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STABLE ISOTOPE INVESTIGATION OF THE MIGRATORY BEHAVIOR OF SILVER-HAIRED BATS (*Lasionycteris noctivagans*) IN EASTERN NORTH AMERICA

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AUTHOR CONTRIBUTIONS

EEF formulated the idea and conducted field and laboratory work. EEF and FJL wrote the manuscript and DB conducted the GIS analyses.
Abstract:

Silver-haired bats (*Lasionycteris noctivagans*) have been typically considered a migratory species, although little is known about their migratory patterns. Our objective was to investigate the latitudinal movements of these bats across the eastern extent of the species’ range. We conducted stable hydrogen isotope analysis of fur samples ($\delta^2$H$_{fur}$) from museum specimens collected across latitudes and at all times of the year. We first used these data to estimate the timing of fur replacement and to develop a model associating $\delta^2$H$_{fur}$ with that of local precipitation ($\delta^2$H$_{precip}$) at the location where fur replacement occurred. We then used this model (i) to identify individuals that had migrated across latitudes, and (ii) to investigate the presence of continental-scale patterns in the estimated distance traveled. Bats were at their location of fur replacement between June 20 and August 26, and there was a strong linear relationship between $\delta^2$H$_{fur}$ and $\delta^2$H$_{precip}$ in bats collected during this time. There was substantial variation in the migratory movements of this species. Twenty-four of 38 females and 14 of 30 males showed isotopic evidence of leaving the area where fur replacement occurred (i.e. migrating across latitudes), whereas the remaining bats were either sedentary or moved at a small scale. Males appeared to migrate consistently, regardless of latitude of origin, while there was a partial leapfrog pattern in female migratory movements. To our knowledge, this is the first evidence of leapfrog migration in bats.

Keywords: Migration, eastern North America, sex, stable hydrogen isotope analysis, silver-haired bat (*Lasionycteris noctivagans*)
Introduction

Animal migration involves a complex and diverse series of processes and outcomes, and it is ubiquitous across a wide range of taxa (Alerstam 2003; Dingle and Drake 2007; Dingle 2014; McGuire and Fraser 2014). While migratory patterns can be described at a population level, the decisions if and how to migrate are individual ones that are likely associated with maximizing individual fitness (Dingle and Drake 2007), and so they may be influenced by a suite of individual-specific characteristics, such as sex, body condition and location. Examples abound of partial and differential migration, where either some individuals migrate while others do not (partial) or among those that do migrate, the distance travelled is highly variable (differential). There is a substantial body of literature investigating the evolutionary processes that lead to individual organisms making the decision to travel hundreds and sometimes thousands of kilometers in migratory journeys (summarized in Dingle 2014).

Migration is a common feature in the life history of many bat species (Fleming and Eby 2003; Bisson et al. 2009; Krauel and McCracken 2013). Because of the small size and cryptic nature of most insectivorous bats, many techniques typically used to investigate the movements of migratory organisms are infeasible (but see Weller et al. 2016). The logistical difficulties involved in tracking individual bats as they move across the landscape means that even basic information about movement is unknown for many common species, making it challenging to test hypotheses about migration theory in bats (Krauel and McCracken 2013, but see McGuire and Guglielmo 2009; McGuire et al. 2012, 2013, 2014; Jonasson and Guglielmo 2016; Jonasson 2017). A better understanding of basic migratory patterns, and the integration of this understanding with more complex hypotheses about migration theory, is a key knowledge gap in our understanding of the ecology of many species of temperate North American bat species. This
gap is particularly relevant given evidence over the past ten years of bat mortality around wind energy facilities in North America during the migratory period (e.g. Arnett et al. 2008; Hein and Schirmacher 2016; Pylant et al. 2016; Frick et al. 2017).

The presence of annual migration by silver-haired bats (*Lasionycteris noctivagans*) has been relatively well-documented (e.g. Barclay 1984; Cryan 2003; Baerwald and Barclay 2009; Dzal et al. 2009; McGuire et al. 2012, 2014; Jonasson and Guglielmo 2016), although the migratory movements of individual bats have not been well-described. *Lasionycteris noctivagans* are widespread across North America (ranging from coast to coast, north into Canada and Alaska, and as far south as some parts of Mexico; Kunz 1982). Based on an analysis of the time and location of capture of animals that are now specimens located in museums, Cryan (2003) inferred that eastern populations of *L. noctivagans* migrate south and west in the autumn and return north and east again in the spring, while western populations migrate in a north-south direction. Annual variation in the sex ratio of captured *L. noctivagans* (e.g. Barclay 1984; Whitaker and Hamilton 1998; Kurta 2010; Weller and Stricker 2012) and museum specimen records (Cryan 2003) have led to the hypothesis that *L. noctivagans* engage in female-biased differential migration, with females completing larger-scale movements than males.

