Estimating natal origins and migratory patterns of juvenile raptors banded during fall migration at Hawk Ridge Duluth, MN

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ABSTRACT

Effective conservation of migratory species requires knowledge of the many geographic locations utilized during their full annual cycle. Determining breeding location can be challenging due to the secretive nature of many raptors on their breeding grounds; however, during migration, these species are relatively easy to study since large numbers of individuals fly through migration corridors. The objective of this research was to improve our understanding of full annual cycle landscape use by identifying the breeding origin and migratory patterns of juvenile raptors utilizing hydrogen stable isotope analysis of feathers (δ^2H_f) collected during fall migration at Hawk Ridge in Duluth, Minnesota. We found that δ^2H_f was able to elucidate temporal migration patterns and broadly assign natal origins. However, assignments remain broad and could be improved by the addition of other techniques. Knowledge of breeding locations and migratory patterns is important for connecting ecological variables on breeding grounds to observed population changes during migration and placing Hawk Ridge's long-term monitoring data within a geographical framework.

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INTRODUCTION

For migratory species, such as raptors, events that occur at any of the many locations utilized during their full annual cycle can affect survival and reproduction. Events such as habitat loss may cause a decline in population size whereas an increase in food availability may cause a rise. However, a species that is less reliant on very specific locations may not be impacted as much by these events due to the ability to use other locations and habitats (Webster et al., 2002). Therefore, knowledge of these locations and how strongly they are connected (i.e., migratory connectivity) is important for informing conservation and management of that species (Bauer et al., 2016; Marra et al., 2018). Unfortunately, many raptor species are inconspicuous during the breeding season and therefore difficult to study during that stage of their life. Monitoring during migration has been used for this reason to establish population trends for raptors.

Raptors are especially easy to study during migration when large numbers of individuals concentrate along migration corridors such as Hawk Mountain, PA, the Goshute Mountains, NV, and Hawk Ridge, MN. This phenomenon is created by landscape features (e.g., mountain ranges), presence of suitable habitat, and weather patterns. Hawk Ridge is located in Duluth, MN, USA (46.85ºN, -92.03ºW) at the westernmost tip of Lake Superior (Inzunza, 2008). Raptors concentrate in this area due to the extension of boreal and transitional Aspen-Parkland habitat into northern MN, the presence of Lake Superior on the eastern side of northern MN that many raptors are reluctant to cross, and favorable flight conditions due to orographic lift created along the basalt ridges of Lake Superior (Goodrich & Smith, 2008). Each fall, about 60,000 raptors are counted migrating through Duluth and on average over 2,500 individuals are banded.

Some of these banded birds are recaptured further south but very few birds are reencountered north of Duluth during their breeding season. As a result, very little is known about the distances traveled from breeding grounds and the timing of passage through Duluth in relation to these natal/breeding grounds.

Raptors are often used as bioindicators of ecosystem health due to their visibility, presence in a variety of different habitats, and their high trophic position which makes them susceptible to biomagnification of environmental contaminants (K. Bildstein, 2001; Movalli et al., 2008). During migration, raptor monitoring sites record count data that suggest trends in species numbers but linking these trends to population changes and their cause is more difficult (Oleyar et al., 2021). With habitat loss, shifting land use, and changing climates, knowledge of migratory connectivity is becoming more urgent for conservation.

Techniques for studying movement

Many techniques can be utilized during migration monitoring to understand full-annual cycle landscape use and migratory connectivity (Norris et al., 2006). Extrinsic techniques such as mark-recapture (e.g., banding) are cheap, but have low rates of return and rely on the recapture of an individual. Satellite, PIT-tagging, GPS, and radio-tracking are also used to understand large-scale movements of individuals (Hobson et al., 2019; Moliner et al., 2015). However, these techniques can be expensive, have the potential to negatively affect an individual's survival, are not all currently available for smaller species, and only provide geographic information after the initial capture (Bodey et al., 2018). Information about the origin of a bird sampled during migration can be acquired using intrinsic techniques such as genetics, trace element, and stable isotope analysis without having to recapture the individual (Hobson et al., 2019). Intrinsic techniques are often relatively inexpensive, non-invasive, and therefore can be used to assess a large number of individuals rather than just a few.

Stable isotope analysis has been successfully used to track movements and geographic origin for many different migratory species (Chamberlain et al., 1997; Hobson & Wassenaar, 1997). Hydrogen is the most commonly implemented isotopic marker for movement studies in North America since hydrogen isotope ratios of precipitation form geographic gradients. The element hydrogen has two stable isotopes, protium (^{1}H) and deuterium (^{2}H), which react differently due to the large mass difference between the two atoms.

Isotope ratios vary across the landscape based on latitude, altitude, temperature, and distance from the coast (Dansgaard, 1964). Generally, in North America there is less deuterium further north and at higher elevations as average annual temperature decreases (Kendall & Coplen, 2001). This continental gradient is subsequently incorporated into animal tissues through diet and drinking water. A mathematical relationship between the isotope ratios of tissue and precipitation at a given location can be identified and used to assign origin to unknown origin tissues. This phenomenon relies on the fact that hydrogen in organisms is derived from drinking water and diet; therefore, an animal that grows tissues on a specific location will have isotope values reflective of the environment in which those tissues were grown. Feathers provide an ideal tissue since they are inert once grown.

In addition, many raptors reliably molt their feathers on breeding grounds before migrating. This means that the feathers collected during migration often possess the isotopic signature of their breeding grounds. Stable hydrogen isotope analysis has been successfully used to estimate geographic origin by comparing hydrogen isotope ratios of unknown feathers (δ^2H_f) to an "isoscape" of known origin feathers (Wassenaar & Hobson, 2006).

An isoscape, or isotopic landscape, is a map showing the unique isotopic ratio for a given geographic location (West et al., 2008). Hydrogen isotopes fractionate as they are incorporated into tissues; therefore, the relationship between δ^2H of precipitation and δ^2H of feather tissue must be understood before geographic assignment can be made. To do this, feather samples from known origin individuals can be analyzed in order to create a regression model with which to connect precipitation and feather δ^2H.

Stable isotope analysis limitations

However, there are some limitations to stable isotope analysis. Of the organically bound hydrogen in feathers, ~8-15% is exchangeable hydrogen which can exchange with ambient water vapor (Hobson et al., 2012). This means that when samples are moved from one environment to another, their hydrogen isotope ratios can change. Therefore, the portion of keratin that is exchangeable hydrogen must be accounted for using a comparative-equilibration approach in which unknown origin samples equilibrate with known standards before analysis (Wassenaar & Hobson, 2003). In addition, laboratories do not always use the same methods and calibration scales which can make comparisons between studies challenging. Part of this problem is that there is no International Atomic Energy Agency (IAEA) reference standard available for keratinous materials which means that values must be expressed in terms of Vienna Standard Mean Ocean Water (VSMOW). In addition, intra- and inter-feather variability has been documented but the processes underlying this variability are not well understood (Smith et al., 2008). Therefore, feather selection and subsampling should be controlled in an isotope study. Past research has also shown unexplained enrichment in adult raptor feathers that are likely due to differences in physiology or evaporative cooling mechanisms (Greenwood & Dawson, 2011; Meehan et al., 2003). Analyses in this study were restricted to juvenile raptors.

Objectives

In this study we wanted to test the utility of hydrogen stable isotope analysis as a method for adding a geographic context to variables taken during the regular banding process at Hawk Ridge (e.g., morphology, contaminant exposure). We selected three species of raptors that represent different life histories but are some of the most commonly banded species at Hawk Ridge. Using hydrogen stable isotope analysis we estimated the most probable natal origins and constrained the assignment with knowledge of breeding ranges and limited band return data to eliminate regions that were unlikely natal origins (USGS Bird Banding Laboratory, 2022). We predicted that the most probable natal origins would be located in Northern MN and Western Canada. Using δ^2H as a proxy for latitude we also assessed patterns in migration timing. We predicted that raptors banded at Hawk Ridge earlier in the migration season migrate from natal origins at lower latitudes than those that are banded later in the season.

METHODS

Unknown origin samples

Feather samples were collected from juvenile Sharp-shinned Hawks (*Accipiter striatus*), Red-tailed Hawks (*Buteo jamaicensis*), and Northern Saw-whet Owls (*Aegolius acadicus*) caught during fall migration 2020 at Hawk Ridge in Duluth, MN. The fall diurnal raptor banding season took place daily from 15 August until mid-December. A combination of mist nets, dho gazas, and bow traps were used to capture *A. striatus* and *B. jamaicensis*. All raptors were fit with an aluminum band, aged, and sexed, when possible. Morphological measurements were recorded per standard banding protocol (weight, wing chord, and tail length). The fall owl banding season took place over 67 nights between 15 September and 20 November. Three net arrays consisting of a total of 3 audio callers and 14 nets were run consistently throughout the season. The *A. acadicus* net array was made up of six 12-meter-long nets located in close proximity to an audio lure which played the *A. acadicus* breeding call. All required federal and state permits were granted for trapping, banding, and feather collection. Feather sampling techniques were approved under the University of Minnesota IACUC protocol (1904-36977A to M. Etterson).

Known origin samples

Published δ^2H data from museum specimens is available for juvenile raptors (Lott & Smith, 2006; Wommack et al., 2020). An additional seven museum samples from known source locations were analyzed to include more resolution to Minnesota and Canada (Table 1; Bell Museum, Minnesota).

