Historic Trends in Deuterium (δD) in Bird Feathers

Honors Thesis

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Abstract

Deuterium, a stable isotope of hydrogen expressed as δD, has been recorded in precipitation around the world since the 1960's and those 40-year averages are often used in the study of avian ecology. Deuterium varies geographically and temporally throughout the year due to temperature changes. This study hypothesized that deuterium may have also increased over time due to temperature increases caused by climate change. Deuterium was investigated in avian museum specimens from the last century in Tompkins County, New York. Specimens were chosen using two different criteria: one including a wide variety of species to investigate general trends and the other restricted to a few species to reduce noise in the data. Across a wide variety of passerine species, δD demonstrated an increasing trend over time, but the explanatory power of time was low (r^2=0.1134). When analysis was restricted to a single species, this relationship disappeared. The relationship between temperature and δD rarely explained more than ten percent of the variation in the data. Statistically significant differences were found between species and between the sexes, suggesting the need for further research in these areas.

I. Introduction

The nucleus of all chemical elements is made up of protons and neutrons. Many chemical elements, such as carbon, nitrogen, sulfur, and hydrogen, have rare forms with more neutrons than their most common form. Different forms are called isotopes and stable isotopes differ from radioactive isotopes in that they do not break down over time (Inger and Bearhop 2008). The different isotopes react differently in the physical and biological environments, making them useful to the study of ecology. For example, scientists have long studied avian diets using stable isotopes of carbon and nitrogen. During photosynthesis, biochemical reactions within different kinds of plants may discriminate against heavier carbon isotopes lending each kind of plant a unique isotopic ratio (Inger and Bearhop 2008). Likewise, the heavier nitrogen isotope is less likely to be lost as nitrogenous waste and therefore increases in abundance as it moves up the food chain (a process called fractionation or enrichment). Nitrogen isotope ratios can thus be used to determine the trophic level where birds are feeding (Inger and Bearhop 2008).

More recently, scientists have begun to utilize an isotope of hydrogen, called deuterium, in avian ecology studies. Whereas the nucleus of the common isotope of hydrogen has one proton and no neutrons, the nucleus of deuterium has one proton and one neutron. The usefulness of this stable isotope arises from the fact that deuterium levels vary predictably across the globe. More deuterium occurs at equatorial latitudes, near coastlines, and at lower elevations, a pattern attributable to deuterium's weight, which is nearly twice that of hydrogen (Inger and Bearhop 2008). More heat energy is required to evaporate water molecules containing deuterium, but its weight causes it to precipitate out of the atmosphere sooner than normal hydrogen. Deuterium in atmospheric water vapor is therefore unable to travel long distances into cooler areas because it will precipitate out of the atmosphere sooner. This property keeps deuterium concentrated in areas with warmer temperatures. Precipitation carries its own ratio of hydrogen to deuterium (expressed as δD, see Methods) which then affects the deuterium ratio of the groundwater where it falls. Precipitation cannot affect the deuterium ratios of large aquatic media, such as the ocean which reflects the deuterium ratio of precipitation not at all, as easily as smaller aquatic media such as lakes or groundwater (Farmer et al. 2003). This is analogous to adding colored dye to a body of water; smaller bodies of water will reflect the color of the dye much more than larger ones. Deuterium's geographic patterns have been used mainly to map the breeding and wintering grounds of birds (Inger and Bearhop 2008), but it has other potential uses. For instance, the possibility of detecting smuggled wildlife in the international wildlife trade was explored in Britain when deuterium values from a British and Russian subspecies of canary were compared and found to be significantly different (Kelly et al. 2008).

Stable isotopes are incorporated into bird tissues through their diet and drinking water (Hobson et al. 1999). Because deuterium is deposited differently in different tissues, tissue choice is a very important consideration in stable isotope studies. Blood and other metabolically active tissues are continuously renewed, reflecting the isotopic signature of food items consumed over the previous few days (Mazerolle and Hobson 2005). In contrast, feathers are grown over a period of days or weeks and are inert once growth ends causing the isotope signature to forever reflect the deuterium value of the location and time period in which that feather was grown (Mazerolle and Hobson 2005). Deuterium has been shown to be similar among species occupying the same trophic level (Hobson and Wassenaar 1997). Because of this, δD in feathers from songbirds and waterfowl has been combined for analysis with no change in the relationship between feather deuterium and precipitation deuterium (Clark et al. 2006). Bird feathers tend to be enriched by approximately 30‰ (parts per thousand) compared to precipitation values, probably due to enrichment lower on the food chain by plants (Hobson and Wassenaar 1997). Feeding experiments with captive red-winged blackbirds found no difference between the deuterium values of food items, in this case commercial turkey grower feed with vitamin supplements, and feathers, indicating no enrichment within the birds (Hobson and Wassenaar 1997). Studies comparing deuterium in feathers to deuterium in precipitation will see different deuterium values in the precipitation and the feathers, but studies comparing deuterium in feathers to deuterium in food items should observe approximately the same deuterium values in the food and the feathers because the enrichment happens within the food items, usually plants, not the birds.

There are many sources of variation in deuterium values that are not yet thoroughly understood, which has led to criticisms concerning the use of deuterium in avian research. Most studies compare deuterium in feathers to the Global Network of Isotopes in Precipitation (GNIP) data administered by the International Atomic Energy Agency (IAEA) and the World Meteorological Organization (Farmer et al. 2008). GNIP data have been collected monthly for over forty years at over 800 stations around the world (Farmer et al. 2008). Each station may not have collected data over the entire forty years, nor are the stations distributed evenly across the globe. Studies often compare feather deuterium values to precipitation deuterium values averaged over forty years, without taking into account interannual variation (Farmer et al. 2008).

With deuterium's increasing importance to avian studies, it is imperative to understand the many potential sources of variation. This study investigated variation in deuterium values in avian museum specimens collected from Tompkins County, New York over the past century.

