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Seasonal patterns in δ^2H values of multiple tissues from Andean birds provide insights into elevational migration

Mariana Villegas,[1,3] Seth D. Newsome,[2] and John G. Blake[1]

[1]*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA*
[2]*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA*

Abstract. Elevational migration is a widespread phenomenon in tropical avifauna but it is difficult to identify using traditional approaches. Hydrogen isotope (δ^2H) values of precipitation decrease with elevation so δ^2H analysis of multiple bird tissues with different isotopic incorporation rates may be a reliable method for characterizing seasonal elevational migration. Here we compare δ^2H values in metabolically inert (feathers and claws) and metabolically active (whole blood) tissues to examine whether an upslope migration occurs prior to the breeding season in the Yungas Manakin (*Chiroxiphia boliviana*). We compare results from *C. boliviana* with data from a known elevational migrant, the Streak-necked Flycatcher (*Mionectes striaticollis*). Opposite to our expectations, tissue δ^2H values increased over time, largely reflecting seasonal patterns in precipitation δ^2H rather than elevational effects; linear mixed-effects models with strongest support included ordinal date, tissue type, and elevation. This seasonal increase in precipitation δ^2H is a general phenomenon in both tropical and temperate mountain ranges. We use these data to propose a hypothetical framework that predicts different patterns in tissue δ^2H values collected in different seasons from residents and elevational migrants. This framework can serve as a reference for future studies that assess elevational migration in birds and other animals.

Key words: Andes; Bolivia; Chiroxiphia boliviana; elevational migration; isoscapes; manakins; Mionectes striaticollis; stable isotopes; δ^2H.

Introduction

Elevational migration is the seasonal movement of individuals along an elevational gradient (Loiselle and Blake 1991, Levey and Stiles 1992). Specifically, it involves annual movements between low-elevation non-breeding habitats and high-elevation breeding sites and is likely common in tropical avifaunas (Stiles 1988). Movements by birds along elevational gradients in the tropics are largely determined by fruit and flower availability and, hence, many elevational migrants are primarily frugivorous or nectarivorous (Loiselle and Blake 1991, Levey and Stiles 1992). Weather can also drive movement across elevations. For example, Boyle et al. (2010) showed that elevational migration in White-ruffed Manakins (*Corapipo altera*) can be driven by severe storm events that can reduce foraging opportunities.

Most reports of elevational migration are based on observations of seasonal changes in abundance at different elevations (e.g., Loiselle and Blake 1991, Chaves-Campos 2004). Radio-transmitters (e.g., Leopold and Hess 2014) and GPS locators or geologgers (e.g., Norbu et al. 2013) have also been used to track elevational migrants but weight or cost, respectively, may limit their use. Hydrogen isotope (δ^2H) analysis has become a powerful alternative technique for studying bird movement across both latitudes and elevations (Rubenstein and Hobson 2004). Typically, δ^2H values of feathers are compared to isoscapes of precipitation δ^2H values (West et al. 2006, Bowen 2010) to determine general breeding locations where such tissues were grown (e.g., Langin et al. 2007, Studds et al. 2012). While isoscapes accurately depict patterns in precipitation δ^2H values across sub-continental scales, they generally have poor resolution over steep elevational gradients that occur across relatively small spatial scales. Elevational lapse rates in precipitation δ^2H values vary from −1‰ to −4‰ for every 100 m increase in elevation; this effect results from Rayleigh distillation and the depletion of precipitation δ^2H values as an air mass rises orographically and rains out moisture (Poage and Chamberlain 2001). Seasonal variation in precipitation δ^2H values

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across mountainous areas has received less attention than elevational patterns but such variation is also potentially important for interpreting tissue isotope data from both residents and elevational migrants.