Sample selection

Past research suggests there is unexplained variation in δ^2H of feathers taken from different feather tracts; therefore, we sampled feathers from the same feather tract within a single species (Smith et al., 2008). Contour feathers (3) from the ventral sternal tract were taken from *A. striatus* and *B. jamaicensis* due to the small size of the feathers and ease of sampling repeatability. In contrast, contour feathers of juvenile *A. acadicus* are not reliably molted on their breeding grounds and may be grown during migration. Instead, a small 1 cm feather clipping was taken from the first primary (P1) of *A. acadicus*. P1 was chosen to allow comparison with past research and to allow future research to assess geographic origins of different age classes since P1 is often retained for multiple years (Ruyck et al., 2013). Feathers were stored in paper coin envelopes at room temperature.

Sample analysis

One hundred feathers each from *A. striatus* and *A. acadicus* and 40 feathers from *B. jamaicensis* spanning the length of the migration season (15 Aug – 30 Nov) were analyzed for feather hydrogen stable isotope ratios (δ^2H_f). *A. acadicus* feathers were cleaned with a 2:1 chloroform/methanol solution, dried for 48 hours, and packaged in clean envelopes. All feather samples were sent to the Central Appalachian Stable Isotope Facility (CASIF) for analysis. *A. striatus* and *B. jamaicensis* feathers were cleaned at CASIF with a 2:1 chloroform/methanol solution. All samples were then cut and weighed to 0.4 mg (+/- 0.05 mg) in silver capsules. Because hydrogen in solid samples is able to exchange with ambient water vapor, feathers were analyzed using the comparative equilibration approach (Wassenaar & Hobson, 2003). Samples were left to equilibrate in the local air alongside standards for 72+ hours before crimping them closed. Sample plates were left in a desiccator for 48 hours before loading them into the zero blank autosampler. Samples were analyzed using a Temperature Conversion Elemental Analyzer (TC/EA) from Thermo Fisher alongside the standards USGS 42, USGS 43, EC-01 (formerly KHS), and EC-02 (formerly CBS). A powdered keratin standard (porcine from Spectrum Chemical) was also included every 10 samples as a QC check (sd = 1.3‰). Values were compared with reference materials to determine δ^2H_f for only the non-exchangeable hydrogen. Stable isotope measurements are expressed as a ratio relative to a standard and reported in delta notation (per mil):

$$\delta \text{ } in \text{ } per \text{ } mil = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000$$

where R is the ratio of the heavy to light isotope. Final values were expressed in delta notation relative to the international standard VSMOW (Vienna Standard Mean Ocean Water). The average difference in δ^2H_f for ten samples run in duplicate was 6.9±3.3‰. All data were calibrated to the reference scale of Soto et. al 2017 (Soto et al., 2017).

Data analysis

For each species we evaluated the assumption of normality of δ^2H_f values by visual assessment of histograms, qqplots, and a Shapiro-Wilk test. We assessed variance of δ^2H_f using Bartlett's test of homogeneity of variance. Mean δ^2H_f values were compared between species and sex of the same species using a non-parametric Kruskal-Wallis and Wilcoxon test. Two *A. acadicus* outliers were removed due to extremely high

δ^2H_f values. All statistical modeling was completed using R version 4.1.3 (R Core Team, 2013). Significance levels were all set at $\alpha = 0.05$ unless otherwise stated.

Migration patterns

Migration patterns were assessed by regressing δ^2H_f against Julian date of banding. Since δ^2H of precipitation in North America follows a mostly latitudinal gradient, δ^2H_f can be used as an estimate of latitudinal origin. For *A. striatus* and *A. acadicus* regressions were run separately for male and female individuals.

Generating a feather isoscape

We created a δ^2H_f isoscape for juvenile raptors using functions within the *assignR* package (Ma et al., 2020). We compiled known origin sample data from this study (n=7) with samples from Lott and Smith 2006 (n=245) and Wommack et al. 2020 (n=30) to be used as the input file for creating a relationship between δ^2H_f and a δ^2H isoscape based on precipitation (Figure 1). Since the data from Lott and Smith 2006 used different methods and reference standards, we also calibrated the values using the *refTrans* function in the *assignR* package. The *refTrans* function uses an algorithm to transform data to a specific calibration scale to make data from different studies more comparable (Magozzi et al., 2021). We used the *calRaster* function to calibrate an average global growing-season precipitation isoscape (GlobalPrecipGS: defined as months with mean temperature greater than 0°C) using the known origin tissue values and obtained the following calibration equation: $\delta^2H_f = 0.843\ \delta^2H_p + 17.05‰$ ($R^2 = 0.64$). The isoscape quality was assessed using the QA function in *assignR* (Figure 2). The QA function partitions the known-origin data into calibration and validation data sets and then runs the *calRaster* and *qtlRaster* functions, calculates descriptive statistics, and returns results in the form of graphs and tables.

Probabilistic assignment of natal origin

For each individual we used the *pdRaster* function in *assignR* to create a continuous probability density of natal origins for each grid cell in the assignment area. The values in these maps are scaled to unity across the assignment area making them estimates of probability density. We created multiple versions of these probability density maps by imposing a series of *a priori* constraints. The first version included all of North America, the second only the known breeding range for each species, and finally a breeding range cropped based on band return data for Minnesota. Breeding range maps were downloaded from the eBird Status and Trends Data Products (eBird, 2021) and cropped using ArcGIS Pro. For each species we used the *unionP* function to combine the individual probability density maps. The values of the resulting maps are the probability density that any individual of that species came from each grid cell in the assignment area.

RESULTS

The δ^2H_f values of 240 juvenile raptor feathers ranged from 8.94 to -142.68‰ (Appendix). Two *A. acadicus* had unexpectedly high δ^2H_f values (Band #1154-19291: 8.94‰; Band #1154-19206: -7.44‰). Banding records indicated that at least one individual had a molt pattern suggesting that it was likely incorrectly assigned as a juvenile (8.94‰; 1154-19291). The other (-7.44‰; 1154-19206) had no associated banding notes. These two samples were excluded from further analysis. In addition, there were two *B. jamaicensis* samples with very low δ^2H_f values. Both of these individuals were the only dark morph *B. jamaicensis* analyzed. Two *A. striatus* samples also had lower δ^2H_f than the rest of the samples analyzed for this species. The values fit within the known breeding range for both species and were therefore included in the analyses of migration patterns and assignment of natal origins.

Within species, δ^2H_f values did not deviate from normality based on a Shapiro-Wilk Test (Figure 3; p-values > 0.05). We rejected the assumption of equal variances based on Bartlett's test for homogeneity of variances (Figure 4). Therefore, non-parametric tests for analysis of variance were used. A Kruskal-Wallis test indicated that there were significant differences between the three species. Mean δ^2H_f values of the three species were all statistically different from each other based on a multiple pairwise-comparison Wilcoxon rank sum test (Table 2). *B. jamaicensis* had the lowest mean (-70.5‰), followed by *A. acadicus* (-63.3‰), and *A. striatus* (-57.2‰) with the most positive mean. Mean δ^2H_f values were not statistically different between sexes of the same species for both *A. striatus* and *A. acadicus* (Table 3). *B. jamaicensis* were not sexed during the banding process.

Temporal migration patterns

Linear regression suggested a significant relationship between δ^2H_f and Julian date of banding for *A. striatus* females, *A. acadicus* females, and *B. jamaicensis* (Figure 5). The relationship between δ^2H_f and banding date for both *A. striatus* females and *B. jamaicensis* was negative. *A. acadicus* females showed the opposite (positive) relationship between δ^2H_f and banding date. Neither *A. striatus* or *A. acadicus* males had a significant relationship between banding date and δ^2H_f.

Isoscape calibration

A significant positive relationship was found between the δ^2H_f values of the known origin samples and the modeled precipitation isotope values for juvenile raptors (Figure 6). Results from the QA function indicated that isoscape quality was adequate for geographic assignment (Figure 2).

Probabilistic assignment

Continuous posterior probability surfaces included high probability densities within each of the species known breeding ranges (Figure 7). However, because of the broad latitudinal gradients of hydrogen isotope ratios, areas outside of the known breeding ranges had probability of origin too. Therefore, maps were sequentially constrained with known breeding range and limited band returns. Spatial polygons including these constraints were provided as the mask for the *pdRaster* function.

DISCUSSION

Migration patterns

Regression of Julian date of banding with δ^2H_f values revealed temporal migration patterns. Female *A. striatus* and all *B. jamaicensis* had a significant negative relationship between Julian banding date and δ^2H_f indicating that southern individuals were in general migrating through Duluth earlier in the season than more northern-breeding individuals. For *A. striatus* this fits with a pattern of chain migration in which birds breeding further north also winter further north. This pattern has been observed in other North American flyways (Smith et al., 2003). However, *A. acadicus* had a significant positive relationship between banding date and δ^2H_f indicating that more northern populations were banded at Hawk Ridge earlier in the season. Knowledge of *A. acadicus* migration patterns are limited and not well understood (Rasmussen et al., 2020). Overall, variation in Julian banding date only explained <30% of the variation in δ^2H_f indicating that these migration patterns are not extremely strong.

