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Stable isotope investigation of the migratory behavior of silverhaired bats (Lasionycteris noctivagans) in eastern North America

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1 **STABLE ISOTOPE INVESTIGATION OF THE MIGRATORY BEHAVIOR OF**

2 **SILVER-HAIRED BATS** *(LASIONYCTERIS NOCTIVAGANS)* **IN EASTERN NORTH**

3 **AMERICA**

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19 **AUTHOR CONTRIBUTIONS**

20 EEF formulated the idea and conducted field and laboratory work. EEF and FJL wrote the

21 manuscript and DB conducted the GIS analyses.

22

23   **Abstract:**

24   Silver-haired bats (*Lasionycteris noctivagans*) have been typically considered a migratory

25   species, although little is known about their migratory patterns. Our objective was to investigate

26   the latitudinal movements of these bats across the eastern extent of the species' range. We

27   conducted stable hydrogen isotope analysis of fur samples (δ^2H_{fur}) from museum specimens

28   collected across latitudes and at all times of the year. We first used these data to estimate the

29   timing of fur replacement and to develop a model associating δ^2H_{fur} with that of local

30   precipitation (δ^2H_{precip}) at the location where fur replacement occurred. We then used this model

31   (i) to identify individuals that had migrated across latitudes, and (ii) to investigate the presence of

32   continental-scale patterns in the estimated distance traveled. Bats were at their location of fur

33   replacement between June 20 and August 26, and there was a strong linear relationship between

34   δ^2H_{fur} and δ^2H_{precip} in bats collected during this time. There was substantial variation in the

35   migratory movements of this species. Twenty-four of 38 females and 14 of 30 males showed

36   isotopic evidence of leaving the area where fur replacement occurred (i.e. migrating across

37   latitudes), whereas the remaining bats were either sedentary or moved at a small scale. Males

38   appeared to migrate consistently, regardless of latitude of origin, while there was a partial

39   leapfrog pattern in female migratory movements. To our knowledge, this is the first evidence of

40   leapfrog migration in bats.

41   **Keywords:** Migration, eastern North America, sex, stable hydrogen isotope analysis, silver-

42   haired bat (*Lasionycteris noctivagans*)

43   **Introduction**

44   Animal migration involves a complex and diverse series of processes and outcomes, and

45   it is ubiquitous across a wide range of taxa (Alerstam 2003; Dingle and Drake 2007; Dingle

46   2014; McGuire and Fraser 2014). While migratory patterns can be described at a population

47   level, the decisions if and how to migrate are individual ones that are likely associated with

48   maximizing individual fitness (Dingle and Drake 2007), and so they may be influenced by a suite

49   of individual-specific characteristics, such as sex, body condition and location. Examples abound

50   of partial and differential migration, where either some individuals migrate while others do not

51   (partial) or among those that do migrate, the distance travelled is highly variable (differential).

52   There is a substantial body of literature investigating the evolutionary processes that lead to

53   individual organisms making the decision to travel hundreds and sometimes thousands of

54   kilometers in migratory journeys (summarized in Dingle 2014).

55   Migration is a common feature in the life history of many bat species (Fleming and Eby

56   2003; Bisson et al. 2009; Krauel and McCracken 2013). Because of the small size and cryptic

57   nature of most insectivorous bats, many techniques typically used to investigate the movements

58   of migratory organisms are infeasible (but see Weller et al. 2016). The logistical difficulties

59   involved in tracking individual bats as they move across the landscape means that even basic

60   information about movement is unknown for many common species, making it challenging to

61   test hypotheses about migration theory in bats (Krauel and McCracken 2013, but see McGuire

62   and Guglielmo 2009; McGuire et al. 2012, 2013, 2014; Jonasson and Guglielmo 2016; Jonasson

63   2017). A better understanding of basic migratory patterns, and the integration of this

64   understanding with more complex hypotheses about migration theory, is a key knowledge gap in

65   our understanding of the ecology of many species of temperate North American bat species. This

66   gap is particularly relevant given evidence over the past ten years of bat mortality around wind

67   energy facilities in North America during the migratory period (e.g. Arnett et al. 2008; Hein and

68   Schirmacher 2016; Pylant et al. 2016; Frick et al. 2017).

69   The presence of annual migration by silver-haired bats (*Lasionycteris noctivagans*) has

70   been relatively well-documented (e.g. Barclay 1984; Cryan 2003; Baerwald and Barclay 2009;

71   Dzal et al. 2009; McGuire et al. 2012, 2014; Jonasson and Guglielmo 2016), although the

72   migratory movements of individual bats have not been well-described. *Lasionycteris noctivagans*

73   are widespread across North America (ranging from coast to coast, north into Canada and

74   Alaska, and as far south as some parts of Mexico; Kunz 1982). Based on an analysis of the time

75   and location of capture of animals that are now specimens located in museums, Cryan (2003)

76   inferred that eastern populations of *L. noctivagans* migrate south and west in the autumn and

77   return north and east again in the spring, while western populations migrate in a north-south

78   direction. Annual variation in the sex ratio of captured *L. noctivagans* (e.g. Barclay 1984;

79   Whitaker and Hamilton 1998; Kurta 2010; Weller and Stricker 2012) and museum specimen

80   records (Cryan 2003) have led to the hypothesis that *L. noctivagans* engage in female-biased

81   differential migration, with females completing larger-scale movements than males.

82   Eastern populations *of L. noctivagans* spend the reproductive season in the northern part

83   of the continent (from Hudson's Bay south to the northern US between Wisconsin and New

84   England, Whitaker and Hamilton 1998) and then migrate to the southern part of the continent

85   (south to Georgia and occasionally Florida) during the winter. There is some overlap in the

86   summer and winter ranges of this species at mid latitudes (Cryan 2003), and both sexes

87   overwinter at mid and southern latitudes. In summer, males are thought to move slightly north,

88   while females migrate earlier and go much farther north to reproduce.

89   Stable hydrogen isotope measurements of bat fur (δ^2H$_{fur}$) can provide information about

90   an individual's location at the time of fur replacement. The stable hydrogen isotope composition

91   of meteoric water (δ^2H$_{precip}$) varies predictably across the North American landscape (e.g. Bowen

92   et al. 2005) with variables such as latitude, elevation, and distance from the coast. Local δ^2H$_{precip}$

93   signatures are incorporated into the tissues of animals through their food and drinking water. The

94   δ^2H of tissues taken from migratory animals can provide information about migratory origin;

95   however, the δ^2H of food and drinking water is not incorporated directly into tissue hydrogen.

96   There is typically an offset between the δ^2H of diet/water and tissue, and this offset varies among

97   species. In order to use stable hydrogen isotope analyses to trace the origins of migratory animals

98   effectively, it is necessary to calibrate the relationship between tissue and environment δ^2H .