Animal tissues have different isotopic incorporation rates and, thus, integrate local hydrogen inputs (water and food) over different time periods (Carleton et al. 2008, Martínez del Rio et al. 2009, Wolf et al. 2012). Feathers are metabolically inert once grown and represent diet and water hydrogen inputs during molt, whereas claws are also inert but grow continuously; an entire passerine claw may contain a ~2–5 month record of ecological information (Bearhop et al. 2003, Mazerolle and Hobson 2005). Metabolically active tissues also have different isotopic incorporation rates. Blood plasma and liver have relatively fast incorporation rates and completely turn over in ~15–30 d, whereas whole blood or muscle integrate hydrogen inputs over ~30–65 d (Wolf et al. 2012) depending on body size. Thus, a comparison among tissues can provide useful information on variation in diet and movement of animals at different periods in their annual life cycle (Mazerolle and Hobson 2005, Newsome et al. 2015), which is essential for characterizing elevational migration.

Few studies have used δ^2H values to study elevational migration in tropical forests and all of them were based in Central and South America. Hobson et al. (2003) reported feather δ^2H, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of eight species of hummingbirds along a large elevational gradient in the Ecuadorian Andes (300–3300 m), and found a strong elevational relationship between feather δ^2H and precipitation δ^2H. Although based on small sample sizes, Fraser et al. (2008) examined δ^2H values in claws and feathers of five bird species in Nicaragua, and suggested that significant differences between these tissues could indicate upslope migration. Hardesty and Fraser (2010) measured δ^2H values in feathers and blood of nectarivores and insectivores across a ~2150 m elevation gradient in Ecuador; they found little evidence of elevational migration, and suggested that use of δ^2H in regions like the Andes, where δ^2H discrimination between precipitation and bird tissues is poorly understood, should be applied with caution. Boyle et al. (2011) examined δ^2H values in claws and showed that individual decisions to migrate in *Corapipo altera* can vary from year to year; for some males, elevational migration may increase survival while for others that do not migrate, residency may be an honest signal of quality to females. Finally, a recent study compared δ^2H, $\delta^{13}C$ and $\delta^{15}N$ values in metabolically inert and active tissues of Ovenbirds (Furnariidae, genus *Cinclodes*) in Chile, and found that individual δ^2H offsets between feather and muscle are a reliable proxy for evaluating elevational migration; this study also reported variation in elevational and latitudinal migration at the species, population, and individual level (Newsome et al. 2015).

Manakins (Pipridae) are frugivorous lekking birds distributed throughout the Neotropics in humid lowland forests (Snow 2004). In this study, we focus on the Yungas Manakin (*Chiroxiphia boliviana*) that inhabits humid hill forests along the eastern slope of the Andes of Bolivia and Peru and generally occurs at higher elevations (600–2600 m) than other members of the genus (Schulenberg et al. 2007, Kirwan and Green 2012). Males begin to display and sing in June (Graves et al. 1983; M. Villegas, *personal observations*) with a peak in breeding between August and December (Merkord 2010). Manakins, in general, have one annual molt at the end of the breeding season (Ryder and Wolfe 2009), which for *C. boliviana* would be in December–January. Evidence for elevational movements by *C. boliviana* is mixed. Merkord (2010) studied seasonal movements of Peruvian bird communities and categorized *C. boliviana* as a resident even though recapture data provided some evidence for seasonal elevational movements. Tobias and Seddon (2007) also suggested that non-breeding individuals may make elevational movements. Previous data on manakins, particularly observations and claw δ^2H values of *Corapipo altera* in Costa Rica, show that some individuals (usually males) migrate downslope for a variable number of months and then return to higher elevations to breed (Loiselle and Blake 1991, Boyle et al. 2010, 2011). Similarly, recent telemetry data for Long-tailed Manakins (*Chiroxiphia linearis*) suggest that some individuals may migrate upslope during the dry season (A. C. Hsuing, *personal communication*).