Deuterium's geographic variation corresponds to temperature, so this study hypothesized that temporal variation across years would likewise correlate with temperature. The climate has warmed 0.83° Celsius (1.5° Fahrenheit) in the northeast United States over the past one hundred years, mostly in the past four decades (Frumhoff et al. 2007). If increases in temperature have increased deuterium in Tompkins County, it would not be appropriate to compare feather values of today's birds to GNIP maps averaged over forty years. Animal tissues have been used to investigate climate change before, but only archaeological samples representing change over millennia (Leyden et al. 2006). However, more rapid deuterium changes due to climate change (on the order of one to three years) have been found in Greenland ice cores (Steffensen et al. 2008). Deuterium values in the ice cores hovered around a mean for decades, but shifts larger than the standard deviations of the previous 150 years reflected abrupt changes in the source region of the precipitation reaching Greenland (Steffensen et al. 2008). The deuterium values shifted because more deuterium was arriving in northern latitudes from warmer regions due to changes in global weather patterns. In this study, museum specimens from the Cornell University Museum of Vertebrates were used to investigate if similar shifts in deuterium could be detected in bird feathers over the last century.

II. Methods

Specimens for this study were collected using two different sampling criteria and analyzed separately. Under the first sampling criteria, test specimens from the order Passeriformes were restricted to those collected in Tompkins County, New York. Twenty-three species were used with sample sizes for each species ranging from one to eight for a total of 49 specimens. Five specimens from a single year were collected for each decade from 1900 to

2010. The decade beginning in 1970 was not represented due to a lack of specimens. Specimens were chosen based on the availability in the collection, but attempts were made to restrict test specimens to birds collected in August or specimens from September through December of species known to be year-long residents in the area. These birds were chosen because most North American passerines undergo a full body molt after breeding but before fall migration, often between July and September (North American Banding Council 2001). Therefore, feathers from these specimens were the most likely to have been grown in Tompkins County. Birds collected under the second sampling criteria were also confined to Tompkins County, but further limited to three species in an attempt to minimize interspecies variation that could affect deuterium values. The three species were the Ruffed Grouse (*Bonasa umbellus*, n=50), the Black-capped Chickadee (*Poecile atricapillus*, n=42), and the Downy Woodpecker (*Picoides pubescens*, n=41). These species were chosen because they are known to be non-migratory and had the largest available sample sizes. These birds were not restricted to certain months or years. Contour feathers were taken from the backs of the birds and molt was recorded when verifiable. Species, sex, relative fat, weight, length, age, and date of location were recorded when available as well as any preparation notes of interest. Complete records of the specimens collected and the accompanying data are available upon request.

Feathers were cut using a razor blade. Only the feather vanes were used when the feather was large enough to discriminate, as the rachis has been found to be deuterium enriched in some instances (Hobson and Wassenaar 2006). A Sartorius MC 5 microbalance was zeroed with a silver capsule before the capsule was filled with feather material weighing 0.3 ± 0.01 mg. The silver capsule was then crushed around the feather material and placed inside a second silver capsule to ensure all feather material was contained. The razor and cutting surface were cleaned with pressurized carbon dioxide between each sample.

Prepared samples were then run on a Thermo Finnigan Delta V mass spectrometer coupled with a Thermo Finnigan TC/EA. Several in-house and international deuterium standards were used to calibrate the results namely CH-7, a polyethylene standard established by the IAEA, NBS 22, an oil standard distributed by the IAEA, and RPG LE, a lipid extracted goose feather standard developed the be Cornell University Stable Isotope Laboratory. Deuterium concentration estimates were expressed as the ratio of hydrogen to deuterium (δD) in parts per thousand (‰) deviation from the Vienna Standard Mean Ocean Water standard. Data were analyzed using analysis of variance tests and linear regressions using SPSS PASW Statistics 18.

About 15% of hydrogen in bird feathers can exchange with hydrogen in ambient water vapor, thereby breaking the assumption that feather deuterium values are inert after the feather is grown (Hobson and Wassenaar 1997). In other words, hydrogen in feather samples can exchange with hydrogen in the air, potentially impacting the deuterium values of the feathers. However, this process takes only two weeks (Hobson and Wassenaar 1997) and museum specimens were housed in the same facility for years, allowing all samples to experience the same hydrogen exchange with the same atmosphere. It is important to note that the specimens from the two sampling criteria were analyzed at different times of the year, the first in September and the second in February. Deuterium values vary over the span of a year due to temperature changes. This was observed in one of the standards used to calibrate the results, RPG LE, which is also feather material. In February the RPG LE standard had a mean δD of -146.75 (SD=1.35) while in September, the RPG LE standard had a mean δD of -137.54 (SD=1.45). This suggests that specimens of the second sampling criteria would be consistently about nine parts per mill less negative than those of the first sampling critera, but the two were analyzed separately, in part to avoid such messy comparisons.

III. Results

A. Trends in δD Across a Wide Range of Species

The δD of the test specimens of the first sampling criteria was found to have increased slightly over time (Figure 1). The positive slope is what would be expected if temperatures increased over time, but the r^2 value of 0.1134 indicates that collection year only explains about 11 percent of the variation in the data. There was no statistically significant difference between all years (*d.f.*=9, *F*=1.261, *P*=0.288), between 1900 and 2008 (*d.f.*=1, *F*=2.116, *P*=0.184), between 1912 and 2008 (*d.f.*=1, *F*=3.273, *P*=0.108), or between 1912 and 1996 (*d.f.*=1, *F*=3.830, *P*=0.086). It is interesting to note the decreasing *P* values as the variation within years chosen for comparison decreased. There was also no statistically significant difference between species (*d.f.*=22, *F*=1.798, *P*=0.076). The most negative specimen from 1990 was from the only Rose-breasted Grosbeak (*Pheucticus ludovicianus*) specimen used. The data were reanalyzed with this specimen removed to see if it was driving the regression (Figure 2). The slope becomes less pronounced and the explanatory power (r^2=0.0292) decreases further, suggesting this point did have a noticeable effect on the regression.