99   The δ^2H$_{fur}$ of samples taken from bat study skins have often been used to investigate bat

100   migration (Cryan et al. 2004; Fraser et al. 2012; Ossa et al. 2012). Pre-existing specimens

101   collected from a range of locations and times allow researchers to ask questions about

102   continental-scale movements. Current knowledge about the annual distribution and migratory

103   movements of *L. noctivagans* is mainly informed by the locations of museum specimen

104   collection (Cryan 2003), accounts of chance encounters with individual bats (e.g. Cowan 1933;

105   Beer 1956; Izor 1979), and the results of mist-netting campaigns (with an emphasis on the sex

106   ratio of bats captured, e.g. Whitaker and Hamilton 1998; Kurta 2010). Our overall objective was

107   to add to this body of knowledge by measuring δ^2H$_{fur}$ for samples taken from museum study

108   skins to investigate the seasonal continental-scale movements of *L. noctivagans* in eastern North

109   America. To do this, we first followed the methods of Cryan et al. (2004) to identify the period

110   of fur replacement for *L. noctivagans* using stable isotope techniques and then to model the

111   relationship between δ^2H$_{fur}$ at the location where fur replacement occurred and local δ^2H$_{precip}$. We

112 then used this model to i) identify individuals whose stable isotope signature indicated that they

113 had migrated across latitudes and ii) investigate variation in the migratory behavior of bats across

114 latitudes and between sexes.

115

116 **Materials and Methods**

117 *Sample collection*

118 We obtained fur samples from study skins kept in the mammal collections of several

119 North American museums (Smithsonian National Museum of Natural History, Washington DC;

120 Field Museum of Natural History, Chicago, IL; Royal Ontario Museum, Toronto, ON; and Texas

121 A&M University Biodiversity Research and Teaching Collections, College Station, TX). We

122 used samples from specimens collected at all times of the year and across the species' range

123 (Figure 1, Supplementary Data S1). In order to achieve our first objective of developing a robust

124 and widespread relationship between δ^2H_{fur} and estimated δ^2H_{precip} at the location of fur

125 replacement, we selected specimens collected between June and August (the likely period when

126 bats would be summer residents, also the time when fur replacement occurs for most North

127 American bat species; Fraser et al. 2013) from across the species' range. Hereafter, bats collected

128 during the period when they replace their fur will be referred to as "summer residents" and those

129 collected outside of the summer residency period as "non-summer individuals." Samples from

130 summer residents are necessary for investigating our first objective because the stable isotope

131 composition of newly grown fur should be reflective of the location where that fur was grown.

132 However, it is important to note that while fur replacement likely occurs during the period of

133 summer residency, the process of fur replacement does not necessarily take the entire summer

134 period. Although the ecological focus of this study was on the eastern population of *L.*

135   *noctivagans*, sampling individuals collected across the species' range allowed us to have

136   representative samples from locations with more distinct δ^2H$_{precip}$ than if we had only sampled

137   summer residents from eastern North America.

138   To achieve our second objective of investigating the migratory behavior of this species in

139   the eastern part of the species' range, we focused our sampling on non-summer individuals in

140   only the eastern half of the continent. We either sampled the specimens ourselves or requested

141   that a representative at the museum collect samples according to our protocol. When available,

142   we obtained coordinates for the site of collection from museum databases. These data were not

143   available for some individuals, in which case we used the Geographic Names Information

144   System (USA; geonames.usgs.gov) and Geographical Names Board of Canada

145   (http://www4.rncan.gc.ca/search-place-names/name.php) as precisely as possible. If specific

146   collection information was not available, we used data from the centroid of the relevant county

147   or state.

148   *Stable isotope analysis*

149   Samples were taken dorsally using surgical scissors and were stored in glass vials until

150   the time of analysis. All analyses were conducted at the Laboratory for Stable Isotope Science at

151   The University of Western Ontario in London, Ontario, Canada. Samples were soaked overnight

152   in a solution of 2:1 chloroform:methanol, rinsed in the same solution, and then left to dry in a

153   fume hood for at least 48 hours. All analyses included five fur standards with known non-

154   exchangeable δ^2H$_{fur}$ – and treated identically to the samples – thus allowing for correction of

155   hydrogen exchange between samples and ambient water vapour. Samples and standards were

156   weighed (175 ± 10 μg) into 3.2×4 mm silver capsules and then left to equilibrate with

157   laboratory air for a minimum of four days before analysis. During analysis, samples were

158 combusted at 1450°C in a high temperature conversion elemental analyzer (Thermo Scientific),

159 and the resultant gas was analyzed for δ^2H using an interfaced isotope ratio mass spectrometer

160 (Thermo Scientific Delta Plus XL) in continuous flow mode. Ten percent of sample analyses

161 were duplicated, and the precision of these duplicates (average difference ± standard deviation)

162 was 3±3‰ (n=20). Stable isotope results are reported in parts per thousand (‰) in the usual δ

163 notation, relative to VSMOW (Vienna Standard Mean Ocean Water), and were calculated as

164 follows:

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

165

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

167 standard.

168 *Precipitation δ^2H*

169 We used estimates of the mean stable hydrogen isotope composition of growing season

170 precipitation available from waterisotopes.org (Bowen et al. 2005) to predict δ^2H$_{precip}$ at the

171 collection sites of each individual bat. Following previous authors (Cryan et al. 2004; Fraser et

172 al. 2012; Pylant et al. 2014), we calculated the difference between δ^2H$_{fur}$ and δ^2H$_{precip}$ for each

173 bat ($\varDelta^2$H$_{fur\text{-}precip}$). For non-summer individuals, $\varDelta^2$H$_{fur\text{-}precip}$ may be used as a proxy for distance

174 travelled across latitudes from the site of summer residency. We visually inspected changes in

175 $\varDelta^2$H$_{fur\text{-}precip}$ over time to identify the time period when *L. noctivagans* were at the site of fur

176 replacement (i.e. when they were summer residents). Based on these data, we made the

177 preliminary conclusion that members of this species can be classified as summer residents

178 between June 2 and September 3, with fur replacement occurring at some point during that

179 period. This fur replacement time frame is supported by data for other bat species (summarized

180 in Fraser et al. 2013) and anecdotal evidence for this species (E. Baerwald, pers. comm.). Based

181   on this estimate for time spent at the site of fur replacement, we used the online tool IsoMAP to

182   create a stable hydrogen isotope isoscape that interpolated δ^2H_{precip} based only on measurements

183   from June, July, and August in North America between 1960 and 2009 (US National

184   Geophysical Data Center 1998; Welker 2000; Mitchell and Jones 2005; PRISM Climate Group

185   2010; IAEA/WMO 2011; Bowen et al. 2014; created by E. Fraser 2014). IsoMAP generated two

186   models, one based on multiple linear regression techniques and one based on geostatistical

187   analysis (Bowen et al. 2016). For fur samples collected during the period of summer residency,

188   we then conducted a simple linear regression between the mean δ^2H_{fur} for all individuals captured

189   at that site and the estimated δ^2H_{precip} at the site, using δ^2H_{precip} for the growing season isoscape

190   as well as both the multiple linear regression and geostatistical June to August isoscapes. The

191   isoscape created using the geostatistical model produced the best fit (based on r^2), and therefore

192   we chose it for use during the remainder of the project.