Both *A. striatus* and *A. acadicus* males did not have a significant relationship between banding date and δ^2H_f. The lack of significant relationship suggests that males are migrating in a broad front pattern. For both species, males are smaller than females, develop and fledge from the nest sooner, and therefore could theoretically begin migration before females. However, banding and count data shows that female *A. striatus* migrate through Duluth before juvenile males (Bildstein et al., 2020; Rasmussen et al., 2020). The δ^2H_f values in this study indicate that while males may fledge before females, they are not necessarily initiating migration sooner. In addition, mean δ^2H_f values of males and females of both species were not statistically different from each other indicating that both males and females were coming from similar geographic regions. One explanation for the lack of migration pattern is that males may use the time post-fledging as a precursor to finding nesting habitat for the next breeding season (Ciaglo et al., 2021; Patchett et al., 2022). This phenomenon of post-fledging prospecting has been reported in a variety of species and may contribute to breeding success the following year.

Estimating natal origins

A. striatus had statistically higher mean δ^2H_f values than either of the other species and *B. jamaicensis* had the lowest mean values. This suggests that juvenile *A striatus* are migrating from further south than the other two species. The variance of δ^2H_f values for *A. striatus* was also smaller than the other two species indicating that the individuals sampled were from relatively similar natal origins versus a broad region.

The lower δ^2H_f values of *B. jamaicensis* indicate that more individuals are coming from further north than the two other species. *B. jamaicensis* migrates different distances throughout its range in North America but northern breeders tend to complete the longest fall migrations (Preston & Beane, 2020).

Based on the *QA function* of *assignR*, the feather δ^2H isoscape was adequate for assigning natal origins. For example, we would expect to exclude 50% of the study area a little more than 90% of the time (Figure 2). While museum specimens like those used in this study provide a unique and convenient opportunity to obtain known-origin samples, there are potential limitations to their use. While specimens were constrained to breeding season, some of these individuals may not have been collected in the location where they hatched. In addition, these specimens come from many different years that could show yearly variation in isotope ratios. As shown in this study, not all specimens have been calibrated to the same reference scales. Going forward, standardization of procedures and techniques will allow for more comparability between studies. Combined with the use of isotope databases like IsoBank this would allow for future studies to use already established data.

Constraining probability density maps with breeding ranges helped to eliminate areas of the broad latitudinal bands of probable origin. However, for all three species these maps still included areas west of the Rocky Mountains that *A. striatus* and *B. jamaicensis* are unlikely to be migrating from. Most of the raptors in the western region of North America are thought to use three main raptor migration routes: the Pacific Flyway, the Intermountain Flyway, and the Rocky Mountain Flyway but individuals with plumage characteristics specific to these regions are occasionally counted at Hawk Ridge in the Mississippi Flyway. When these regions were excluded for *A. striatus* and *B. jamaicensis*, the highest probability density areas were in western Ontario, southern Manitoba, Saskatchewan, and into Alberta. These constraints were not as useful for *A. acadicus* which are known to make large East-West movements (Rasmussen et al., 2020). This suggests that hydrogen isotope analysis alone may be less useful for understanding the movements of this species.

Outliers

Two *A. acadicus* individuals had unusually high δ^2H_f values. Based on banding notes at least one appears to have been incorrectly aged as juvenile. More research should be devoted to studying raptors from known origin locations to evaluate whether this technique could be useful in the future for all ages of raptors.

A few other individuals were considered outliers with very low δ^2H_f values. They were included in the creation of assignment maps since the low values were still within the known breeding ranges of these species. One individual was a dark morph *B. jamaicensis* that was suspected to be a *harlani* subspecies based on distinctive plumage (Band #2187−05377; δ^2H_f = -142.68‰**)**. The *B. j. harlani* subspecies is thought to breed from central Alaska into northern Canada (Preston & Beane, 2020). Based on the δ^2H_f value for this individual the suspected natal origins align with the breeding range for this subspecies (Figure 8). This assignment helped to confirm that the values for these outliers were not likely due to analytical error or unexplained depletion of ^2H. The other *B. jamaicensis* outlier was also a dark morph (Band #2187-05379; δ^2H_f = -119.81‰) but did not have the same markings as a typical *B. j. harlani*. This individual also likely hatched in western Canada, but is of unknown subspecies origin. These two individuals were banded within one day of each other.

Two *A. striatus* possessed δ^2H_f values that were outside the normal distribution of values (Band #1893-46824, δ^2H_f = -115.21‰ and Band #1893-46806, δ^2H_f = -113.59‰). Both of these individuals were female and had highest probability density regions in northwestern Canada. Only one band return from Hawk Ridge has been reported in this region (USGS Bird Banding Laboratory, 2022). Perhaps individuals coming from these regions in Canada are more common than banding return data suggests. It is also possible that this long-distance migration is more common in juvenile birds than adults.

As in previous studies, we found that δ^2H values of juvenile raptor feathers can be used to broadly assign natal origin of birds on a broad spatial scale (Crowley et al., 2021; Ruyck et al., 2013; R. B. Smith et al., 2003; Wommack et al., 2020). Probabilistic assignments using the *assignR* package had highest probability densities of natal origin north of Duluth. However, hydrogen isotopes have broad latitudinal bands across North America which means that assignments are not constrained on an East-West direction and therefore this technique has limitations for gaining understanding of more precise natal origins. Future studies at Hawk Ridge using stable isotopes could incorporate a dual- or multi-isotope approach that has complementary gradients to hydrogen isotopes (Crowley et al., 2021; Wommack et al., 2020). In addition, the combined use of extrinsic techniques like transmitters could help to verify assignments made with isotopes. Other intrinsic techniques like genetics or trace metal analysis could also be used to further refine assignments by isotope analysis.

CONCLUSION

We demonstrated that hydrogen isotope analysis can be useful for evaluating temporal migration patterns and determining natal origins for juvenile raptors banded at Hawk Ridge. We found that migration timing through Duluth in relation to natal origins depends on both species and sex. While hydrogen isotope analysis shows promise for understanding variables collected during migration at Hawk Ridge, the addition of other techniques or isotopes would allow for more precise assignments than the broad latitudinal gradients of hydrogen isotopes. More research is needed to understand the connection between migration at Hawk Ridge and other parts of a raptors full annual cycle. This knowledge will help future research to determine if changes noticed during migration are due to events occurring at specific geographic locations and also has the potential to track changes in yearly migration patterns and routes. Habitat loss and a changing climate continue to pose risks to raptors and other species; therefore, knowledge of landscape usage is becoming increasingly urgent for conservation.

TABLES AND FIGURES

Table 1. Known-origin museum specimens. Seven *A. striatus* museum specimens from the Bell Museum were analyzed for δ^2H_f. Specimens were all juvenile and from MN or Canada. These samples were used to calibrate a feather isoscape based on hydrogen isotope ratios of precipitation.

Sample ID	Species	Age	δ^2H (‰)	δ^2H SD (‰)	State/Province	Country	Latitude (°)	Longitude (°)
SS-45433	*Accipiter striatus*	juvenile	-33.92	1.33	MN	USA	46.37	-91.71
SS-6365	*Accipiter striatus*	juvenile	-38.67	1.33	MN	USA	47.53	-91.09
SS-25443	*Accipiter striatus*	juvenile	-33.85	1.33	MN	USA	47.45	-92.61
SS-21872	*Accipiter striatus*	juvenile	-45.87	1.33	MN	USA	47.45	-92.61
SS-6132	*Accipiter striatus*	juvenile	-39.18	1.33	MN	USA	45.30	-93.57
SS-7976	*Accipiter striatus*	juvenile	-72.7	1.33	MB	Canada	53.70	-100.33
SS-38957	*Accipiter striatus*	juvenile	-65.86	1.33	MN	USA	46.69	-94.25

Table 2. Results from the pairwise-comparison Wilcoxon rank sum test. Mean δ^2H_f values differ between each of the three species.

	A. striatus	***A. acadicus***	***B. jamaicensis***
A. striatus	-	0.0032	-
A. acadicus	-	-	0.011
B. jamaicensis	<0.0001	-	-

Table 3. Results from a paired t-test of δ^2H_f values between sexes.
B. jamaicensis were not included since they were not sexed. There were no statistical differences between δ^2H_f values of different sexes indicating that males and females from the same species migrate from similar natal origins.