The sex was available for 87% of specimens. There was a statistically significant difference between the sexes (*d.f.*=1, *F*=8.071, *P*=0.007). Females had less negative δD, though there were only 9 females and 34 males (Figure 3). A linear regression was conducted to examine the relationship between sex and deuterium, controlling for species. The β coefficient for sex was 0.4, suggesting that females (which were coded as 1) were still less negative than males after controlling for species because the β value was positive. Length, relative fat, molt, and age were not analyzed because most specimens lacked this data.

To more directly analyze the relationship between δD and temperature, temperature data were obtained from the National Climate Data Center website run by the National Oceanic and Atmospheric Association. Temperature data for some months are incomplete or missing, though this was rare. Temperature data for Ithaca, NY were only available from 1931 to 2010. The opposite relationship than predicted was found between the mean temperature of each specimen's collection month and δD (Figure 4). As temperatures increased, δD decreased. The r^2 value was 0.107 and therefore the mean temperature of the collection month did not explain much of the variation in the data. However, the birds may not have grown their feathers during the collection month. The mean growing season temperature was obtained for each year by averaging all monthly means greater than zero degrees Celsius. The mean growing season temperature was chosen rather than the mean annual temperature because deuterium only enters the biological cycle when plants take water up into their tissues during the growing season, which are then consumed by birds or by other organisms which are then consumed by birds. The δD of birds collected between January and June was compared to the mean growing season temperature of the previous year because feathers had not yet been molted and therefore reflected the previous year's δD. This relationship explains even less of the variation in the data (r^2=0.05), though again the regression suggests the opposite relationship than expected between temperature and δD (Figure 5).

B. Trends in δD Within Three Resident Species

To reduce possible interspecies variation, δD was plotted against time in years for *Bonasa umbellus*, *Poecile atricapillus*, and *Picoides pubescens* (Figure 6, 7, and 8 respectively).

The slopes and r^2 values in all three figures were very close to zero, meaning collection year explained nearly none of the variation in the data within each species. *Bonasa umbellus* had significantly lower δD values than the other species (Figure 9, *d.f.*=2, *F*=49.915, *P*<0.001). Across species, there was no significant difference between the sexes (*d.f.*=1, *F*=3.177, *P*=0.077). The relationship between sex and δD across these three species (Figure 10) was opposite that found in the first sampling criteria (see Figure 3), though again sampling of each sex was not equal with 73 males and 50 females.

Linear regressions were conducted for the specimens of the second sampling criteria. Because δD was found to differ between the species, species was entered as an independent variable in all linear regressions to control for this effect. The regression of δD on mean monthly temperature for the month of collection had a r^2 value of 0.116, but when species was added as an independent variable this increased to 0.235. The β coefficient for the monthly temperature, controlling for species, was -0.286, suggesting that the relationship between mean monthly temperature of the collection month and δD was negative, again opposite what was expected. The β coefficient for sex, controlling for species, was -0.097, suggesting that females (which were coded as 1) were slightly more negative than males.

The linear regression of δD on mean growing season temperature had a r^2 value of 0.028, but when species was added as an independent variable this increased to 0.168. The β coefficient of mean growing season temperature was -0.113, again suggesting that the relationship between mean monthly temperature of the collection month and δD was negative, opposite what was expected. There was considerable interannual variation in mean growing season temperature, but there has not been a consistent increase in temperature over time (Figure 11). In fact, the regression shows mean growing season temperature has decreased slightly over time, thus discrediting the initial assumption that climate change had increased temperatures and therefore increased deuterium. However, the variance in mean growing season temperature between 1990 and 2010 (2.246) was more than double the variance of the previous 60 years (0.878) and nearly quadruple the variance of the previous 20 years (0.539). A linear regression of δD against mean growing season temperature for 1990-2010 was conducted, controlling for species, but the explanatory power remained low (r^2=0.174).

IV. Discussion

If climate change had increased temperatures in Tompkins County, New York δD in bird feathers was expected to increase. The correlation between years and deuterium did not explain the majority of the data and only exhibited the expected relationship when data from a wide variety of species were examined together. Even when δD was regressed against temperature, the opposite relationship than expected was found, though temperature never explained a majority of the data. Climate change has not caused much change in mean growing season temperature in Tompkins County (Figure 11). The data did suggest that climate change has caused mean growing season temperature to be more variable from year to year, but when δD from the last 20 years was regressed against mean growing season temperature, the explanatory power did not increase. These data suggested climate change has had no effect on δD values in bird feathers within a single species in Tompkins County over the last century, lending credence to studies using forty year averages of GNIP data.

Significant differences were found between *Bonasa umbellus* and two other species (*Poecile atricapillus* and *Picoides pubescens*). This may contradict earlier findings that δD is independent of species occupying a particular trophic level (Hobson and Waasenaar 1997).

However, it is questionable whether the Ruffed Grouse occupies the same trophic level as the two other species because its diet consists almost entirely of plants, while the other two consume a mix of insects and plant material (Cornell 2010). The differences in the analysis of the two sets of specimens should provide a cautionary tale to researchers examining δD across a wide variety of species. If differences in diet contribute to differences in δD, studies across a wide variety of species will have to control for dietary differences, otherwise trends in δD could be caused by diet, but interpreted as something else. Dietary differences could have contributed to the trend seen in the specimens of the first sampling criteria because δD was nearly significantly different among the species (*d.f.*=22, F=1.798, P=0.076) and because the regression changed considerably when the single *Pheucticus ludovicianus* specimen was removed. Another consideration not investigated in this study concerns the influence of human-provided feed on δD. If the species examined had consumed mostly feeder food, their δD values would not reflect the δD of Tompkins County. Additionally, studies across a wide variety of species will have to include only non-migratory species in order to ensure that δD in feathers reflects only the study area. This study attempted to control for migration in the first set of specimens by selecting birds from a single county during a certain time of year and in the second set of specimens by selecting only resident species.