Eastern populations of *L. noctivagans* spend the reproductive season in the northern part of the continent (from Hudson’s Bay south to the northern US between Wisconsin and New England, Whitaker and Hamilton 1998) and then migrate to the southern part of the continent (south to Georgia and occasionally Florida) during the winter. There is some overlap in the summer and winter ranges of this species at mid latitudes (Cryan 2003), and both sexes overwinter at mid and southern latitudes. In summer, males are thought to move slightly north, while females migrate earlier and go much farther north to reproduce.
Stable hydrogen isotope measurements of bat fur ($\delta^2$H$_{fur}$) can provide information about an individual’s location at the time of fur replacement. The stable hydrogen isotope composition of meteoric water ($\delta^2$H$_{precip}$) varies predictably across the North American landscape (e.g. Bowen et al. 2005) with variables such as latitude, elevation, and distance from the coast. Local $\delta^2$H$_{precip}$ signatures are incorporated into the tissues of animals through their food and drinking water. The $\delta^2$H of tissues taken from migratory animals can provide information about migratory origin; however, the $\delta^2$H of food and drinking water is not incorporated directly into tissue hydrogen. There is typically an offset between the $\delta^2$H of diet/water and tissue, and this offset varies among species. In order to use stable hydrogen isotope analyses to trace the origins of migratory animals effectively, it is necessary to calibrate the relationship between tissue and environment $\delta^2$H.

The $\delta^2$H$_{fur}$ of samples taken from bat study skins have often been used to investigate bat migration (Cryan et al. 2004; Fraser et al. 2012; Ossa et al. 2012). Pre-existing specimens collected from a range of locations and times allow researchers to ask questions about continental-scale movements. Current knowledge about the annual distribution and migratory movements of *L. noctivagans* is mainly informed by the locations of museum specimen collection (Cryan 2003), accounts of chance encounters with individual bats (e.g. Cowan 1933; Beer 1956; Izor 1979), and the results of mist-netting campaigns (with an emphasis on the sex ratio of bats captured, e.g. Whitaker and Hamilton 1998; Kurta 2010). Our overall objective was to add to this body of knowledge by measuring $\delta^2$H$_{fur}$ for samples taken from museum study skins to investigate the seasonal continental-scale movements of *L. noctivagans* in eastern North America. To do this, we first followed the methods of Cryan et al. (2004) to identify the period of fur replacement for *L. noctivagans* using stable isotope techniques and then to model the relationship between $\delta^2$H$_{fur}$ at the location where fur replacement occurred and local $\delta^2$H$_{precip}$. We
then used this model to i) identify individuals whose stable isotope signature indicated that they had migrated across latitudes and ii) investigate variation in the migratory behavior of bats across latitudes and between sexes.

**Materials and Methods**

*Sample collection*

We obtained fur samples from study skins kept in the mammal collections of several North American museums (Smithsonian National Museum of Natural History, Washington DC; Field Museum of Natural History, Chicago, IL; Royal Ontario Museum, Toronto, ON; and Texas A&M University Biodiversity Research and Teaching Collections, College Station, TX). We used samples from specimens collected at all times of the year and across the species’ range (Figure 1, Supplementary Data S1). In order to achieve our first objective of developing a robust and widespread relationship between δ²H_fur and estimated δ²H_precip at the location of fur replacement, we selected specimens collected between June and August (the likely period when bats would be summer residents, also the time when fur replacement occurs for most North American bat species; Fraser et al. 2013) from across the species’ range. Hereafter, bats collected during the period when they replace their fur will be referred to as “summer residents” and those collected outside of the summer residency period as “non-summer individuals.” Samples from summer residents are necessary for investigating our first objective because the stable isotope composition of newly grown fur should be reflective of the location where that fur was grown. However, it is important to note that while fur replacement likely occurs during the period of summer residency, the process of fur replacement does not necessarily take the entire summer period. Although the ecological focus of this study was on the eastern population of *L.*
noctivagans, sampling individuals collected across the species’ range allowed us to have representative samples from locations with more distinct $\delta^2\text{H}_{\text{precip}}$ than if we had only sampled summer residents from eastern North America.