Species	**t**	**df**	**p-value**
A. striatus	0.76	96	0.45
A. acadicus	-0.94	96	0.35

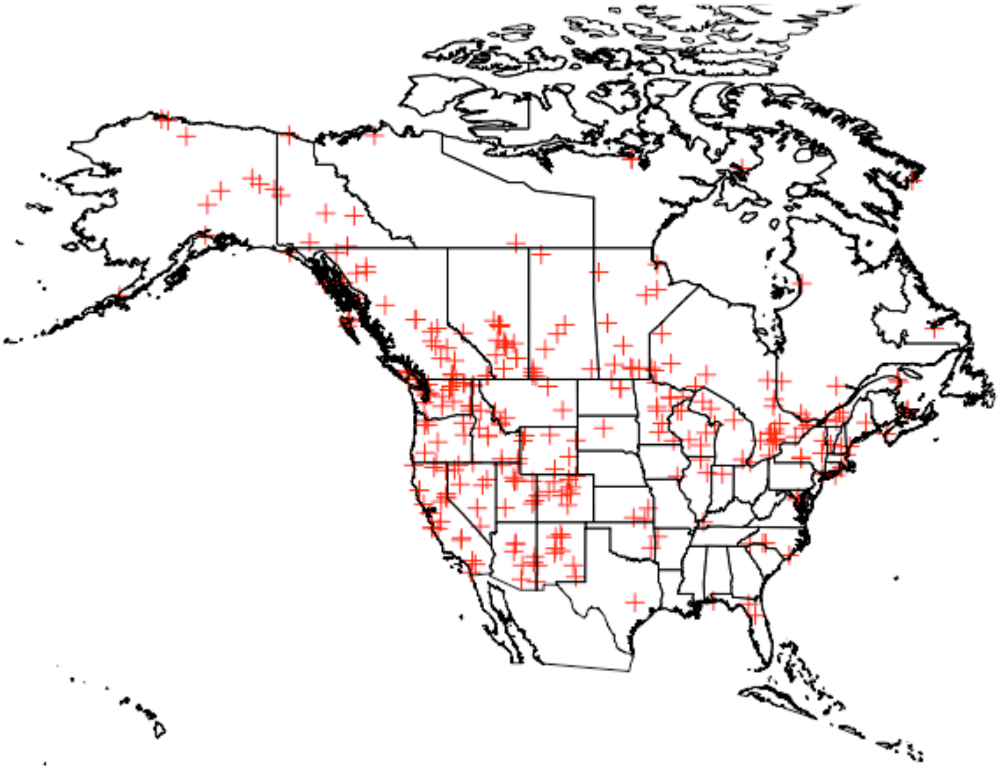

Figure 1. Map of locations of all known-origin museum specimens used for isoscape calibration.
Samples were compiled from two previous studies and seven museum specimens analyzed for this study from the Bell Museum. Some areas of western Canada are still not well represented.

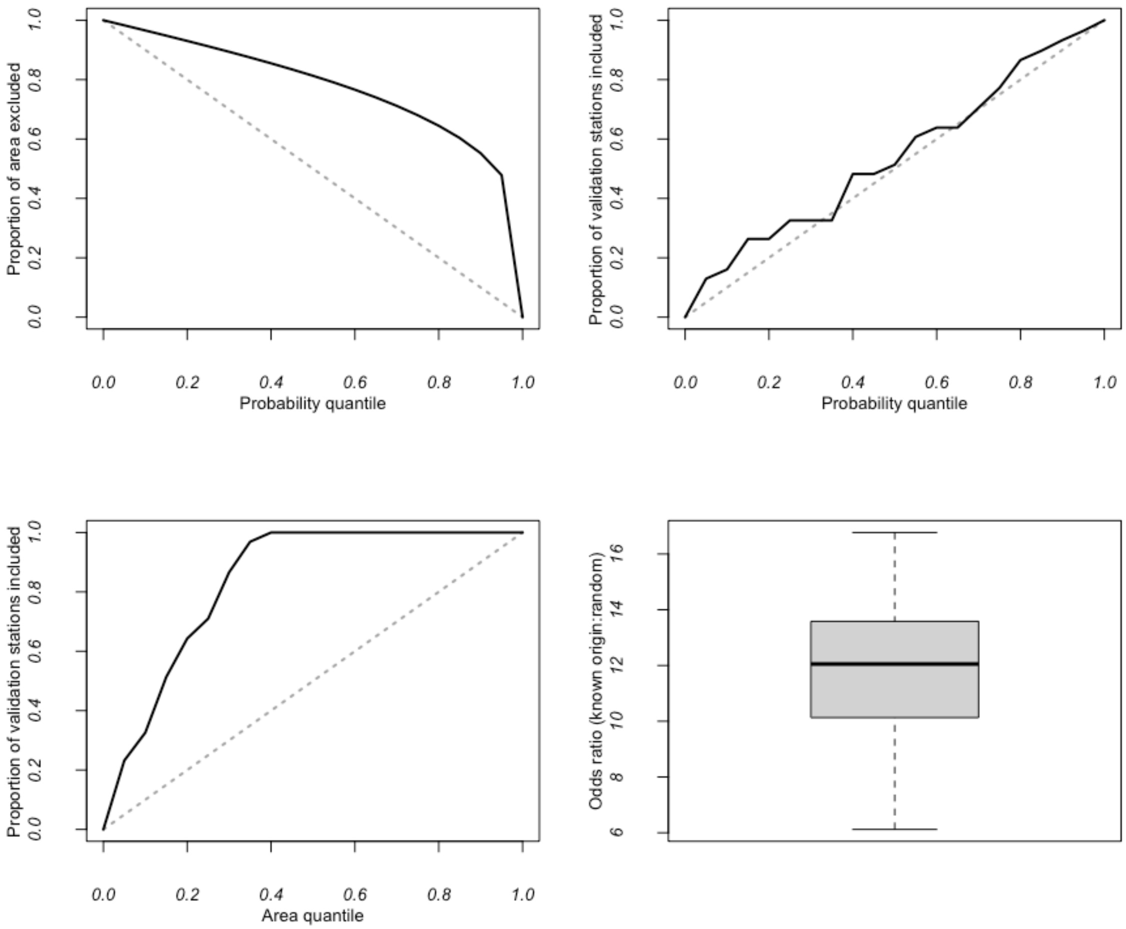

Figure 2. Plots showing isoscape quality using the QA function in the assignR package.
(a) The top left plot shows the proportion of the study area excluded from the assignment as a function of the probability threshold. Larger numbers across the range of probability quantiles suggest that the plot is more “granular” which gives more specific geographic assignments. (b) The top right plot shows the proportion of validation samples that are correctly assigned. Deviations from 1:1 ratio suggest bias. (c) The bottom left plot shows the proportion of correctly assigned validation samples as a function of area. This is a measure of sensitivity and higher values indicate a “better” isoscape. (d) The bottom right plot shows an odds ratio of the posterior probabilities of known locations compared to random (=1). A higher value indicates a “better” isoscape.

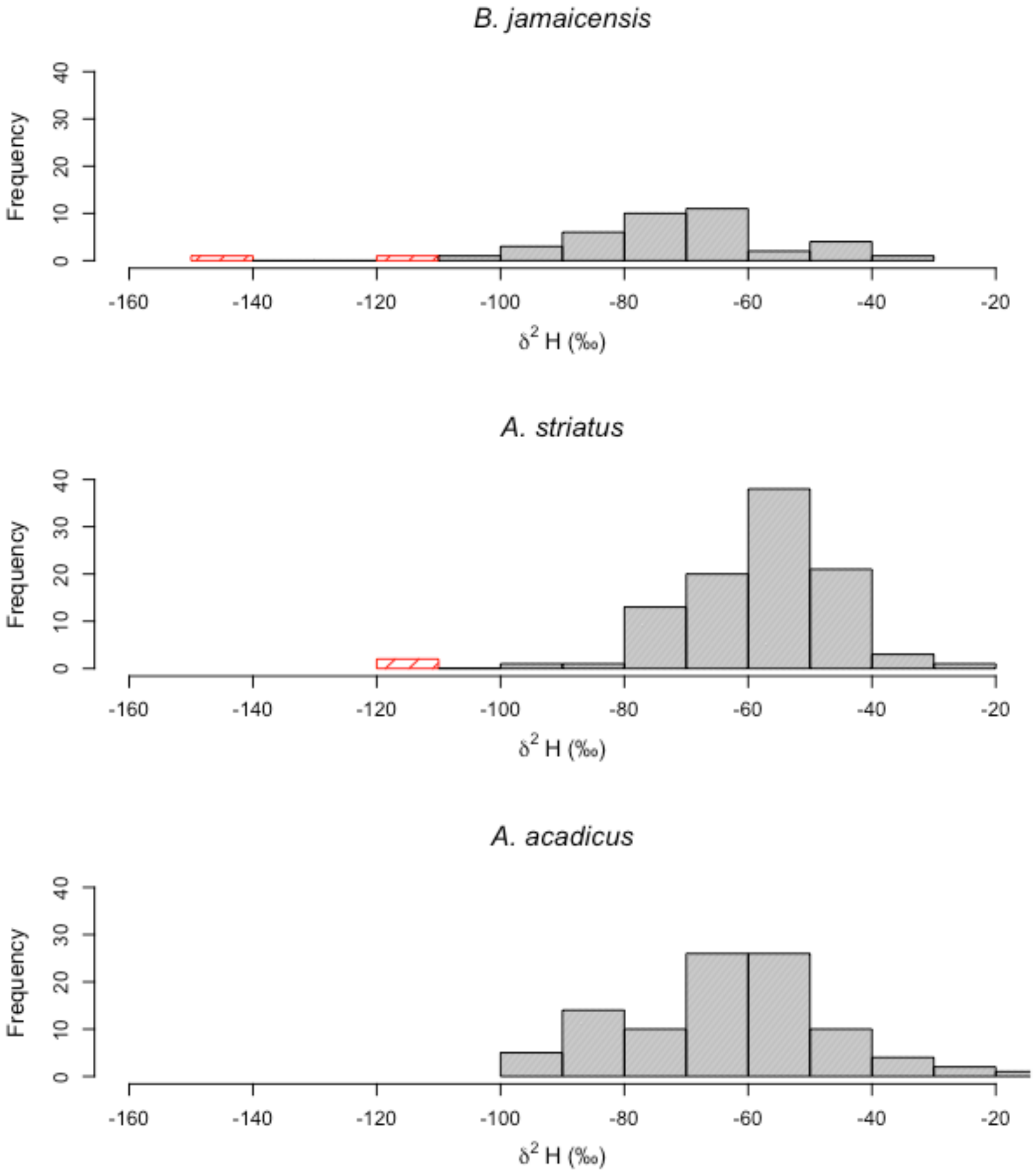

Figure 3. Histogram showing the distribution of δ^2H_f values for each species. Values with diagonal shading were considered outliers but were included in determining migration tests and assigning natal origin since they fit within the known breeding range for each species. With outliers removed, a Shapiro-Wilk Test failed to detect departures from normality (*B. jamaicensis* W=0.97, p-value = 0.42; *A. striatus* W=0.98, p-value = 0.20; *A. acadicus* W=0.98, p-value = 0.17). Values on the y-axis are counts of individual species.