In this study, we ask if *C. boliviana* in the central Andes of Bolivia makes elevational movements during its annual life cycle, and specifically if it moves to higher elevations (upslope) to breed. We address this question by comparing δ^2H values between metabolically inert (feathers and claws) and metabolically active (whole blood) tissues collected during the breeding season from June to October. We expected feather δ^2H values to remain constant across elevations or over time because they represent a short period of the annual life cycle when birds are molting after the breeding season. In contrast, we expected claws and blood δ^2H values to decrease over time as the birds moved upslope to breed, as these tissues can record movement (e.g., elevational shifts) over several months prior to capture. We hypothesize that this variation can be used as an indication of upslope movement that occurred prior to the breeding season. We also test whether *C. boliviana* is an elevational migrant by comparing its tissue δ^2H patterns with the Streak-necked Flycatcher (*Mionectes striaticollis*), an elevational migrant (Walker et al. 2006, Merkord 2010) with a similar elevational range (550–2750 m).

Methods

Study area and sample collection

Birds were sampled at three sites in Yungas primary and secondary montane tropical forests near La Paz, Bolivia along the eastern slopes of the Andes: Sandillani

(16°13′ S, 67°52′ W, 1700–2000 m) and El Jiri (16°11′ S, 67°45′ W, 1300–1550 m) located in Cotapata National Park, and Carmen Pampa (16°15′ S, 67°41′ W, 1800–2200 m) located on the northeastern slope of Uchumachi Mountain. All three sites represent breeding elevations. We collected tissues from 69 individuals of *C. boliviana* and 39 individuals of *M. striaticollis* from June to October 2013 and from July to September 2014. Upon capture of each bird, we took a 2–3 mm sample of the tip of the claw from the middle toe of both feet, and plucked an outer tail feather. Claws and feathers were stored in small paper envelopes. In July–September 2014, we also collected whole blood from the brachial vein of the left wing from each bird; blood was stored in microcentrifuge tubes and dried in an oven at ~70°C.

Sample preparation and isotope analysis

Surface contaminants were removed from claws and feathers by rinsing them in a 2:1 chloroform:methanol solvent solution, after which samples were air dried. We then sealed ~0.2–0.4 mg of each tissue into a silver capsule. We typically weighed the entire claw sample for a single analysis; for tail feathers, we clipped a small portion (~1 cm) of the tip of the vane with scissors and homogenized it with surgical scissors prior to weighing. Dried whole blood was directly weighed into silver capsules.

δ²H values were measured with a high-temperature conversion elemental analyzer (TCEA) coupled to a Delta V isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) at the University of New Mexico Center for Stable Isotopes (UNM–CSI). Isotope results are expressed as δ values as $\delta^2H = 1000 \times [(R_{sample} - R_{standard})/R_{standard}]$, where R is the $^2H/^1H$ ratio of the sample and standard, and the units are expressed as parts per thousand or per mil (‰). The internationally accepted standard for hydrogen is Vienna Standard Mean Ocean Water (VSMOW). δ²H values were corrected for hydrogen exchange with ambient water vapor using three keratin and three whole blood internal reference materials for which non-exchangeable δ²H values were measured by comparative bench-top equilibration experiments (Bowen et al. 2005), followed by external verification with two other laboratories. The within-run analytical precision (SD) of these reference materials was ≤3‰. We also downloaded data from the Global Network of Isotopes in Precipitation (GNIP; IAEA/WMO 2015) from four meteorological stations that were in close proximity (~5–53 km) to our collection sites.

Statistical analyses

We used both general linear models (i.e., ANCOVA) and general linear mixed-effects models (LMM) to test for differences in δ²H values as a function of several explanatory variables (Appendix S1: Table S1): tissue (categorical with three levels: feathers, claws, and blood),

ordinal date of capture (continuous), elevation of capture (continuous), and sex/age (categorical, with four levels). Since we had δ²H data for multiple tissues from each bird, we used LMM models with individual as a random factor to test for individual variability; models were performed with the lme4 package (Bates et al. 2014) in R (R Core Team 2015). P values were obtained by likelihood-ratio tests of different models with and without the effects in question. The best models were selected based on the Akaike information criterion (AIC) score.

