance was set at $P \leq 0.05$ and values are given as means ±1 SD.

RESULTS

Variation in $\Delta\delta D_{hp}$ depended on time of year. The least deviation from expected offset values (approximately -25‰) occurred between about 20 June and 23 August (Fig. 2). This period is presumed to represent the molting period. The breakpoint of the 2-phase regression fit to these data for juvenile bats fell on Julian day 207 (26 July), whereas male and female breakpoints fell on days 219 (7 August) and 225 (13 August), respectively. Within the molting period, δD_h averaged $-76.7 \pm 18.6\text{‰}$ (range -123 to -30‰), with no significant differences between sexes ($t = -0.62$, *d.f.* = 102, $P = 0.54$). Outside of the molting period, δD_h averaged $-80.9 \pm 21.0\text{‰}$ (range -136 to -38‰) and there were no significant differences between sexes ($t = -1.44$, *d.f.* = 131, $P = 0.15$).

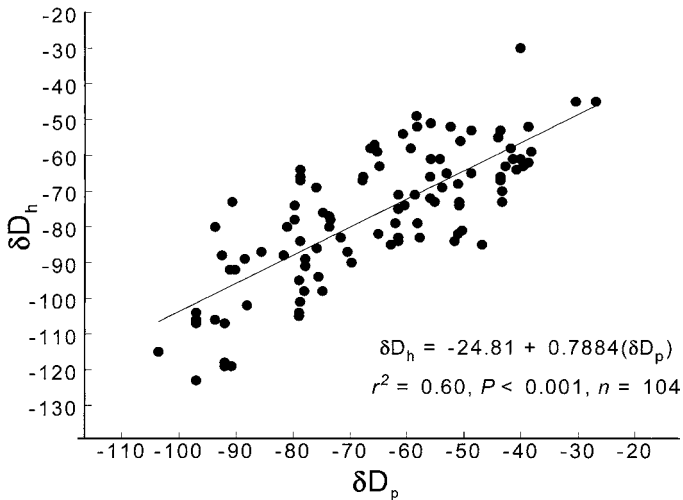


FIG. 3.—Relationship between the stable hydrogen isotope ratio of bat hair (δD_h) and altitude-corrected mean growing-season precipitation (δD_p) at the site of capture. Samples included in this analysis were collected during the period when bats were presumably growing their hair (between 20 June and 23 August). During this period, there was a significant relationship between δD_h and δD_p ($\delta D_h = -24.81 + 0.7884[\delta D_p]$, $r^2 = 0.60$, $P < 0.001$).

During the molting period, there was a significant relationship between δD_h and δD_p ($\delta D_h = -24.81 + 0.7884[\delta D_p]$, $r^2 = 0.60$, $P < 0.001$; Fig. 3). Residuals from this regression model, plotted as a function of time, showed no evidence that variation in the relationship between δD_p and δD_h was systematically related to either day or year of capture. We rearranged the regression model to solve for δD_p and thus estimated precipitation values for the location where hair was grown using the following formula: $\delta D_p = \delta D_h + 24.81/0.7884$.

The minimum distance between capture locality of *L. cinereus* and nearest potential hair growth locality, excluding records from Mexico, was 412 ± 545 km and ranged from 1 to 2,670 km. No significant differences were detected in the minimum distance measured between sexes ($F = 0.58$, $d.f. = 1$, 133 , $P = 0.45$) and the sex-by-season interaction was not significant ($F = 0.66$, $d.f. = 3$, 133 , $P = 0.19$), but there were significant differences among seasons ($F = 3.12$, $d.f. = 3$, 133 , $P < 0.05$). Minimum distance measured between capture locality and nearest potential hair growth locality during summer was less (260 ± 420 km) than other seasons.

The average δD_h value for samples collected in Mexico ($n = 24$; Fig. 1) was -67.3‰ (range -23 to -122‰) and there was no significant difference between the sexes ($t = 0.23$, $d.f. = 22$, $P = 0.82$).