An avenue of research prompted by this study is whether males and females have different δD values in their feathers. When a wide variety of species were examined together, females were found to be less negative by about 15‰ whereas across the three species of the second set of specimens females were found to be more negative by about 4‰, though the latter relationship was not significant at the P<0.05 level. After controlling for species in the first sampling criteria, females were still found to have less negative δD (β=0.4). After controlling for species in the second sampling criteria, females were still found to have more negative δD (β=-0.097), though the magnitude of the difference was small. Some studies have found significant differences between the sexes (Hobson et al. 2009) or no difference between the sexes (Smith and Dufty 2005). Hobson et al. (2009) found females to be more negative as well (β=0.591), but were unable to explain why. They suggested physiological or ecological reasons; perhaps females undergo more evaporative cooling because they are more active or perhaps females exhibited more site philopatry. Both studies cited above examined only one species (Northern Goshawks in Smith and Dufty 2005 and House Sparrows in Hobson et al. 2009).

Additional opportunities for further research could expand deuterium studies to taxa beyond birds. There is an interest in applying such studies to reptiles in the international wildlife trade among Fish and Wildlife Service Law Enforcement officers at the Miami International Airport (pers. comm.). Deuterium could potentially serve as a tool to discover species that originated from regions other than those indicated on their CITES permits, which is important for Appendix III species that cannot be exported from certain countries but are allowed to be exported from others. Additionally, deuterium has been found to have less variance in captive bred canaries than wild-caught canaries (Kelly et al. 2008), another important distinction for CITES permits, which often prohibit the trade in wild-caught individuals, but not captive-bred individuals.

This study used two very different sampling methods, one which utilized a wide variety of species to investigate general relationships and another which investigated a select few species to control for variation, causing conflicting relationships to be found in the data. This study also does not account for other sources of variation such as geographic or elevation variation in δD within Tompkins County, the effect of evaporative cooling on δD, metabolic differences between adults and juveniles, the diets of species examined including differences between natural and human-provided food items, or variation within months in δD. In spite of these limitations, this study represents the first investigation of variation in δD in historic museum specimens (though other studies have used museum specimens to support investigations of contemporary populations), lends credence to the use of deuterium values averaged over 40 years from GNIP maps in research concerning a single species, provides a cautionary tale to researchers attempting to study δD across a wide range of species, and suggests the need for further research into sex and species differences in δD in bird feathers.

V. Acknowledgments

This research was funded by the National Science Foundation. I am grateful to Kimberly Bostwick for her help with the design of this study especially species selection, Kimberlee Sparks for teaching me how to prepare samples for stable isotope analysis and for running the samples, Myra Shulman for guidance throughout the process, and the Cornell Museum of Vertebrates for use of their bird collection. All three of the aforementioned researchers as well as Sean Griffin and two anonymous reviewers helped to improve this manuscript by assisting with results interpretation and writing clarification.

VI. Figures

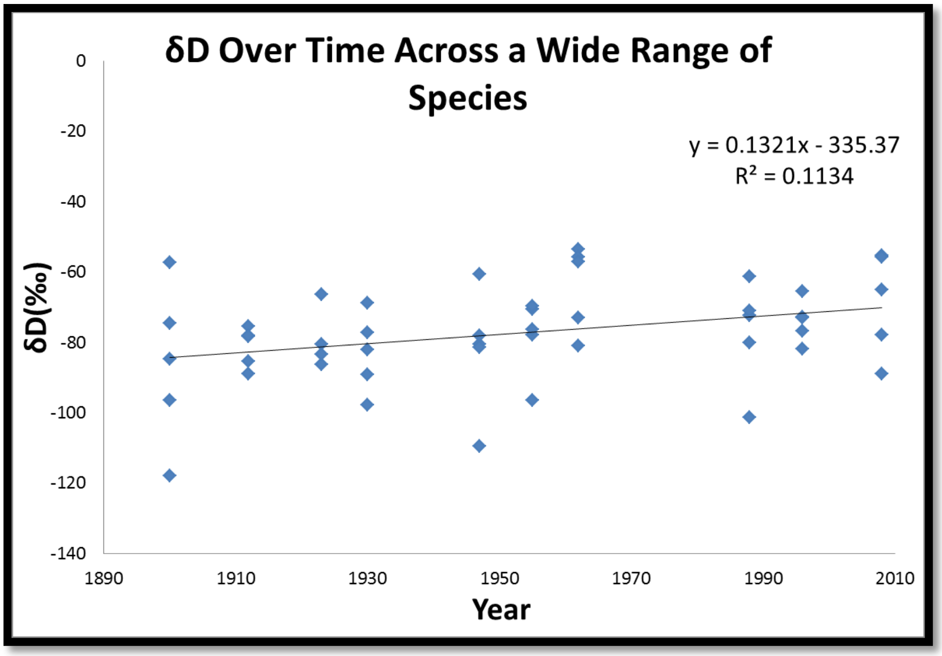

Figure 1. δD plotted against time in years for the specimens of the first sampling criteria.