Results

Seasonal variation in precipitation

GNIP data revealed variation in precipitation δ²H values related to both elevation and season at four stations in the study area that ranged from 600 to 3100 m in elevation (Fig. 1). In general, precipitation δ²H decreases with elevation, however, the magnitude of the decrease is much smaller than the seasonal increase in precipitation δ²H values from the rainy season (November–March) to the dry season (May–August).

Bird tissue isotope values and models

Overall, *C. boliviana* had lower δ²H values than *M. striaticollis* (Fig. 2; Appendix S1: Table S2). Blood had the lowest mean (±SD) δ²H values, followed by feathers and claws for both *C. boliviana* and *M. striaticollis* (Appendix S1: Table S2). The slope of the positive linear relationship between tissue δ²H values and ordinal date (Fig. 2; Appendix S1: Table S3) was not significantly different between *C. boliviana* and *M. striaticollis* for claws ($z = 0.78$, $P = 0.22$) or blood ($z = -0.07$, $P = 0.47$); for feathers, there was no significant relationship between δ²H values and ordinal date in either species (Appendix S1: Table S3).

For *C. boliviana*, the model with the lowest AIC score and strongest support included ordinal date, tissue type, and elevation as variables ($R^2 = 0.56$, $n = 69$, $F_{4,147} = 45.56$, $P < 0.001$). In this model, ordinal date and elevation had a positive and significant combined effect on δ²H values of all *C. boliviana* tissues (Fig. 2; Appendix S1: Table S4). The model that included sex/age also had high support but there was no significant effect of the different sex/age categories. The mixed-effects model was significant, suggesting individual variability in δ²H values (Appendix S1: Table S4).

For *M. striaticollis*, the model with strongest support included only ordinal date and tissue type as variables ($R^2 = 0.66$, $n = 39$, $F_{3,83} = 54.44$, $P < 0.001$) with individual as a random effect. δ²H values and ordinal date were significantly correlated: positive for claws and blood but slightly negative for feathers (Fig. 2; Appendix S1: Table S4). The model that included elevation also had high support, but we found no significant relationship between δ²H values and elevation.
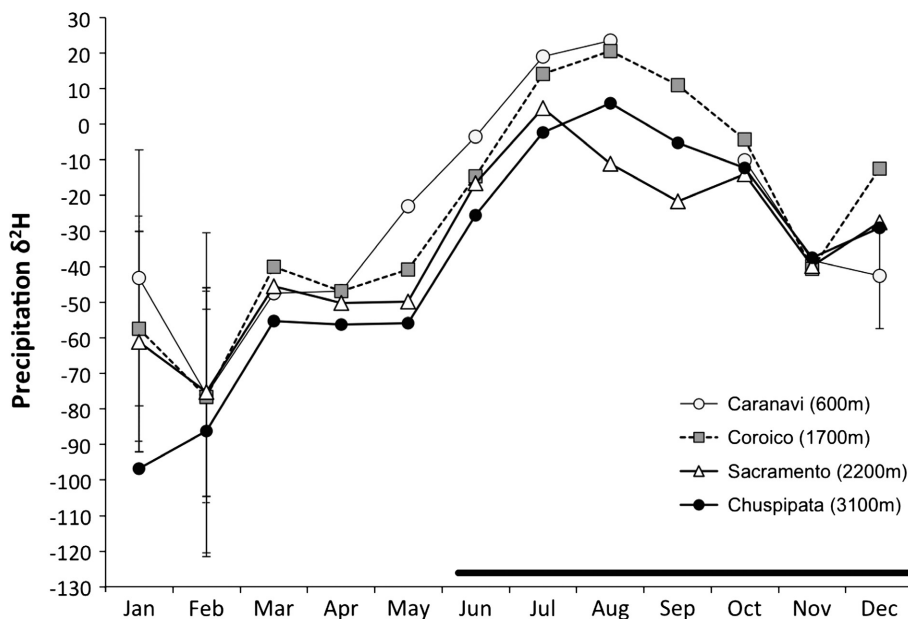
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Fig. 1.   Annual mean δ^2H values of precipitation at four stations in the study area; some stations include error bars (±SD) for data from Dec–Feb because precipitation was sampled for several years at those sites (IAEA/WMO 2015). The horizontal black bar above the *x*-axis denotes the estimated breeding season of the two study species.