193   Using these improved estimates for δ^2H_{precip}, we re-examined $\Delta^2H_{fur\text{-}precip}$ over time

194   (Figure 2) and refined our estimate for the time of summer residency to between June 20 and

195   August 26. We then conducted a subsequent linear regression between δ^2H_{fur} and $\delta^2H_{precip,}$ using

196   only fur samples that were collected during the revised summer residency period (Figure 3).

197   *Data analysis*

198   The focus of this study was on the eastern population of North American *L. noctivagans,*

199   and so we arbitrarily chose -100° longitude as the boundary of our study. We considered all

200   samples collected east of this line in our investigation of individual migratory movements for

201   non-summer individuals. We quantified the movements of these individuals in two ways. First,

202   we used the linear relationship between δ^2H_{fur} and δ^2H_{precip} to calculate the predicted δ^2H_{precip}

203   associated with the fur of each non-summer individual. We then conducted a proximity analysis

204   in ArcMap (ESRI 2016) using our map of δ^2H_{precip} during the period of summer residency to

205   calculate the distance (hereafter referred to as estimated distance travelled) between the

206   individual's location of collection and the nearest location with the relevant δ^2H_{precip} (hereafter

207   referred to as the estimated latitude of origin). There is substantial variation in δ^2H_{fur} within a

208   population, as well as δ^2H_{precip} across the landscape. Hence, we do not anticipate that our

209   calculated estimated distances travelled or estimated latitudes of origin will provide exact

210   measures of individual movements. Rather, they act as a proxy of movement that is standardized

211   and can be compared among individuals across latitudes and of different sexes, and we used

212   these values in the subsequent statistical tests described below.

213   Second, we used the linear relationship between δ^2H_{fur} and δ^2H_{precip} and the associated

214   variation (standard deviation of the residuals = 9.5‰) to run the origin assignment function in

215   Isomap to create probability density analyses of the location of origin for each individual bat. We

216   then identified the area from which there was a 75% probability that each bat had originated

217   (hereafter referred to as the area of probable origin) (following Van Wilgenburg and Hobson

218   2011) and categorized bats as having been collected either in or out of their respective areas of

219   probable origin (Figure 4). Individuals collected within their areas of probable origin were likely

220   more sedentary than those outside but were not necessarily non-migrants. Any migratory

221   movements that they did complete, however, were at a scale less likely to be detected using

222   stable isotope techniques than the larger scale movements of bats that were collected outside of

223   their areas of probable origin. Bats identified as having made smaller-scale movements may

224   indeed have been shorter distance migrants than some other individuals, or may have been

225   captured mid-migration. The 75% probability threshold is arbitrary but was selected to balance

226   the natural variation inherent in environmental stable hydrogen isotope composition with the

227   need to conduct accurate origin assignment (Van Wilgenburg and Hobson 2011).

228   We then conducted univariate general linear models incorporating estimated latitude of

229   origin of all non-summer individuals as the dependent variable and sex and latitude of collection

230   as independent variables. We further included season as a third independent variable, classifying

231   non-summer individuals as either overwintering or potential migrants. We considered individuals

232   collected between October 15 and March 15 as likely overwintering and those collected outside

233   of both the summer resident and overwintering periods as potential migrants. Stable isotope

234   results indicated that most bats were collected south of their estimated latitude of origin, though

235   some were north. In an attempt to identify widespread patterns in the movements of *L.*

236   *noctivagans*, we conducted the analyses described above only on the majority of individuals that

237   were collected south of their estimated latitude of origin. Before conducting these tests, we

238   confirmed that all relevant data were normally distributed using Shapiro-Wilkes tests and that

239   groups displayed homogeneity of variance using Levene's tests.

240

241   **Results**

242   We sampled fur and obtained δ^2H_{fur} for 112 *Lasionycteris noctivagans* study skins (55

243   males, 57 females) that were originally collected between 1886 and 2008 on dates spanning the

244   calendar year (Figure 1). Nonexchangeable δ^2H_{fur} of these samples ranged from -124 to -42 ‰

245   VSMOW (Supplemental Data S1). There were strongly significant linear relationships between

246   the δ^2H_{fur} of summer residents and all three estimates of δ^2H_{precip} at their location of capture [(1)

247   Waterisotope.org isoscape (growing season) (Bowen et al. 2014): $\delta^2H_{fur} = 0.71 \times \delta^2H_{precip} -$

248   33.18, $r^2 = 0.58$, $p<0.001$; (2) Isomap isoscape (June to August), multiple linear regression

249   method (Fraser 2014): $\delta^2H_{fur} = 0.77 \times \delta^2H_{precip} - 35.20$, $r^2 = 0.60$, $p<0.001$; (3) Isomap isoscape

250   (June to August), geostatistical model (Fraser 2014): $\delta^2H_{fur} = 0.70 \times \delta^2H_{precip} - 40.65$, $r^2 = 0.67$,

251    $p<0.001$] . The Isomap isoscape (June to August), geostatistical model, provided the best fit and

252   therefore was used for the remainder of the project.

253   We had δ^2H_{fur} for samples from 68 non-summer individuals (38 females and 30 males)

254   from our study area in the eastern part of the continent. These results suggested that 58 bats (32

255   females and 26 males) were collected to the south, and 10 bats (6 females and 4 males) were

256   collected to the north, of their locations of fur growth. Fourteen females and 16 males, including

257   all individuals with δ^2H_{fur} values indicating that they were north of their estimated latitude of

258   origin, were collected within their areas of 75% probable origin. The remaining 24 females and

259   14 males were collected south of their areas of 75% probable origin (Figure 5a) and were

260   collected during the non-summer period (Figure 5b). The distance between location of collection

261   and the nearest location at the estimated latitude of origin ranged from 38 to 2774 km among all

262   individuals collected during the non-summer period (i.e. overwintering individuals plus potential

263   migrants) and from 125 to 2189 km among individuals collected between October 15 and March

264   15 (i.e. overwintering individuals only) (Figure 6).