To achieve our second objective of investigating the migratory behavior of this species in the eastern part of the species’ range, we focused our sampling on non-summer individuals in only the eastern half of the continent. We either sampled the specimens ourselves or requested that a representative at the museum collect samples according to our protocol. When available, we obtained coordinates for the site of collection from museum databases. These data were not available for some individuals, in which case we used the Geographic Names Information System (USA; geonames.usgs.gov) and Geographical Names Board of Canada (http://www4.rncan.gc.ca/search-place-names/name.php) as precisely as possible. If specific collection information was not available, we used data from the centroid of the relevant county or state.

**Stable isotope analysis**

Samples were taken dorsally using surgical scissors and were stored in glass vials until the time of analysis. All analyses were conducted at the Laboratory for Stable Isotope Science at The University of Western Ontario in London, Ontario, Canada. Samples were soaked overnight in a solution of 2:1 chloroform:methanol, rinsed in the same solution, and then left to dry in a fume hood for at least 48 hours. All analyses included five fur standards with known non-exchangeable $\delta^2\text{H}_{\text{fur}}$ – and treated identically to the samples – thus allowing for correction of hydrogen exchange between samples and ambient water vapour. Samples and standards were weighed (175 ± 10 µg) into 3.2 × 4 mm silver capsules and then left to equilibrate with laboratory air for a minimum of four days before analysis. During analysis, samples were
combusted at 1450°C in a high temperature conversion elemental analyzer (Thermo Scientific), and the resultant gas was analyzed for $\delta^2$H using an interfaced isotope ratio mass spectrometer (Thermo Scientific Delta Plus XL) in continuous flow mode. Ten percent of sample analyses were duplicated, and the precision of these duplicates (average difference ± standard deviation) was 3±3‰ (n=20). Stable isotope results are reported in parts per thousand (‰) in the usual $\delta$ notation, relative to VSMOW (Vienna Standard Mean Ocean Water), and were calculated as follows:

$$\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right)$$

where $R_{\text{sample}}$ refers to the ratio of $^2$H:$^1$H in the sample, and $R_{\text{standard}}$ refers to the same ratio in the standard.

**Precipitation $\delta^2$H**

We used estimates of the mean stable hydrogen isotope composition of growing season precipitation available from waterisotopes.org (Bowen et al. 2005) to predict $\delta^2$H$_{\text{precip}}$ at the collection sites of each individual bat. Following previous authors (Cryan et al. 2004; Fraser et al. 2012; Pylant et al. 2014), we calculated the difference between $\delta^2$H$_{\text{fur}}$ and $\delta^2$H$_{\text{precip}}$ for each bat ($\Delta^2$H$_{\text{fur-precip}}$). For non-summer individuals, $\Delta^2$H$_{\text{fur-precip}}$ may be used as a proxy for distance travelled across latitudes from the site of summer residency. We visually inspected changes in $\Delta^2$H$_{\text{fur-precip}}$ over time to identify the time period when *L. noctivagans* were at the site of fur replacement (i.e. when they were summer residents). Based on these data, we made the preliminary conclusion that members of this species can be classified as summer residents between June 2 and September 3, with fur replacement occurring at some point during that period. This fur replacement time frame is supported by data for other bat species (summarized in Fraser et al. 2013) and anecdotal evidence for this species (E. Baerwald, pers. comm.). Based
on this estimate for time spent at the site of fur replacement, we used the online tool IsoMAP to create a stable hydrogen isotope isoscape that interpolated $\delta^2$H$_{precip}$ based only on measurements from June, July, and August in North America between 1960 and 2009 (US National Geophysical Data Center 1998; Welker 2000; Mitchell and Jones 2005; PRISM Climate Group 2010; IAEA/WMO 2011; Bowen et al. 2014; created by E. Fraser 2014). IsoMAP generated two models, one based on multiple linear regression techniques and one based on geostatistical analysis (Bowen et al. 2016). For fur samples collected during the period of summer residency, we then conducted a simple linear regression between the mean $\delta^2$H$_{fur}$ for all individuals captured at that site and the estimated $\delta^2$H$_{precip}$ at the site, using $\delta^2$H$_{precip}$ for the growing season isoscape as well as both the multiple linear regression and geostatistical June to August isoscapes. The isoscape created using the geostatistical model produced the best fit (based on $r^2$), and therefore we chose it for use during the remainder of the project.