DISCUSSION

We found evidence that *L. cinereus* undergoes a single annual molt during late summer, prior to autumn migration. Considering the wide geographic range across which these samples were collected, the minimal variation in $\Delta\delta D_{hp}$ during late summer (Fig. 2) likely reflects molt into new hair and

incorporation of local hydrogen isotopes from precipitation. Greater variation in $\Delta\delta D_{hp}$ values during autumn, winter, and spring suggests that bats collected during those seasons were less likely to have grown their hair at the capture site. The timing of molt, as indicated by the isotope data, coincides with the expected molt period for *L. cinereus* and other North American bat species. In the few bat species for which molt data are available, pelage replacement generally occurs between mid-July and mid-August (Constantine 1957, 1958; Jones and Genoways 1967). Furthermore, available evidence suggests that, relative to males, females typically delay molt until lactation ceases (Jones and Genoways 1967; Quay 1970). The breakpoints of our 2-phase regression models indicated that the molt of female *L. cinereus* was indeed delayed, as the first groups to exhibit δD_h values close to local δD_p were juveniles and then males. Parturition in *L. cinereus* occurs from late May through June (Shump and Shump 1982), followed by a 3–4-week lactation period (Bogan 1972) that extends to the end of July in some regions (Turner 1974). Assuming that lactation in female *L. cinereus* ends between early July and early August, our isotope data suggest that growth of new hair, at least on the dorsal pelage where we sampled, occurs in a relatively short time (about 2 weeks). Although new pelage is often apparent on hoary bats during autumn, evidence of active molt (i.e., molt lines) is not easily discernible (Bogan 1972). Stable isotope analysis offers a new method for studying molt in *L. cinereus* as well as other mammal species with cryptic patterns of hair replacement.

The strong positive relationship that we observed between δD_h and δD_p is similar to relationships observed between δD of bird feathers and water in other studies (Table 1). Although mammal hair is comprised of α -keratin and bird feathers are made of β -keratin, processes of hydrogen uptake from food and water into these tissues are apparently similar. Within the molting period, δD_p explained 60% of the variation in δD_h in *L. cinereus*. The unexplained variation may be due to differences in temperature (McKechnie et al., in press) or relative humidity (Cormie et al. 1994) across collection sites or years, input of water from sources other than precipitation (Wassenaar and Hobson 2000a), error in δD_p estimates, or movement by bats shortly after they grow new hair. In the last case, northward dispersal by hoary bats during late summer and autumn (Cryan 2003) may help explain some of the relatively enriched values for hair seen between early June and late October ($\Delta\delta D_{hp} > 0$; Fig. 2).

Although bats analyzed in this study were collected over a time period spanning 97 years, we found no evidence that year or day of capture influenced the average relationship between δD_h and δD_p . Therefore, we agree with Lott et al. (2003) that museum specimens, regardless of collection year, are an important resource for isotopic studies.

Our relatively large differences between δD_h and the corrected value of local δD_p in *L. cinereus* (e.g., -76‰) provide the first physical evidence of long-distance movement by individual hoary bats. While the dispersal abilities of *L. cinereus* were previously assumed, stable isotope methods offer a means of not only verifying, but also quantifying, such movements. For example, the δD_h value of a male taken during

TABLE 1.—Relationship between stable hydrogen isotope ratios of various sources of water (δD_w) and bird feathers (δD_f) measured in other studies, compared with the relationship between the stable hydrogen isotope ratio of precipitation (δD_p) and bat hair (δD_h) measured in this study.

Species	Equation	r^2	Source
Red-winged blackbird	$\delta D_f = -27 + 1.1\delta D_w$	0.83	Wassenaar and Hobson 2000a
Black-throated warbler	$\delta D_f = -51 + 0.5\delta D_w$	0.86	Chamberlain et al. 1997
Bicknell's thrush	$\delta D_f = -26 + 0.7\delta D_w$	0.48	Hobson et al. 2001
Cooper's hawk	$\delta D_f = -34 + 1.0\delta D_w$	0.83	Meehan et al. 2001
8 raptor species	$\delta D_f = -41 + 0.6\delta D_w$	0.46	Lott et al. 2003
6 songbird species	$\delta D_f = -31 + 0.9\delta D_w$	0.83	Hobson and Wassenaar 1997
Hoary bat	$\delta D_h = -25 + 0.8\delta D_p$	0.60	This study

September in the state of Chihuahua, Mexico, indicated that δD_p where it grew the hair was -123‰ . The closest region with δD_p values near -123‰ was located north of the Canadian border, more than 2,000 km from where this bat was captured. One of the lowest δD_h values observed during this study ($\delta D_h = -132\text{‰}$) came from a female captured in southern Arizona during October. This value indicated that her hair was also grown in an area north of the Canadian border and provides evidence for dispersal by female hoary bats of $>1,800$ km.