265   Both sex and latitude of collection, but not season, were significant main effects on the

266   estimated latitudes of origin. There was also a significant interaction effect between sex and

267   latitude, but not among any of the other independent variables (General linear model: sex –

268    $F_{1,57}=7.806$, $p=0.007$ [mean ± standard deviation – 46.1±3.9 (females); – 43.7 ± 4.9 (males)];

269   latitude of collection – $F_{1,57}=7.392$, $p=0.009$; latitude of collection - $F_{1,57}=7.392$, $p=0.009$; season

270   – $F_{1,57}=2.985$, $p=0.091$; full model – $F_{4,57}=5.130$, $p=0.001$). Females originated from slightly

271   more northern latitude than did males. For female bats, there was a quadratic relationship

272   between latitude of collection and estimated latitude of origin, with females at the southern- and

273   northern-most collection points having the most northern predicted latitudes of origin (Quadratic

274   regression: $F_{2,30}$=6.724, p=0.004, r^2=0.325, Figure 7a). For male bats, latitude of origin

275   decreased slightly with latitude of collection (Simple linear regression: $F_{1,25}$=11.033, p=0.003,

276   r^2=0.315, Figure 7b).

277

278   **Discussion**

279   Our investigation of the migratory patterns of *L. noctivagans* in eastern North America using

280   stable hydrogen isotope techniques suggests intraspecific variability in the migratory tendencies

281   of this species. Many individuals either do not migrate at all or conduct latitudinal migration at

282   too small a scale to be reliably detected using stable hydrogen isotope techniques, while others

283   likely traverse thousands of kilometers. Further, we present evidence for sex-specific differences

284   in migratory tendency. Females spent summer at slightly more northern latitudes than did males,

285   and some of the most northern summer resident females then migrated to some of the most

286   southern overwintering locations.

287   *Stable isotope assignment techniques*

288   Most studies using stable hydrogen isotope evidence to investigate bat migration have

289   used estimates of local δ^2H_{precip} that were based on data for the entire growing season (Fraser et

290   al. 2012; Cryan et al. 2014) or the entire year (Ossa et al. 2012; Popa-Lisseanu et al. 2012; but

291   see Pylant et al. 2014, 2016). In most locations, the growing season likely far exceeds the time

292   period of new fur growth for many temperate bat species (Fraser et al. 2013), and a more refined

293   model that incorporates a customized suite of environmental variables and considers only the

294   relevant time period may better explain the variation in δ^2H_{fur}, although this is not always the

295   case (Hobson et al. 2012; Pylant et al. 2016). In our study, the model based only on the expected

296   time period of fur replacement explained the variation in *L. noctivigans* δ^2H$_{fur}$ values slightly

297   better than a precipitation model based on the entire growing season, and this model also allowed

298   us to refine the timing of summer residency more precisely.

299   *Timing of migration*

300   A limitation of the present study is that little is known about the exact timing of migration

301   for the study species at the levels of both the population and the individual. Because the period of

302   summer residency was defined as ending when there was first evidence of bats having migrated,

303   some individuals collected outside the defined period of summer residency may have been mid-

304   migration or even pre- (in autumn) or post- (in spring) migration, resulting in underestimates of

305   their total migratory journeys. Most *L. noctivagans* collected as mortalities around wind energy

306   facilities are found during late summer and early fall (Arnett et al. 2010), suggesting that at a

307   continental scale, the migratory period for the species lasts more than a month. Less is known

308   about spring migratory movements (but see Jonasson and Guglielmo 2016, Jonasson 2017). A

309   further key knowledge gap is the time required for an individual bat's migratory journey: if

310   migration is completed in relatively little time, then bats are less likely to be collected during

311   migration than if migration is lengthy. Modelling work suggests that *L. noctivagans* are

312   physically capable of completing their migratory movements quickly through the use of torpor-

313   assisted migration (McGuire et al. 2012, 2014) but, recent radio tracking evidence from autumn

314   migrating individuals in Ontario suggests that migration is more protracted (Jonasson 2017). In

315   the present study, it is likely that some of the non-summer individuals collected within their area

316   of probable origin were mid-migration or not migrating, but limited knowledge about *L.*

317   *noctivagans* outside of summer residency make it challenging to assess the extent to which this is

318   the case. Despite this uncertainty, the lack of statistical significance of the season variable

319   (overwintering vs. potential migrant) in our model as well as the presence of relatively sedentary

320   individuals at all times of the year including mid-winter suggest that the main findings of the

321   study accurately reflect continental trends in *L. noctivagans* migration.

322   *Variation in migratory patterns*

323   Our findings suggest the presence of partial migration among eastern North American *L.*

324   *noctivagans*. While some individuals appear to travel thousands of kilometers across latitudes, a

325   subset of the eastern population (including members of both sexes) is either sedentary or engages

326   in relatively short-distance annual movements. Partial migration is common among a wide

327   diversity of taxa, and evolutionary arguments are usually invoked to explain the decision by

328   some individuals to migrate, while others do not (e.g. Dingle and Drake 2007). The decision to

329   migrate may be driven by resource availability, predation risk, body condition, environmental

330   stochasticity, and/or individual dominance (Dingle 2014).

331   We observed bats that were collected within their area of probable origin at all times of

332   year, including the mid-winter, supporting the idea that some individuals never undertook large-

333   scale latitudinal migratory movements. These findings complement numerous records of this

334   species overwintering in relatively northern locations (e.g. Michigan (Gosling 1977; Sherwood

335   and Kurta 1999; Kurta 2008), Minnesota (Beer 1956), Illinois (Izor 1979), Indiana (Whitaker and

336   Hamilton 1998) and British Columbia (Cowan 1933; Nagorsen et al. 1993). While it is unknown

337   where these northern overwintering individuals spent the summer, their presence at northern

338   latitudes during the winter season indicate that they have not engaged in trans-continental scale

339   migratory movements. Most reports of *L. noctivagans* overwintering at northern latitudes discuss

340   only one or a few individual bats, and it is unclear whether they represent exceptions, or provide

341   evidence for a greater trend. Our finding of numerous non-summer individuals across latitudes

342   remaining sedentary or travelling relatively short distances during the non-summer period

343   suggests that *L. noctivagans* overwintering at more northern latitudes may be more common than

344   previously thought. Studies of the overwintering ecology of other latitudinal migrant species

345   indicate that they are capable of spending weeks or months in torpor (eastern red bats, *Lasiurus*

346   *borealis,* Mormann and Robbins 2007; and hoary bats, *Lasiurus cinereus,* Weller et al. 2016),

347   which would make them less detectable. Further, the overwintering ecology of North American

348   bat species that migrate across latitudes is not well described. The assumption that members of

349   these species overwinter at one location in the manner that is typical of many migratory birds

350   may be overly simplistic (e.g. Weller et al. 2016.)