Using these improved estimates for $\delta^2$H$_{precip}$, we re-examined $\Delta^2$H$_{fur-precip}$ over time (Figure 2) and refined our estimate for the time of summer residency to between June 20 and August 26. We then conducted a subsequent linear regression between $\delta^2$H$_{fur}$ and $\delta^2$H$_{precip}$, using only fur samples that were collected during the revised summer residency period (Figure 3).

Data analysis

The focus of this study was on the eastern population of North American L. noctivagans, and so we arbitrarily chose -100° longitude as the boundary of our study. We considered all samples collected east of this line in our investigation of individual migratory movements for non-summer individuals. We quantified the movements of these individuals in two ways. First, we used the linear relationship between $\delta^2$H$_{fur}$ and $\delta^2$H$_{precip}$ to calculate the predicted $\delta^2$H$_{precip}$ associated with the fur of each non-summer individual. We then conducted a proximity analysis
in ArcMap (ESRI 2016) using our map of $\delta^2$H$_{\text{precip}}$ during the period of summer residency to calculate the distance (hereafter referred to as estimated distance travelled) between the individual’s location of collection and the nearest location with the relevant $\delta^2$H$_{\text{precip}}$ (hereafter referred to as the estimated latitude of origin). There is substantial variation in $\delta^2$H$_{\text{fur}}$ within a population, as well as $\delta^2$H$_{\text{precip}}$ across the landscape. Hence, we do not anticipate that our calculated estimated distances travelled or estimated latitudes of origin will provide exact measures of individual movements. Rather, they act as a proxy of movement that is standardized and can be compared among individuals across latitudes and of different sexes, and we used these values in the subsequent statistical tests described below.

Second, we used the linear relationship between $\delta^2$H$_{\text{fur}}$ and $\delta^2$H$_{\text{precip}}$ and the associated variation (standard deviation of the residuals = 9.5‰) to run the origin assignment function in Isomap to create probability density analyses of the location of origin for each individual bat. We then identified the area from which there was a 75% probability that each bat had originated (hereafter referred to as the area of probable origin) (following Van Wilgenburg and Hobson 2011) and categorized bats as having been collected either in or out of their respective areas of probable origin (Figure 4). Individuals collected within their areas of probable origin were likely more sedentary than those outside but were not necessarily non-migrants. Any migratory movements that they did complete, however, were at a scale less likely to be detected using stable isotope techniques than the larger scale movements of bats that were collected outside of their areas of probable origin. Bats identified as having made smaller-scale movements may indeed have been shorter distance migrants than some other individuals, or may have been captured mid-migration. The 75% probability threshold is arbitrary but was selected to balance
the natural variation inherent in environmental stable hydrogen isotope composition with the need to conduct accurate origin assignment (Van Wilgenburg and Hobson 2011).

We then conducted univariate general linear models incorporating estimated latitude of origin of all non-summer individuals as the dependent variable and sex and latitude of collection as independent variables. We further included season as a third independent variable, classifying non-summer individuals as either overwintering or potential migrants. We considered individuals collected between October 15 and March 15 as likely overwintering and those collected outside of both the summer resident and overwintering periods as potential migrants. Stable isotope results indicated that most bats were collected south of their estimated latitude of origin, though some were north. In an attempt to identify widespread patterns in the movements of *L. noctivagans*, we conducted the analyses described above only on the majority of individuals that were collected south of their estimated latitude of origin. Before conducting these tests, we confirmed that all relevant data were normally distributed using Shapiro-Wilkes tests and that groups displayed homogeneity of variance using Levene’s tests.