Stable isotope ratios from *L. cinereus* collected in Mexico were not included in our analyses, but offer insight into the distribution of the species during the molting period. Values of δD_h from Mexico samples that ranged between -23‰ and -122‰ suggest that hoary bats occur over a wide range of latitudes and elevations during the molting period. For example, the δD_h values of 4 *L. cinereus* collected in the Mexican state of Guerrero were -57 , -71 , -100 , and -104‰ . These values imply that some of the bats occurring in Mexico are year-round residents of lowland areas in the southwestern United States and Mexico, while others may be molting during summer in areas farther north or at higher elevations. Hobson and Wassenaar (2001) observed similar variation in hydrogen isotope signatures among wintering shrikes collected in Mexico.

Because isotopic signatures of water decrease with increasing elevation (about -0.28‰ per 100 m—Bowen and Wilkinson 2002; Hobson et al. 2003; Poage and Chamberlain 2001) as they do with increasing latitude, our calculations of the minimum distances moved by *L. cinereus* may underestimate actual movements. For example, if an isotope signature for hair actually reflected precipitation isotope ratios of high latitudes, rather than nearby high-elevation sites, our methodology likely underestimated the distance traveled. Such underestimation may have been particularly sizeable among female *L. cinereus* collected from western parts of the continent. Unlike males, female hoary bats are uncommon in western North America during the molting period (June–August—Cryan 2003; Findley and Jones 1964). For instance, among the museum records reported by Cryan (2003), 353 female *L. cinereus* were collected between 20 June and 15 August in North America and only 21 of these occurred west of the Continental Divide, the majority ($n = 15$) after the 1st week of August. In addition, female bats in mountainous regions of temperate North America generally tend to avoid higher

elevation sites during the reproductive period (Cryan et al. 2000). If most female *L. cinereus* indeed molt hair at relatively low-elevation sites in eastern North America, many of the high δD_h values observed among females during this study likely reflect northern latitudes rather than the high-elevation sites of the West. If we assume that female hoary bats do not grow new hair in mountainous western regions and measure the distance to the nearest predicted δD_p east of the Continental Divide, minimum distance moved by females = $1,193 \pm 826$ km (range 3–3,096 km). This illustrates how mountainous regions of western North America complicate interpretation of migration studies that are based on δD analysis alone.

Our results demonstrate that the major assumptions of stable isotope migration studies for birds and insects (Hobson 1999) hold also for bats. Given the relative ease of collecting samples, the minuscule quantities of hair needed for analysis, and the potential to increase geographic resolution by incorporating other stable isotopes (e.g., carbon and nitrogen—Chamberlain et al. 1997; Fleming et al. 1993), stable isotope analysis provides a useful new tool for the study of bat migration.