351   Our results suggest a more complicated picture of sex-biased migration than has

352   previously been proposed. Males collected across latitudes and outside of summer residency

353   engaged in relatively short migratory movements or remained sedentary. Females collected at

354   mid-latitudes generally engaged in a relatively consistent pattern of shorter, parallel southern

355   movements. However, the most northern female summer residents engaged in the greatest

356   migratory movements, apparently passing over more southern summer residents to overwinter at

357   the most southern locations, suggesting a partial pattern of leapfrog migration. To our

358   knowledge, ours is the first description of leapfrog migration in a bat species, although this

359   pattern has frequently been documented among bird species (e.g. Boland 1990; Kelly et al. 2002;

360   Bell 2005; Nelson et al. 2015).

361   There are several commonly cited hypotheses to explain the evolution of a leap-frog

362   pattern of migration among birds (Alerstam and Högstedt 1980; Greenberg 1980; Pienkowski et

363   al. 1985; Bell 1996, 1997), each based on the assumption that individuals will time their

364   migration and select their migratory destination in order to optimize access to resources,

365   particularly by reducing competition. In all cases, these competing hypotheses were generated

366   based on the basic characteristics of bird life history, which differ significantly from that of bats

367   (e.g. Fleming and Eby 2003; McGuire 2009; Willis et al. 2010). For example, implicit in some

368   hypotheses (Alerstam and Högstedt 1980; Pienkowski et al. 1985) is the assumption that

369   overwintering birds compete for resources and so disperse widely across overwintering areas.

370   While numerous studies have investigated both dietary resource partitioning and overlap among

371   sympatric bat species (e.g. Arlettz et al. 1997, 2000; Emrich et al. 2013; Krüger et al. 2014),

372   there is currently very little direct evidence that insectivorous bats compete for food or roost

373   resources.

374   The time allocation hypothesis for leapfrog migration (proposed by Greenberg 1980, later

375   extended by Bell 1996, 1997) may be most relevant to insectivorous bats. This hypothesis

376   suggests that individual birds breeding at more northern latitudes will spend a shorter period on

377   breeding grounds than those breeding at more southern latitudes and so will prioritize travelling

378   to overwintering locations with optimal conditions more than individuals who breed at more

379   southern latitudes and so spend less time at their overwintering site. If female *L. noctivagans*

380   across latitudes similarly vary in summer residency time, more northern individuals may benefit

381   from migrating to more southern locations if those locations have better or more resources

382   available. Certainly, female *L. noctivagans* engaged in spring migration are under major

383   energetic constraints and would likely benefit from overwintering in locations with energetically

384   favourable conditions. *Lasionycteris noctivagans* mate during autumn (Cryan et al. 2012), with

385   females storing sperm all winter. At the time of spring migration, females may already be

386   pregnant and need to complete their migratory movements with sufficient fuel stores for

387 gestation and lactation once they arrive at their site of summer residency. Experimental work on

388 *L. cinereus*, another long-distance migrant, indicates that females during spring migration are

389 less likely than males to enter torpor, a strategy that likely benefits embryonic growth, but further

390 increases the energetic cost of migration (Cryan and Wolf 2003). Females of this species are

391 likely under strong selective pressure to begin the spring migration with substantial fuel stores

392 and Jonasson and Guglielmo (2016) found that in two out of three years, female spring migrant

393 *L. noctivagans* captured in southern Ontario carried greater fat stores than did males captured at

394 the same site and migrated ahead of males. The heightened energetic costs faced by spring

395 migrant females, particularly those making the greatest journeys to the most northern locations of

396 summer residency in spring, may make them good candidates for selecting high resource

397 overwintering sites where they can deposit substantial fat stores before spring migration.

398   Finally, there is often a temporal component to leapfrog migration, with clear variation in

399 the timing of migration by northern and southern populations (e.g. Bell 1996; Kelly et al. 2002;

400 Paxton et al. 2007). The structure of the present study did not allow us to test for intraspecific

401 variation in migration timing, although to date, previous research on migratory *L. noctivagans* in

402 Ontario (Fraser 2011) and Alberta (Baerwald et al. 2014), *L. cinereus* in New Mexico (another

403 latitudinal migrant Cryan et al. 2014), and *L. borealis* in the central Appalachian mountains

404 (Pylant et al. 2016) found no such temporal patterns. Given the large numbers of *L. noctivagans*

405 that are killed each year at wind energy facilities, there is an opportunity to replicate these kinds

406 of studies at a greater scale.

407

408   *Summary*

409   Stable hydrogen isotope results for the fur of *L. noctivagans* collected during the non-

410   summer period indicate that members of this species in eastern North America engage in variable

411   migratory strategies. Some individuals of both sexes appeared to be sedentary or to complete

412   relatively short-distance migratory movements, while others traversed the continent with

413   evidence for a pattern of leapfrog migration among female populations. Intraspecific variation in

414   migratory patterns is common in many species, and individual-specific evolutionary arguments

415   are usually invoked to explain these patterns.

416

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431 **SUPPLEMENTARY DATA**

432 Supplementary Data S1. List of all museum specimens that were used in the study, including the

433 institution where they are stored, their date and location of collection, and the non-exchangeable

434 stable hydrogen isotope composition ($\delta^2\text{H}_{\text{fur}}$) of their fur.

435

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603   Figure Legends:

604   Figure 1. Collection locations for all *Lasionycteris noctivagans* individuals included in the study.

605   Fur samples were taken from study skins held in museum collections. Sampling included

606   individuals collected during the period of summer residency (June – August) from across North

607   America and during the non-summer period in eastern North America only.

608

609   Figure 2. The period of summer residency for *Lasionycteris noctivagans* was defined by

610   identifying the time period when bat δ^2H_{fur} was most similar to δ^2H_{precip} at the location of

611   collection (i.e. when $\Delta^2H_{fur\text{-}precip}$ was closest to zero).

612

613   Figure 3. Linear relationship between δ^2H_{fur} of *L. noctivagans* captured during the period of

614   summer residency and mean δ^2H_{precip} (estimated June through August) at the locations of

615   capture. For sites where multiple bats were sampled, variation in δ^2H_{fur} is indicated by error bars

616   showing one standard deviation from the mean.

617

618   Figure 4. Identification of *Lasionycteris noctivagans* as in or out of their locations of probable

619   origin. The 75% probability of origin was determined for each individual collected during the

620   non-summer period. Bats were categorized as either (a) outside their area of probable origin

621   (Individual ROM78278 shown here as an example) or (b) inside their area of probable origin

622   (ROM2204201396 shown as an example).

623

624

625

626   Figure 5. (a) Migratory status of male (squares) and female (circles) bats captured during the

627   non-summer period. Thirty-eight bats (14 males and 24 females) were captured outside of their

628   area of probable origin (indicated by grey symbols), and thirty bats (16 males and 14 females)

629   were captured inside their area of probable origin (indicated by filled symbols). (b) Bats were

630   captured within their area of probable origin at all times of the year, including mid-winter. The

631   dashed vertical line indicates the period of summer residency (June 21st to August 25th), for

632   which data are not shown.

633

634   Figure 6. The distance between collection site and the estimated latitude of origin was less than

635   1000 km for most *L. noctivagans* collected between Oct 15 and March 15 (defined here as the

636   overwintering period) and greater than 2000 km for a few individuals. Distance estimates were

637   obtained by calculating the distance between each bat's location of collection and the nearest

638   location with the relevant $\delta^2 H_{precip}$ (calculated based on the described relationship between $\delta^2 H_{fur}$

639   and $\delta^2 H_{precip}$). Data from females is shown with black bars and from males with open bars.