DISCUSSION

Our study is one of the few to compare δ^2H values among metabolically inert and active tissues collected from the same individual animal. Given that field observations indicate a lower abundance of birds in May (M. Villegas, *personal observations*), we assumed they were moving upslope to breed at the beginning of June. Thus, if elevation was the only factor driving tissue δ^2H patterns, we would expect tissue δ^2H values to decrease over time as birds moved upslope from the non-breeding to the breeding season. Opposite to our expectations, δ^2H values of metabolically active (blood) or metabolically inert but continuously growing tissues (claws) in both *C. boliviana* and *M. stricaticollis* increased over time (Fig. 2). This pattern suggests that claw and blood tissues of both species primarily reflect seasonal patterns in precipitation δ^2H. The seasonal increase in tissue δ^2H values is opposite to what would be expected if elevational δ^2H lapse rates in precipitation were the primary driver of tissue hydrogen isotope composition, since precipitation δ^2H values decrease with increasing elevation (Poage and Chamberlain 2001, Bowen and Revenaugh 2003). In contrast to claws and blood, tail feathers, as expected, showed no trend with elevation or time of capture as they are metabolically inert and are grown in a short period (~2–3 weeks) during molt (Fig. 2A). In contrast, claws grow continuously and integrate dietary and habitat isotope signatures over 2–5 months prior to sampling (Bearhop et al. 2003) and, thus, provide a useful alternative to feathers when studying elevational migration (Mazerolle and Hobson 2005, Hardesty and Fraser

2010). Our results suggest that like *M. striaticollis*, *C. boliviana* is an elevational migrant because claws and blood show similar patterns for both species (Fig. 2). However, since we do not have data for a resident species that could serve as a control, we admit these conclusions should be viewed with caution.

In the Andes, GNIP data show that at any given elevation, precipitation δ^2H values are higher during the breeding season (~June–December) by ~50–60‰ as opposed to the non-breeding season (~January–May). Furthermore, the magnitude of the seasonal increase in precipitation δ^2H is approximately twice as large as the decrease in precipitation δ^2H observed along the steep elevational gradient for which data are available (600–3100 m; Fig. 1). Thus, if birds are moving upslope to breed, the seasonal variation in precipitation δ^2H values (Fig. 1) must be considered to accurately interpret δ^2H patterns in bird tissues collected from the Andes and elsewhere. Examination of GNIP data from other mountainous areas in temperate and tropical regions shows that this seasonal increase in precipitation δ^2H values between dry and rainy (tropical) or winter and summer (temperate) seasons is a pervasive pattern (Appendix S1: Table S5).