**Results**

We sampled fur and obtained $\delta^2$H$_{\text{fur}}$ for 112 *Lasionycteris noctivagans* study skins (55 males, 57 females) that were originally collected between 1886 and 2008 on dates spanning the calendar year (Figure 1). Nonexchangeable $\delta^2$H$_{\text{fur}}$ of these samples ranged from $\sim$124 to $\sim$42 ‰ VSMOW (Supplemental Data S1). There were strongly significant linear relationships between the $\delta^2$H$_{\text{fur}}$ of summer residents and all three estimates of $\delta^2$H$_{\text{precip}}$ at their location of capture [(1) Waterisotope.org isoscape (growing season) (Bowen et al. 2014): $\delta^2$H$_{\text{fur}} = 0.71 \times \delta^2$H$_{\text{precip}} – 33.18$, $r^2 = 0.58$, $p<0.001$; (2) Isomap isoscape (June to August), multiple linear regression
method (Fraser 2014): \[ \delta^{2}H_{\text{fur}} = 0.77 \times \delta^{2}H_{\text{precip}} - 35.20, r^2 = 0.60, p<0.001 \]; (3) Isomap isoscape (June to August), geostatistical model (Fraser 2014): \[ \delta^{2}H_{\text{fur}} = 0.70 \times \delta^{2}H_{\text{precip}} - 40.65, r^2 = 0.67, p<0.001 \]. The Isomap isoscape (June to August), geostatistical model, provided the best fit and therefore was used for the remainder of the project.

We had \( \delta^{2}H_{\text{fur}} \) for samples from 68 non-summer individuals (38 females and 30 males) from our study area in the eastern part of the continent. These results suggested that 58 bats (32 females and 26 males) were collected to the south, and 10 bats (6 females and 4 males) were collected to the north, of their locations of fur growth. Fourteen females and 16 males, including all individuals with \( \delta^{2}H_{\text{fur}} \) values indicating that they were north of their estimated latitude of origin, were collected within their areas of 75% probable origin. The remaining 24 females and 14 males were collected south of their areas of 75% probable origin (Figure 5a) and were collected during the non-summer period (Figure 5b). The distance between location of collection and the nearest location at the estimated latitude of origin ranged from 38 to 2774 km among all individuals collected during the non-summer period (i.e. overwintering individuals plus potential migrants) and from 125 to 2189 km among individuals collected between October 15 and March 15 (i.e. overwintering individuals only) (Figure 6).

Both sex and latitude of collection, but not season, were significant main effects on the estimated latitudes of origin. There was also a significant interaction effect between sex and latitude, but not among any of the other independent variables (General linear model: sex – \( F_{1,57}=7.806, p=0.007 \) [mean ± standard deviation – 46.1±3.9 (females); – 43.7 ± 4.9 (males)]; latitude of collection – \( F_{1,57}=7.392, p=0.009 \); latitude of collection - \( F_{1,57}=7.392, p=0.009 \); season – \( F_{1,57}=2.985, p=0.091 \); full model – \( F_{4,57}=5.130, p=0.001 \). Females originated from slightly more northern latitude than did males. For female bats, there was a quadratic relationship
between latitude of collection and estimated latitude of origin, with females at the southern- and
northern-most collection points having the most northern predicted latitudes of origin (Quadratic
regression: $F_{2,30}=6.724, p=0.004, r^2=0.325$, Figure 7a). For male bats, latitude of origin
decreased slightly with latitude of collection (Simple linear regression: $F_{1,25}=11.033, p=0.003,$
$r^2=0.315$, Figure 7b).

**Discussion**

Our investigation of the migratory patterns of *L. noctivagans* in eastern North America using
stable hydrogen isotope techniques suggests intraspecific variability in the migratory tendencies
of this species. Many individuals either do not migrate at all or conduct latitudinal migration at
too small a scale to be reliably detected using stable hydrogen isotope techniques, while others
likely traverse thousands of kilometers. Further, we present evidence for sex-specific differences
in migratory tendency. Females spent summer at slightly more northern latitudes than did males,
and some of the most northern summer resident females then migrated to some of the most
southern overwintering locations.

**Stable isotope assignment techniques**

Most studies using stable hydrogen isotope evidence to investigate bat migration have
used estimates of local $\delta^2$H$_{\text{precip}}$ that were based on data for the entire growing season (Fraser et
al. 2012; Cryan et al. 2014) or the entire year (Ossa et al. 2012; Popa-Lisseanu et al. 2012; but
see Pylant et al. 2014, 2016). In most locations, the growing season likely far exceeds the time
period of new fur growth for many temperate bat species (Fraser et al. 2013), and a more refined
model that incorporates a customized suite of environmental variables and considers only the
relevant time period may better explain the variation in $\delta^2$H$_{\text{fur}}$, although this is not always the
case (Hobson et al. 2012; Pylant et al. 2016). In our study, the model based only on the expected time period of fur replacement explained the variation in \( L. \text{noctivigans} \delta^2\text{H}_{\text{fur}} \) values slightly better than a precipitation model based on the entire growing season, and this model also allowed us to refine the timing of summer residency more precisely.