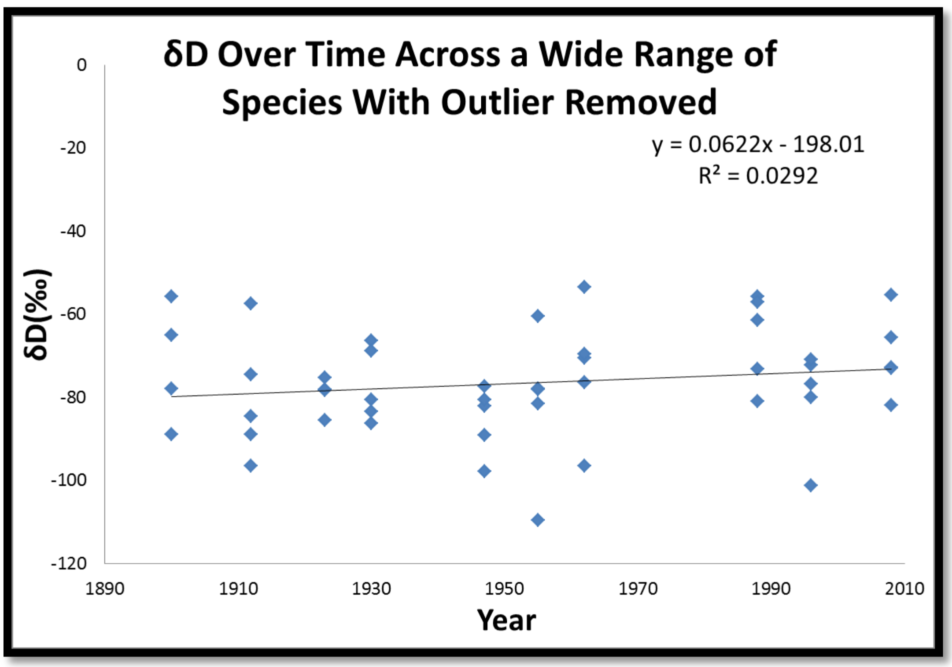

Figure 2. δD plotted against time in years for the specimens of the first sampling criteria with the most negative 1990 specimen removed.

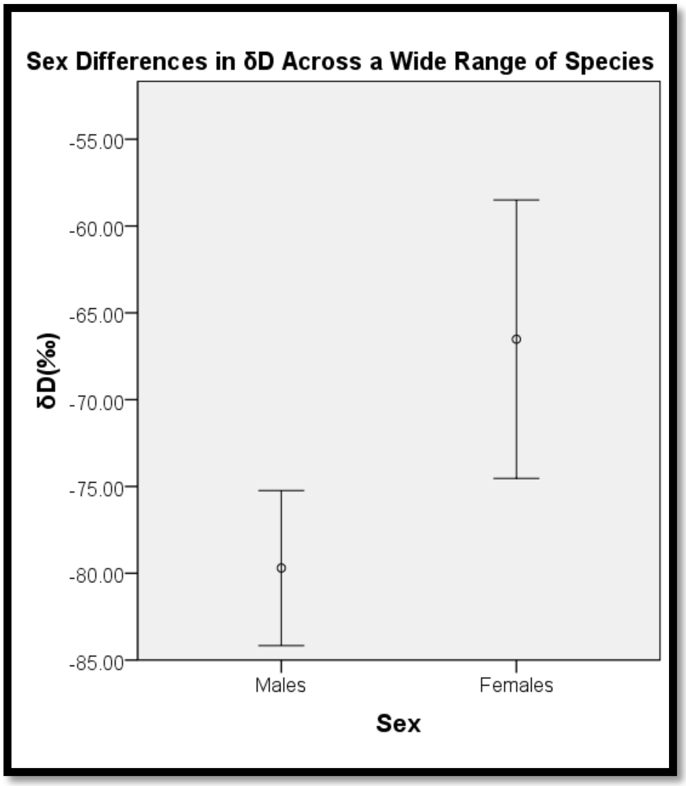

Figure 3. There is a statistically significant difference between the sexes, though sampling was uneven with 9 females and 34 males.

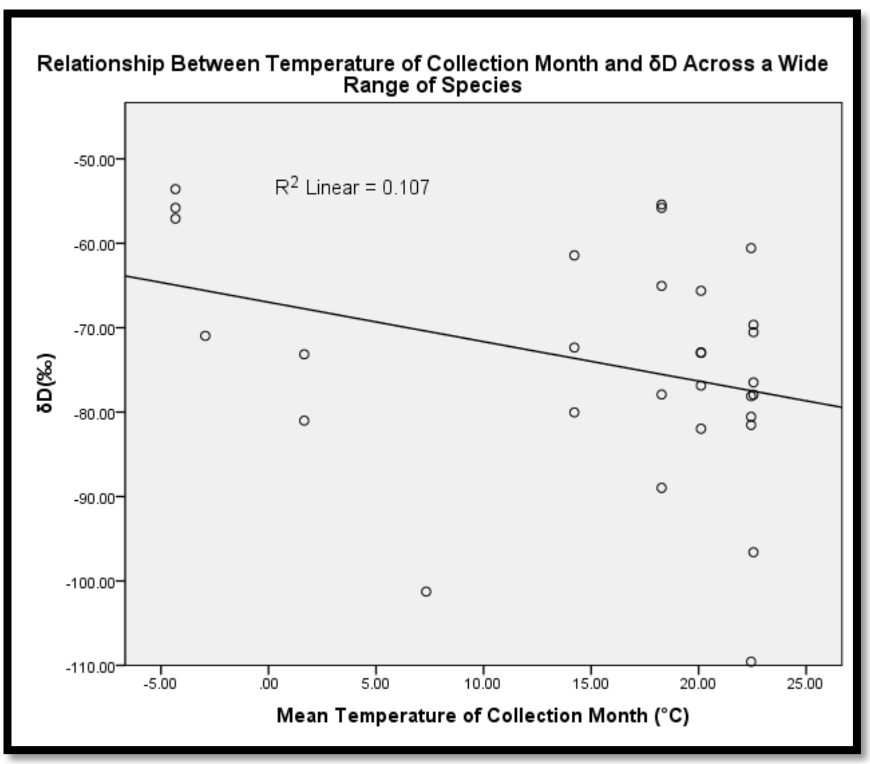

Figure 4. Linear regression of δD against temperature in degrees Celsius for the specimen's month of collection.