Previous studies with Andean birds have shown that whole blood had significantly lower δ^2H values at a given elevation than feathers (Hardesty and Fraser 2010, Newsome et al. 2015), a pattern also observed in our data (Fig. 2C). This pattern has also been observed in controlled feeding experiments on captive birds that were fed isotopically homogenous food and water (Hobson et al. 1999, Wolf et al. 2011, 2012). A likely explanation for this
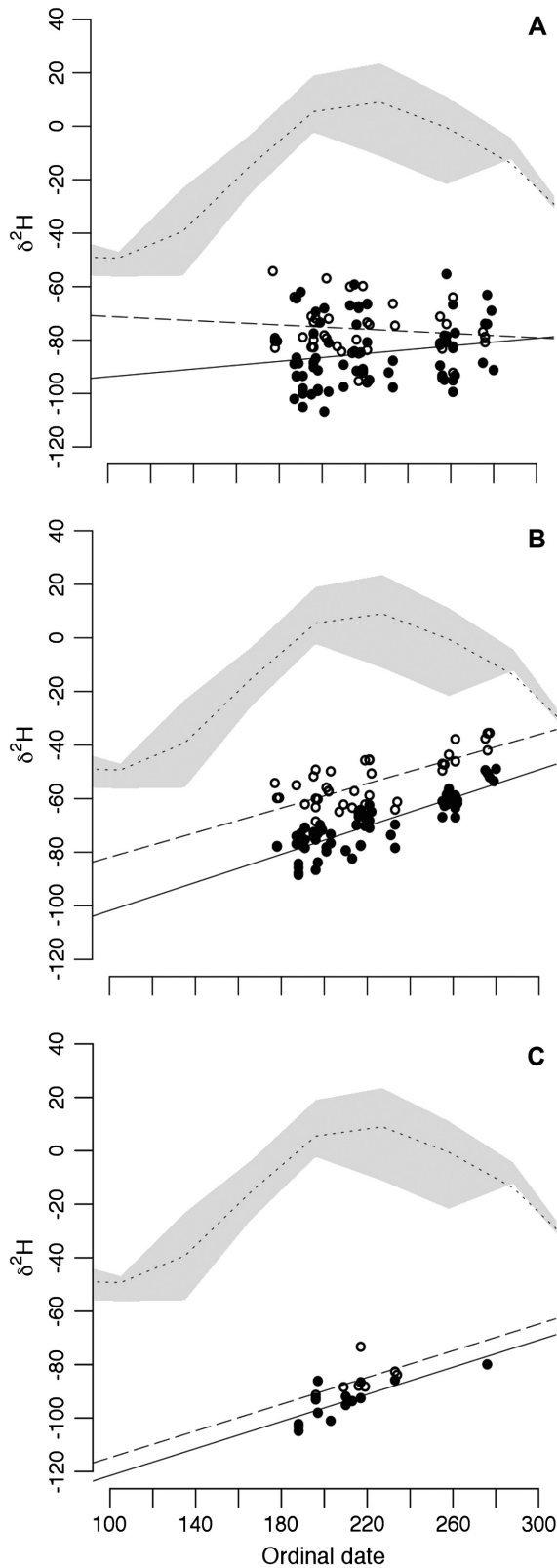
Fig. 2.   δ²H values of (A) feathers, (B) claws, and (C) blood for *Chiroxiphia boliviana* (black circles) and *Mionectes striaticollis* (white circles). The dotted line represents a smoothed curve of the mean monthly precipitation δ²H values from April to October from the four precipitation stations shown in Fig. 1, and the gray band encompasses the monthly range in these values. The lines represent linear relationships between tissue δ²H values and ordinal date (Appendix S1: Table S3); slopes were not significantly different between *Chiroxiphia boliviana* (solid line) and *Mionectes striaticollis* (dashed line) for claws (B) or blood (C). Results from this analysis, and from the general linear and linear mixed-effects models are reported in the *Results* and supplementary material (Appendix S1: Tables S3 and S4).

pattern is that tissues can have different δ²H values irrespective of ecology, a phenomenon known as tissue-specific discrimination that is hypothesized to result from δ²H variation among amino acids from which tissues are constructed (Wolf et al. 2011, 2012, Newsome et al. 2015, Fogel et al. 2016).