640

641   Figure 7. The relationship between latitude of collection and estimated latitude of origin for (a)

642   female *Lasionycteris noctivagans* collected during the non-summer period was quadratic

643   (*p*=0.004), with those individuals collected at the most northern and southern latitudes

644   originating from the most northern locations, whereas (b) for males it was linear (*p*=0.003), with

645   those collected at the most southern locations also originating from southern latitudes. For both

646   panels, the dashed line illustrates the points where latitude of collection is equal to estimated

647   latitude of origin (the 1:1 line.)

y = 0.69x - 40.65
r^2 = 0.666

a

$y = 0.08x^2 - 6.13x + 159.57$
$r^2 = 0.325$

b

$y = 0.67x + 17.89$
$r^2 = 0.315$

Latitude of collection (°N)
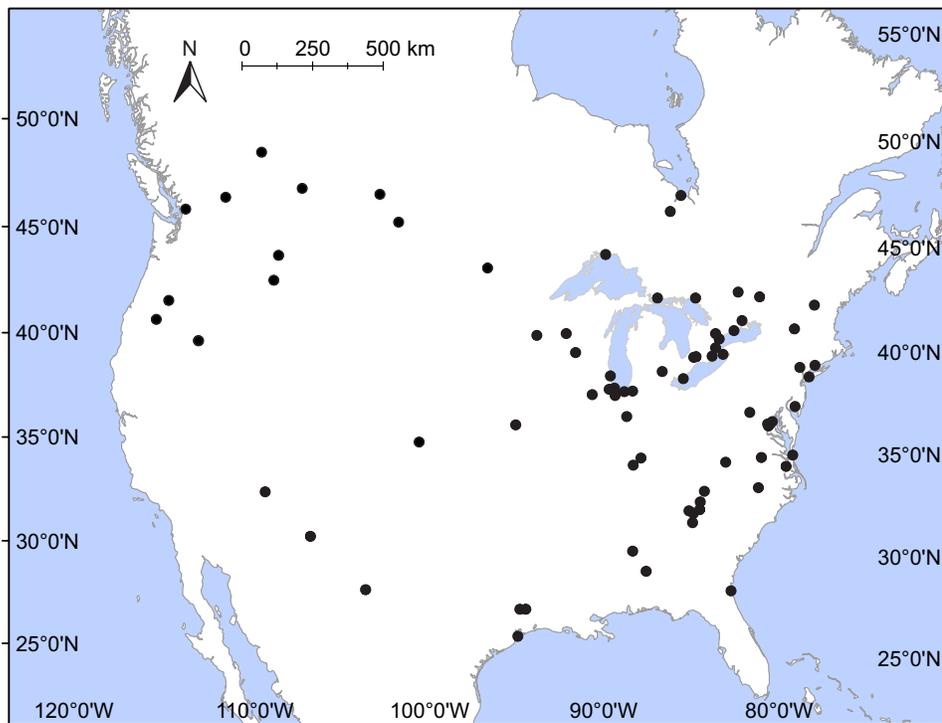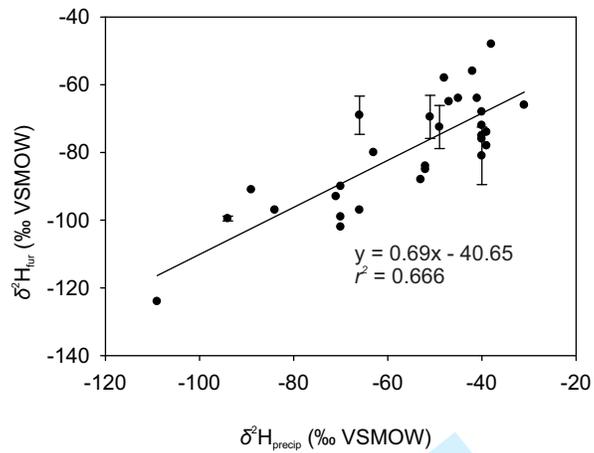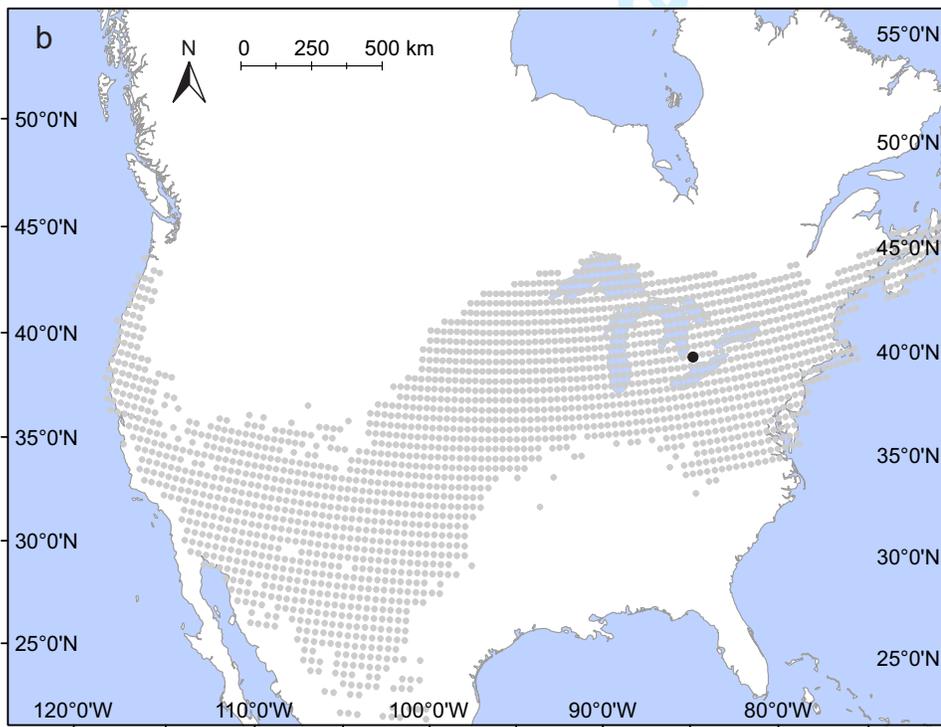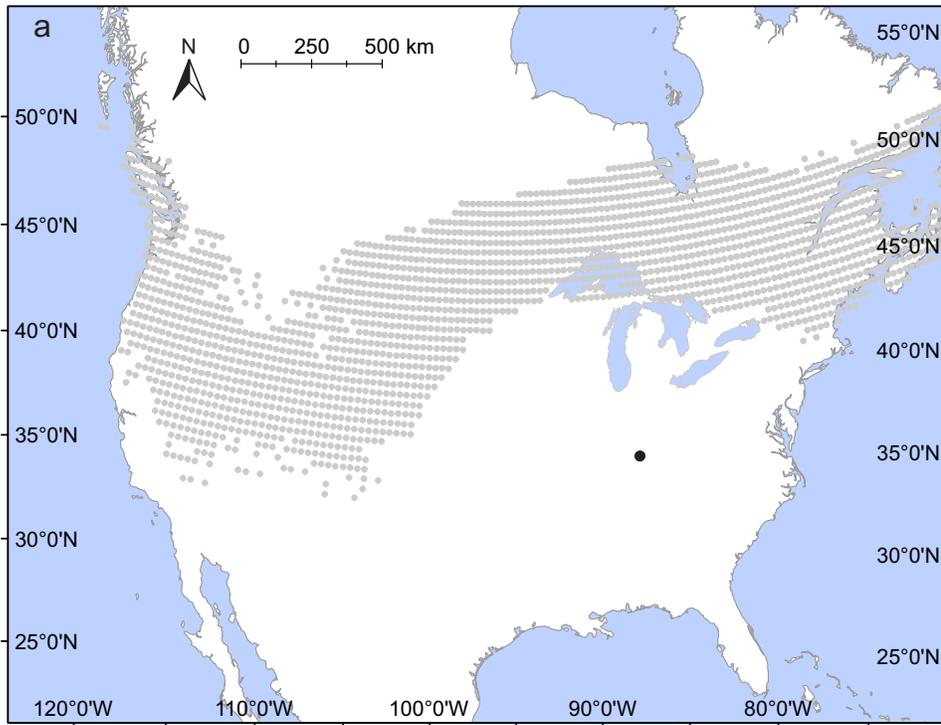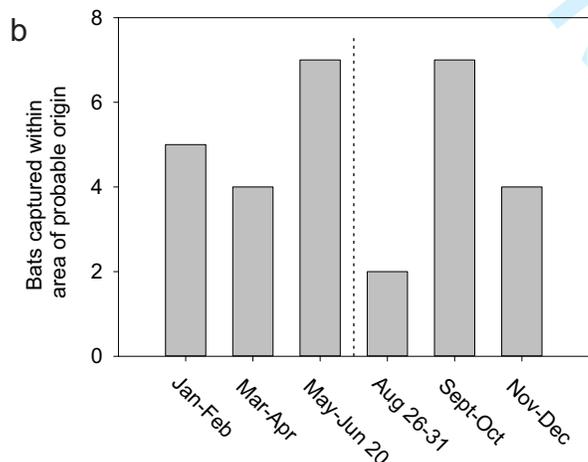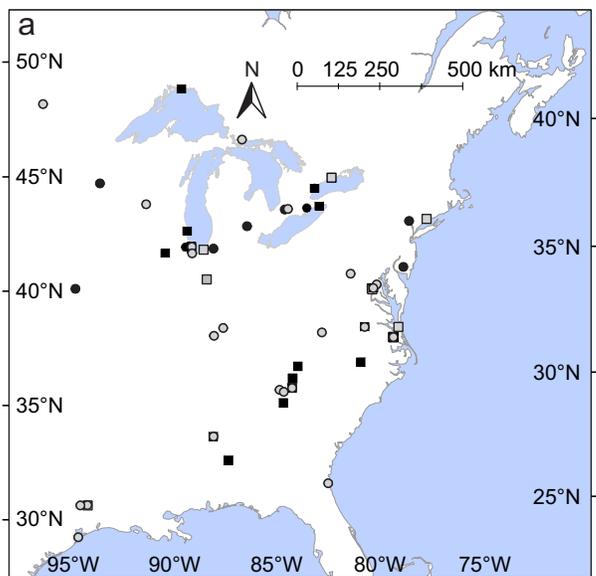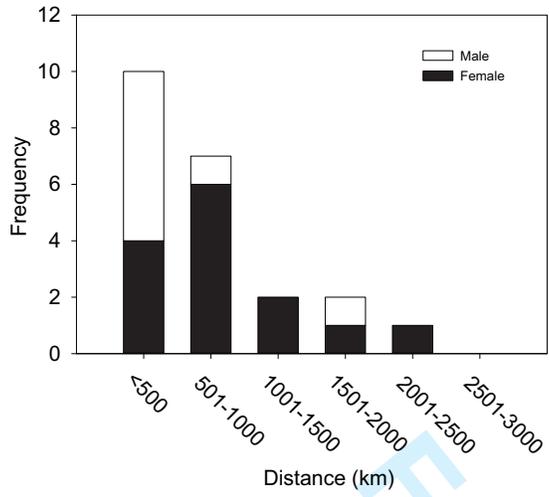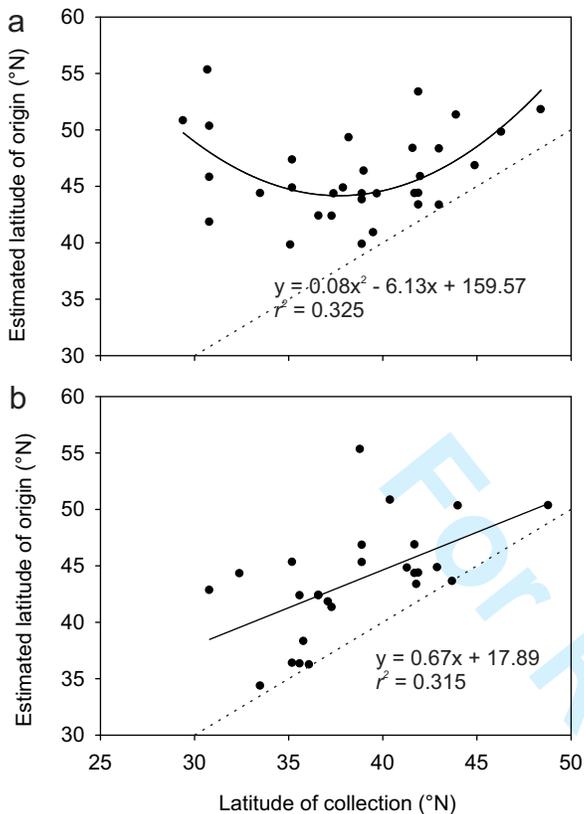
TITLE: STABLE ISOTOPE INVESTIGATION OF THE MIGRATORY BEHAVIOR OF SILVER-HAIRED BATS (*LASIONYCTERIS NOCTIVAGANS*) IN EASTERN NORTH AMERICA
AUTHORS: ERIN E. FRASER, DARIN BROOKS, FRED J. LONGSTAFFE
SUPPLEMENTARY DATA S1: MUSEUM STUDY SKINS AND ASSOCIATED COLLECTION INFORMATION AND $\delta^2 H_{fur}$