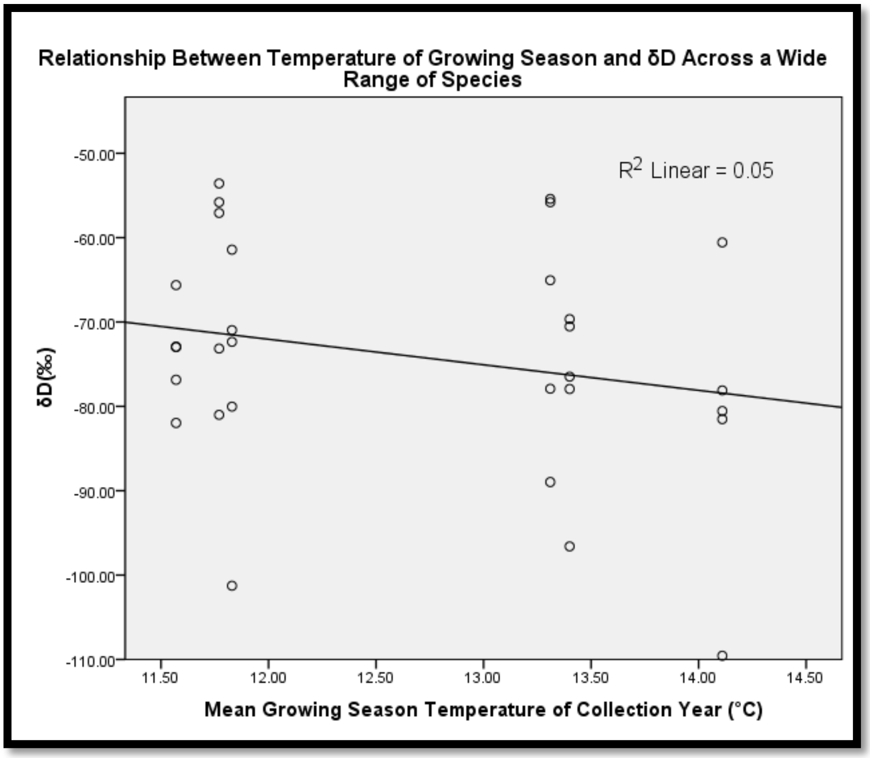

Figure 5. Linear regression of δD against temperature in degrees Celsius for the mean growing season of the specimen's year of collection.