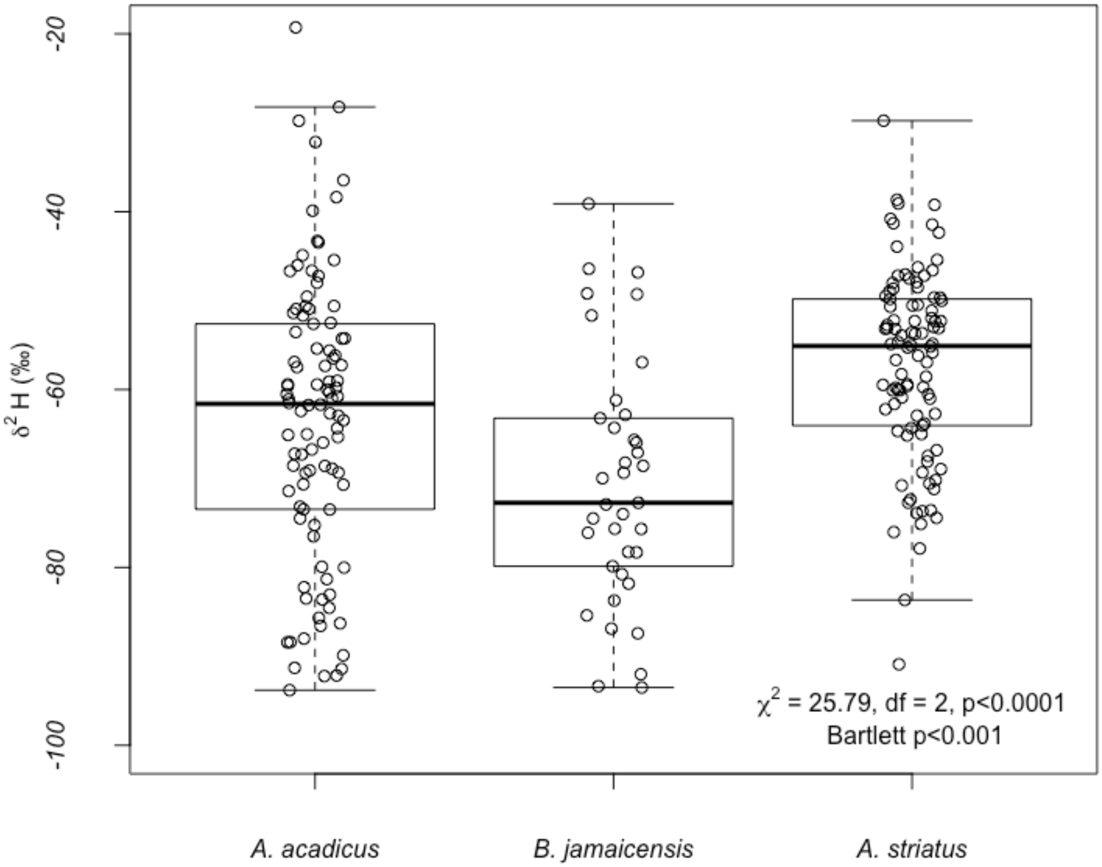

Figure 4. Boxplot showing the δ^2H_f values for each species.
Results from a Kruskal-Wallis test are shown indicating a difference in the three group ($p<0.0001$). Additionally, a Wilcoxon rank sum test indicated that there are statistical differences in mean δ^2H_f values between all three species. Results from Bartlett's test for homogeneity of variances is also shown and indicates that variances differ between the three species, therefore non-parametric tests for analysis of variance were used.

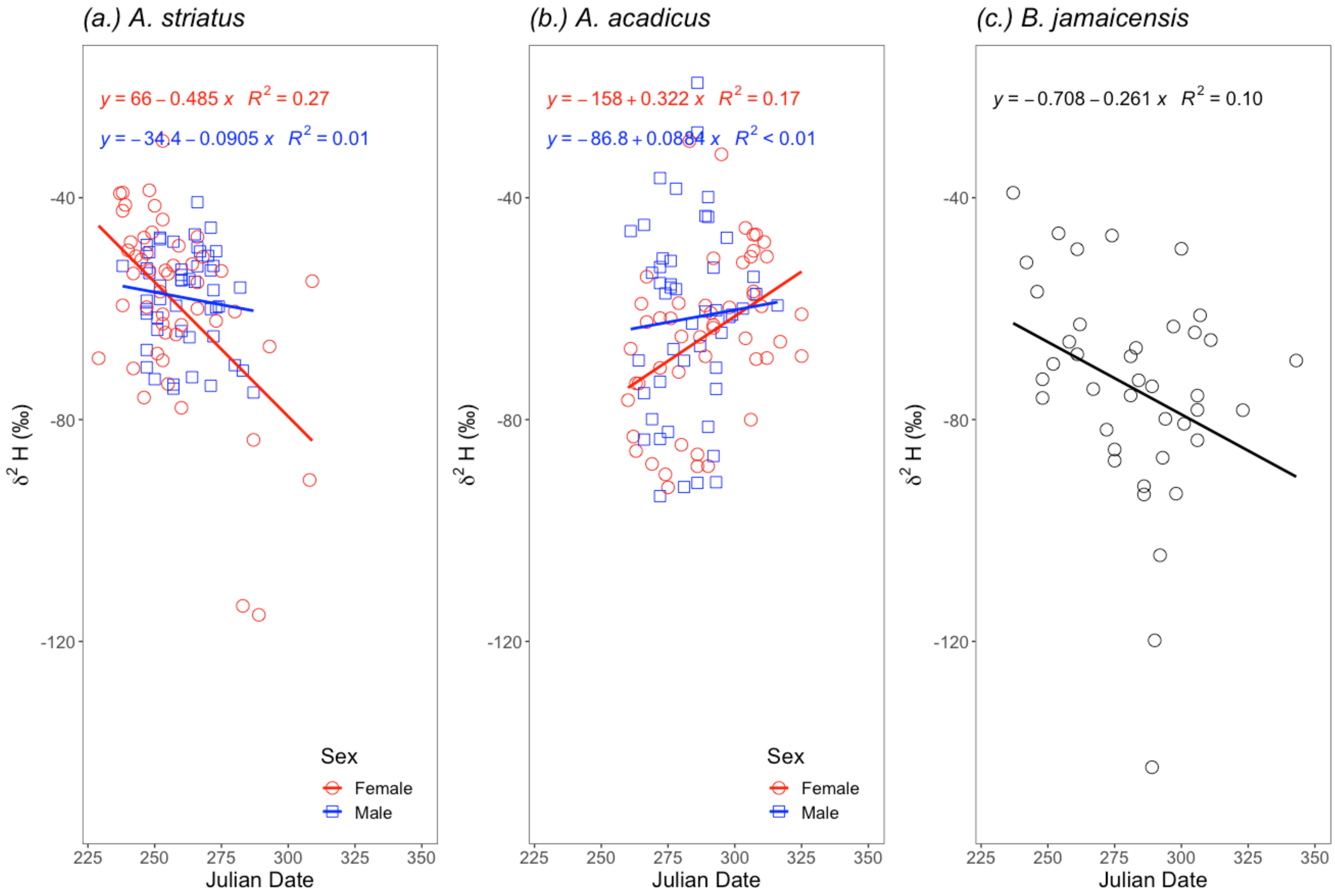
(a.) A. striatus
y = 66 – 0.485 x R² = 0.27
y = – 34.4 – 0.0905 x R² = 0.01
-40
-80
-120
δ² H (‰)
Sex
Female
Male
225
250
275
300
325
350
Julian Date
(b.) A. acadicus
y = – 158 + 0.322 x R² = 0.17
y = – 86.8 + 0.0884 x R² < 0.01
-40
-80
-120
δ² H (‰)
Sex
Female
Male
225
250
275
300
325
350
Julian Date
(c.) B. jamaicensis
y = – 0.708 – 0.261 x R² = 0.10
-40
-80
-120
δ² H (‰)
225
250
275
300
325
350
Julian Date

Figure 5. Regressions of δ^2H_f against Julian date of banding.

(a) Female *A. striatus* have a negative relationship between Julian date of banding and δ^2H_f ($p < 0.001$). Male *A. striatus* showed no significant relationship between Julian banding date and δ^2H_f ($p = 0.42$). (b) Female *A. acadicus* have a positive relationship between Julian date of banding and δ^2H_f ($p < 0.01$). Male *A. acadicus* showed no significant relationship between Julian banding date and δ^2H_f ($p = 0.66$). (c) *B. jamaicensis* feathers have a negative relationship between Julian date of banding and δ^2H_f ($p = 0.046$).