**Timing of migration**

A limitation of the present study is that little is known about the exact timing of migration for the study species at the levels of both the population and the individual. Because the period of summer residency was defined as ending when there was first evidence of bats having migrated, some individuals collected outside the defined period of summer residency may have been mid-migration or even pre- (in autumn) or post- (in spring) migration, resulting in underestimates of their total migratory journeys. Most \( L. \text{noctivagans} \) collected as mortalities around wind energy facilities are found during late summer and early fall (Arnett et al. 2010), suggesting that at a continental scale, the migratory period for the species lasts more than a month. Less is known about spring migratory movements (but see Jonasson and Guglielmo 2016, Jonasson 2017). A further key knowledge gap is the time required for an individual bat’s migratory journey: if migration is completed in relatively little time, then bats are less likely to be collected during migration than if migration is lengthy. Modelling work suggests that \( L. \text{noctivagans} \) are physically capable of completing their migratory movements quickly through the use of torpor-assisted migration (McGuire et al. 2012, 2014) but, recent radio tracking evidence from autumn migrating individuals in Ontario suggests that migration is more protracted (Jonasson 2017). In the present study, it is likely that some of the non-summer individuals collected within their area of probable origin were mid-migration or not migrating, but limited knowledge about \( L. \text{noctivagans} \) outside of summer residency make it challenging to assess the extent to which this is
the case. Despite this uncertainty, the lack of statistical significance of the season variable
(overwintering vs. potential migrant) in our model as well as the presence of relatively sedentary
individuals at all times of the year including mid-winter suggest that the main findings of the
study accurately reflect continental trends in L. noctivagans migration.

Variation in migratory patterns

Our findings suggest the presence of partial migration among eastern North American L.
noctivagans. While some individuals appear to travel thousands of kilometers across latitudes, a
subset of the eastern population (including members of both sexes) is either sedentary or engages
in relatively short-distance annual movements. Partial migration is common among a wide
diversity of taxa, and evolutionary arguments are usually invoked to explain the decision by
some individuals to migrate, while others do not (e.g. Dingle and Drake 2007). The decision to
migrate may be driven by resource availability, predation risk, body condition, environmental
stochasticity, and/or individual dominance (Dingle 2014).

We observed bats that were collected within their area of probable origin at all times of
year, including the mid-winter, supporting the idea that some individuals never undertook large-
scale latitudinal migratory movements. These findings complement numerous records of this
species overwintering in relatively northern locations (e.g. Michigan (Gosling 1977; Sherwood
and Kurta 1999; Kurta 2008), Minnesota (Beer 1956), Illinois (Izor 1979), Indiana (Whitaker and
Hamilton 1998) and British Columbia (Cowan 1933; Nagorsen et al. 1993). While it is unknown
where these northern overwintering individuals spent the summer, their presence at northern
latitudes during the winter season indicate that they have not engaged in trans-continental scale
migratory movements. Most reports of L. noctivagans overwintering at northern latitudes discuss
only one or a few individual bats, and it is unclear whether they represent exceptions, or provide
evidence for a greater trend. Our finding of numerous non-summer individuals across latitudes
remaining sedentary or travelling relatively short distances during the non-summer period
suggests that *L. noctivagans* overwintering at more northern latitudes may be more common than
previously thought. Studies of the overwintering ecology of other latitudinal migrant species
indicate that they are capable of spending weeks or months in torpor (eastern red bats, *Lasiurus
which would make them less detectable. Further, the overwintering ecology of North American
bat species that migrate across latitudes is not well described. The assumption that members of
these species overwinter at one location in the manner that is typical of many migratory birds
may be overly simplistic (e.g. Weller et al. 2016.)

Our results suggest a more complicated picture of sex-biased migration than has
previously been proposed. Males collected across latitudes and outside of summer residency
engaged in relatively short migratory movements or remained sedentary. Females collected at
mid-latitudes generally engaged in a relatively consistent pattern of shorter, parallel southern
movements. However, the most northern female summer residents engaged in the greatest
migratory movements, apparently passing over more southern summer residents to overwinter at
the most southern locations, suggesting a partial pattern of leapfrog migration. To our
knowledge, ours is the first description of leapfrog migration in a bat species, although this
pattern has frequently been documented among bird species (e.g. Boland 1990; Kelly et al. 2002;
Bell 2005; Nelson et al. 2015).