We propose a hypothetical framework for interpreting bird tissue δ²H values that can serve as a reference for future studies on elevational migration in the Andes (Fig. 3), and perhaps other montane areas that show similar seasonal patterns in precipitation δ²H values (Appendix S1: Table S5). We encourage future studies to compare δ²H values among different tissues, such as metabolically active (e.g., blood) and continuously growing inert tissues (e.g., claws), of both resident and elevational migrant bird species. The general expectation in tropical or temperate latitudes is that birds remain at low elevations outside of the breeding season and move upslope to breed. We expect tissues that reflect time spent at high elevations to have lower δ²H values compared with tissues representing low elevations. Given the observed seasonal variation in precipitation δ²H in the Andes and other tropical and temperate mountain ranges (Appendix S1: Table S5), however, we expect residents to show more variation in tissue δ²H values among seasons (Fig. 3). Specifically, an elevational migrant moving upslope to breed would have a smaller offset in δ²H values between tissues representing non-breeding and breeding seasons than would a resident bird, because the seasonal variation in precipitation δ²H at a single site is larger in magnitude and opposite in direction in comparison to elevational δ²H lapse rates in precipitation δ²H (Fig. 1). Therefore, the tissues of a bird that seasonally moves upslope would reflect the seasonal pattern in precipitation δ²H at both low and high elevations, which combine to create a smaller difference in tissue δ²H collected across the seasons. In contrast, a bird that remains at the same site would reflect the large seasonal precipitation δ²H patterns at that elevation. Thus, the temporal trend in δ²H values of metabolically active (e.g., blood) or continuously growing metabolically inert (e.g., claws) tissues vs. ordinal date of collection for a resident bird
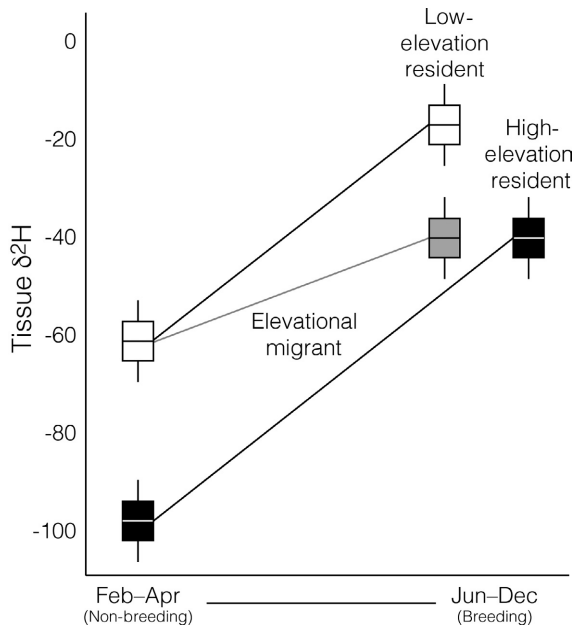
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Fig. 3. Hypothetical framework for identifying elevational migration vs. residency in the Andes. The *x*-axis represents a time scale from the non-breeding season to the breeding season. Box plots represent hypothetical tissue δ^2H values (mean, 95% confidence intervals, ± maximum and minimum) for a low-elevation resident (white), for a high-elevation resident (black) and for an elevational migrant (gray). Lines connecting the boxplots approximate the variation of tissue δ^2H values over-time; the magnitude of variation approximates that observed in our tissue δ^2H dataset.

would produce a steeper slope in comparison to that observed in an elevational migrant (Fig. 3).

Our study has confirmed that comparing δ^2H values among different tissues is a useful approach for studying elevational migration in mountainous areas like the Andes, where precipitation δ^2H varies both seasonally and across small geographical areas because of steep elevational gradients. We emphasize the importance of considering seasonal variation in precipitation δ^2H to interpret patterns in animal tissues, and we recommend the analysis of local precipitation to better refine δ^2H isoscapes in mountainous areas where large isotopic gradients occur across short distances. Lastly, this study resulted in a model framework worth testing against other elevational migrants and low- and high-elevation resident species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1456/suppinfo

DATA AVAILABILITY

Data associated with this paper have been deposited in a Dryad digital repository http://dx.doi.org/10.5061/dryad.dd804

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