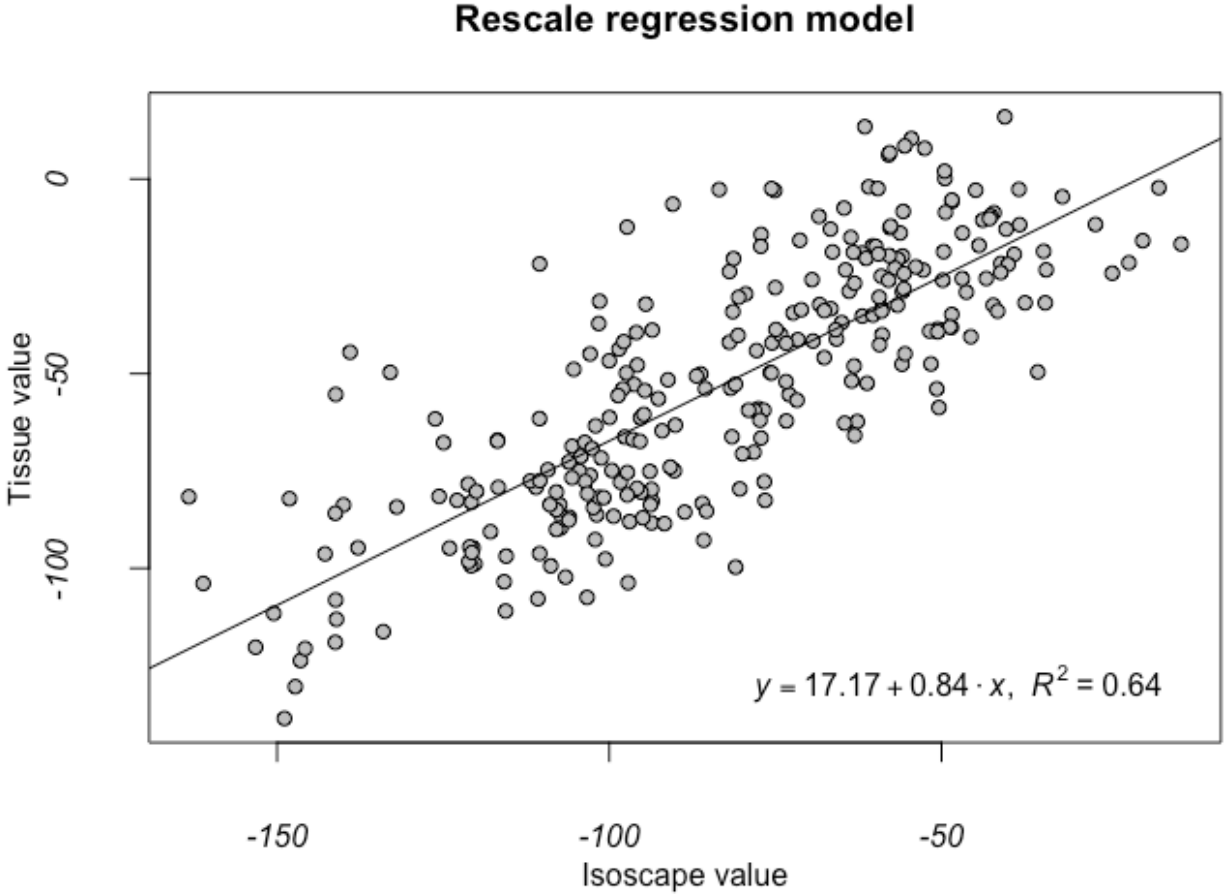

Figure 6. Regression model of feather δ^2H (y-axis) and precipitation δ^2H (x-axis).
About 64% of the variation in feather δ^2H is explained by variation in precipitation δ^2H.

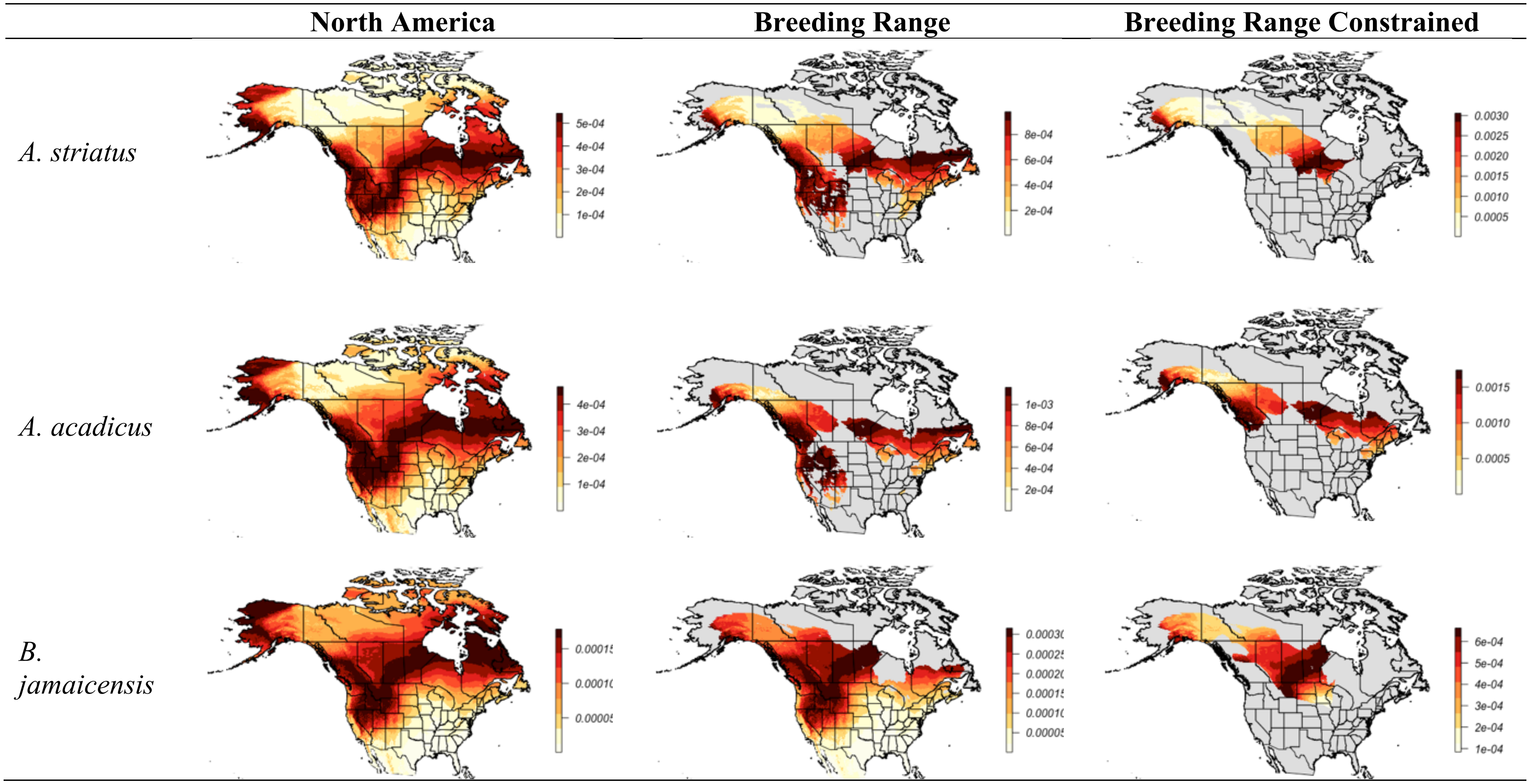

Figure 7. Continuous probability surfaces for each species.

Each map represents the union probability for all species constrained to a different part of North America. The middle panel shows assignments constrained to just the known breeding range for each species and the right panel shows that breeding range further constrained based on band return data from MN (USGS Bird Banding Laboratory, 2022).