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APPENDIX I

Specimens examined.—The following list of specimens is organized alphabetically by country and state or province from which bats were sampled for stable isotope analysis. Numbers in parentheses represent total number of bats sampled from each area and are followed by catalog numbers of samples taken from museum specimens; the remainder came from bats that were captured and released or else not retained as specimens (e.g., decomposed carcasses). Museum acronyms follow those listed in Hafner et al. (1997). CANADA: Alberta (6), USNM 159407; British Columbia (5), UBC 547, UBC 5390, UBC 5391, UBC 9020, UBC 16814; Ontario (2), JMM 2482, UGDZ 287; Ontario (2), JMM 2482, UGDZ 287; Saskatchewan (4). MEXICO: Baja California (2), MVZ 35429, UNM 43034; Baja California Sur (2), USNM 525312, USNM 531341; Chihuahua (2), MVZ 132194, UNM 27749; Coahuila (1), KU 44746; Guerrero (4), MVZ 106505, MVZ 106850, USNM 329588, USNM 329593; Jalisco (2), KU 92950, KU 100398; Michoacan (2), AMNH 175011, LSUMZ 25095; Nayarit (3), USNM 508889, USNM 508890, USNM 511531; Nuevo Leon (1), KU 98487; San Luis Potosi (1), LSUMZ 4958; Sonora (4), UNM 18305, UNM 19595, UNM 49725, USNM 507126. UNITED STATES: Alabama (1), USNM 178141; Arizona (5), MVZ 71588, UCLA 623; Arkansas (1), LSUMZ 11606; California (31), CSUN 464, CSUN 465, CSUN 1276, MVZ 5148, MVZ 6944, MVZ 20815, MVZ 69087, MVZ 71584, MVZ 80797, MVZ 84261, MVZ 182422, MVZ 182424, SBMNH 206, SBMNH 376, SBMNH 644, SBMNH 718, SBMNH 719, SBMNH 768, SBMNH 782, SBMNH 939, SBMNH 964, UCLA 7753, UCLA 9088, UNM 40648, USNM 187827, UWBM 31877, UWBM 32565; Colorado (15), UCM 6175, UCM 6176, UCM 11458, UCM 18509, UNM 10237, USNM 347568; Florida (2), JMM 3096; Georgia (2), MCZ b6213, USNM 276571;

Idaho (1), MVZ 46945; Illinois (2), BMNHC 6001, MVZ 94699; Indiana (11), AMNH 125637, JMM 995, JMM 2010, JMM 2908, USNM 296436, USNM 363850, USNM 363856, USNM 363857, USNM 363860, USNM 363864, USNM 363866; Iowa (1), KU 112026; Kansas (4), KU 13219, KU 13220, KU 52432, KU 139193; Louisiana (4), LSUMZ 1703, LSUMZ 9234, LSUMZ 11607, LSUMZ 30040; Minnesota (9), MMNH 1042, MMNH 15160, MMNH 18385, UCLA 12033; Missouri (3), UCM 17207; Montana (6), KU 83756, KU 123236, KU 123237, KU 123242, MMNH 9798; Nebraska (5), AMNH 175427, JMM 415, KU 124966; Nevada (1); New Mexico (48), MCZ 18697, NMMNH 2631, UNM 9257, UNM 10019, UNM 11747, UNM 11770, UNM 12739, UNM 13016, UNM 14692, UNM 14693, UNM 16781, UNM 18204, UNM 18205, UNM 21633, UNM 21708, UNM 21708, UNM 25043, UNM 25044, UNM 49728, UNM 64700, UNM 64700, UTEP 5394, UNM 16449, UNM 12827; New York (1), MVZ 167532; North Carolina (10), DMNH 57, NCSM 375, NCSM 376, NCSM 408, NCSM 803, NCSM 5320, NCSM 7691, NCSM 7692, NDSU 993, USNM 209475; Oklahoma (2), OMNH 16369, OMNH 19035; Oregon (11), KU 146494, KU 146494, MVZ 94200, OSUFW 3008, OSUFW 6000, OSUFW 6001, UCLA 17329, USNM 228293, UWBM 48277; Pennsylvania (5), AMNH 258283, AMNH 258285; South Carolina (1), MCZ 17418; South Dakota (8), KU 101651, KU 116364, KU 116367; Tennessee (1), KU 130353; Texas (11), ASNHC 1103, ASNHC 4560, ASNHC 5361, ASNHC 7531, ASNHC 7532, ASNHC 7585, ASNHC 10660, ASNHC 10662, UTEP 1867, UTEP 8341; Utah (5), UMNH 4385, UMNH 6273, UMNH 8007, UMNH 27249, UMNH 28955; Vermont (1); Virginia (1), USNM 565932; Washington (5), UWBM 9219, UWBM 9531, UWBM 39407, UWBM 39407, WCW W44; Wisconsin (4), USNM 227057, UWSP 6087, UWSP 6091, UWSP 6092; Wyoming (6).