There are several commonly cited hypotheses to explain the evolution of a leap-frog
pattern of migration among birds (Alerstam and Högstedt 1980; Greenberg 1980; Pienkowski et
al. 1985; Bell 1996, 1997), each based on the assumption that individuals will time their
migration and select their migratory destination in order to optimize access to resources, particularly by reducing competition. In all cases, these competing hypotheses were generated based on the basic characteristics of bird life history, which differ significantly from that of bats (e.g. Fleming and Eby 2003; McGuire 2009; Willis et al. 2010). For example, implicit in some hypotheses (Alerstam and Högstedt 1980; Pienkowski et al. 1985) is the assumption that overwintering birds compete for resources and so disperse widely across overwintering areas. While numerous studies have investigated both dietary resource partitioning and overlap among sympatric bat species (e.g. Arlettz et al. 1997, 2000; Emrich et al. 2013; Krüger et al. 2014), there is currently very little direct evidence that insectivorous bats compete for food or roost resources.

The time allocation hypothesis for leapfrog migration (proposed by Greenberg 1980, later extended by Bell 1996, 1997) may be most relevant to insectivorous bats. This hypothesis suggests that individual birds breeding at more northern latitudes will spend a shorter period on breeding grounds than those breeding at more southern latitudes and so will prioritize travelling to overwintering locations with optimal conditions more than individuals who breed at more southern latitudes and so spend less time at their overwintering site. If female *L. noctivagans* across latitudes similarly vary in summer residency time, more northern individuals may benefit from migrating to more southern locations if those locations have better or more resources available. Certainly, female *L. noctivagans* engaged in spring migration are under major energetic constraints and would likely benefit from overwintering in locations with energetically favourable conditions. *Lasionycteris noctivagans* mate during autumn (Cryan et al. 2012), with females storing sperm all winter. At the time of spring migration, females may already be pregnant and need to complete their migratory movements with sufficient fuel stores for
gestation and lactation once they arrive at their site of summer residency. Experimental work on
*L. cinereus*, another long-distance migrant, indicates that females during spring migration are
less likely than males to enter torpor, a strategy that likely benefits embryonic growth, but further
increases the energetic cost of migration (Cryan and Wolf 2003). Females of this species are
likely under strong selective pressure to begin the spring migration with substantial fuel stores
and Jonasson and Guglielmo (2016) found that in two out of three years, female spring migrant
*L. noctivagans* captured in southern Ontario carried greater fat stores than did males captured at
the same site and migrated ahead of males. The heightened energetic costs faced by spring
migrant females, particularly those making the greatest journeys to the most northern locations of
summer residency in spring, may make them good candidates for selecting high resource
overwintering sites where they can deposit substantial fat stores before spring migration.

Finally, there is often a temporal component to leapfrog migration, with clear variation in
the timing of migration by northern and southern populations (e.g. Bell 1996; Kelly et al. 2002;
Paxton et al. 2007). The structure of the present study did not allow us to test for intraspecific
variation in migration timing, although to date, previous research on migratory *L. noctivagans* in
Ontario (Fraser 2011) and Alberta (Baerwald et al. 2014), *L. cinereus* in New Mexico (another
latitudinal migrant Cryan et al. 2014), and *L. borealis* in the central Appalachian mountains
(Pylant et al. 2016) found no such temporal patterns. Given the large numbers of *L. noctivagans*
that are killed each year at wind energy facilities, there is an opportunity to replicate these kinds
of studies at a greater scale.
Summary

Stable hydrogen isotope results for the fur of *L. noctivagans* collected during the non-summer period indicate that members of this species in eastern North America engage in variable migratory strategies. Some individuals of both sexes appeared to be sedentary or to complete relatively short-distance migratory movements, while others traversed the continent with evidence for a pattern of leapfrog migration among female populations. Intraspecific variation in migratory patterns is common in many species, and individual-specific evolutionary arguments are usually invoked to explain these patterns.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY DATA

Supplementary Data S1. List of all museum specimens that were used in the study, including the institution where they are stored, their date and location of collection, and the non-exchangeable stable hydrogen isotope composition ($\delta^2$H_{fur}) of their fur.
REFERENCES


https://mc.manuscriptcentral.com/jmamm
Bell CP (2005) Inter- and intrapopulation migration patterns In: Greenberg R, Marra PP (eds) 
Birds of two worlds: The ecology and evolution of migration. The Johns Hopkins University Press, Baltimore, pp 41-52


Cowan IM (1933) Some notes on the hibernation of Lasionycteris noctivagans. Can Field Nat 47:74-75


Pienkowski MW, Evans PR, Townshend DJ (1985) Leap-frog and other migration patterns of waders: A critique of the Alerstam and Högstedt hypothesis, and some alternatives. Ornis Scandinavica (Scan J Ornithol) 16(1):61-70

PRISM Climate Group (2005) Gridded climate data for contiguous USA.
http://prism.oregonstate.edu


US National Geophysical Data Center (1998) ETOPO-5 five minute gridded world elevation, NGDC, Boulder, CO, USA.