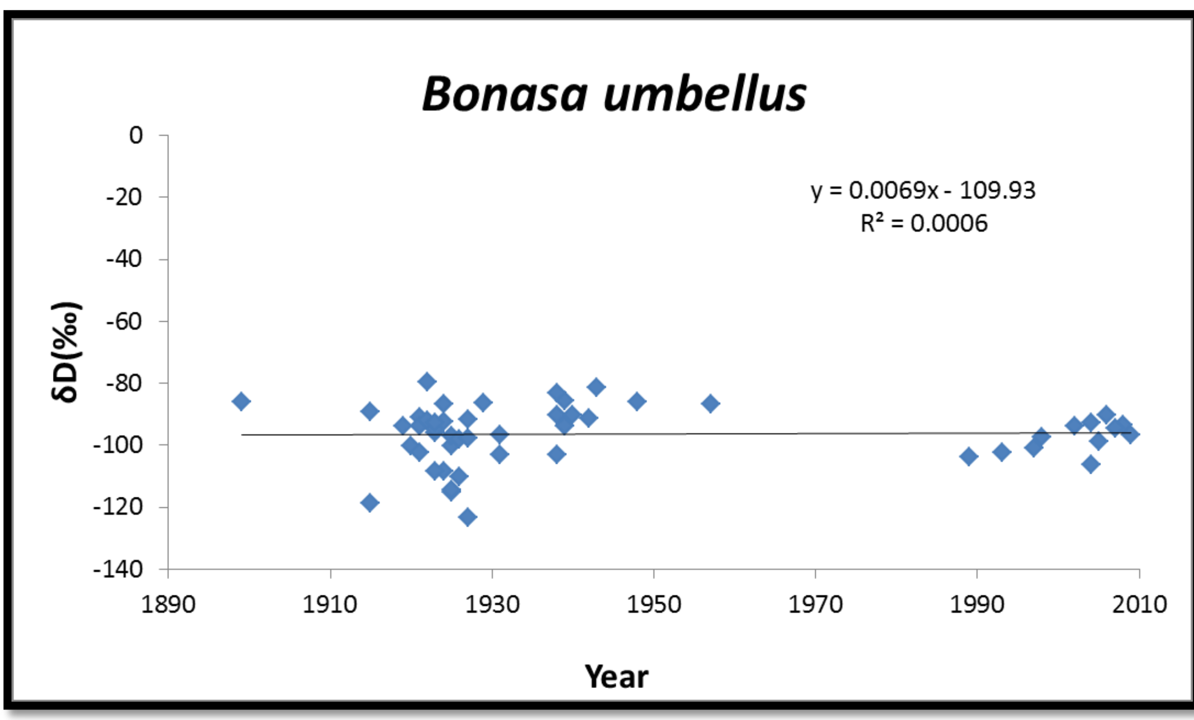

Figure 6. δD plotted against time in years for *Bonasa umbellus*. n=50

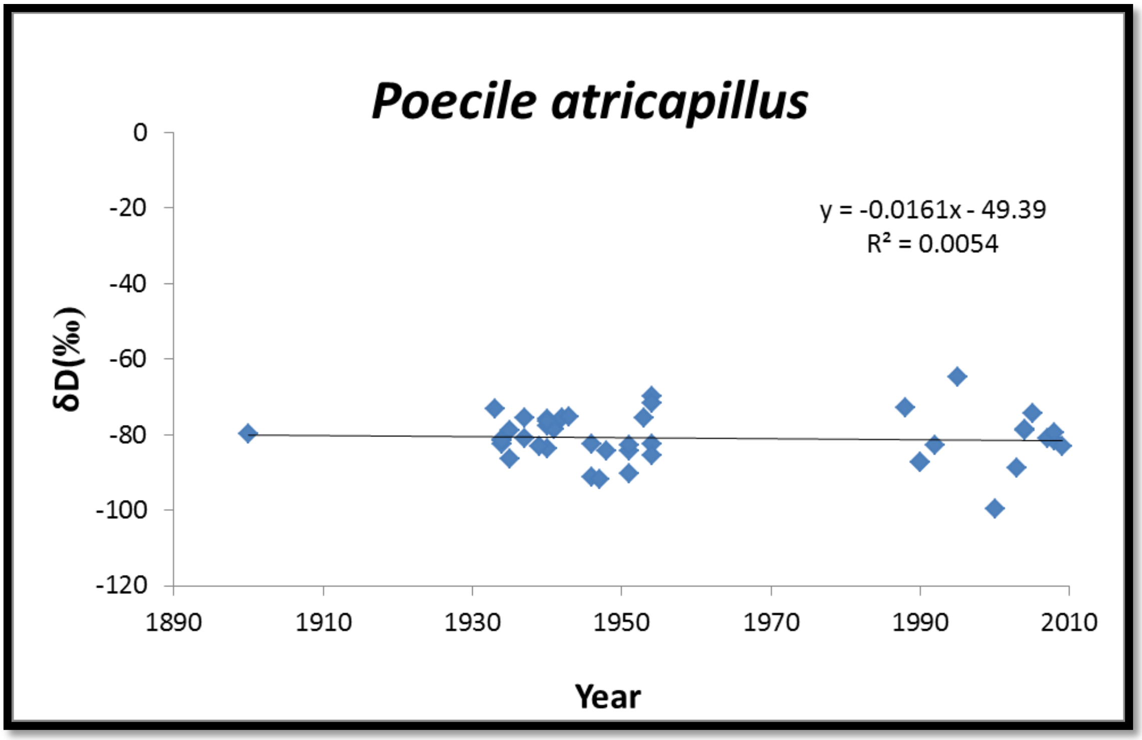

Figure 7. δD plotted against time in years for *Poecile atricapillus.* n=42

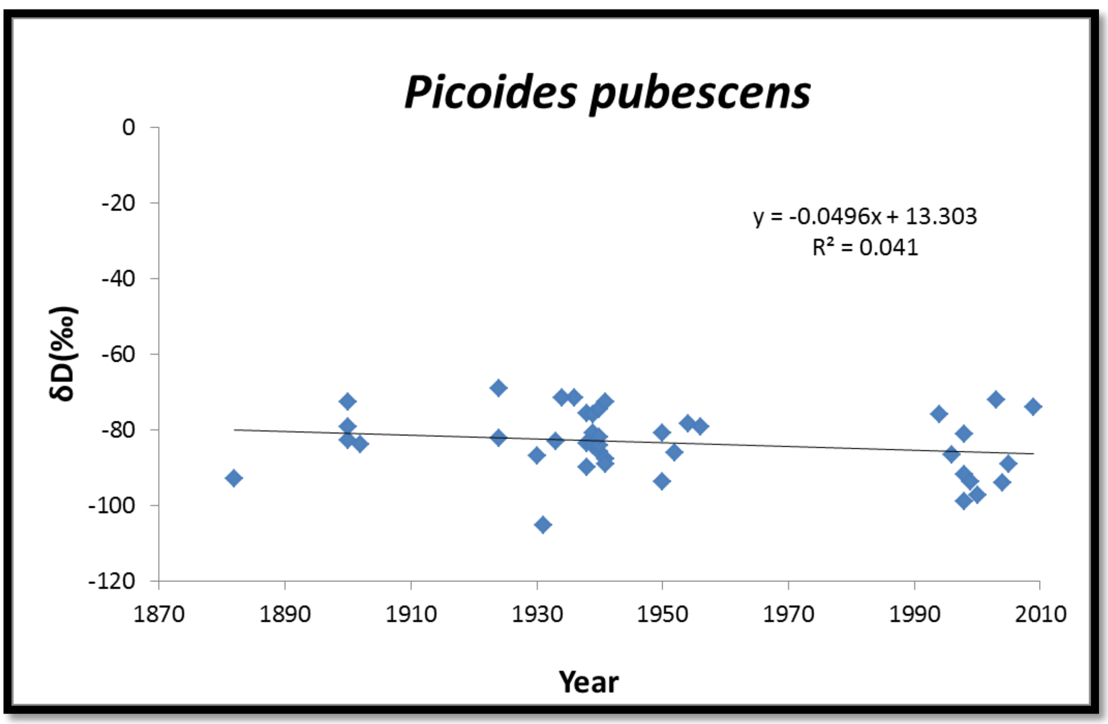

Figure 8. δD plotted against time in years for *Picoides pubescens*. n=41

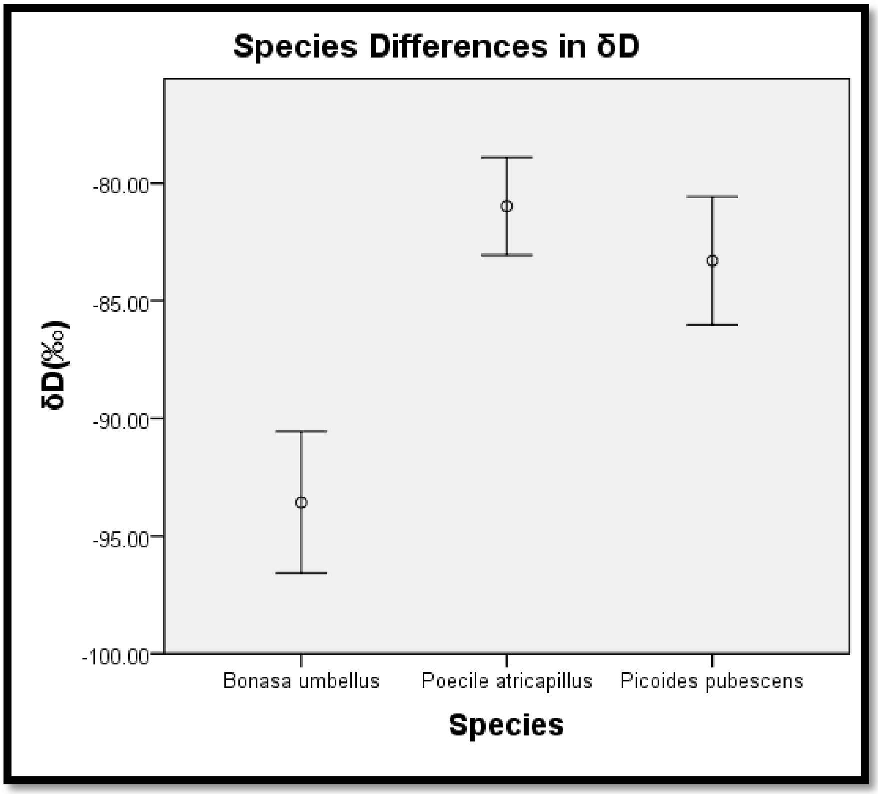

Figure 9. Mean δD for each species.