Institution	Specimen ID	Specimen sex	Collection date (Julian date)	Collection year	$\delta^2 H_{fur}$ (‰ VSMOW)
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM155572	unknown	227	1891	-48
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM267304	unknown	292	1937	-62
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM147924	male	279	1906	-78
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM178454	male	102	1912	-54
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM178455	male	108	1912	-74
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM178456	male	108	1912	-42
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM204428	male	203	1914	-65
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM204429	male	204	1914	-73
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM212049	male	147	1916	-50
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM216065	male	235	1916	-99
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM248261	male	121	1928	-78
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM249302	male	4	1930	-61
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM251426	male	356	1933	-60
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM251427	male	356	1933	-73
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM254297	male	267	1894	-121
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM264724	male	68	1939	-68
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM271224	male	278	1943	-83
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM271333	male	31	1944	-48
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM344970	male	354	1951	-63
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM448242	male	76	1984	-75
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM448243	male	76	1984	-75
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM54094	male	160	1893	-55
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM555633	male	320	1980	-111
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM568097	male	242	1996	-81
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM63001	male	246	1895	-71
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM94341	male	154	1897	-114
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM125364	female	134	1903	-79
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM169220	female	170	1910	-115
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM178453	female	102	1912	-73
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM187528	female	214	1884	-78
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM187578	female	108	1886	-66
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM207449	female	162	1915	-102
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM226405	female	181	1917	-80
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM238136	female	4	1922	-68
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM248262	female	123	1928	-75
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM249364	female	290	1918	-67
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM254298	female	275	1899	-60
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM256494	female	241	1931	-71
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM265026	female	111	1939	-73
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM293331	female	291	1941	-80
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM448241	female	43	1984	-75
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM505470	female	10	1971	-80
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM543066	female	342	1981	-76
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM554340	female	124	1968	-44
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM567583	female	317	1943	-82

Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM568099	female	249	1985	-110
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM570150	female	334	2007	-56
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM570485	female	105	2008	-80
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM67720	female	225	1894	-77
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM67721	female	225	1894	-68
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM80765	female	238	1896	-97
Smithsonian National Museum of Natural History (NMNH, specimens identified as USNM)	USNM82724	female	247	1890	-94
Royal Ontario Museum (ROM)	ROM17932	unknown	242	1916	-74
Royal Ontario Museum (ROM)	ROM3202290014	unknown	230	1931	-97
Royal Ontario Museum (ROM)	ROM3306200985	unknown	222	1908	-75
Royal Ontario Museum (ROM)	ROM3306200988	unknown	222	1908	-87
Royal Ontario Museum (ROM)	ROM10938	male	242	1937	-89
Royal Ontario Museum (ROM)	ROM13622	male	215	1939	-90
Royal Ontario Museum (ROM)	ROM13624	male	223	1939	-93
Royal Ontario Museum (ROM)	ROM16114	male	257	1943	-95
Royal Ontario Museum (ROM)	ROM17934	male	192	1890	-84
Royal Ontario Museum (ROM)	ROM22030	male	245	1912	-70
Royal Ontario Museum (ROM)	ROM2204201407	male	217	1920	-74
Royal Ontario Museum (ROM)	ROM23450	male	176	1953	-65
Royal Ontario Museum (ROM)	ROM24679	male	217	1930	-68
Royal Ontario Museum (ROM)	ROM2909160001	male	208	1929	-64
Royal Ontario Museum (ROM)	ROM29539	male	243	1941	-102
Royal Ontario Museum (ROM)	ROM32735	male	245	1954	-75
Royal Ontario Museum (ROM)	ROM3306200989	male	220	1914	-76
Royal Ontario Museum (ROM)	ROM78279	male	246	1959	-79
Royal Ontario Museum (ROM)	ROM83899	male	210	1936	-64
Royal Ontario Museum (ROM)	ROM86741	male	249	1968	-91
Royal Ontario Museum (ROM)	ROM10572	female	210	1937	-74
Royal Ontario Museum (ROM)	ROM10574	female	215	1937	-65
Royal Ontario Museum (ROM)	ROM13623	female	215	1939	-102
Royal Ontario Museum (ROM)	ROM17930	female	189	1890	-85
Royal Ontario Museum (ROM)	ROM19783	female	206	1949	-99
Royal Ontario Museum (ROM)	ROM19784	female	206	1949	-100
Royal Ontario Museum (ROM)	ROM2204201396	female	170	1918	-70
Royal Ontario Museum (ROM)	ROM22946	female	226	1939	-91
Royal Ontario Museum (ROM)	ROM22947	female	100	1950	-89
Royal Ontario Museum (ROM)	ROM2404140074	female	154	1906	-113
Royal Ontario Museum (ROM)	ROM24682	female	239	1930	-85
Royal Ontario Museum (ROM)	ROM27944	female	257	1957	-77
Royal Ontario Museum (ROM)	ROM3012190006	female	234	1930	-124
Royal Ontario Museum (ROM)	ROM32571	female	256	1947	-61
Royal Ontario Museum (ROM)	ROM3508010181	female	179	1935	-88
Royal Ontario Museum (ROM)	ROM3511250220	female	249	1935	-88
Royal Ontario Museum (ROM)	ROM3601020007	female	223	1929	-72
Royal Ontario Museum (ROM)	ROM74799	female	132	1975	-65
Royal Ontario Museum (ROM)	ROM78278	female	108	1955	-86
Royal Ontario Museum (ROM)	ROM78280	female	310	1959	-72
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC15155	male	169	1965	-79
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC15156	male	169	1965	-77

Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC15157	male	169	1965	-84
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC15158	male	169	1965	-46
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC15159	male	169	1965	-91
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC22560	male	152	1968	-89
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC22561	male	152	1968	-51
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC22562	male	153	1968	-109
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC28524	male	170	1974	-88
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC28526	male	197	1969	-58
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC33413	male	77	1978	-75
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC30227	female	267	1975	-98
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC33412	female	324	1977	-73
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC33414	female	6	1978	-93
Texas A&M University Biodiversity Research and Teaching Collections (TCWC)	TCWC33415	female	6	1978	-81
The Field Museum of Natural History (FMNH)	FMNH167017	male	307	1925	-69
The Field Museum of Natural History (FMNH)	FMNH175333	male	256	1999	-53
The Field Museum of Natural History (FMNH)	FMNH17855	male	36	1910	-71
The Field Museum of Natural History (FMNH)	FMNH5834	male	262	1898	-66
The Field Museum of Natural History (FMNH)	FMNH124583	female	62	1983	-70
The Field Museum of Natural History (FMNH)	FMNH134585	female	70	1987	-100
The Field Museum of Natural History (FMNH)	FMNH137328	female	264	1915	-84
The Field Museum of Natural History (FMNH)	FMNH175334	female	8	2002	-66
The Field Museum of Natural History (FMNH)	FMNH64436	female	221	1948	-56
The Field Museum of Natural History (FMNH)	FMNH6618	female	235	1899	-66
The Field Museum of Natural History (FMNH)	FMNH73997	female	166	1950	-48