Welker JM (2000) Isotopic (δ¹⁸O) characteristics of weekly precipitation collected across the USA: An initial analysis with application to water source studies. Hydro Proc 14:1449-1464


Figure Legends:

Figure 1. Collection locations for all *Lasionycteris noctivagans* individuals included in the study. Fur samples were taken from study skins held in museum collections. Sampling included individuals collected during the period of summer residency (June – August) from across North America and during the non-summer period in eastern North America only.

Figure 2. The period of summer residency for *Lasionycteris noctivagans* was defined by identifying the time period when bat $\delta^2 H_{\text{fur}}$ was most similar to $\delta^2 H_{\text{precip}}$ at the location of collection (i.e. when $\Delta \delta^2 H_{\text{fur-precip}}$ was closest to zero).

Figure 3. Linear relationship between $\delta^2 H_{\text{fur}}$ of *L. noctivagans* captured during the period of summer residency and mean $\delta^2 H_{\text{precip}}$ (estimated June through August) at the locations of capture. For sites where multiple bats were sampled, variation in $\delta^2 H_{\text{fur}}$ is indicated by error bars showing one standard deviation from the mean.

Figure 4. Identification of *Lasionycteris noctivagans* as in or out of their locations of probable origin. The 75% probability of origin was determined for each individual collected during the non-summer period. Bats were categorized as either (a) outside their area of probable origin (Individual ROM78278 shown here as an example) or (b) inside their area of probable origin (ROM2204201396 shown as an example).
Figure 5. (a) Migratory status of male (squares) and female (circles) bats captured during the non-summer period. Thirty-eight bats (14 males and 24 females) were captured outside of their area of probable origin (indicated by grey symbols), and thirty bats (16 males and 14 females) were captured inside their area of probable origin (indicated by filled symbols). (b) Bats were captured within their area of probable origin at all times of the year, including mid-winter. The dashed vertical line indicates the period of summer residency (June 21st to August 25th), for which data are not shown.

Figure 6. The distance between collection site and the estimated latitude of origin was less than 1000 km for most L. noctivagans collected between Oct 15 and March 15 (defined here as the overwintering period) and greater than 2000 km for a few individuals. Distance estimates were obtained by calculating the distance between each bat’s location of collection and the nearest location with the relevant $\delta^2H_{\text{precip}}$ (calculated based on the described relationship between $\delta^2H_{\text{fur}}$ and $\delta^2H_{\text{precip}}$). Data from females is shown with black bars and from males with open bars.

Figure 7. The relationship between latitude of collection and estimated latitude of origin for (a) female Lasionycteris noctivagans collected during the non-summer period was quadratic ($p=0.004$), with those individuals collected at the most northern and southern latitudes originating from the most northern locations, whereas (b) for males it was linear ($p=0.003$), with those collected at the most southern locations also originating from southern latitudes. For both panels, the dashed line illustrates the points where latitude of collection is equal to estimated latitude of origin (the 1:1 line.)
\[ \delta H_{\text{fur}} (\text{‰ VSMOW}) = 0.69x - 40.65 \]

\[ r^2 = 0.666 \]
b

Bats captured within area of probable origin

Jan-Feb  Mar-Apr  May-Jun 20  Aug 26-31  Sept-Oct  Nov-Dec

0 2 4 6 8
Estimated latitude of origin (°N)

Latitude of collection (°N)

\[ y = 0.08x^2 - 6.13x + 159.57 \]
\[ r^2 = 0.325 \]

\[ y = 0.67x + 17.89 \]
\[ r^2 = 0.315 \]
**Institution** | Specimen ID | Specimen sex | Collection date (Julian date) | Collection year | $\delta^{13}$H_{\text{fur}}$ (%) VSMOW
---|---|---|---|---|---
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM) | USNM155572 | unknown | 227 | 1891 | -48
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