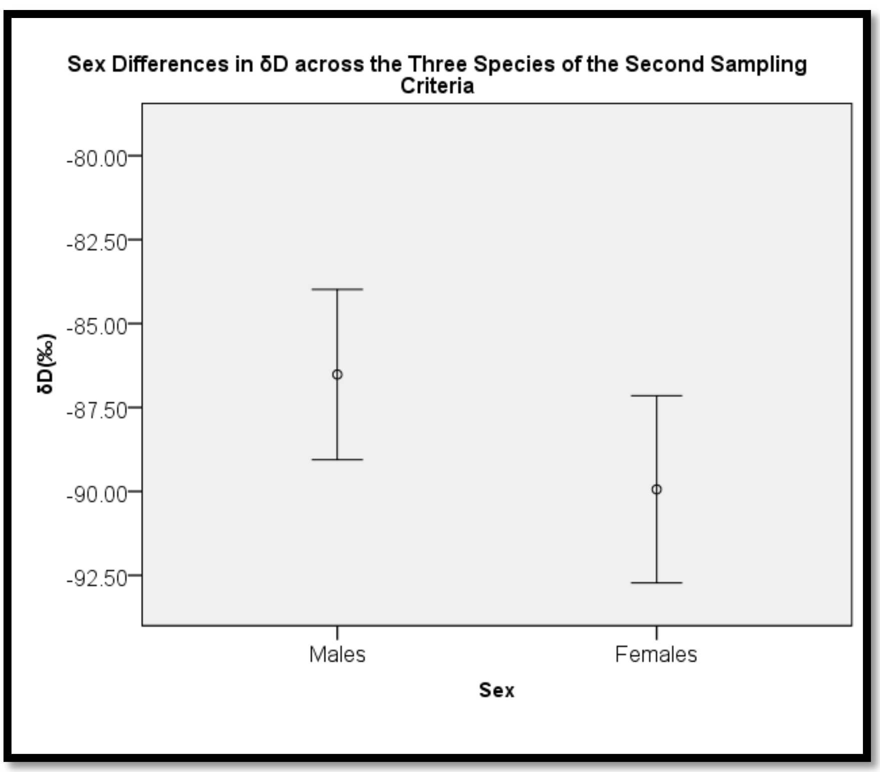

Figure 10. Mean δD for each sex across all three species though sampling was uneven with 73 males and 50 females.

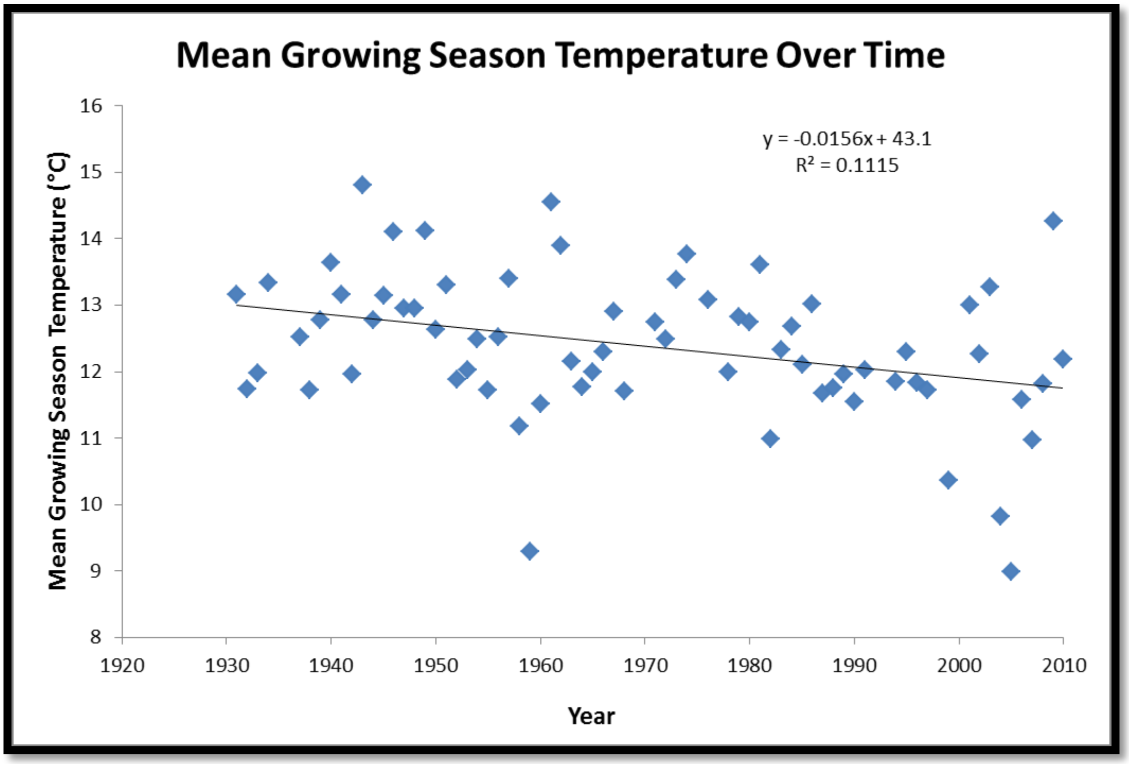

Figure 11. Mean growing season temperature in degrees Celsius plotted over time.

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