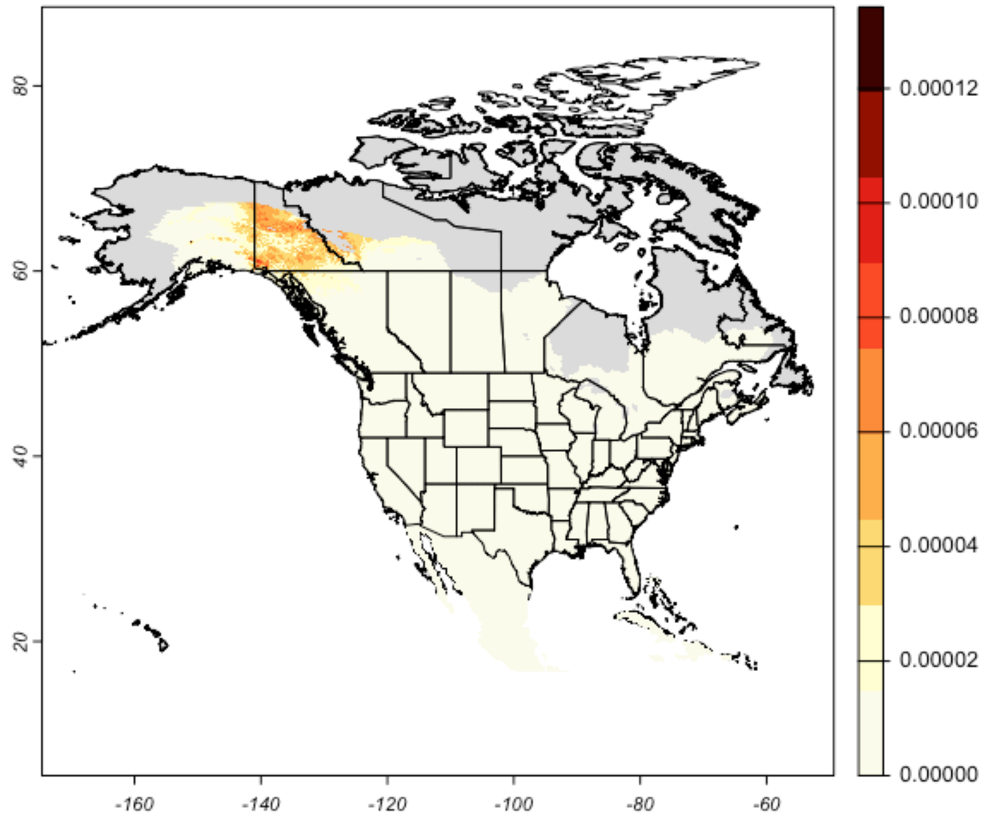

Figure 8. Map showing the posterior probability surface for individual with Band #2187−05377, a dark morph B. jamacensis with harlani characteristics. Highest probabilities of natal origin are in the Yukon which is part of the *B. j. harlani* breeding range.

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APPENDIX

Table 4. δ^2H_f values for all unknown origin individuals analyzed in this study.

Banding Date	Species	Band Number	Sex	δ^2H (‰)
9/16/20	*A. acadicus*	1154-09514	F	-76.5
9/17/20	*A. acadicus*	1154-09638	F	-67.22
9/18/20	*A. acadicus*	1154-09663	F	-83.06
9/19/20	*A. acadicus*	1154-09669	F	-73.46
9/20/20	*A. acadicus*	1154-09670	F	-73.49
9/21/20	*A. acadicus*	1154-09679	F	-59.11
9/23/20	*A. acadicus*	1154-09748	F	-62.41
9/23/20	*A. acadicus*	1154-09749	F	-54.24
9/25/20	*A. acadicus*	1154-09782	F	-88
9/19/20	*A. acadicus*	1114-16977	F	-85.67
10/5/20	*A. acadicus*	1154-19142	F	-71.41
10/5/20	*A. acadicus*	1154-19143	F	-59.01
10/6/20	*A. acadicus*	1154-19164	F	-84.54
10/6/20	*A. acadicus*	1154-19165	F	-65.02
10/9/20	*A. acadicus*	1154-19285	F	-29.78
10/12/20	*A. acadicus*	1154-19352	F	-86.28
10/12/20	*A. acadicus*	1154-19355	F	-88.42
10/13/20	*A. acadicus*	1154-19397	F	-65.1
10/15/20	*A. acadicus*	1154-19535	F	-59.43
10/15/20	*A. acadicus*	1154-19655	F	-68.59
10/16/20	*A. acadicus*	1154-19659	F	-88.4
10/17/20	*A. acadicus*	1154-19735	F	-60.78
10/18/20	*A. acadicus*	1154-19764	F	-62.94
10/18/20	*A. acadicus*	1154-19777	F	-63.45
10/18/20	*A. acadicus*	1154-19780	F	-50.92
10/21/20	*A. acadicus*	1154-19897	F	-32.17
10/24/20	*A. acadicus*	1154-19911	F	-59.78
10/29/20	*A. acadicus*	1154-23520	F	-51.67
10/30/20	*A. acadicus*	1154-23526	F	-65.34
10/30/20	*A. acadicus*	1154-23533	F	-45.44
11/1/20	*A. acadicus*	1154-23539	F	-80.02
11/1/20	*A. acadicus*	1154-23546	F	-50.64
11/2/20	*A. acadicus*	1154-23554	F	-49.56
11/2/20	*A. acadicus*	1154-23558	F	-57.48

Banding Date	Species	Band Number	Sex	δ^2H (‰)
11/2/20	*A. acadicus*	1154-23562	F	-46.67
11/2/20	*A. acadicus*	1154-23563	F	-56.9
11/3/20	*A. acadicus*	1154-23568	F	-46.64
11/3/20	*A. acadicus*	1154-23576	F	-69.09
11/5/20	*A. acadicus*	1154-23601	F	-59.57
11/6/20	*A. acadicus*	1154-23616	F	-47.99
11/7/20	*A. acadicus*	1154-23627	F	-50.6
11/7/20	*A. acadicus*	1154-23629	F	-68.9
11/12/20	*A. acadicus*	1154-23641	F	-65.96
11/20/20	*A. acadicus*	1154-23656	F	-61.01
11/20/20	*A. acadicus*	1154-23657	F	-68.55
9/28/20	*A. acadicus*	1094-71232	F	-61.7
9/28/20	*A. acadicus*	1094-71234	F	-70.69
9/30/20	*A. acadicus*	1094-71313	F	-89.88
10/1/20	*A. acadicus*	1094-71353	F	-92.22
10/2/20	*A. acadicus*	1094-71402	F	-61.75
9/17/20	*A. acadicus*	1154-09651	M	-46.02
9/20/20	*A. acadicus*	1154-09671	M	-69.34
9/22/20	*A. acadicus*	1154-09684	M	-83.6
9/22/20	*A. acadicus*	1154-09723	M	-44.9
9/22/20	*A. acadicus*	1154-09732	M	-75.24
9/25/20	*A. acadicus*	1154-09762	M	-79.93
9/25/20	*A. acadicus*	1154-09786	M	-53.53
10/3/20	*A. acadicus*	1154-19112	M	-67.29
10/4/20	*A. acadicus*	1154-19136	M	-38.37
10/4/20	*A. acadicus*	1154-19138	M	-56.49
10/7/20	*A. acadicus*	1154-19177	M	-92.15
10/7/20	*A. acadicus*	1154-19206	M	-7.44
10/7/20	*A. acadicus*	1154-19215	M	-69.38
10/10/20	*A. acadicus*	1154-19289	M	-62.68
10/10/20	*A. acadicus*	1154-19291	M	8.94
10/12/20	*A. acadicus*	1154-19313	M	-19.28
10/12/20	*A. acadicus*	1154-19338	M	-91.41
10/12/20	*A. acadicus*	1154-19350	M	-28.23
10/13/20	*A. acadicus*	1154-19394	M	-66.74
10/15/20	*A. acadicus*	1154-19611	M	-43.29
10/16/20	*A. acadicus*	1154-19667	M	-43.46
10/16/20	*A. acadicus*	1154-19681	M	-39.89

Banding Date	Species	Band Number	Sex	δ^2H (‰)
10/16/20	*A. acadicus*	1154-19715	M	-81.31
10/18/20	*A. acadicus*	1154-19751	M	-86.57
10/18/20	*A. acadicus*	1154-19760	M	-52.61
10/19/20	*A. acadicus*	1154-19781	M	-70.65
10/19/20	*A. acadicus*	1154-19842	M	-74.49
10/19/20	*A. acadicus*	1154-19867	M	-91.29
10/19/20	*A. acadicus*	1154-19873	M	-60.28
10/21/20	*A. acadicus*	1154-19892	M	-64.34
10/23/20	*A. acadicus*	1154-19899	M	-47.22
10/24/20	*A. acadicus*	1154-19945	M	-61.5
10/25/20	*A. acadicus*	1154-19992	M	-61.1
10/29/20	*A. acadicus*	1154-23519	M	-59.99
11/2/20	*A. acadicus*	1154-23549	M	-54.27
11/3/20	*A. acadicus*	1154-23577	M	-57.34
11/11/20	*A. acadicus*	1154-23635	M	-59.42
10/15/20	*A. acadicus*	1144-25769	M	-60.52
10/2/20	*A. acadicus*	1104-47922	M	-55.62
9/28/20	*A. acadicus*	1094-71218	M	-36.46
9/28/20	*A. acadicus*	1094-71219	M	-55.39
9/28/20	*A. acadicus*	1094-71237	M	-73.17
9/28/20	*A. acadicus*	1094-71238	M	-83.49
9/28/20	*A. acadicus*	1094-71245	M	-52.5
9/28/20	*A. acadicus*	1094-71246	M	-93.8
9/29/20	*A. acadicus*	1094-71269	M	-50.94
9/30/20	*A. acadicus*	1094-71309	M	-57.25
10/1/20	*A. acadicus*	1094-71348	M	-82.23
10/2/20	*A. acadicus*	1094-71403	M	-51.39
10/2/20	*A. acadicus*	1094-71421	M	-56.18
9/4/20	*B. jamaicensis*	1787-00913	U	-72.73
9/4/20	*B. jamaicensis*	1787-00914	U	-76.1
10/7/20	*B. jamaicensis*	2187-05349	U	-75.65
10/12/20	*B. jamaicensis*	2187-05350	U	-93.5
11/1/20	*B. jamaicensis*	2187-05353	U	-83.72
8/29/20	*B. jamaicensis*	2187-05362	U	-51.67
9/8/20	*B. jamaicensis*	2187-05365	U	-69.97
9/10/20	*B. jamaicensis*	2187-05366	U	-46.42
9/23/20	*B. jamaicensis*	2187-05368	U	-74.49
9/30/20	*B. jamaicensis*	2187-05369	U	-46.82

Banding Date	Species	Band Number	Sex	δ^2H (‰)
10/9/20	*B. jamaicensis*	2187-05371	U	-67.08
10/10/20	*B. jamaicensis*	2187-05372	U	-72.92
10/15/20	*B. jamaicensis*	2187-05377	U	-142.68
10/16/20	*B. jamaicensis*	2187-05379	U	-119.81
10/20/20	*B. jamaicensis*	2187-05381	U	-79.87
9/17/20	*B. jamaicensis*	2187-05387	U	-68.22
9/18/20	*B. jamaicensis*	2187-05388	U	-62.84
9/28/20	*B. jamaicensis*	2187-05391	U	-81.82
10/1/20	*B. jamaicensis*	2187-05393	U	-85.39
10/12/20	*B. jamaicensis*	2187-05400	U	-92.01
10/18/20	*B. jamaicensis*	1947-07130	U	-104.46
10/19/20	*B. jamaicensis*	2187-10406	U	-86.88
10/24/20	*B. jamaicensis*	2187-10416	U	-93.35
10/31/20	*B. jamaicensis*	2187-10428	U	-64.3
11/1/20	*B. jamaicensis*	2187-10431	U	-75.67
11/2/20	*B. jamaicensis*	2187-10434	U	-61.2
11/18/20	*B. jamaicensis*	2187-10444	U	-78.3
12/8/20	*B. jamaicensis*	2187-10446	U	-69.35
10/26/20	*B. jamaicensis*	2187-10456	U	-49.2
10/27/20	*B. jamaicensis*	2187-10462	U	-80.76
11/6/20	*B. jamaicensis*	2187-10472	U	-65.66
10/1/20	*B. jamaicensis*	1947-20969	U	-87.41
10/7/20	*B. jamaicensis*	1947-20973	U	-68.58
10/15/20	*B. jamaicensis*	1947-20976	U	-74
8/24/20	*B. jamaicensis*	1957-27285	U	-39.11
9/2/20	*B. jamaicensis*	1957-27288	U	-56.94
9/14/20	*B. jamaicensis*	1957-27289	U	-65.97
9/17/20	*B. jamaicensis*	1957-27290	U	-49.28
10/23/20	*B. jamaicensis*	1947-48212	U	-63.22
11/1/20	*B. jamaicensis*	1947-48245	U	-78.26
8/16/20	*A. striatus*	1893-17873	F	-68.94
8/24/20	*A. striatus*	1893-17879	F	-39.22
8/25/20	*A. striatus*	1893-17883	F	-59.41
8/25/20	*A. striatus*	1893-17887	F	-42.35
8/25/20	*A. striatus*	1893-17892	F	-39.08
8/26/20	*A. striatus*	1893-17896	F	-41.3
8/27/20	*A. striatus*	1893-17899	F	-49.48
8/28/20	*A. striatus*	1893-17900	F	-48.01

Banding Date	**Species**	**Band Number**	**Sex**	**δ^2H (‰)**
8/29/20	*A. striatus*	1893-31404	F	-53.66
8/29/20	*A. striatus*	1893-31408	F	-70.78
8/30/20	*A. striatus*	1893-31417	F	-50.54
9/1/20	*A. striatus*	1893-31421	F	-51.13
9/2/20	*A. striatus*	1893-31427	F	-47.19
9/2/20	*A. striatus*	1893-31429	F	-76.02
9/3/20	*A. striatus*	1893-31433	F	-59.73
9/3/20	*A. striatus*	1893-31437	F	-50.01
9/4/20	*A. striatus*	1893-31449	F	-53.16
9/4/20	*A. striatus*	1893-31453	F	-38.66
9/5/20	*A. striatus*	1893-31463	F	-46.26
9/6/20	*A. striatus*	1893-31468	F	-41.45
9/7/20	*A. striatus*	1893-31606	F	-68.1
9/8/20	*A. striatus*	1893-31622	F	-56.93
9/9/20	*A. striatus*	1893-31628	F	-61.02
9/9/20	*A. striatus*	1893-31629	F	-29.77
9/9/20	*A. striatus*	1893-31636	F	-43.93
9/9/20	*A. striatus*	1893-31638	F	-69.32
9/9/20	*A. striatus*	1893-31639	F	-62.73
9/10/20	*A. striatus*	1893-31643	F	-64.33
9/10/20	*A. striatus*	1893-31645	F	-53.1
9/11/20	*A. striatus*	1893-31654	F	-53.72
9/11/20	*A. striatus*	1893-31657	F	-73.58
9/13/20	*A. striatus*	1893-31663	F	-52.22
9/14/20	*A. striatus*	1893-31679	F	-64.66
9/15/20	*A. striatus*	1893-31698	F	-48.66
9/16/20	*A. striatus*	1893-46028	F	-77.87
9/16/20	*A. striatus*	1893-46044	F	-62.93
9/20/20	*A. striatus*	1893-46088	F	-51.97
9/22/20	*A. striatus*	1893-46164	F	-55.27
9/22/20	*A. striatus*	1893-46166	F	-47.06
9/22/20	*A. striatus*	1893-46187	F	-59.99
9/24/20	*A. striatus*	1893-46245	F	-50.67
9/29/20	*A. striatus*	1893-46555	F	-62.21
10/1/20	*A. striatus*	1893-46578	F	-53.2
10/6/20	*A. striatus*	1893-46593	F	-60.52
10/9/20	*A. striatus*	1893-46806	F	-113.59
10/13/20	*A. striatus*	1893-46820	F	-83.66

Banding Date	Species	Band Number	Sex	δ^2H (‰)
10/15/20	*A. striatus*	1893-46824	F	-115.21
10/19/20	*A. striatus*	1893-46830	F	-66.82
11/3/20	*A. striatus*	1893-46832	F	-90.89
11/4/20	*A. striatus*	1893-46833	F	-55.04
8/25/20	*A. striatus*	1412-64723	M	-52.3
9/3/20	*A. striatus*	1412-64736	M	-48.51
9/3/20	*A. striatus*	1412-64738	M	-60.07
9/3/20	*A. striatus*	1412-64739	M	-58.55
9/3/20	*A. striatus*	1412-64740	M	-67.45
9/3/20	*A. striatus*	1412-64741	M	-52.74
9/3/20	*A. striatus*	1412-64743	M	-70.57
9/3/20	*A. striatus*	1412-64744	M	-60.89
9/4/20	*A. striatus*	1412-64749	M	-53.59
9/4/20	*A. striatus*	1412-64902	M	-49.82
9/6/20	*A. striatus*	1412-64905	M	-72.72
9/7/20	*A. striatus*	1412-64910	M	-61.62
9/7/20	*A. striatus*	1412-64915	M	-63.82
9/8/20	*A. striatus*	1412-64924	M	-58.27
9/8/20	*A. striatus*	1412-64928	M	-47.51
9/8/20	*A. striatus*	1412-64940	M	-47.19
9/8/20	*A. striatus*	1412-64941	M	-55.83
9/13/20	*A. striatus*	1412-64956	M	-47.92
9/13/20	*A. striatus*	1412-64958	M	-73.68
9/13/20	*A. striatus*	1412-64959	M	-74.42
9/14/20	*A. striatus*	1412-64964	M	-59.47
9/16/20	*A. striatus*	1412-64984	M	-64.05
9/16/20	*A. striatus*	1412-64990	M	-53.92
9/16/20	*A. striatus*	1412-65000	M	-52.96
9/16/20	*A. striatus*	1412-65011	M	-54.88
9/16/20	*A. striatus*	1412-65020	M	-54.85
9/19/20	*A. striatus*	1412-65036	M	-54.67
9/19/20	*A. striatus*	1412-65042	M	-65.16
9/20/20	*A. striatus*	1412-65046	M	-72.36
9/21/20	*A. striatus*	1412-65052	M	-55.16
9/21/20	*A. striatus*	1412-65063	M	-46.6
9/22/20	*A. striatus*	1412-65068	M	-52.35
9/22/20	*A. striatus*	1412-65071	M	-40.81
9/22/20	*A. striatus*	1412-65081	M	-48.95

Banding Date	**Species**	**Band Number**	**Sex**	**δ^2H (‰)**
9/23/20	*A. striatus*	1412-65094	M	-49.67
9/28/20	*A. striatus*	1412-80605	M	-56.67
9/29/20	*A. striatus*	1412-80616	M	-59.79
9/29/20	*A. striatus*	1412-80619	M	-49.65
9/30/20	*A. striatus*	1412-80627	M	-59.6
10/6/20	*A. striatus*	1412-80659	M	-70.19
10/8/20	*A. striatus*	1412-80675	M	-56.19
10/9/20	*A. striatus*	1412-80692	M	-71.18
10/13/20	*A. striatus*	1412-80809	M	-75.11
9/26/20	*A. striatus*	1412-80927	M	-50.48
9/27/20	*A. striatus*	1412-80938	M	-45.41
9/27/20	*A. striatus*	1412-80942	M	-73.9
9/27/20	*A. striatus*	1412-80944	M	-53.1
9/27/20	*A. striatus*	1412-80946	M	-60.08
9/28/20	*A. striatus*	1412-80998	M	-52.3
9/28/20	*A. striatus*	1412-80999	M	-65