Analysis of temporal range change in neotropical passerine migrants using stable hydrogen isotope techniques

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ABSTRACT

Avian feathers contain an intrinsic hydrogen isotope signature that indicates the latitude where the feather was grown. When breeding latitudes, determined by analyzing stable hydrogen, are compared between two distinct time periods, changes in range use can be discerned. This technique could prove especially useful for neotropical migrants which are vulnerable to habitat loss and climate change throughout the various portions of the avian life cycle. During migration in 2014, prebasic tail feathers were collected from magnolia warblers by the Powdermill Avian Research Center to determine current breeding latitudes. Prebasic body feathers were collected from study skins of the same species at the Carnegie Museum of Natural History to determine breeding latitudes from 1895-1985. Feather samples were sent to the Stable Isotope Lab at Cornell University for analysis and the resulting isotope data was manipulated using a spatial analyst operation in GIS to model tolerance limits based on an interpolation of stable hydrogen in precipitation. Several comparison models of older feathers and current feathers were created and anova tests suggest the area of occupancy has shifted through time, though the reasons for change may vary. Between urbanization and land conversion for agriculture, the magnolia warbler may be experiencing varying levels of habitat loss along its southern breeding boundary. Changes seen along the northern boundaries are more likely northern colonization in response to climate warming. Nevertheless, the use of stable hydrogen to analyze temporal range change was successful and should continue to be used as a method for detecting range change in threatened or endangered neotropical avian migrants. If a species is shifting over time, natural resource managers could adapt management plans accordingly.

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Introduction

The use of stable isotope techniques in ecological research has grown steadily throughout the past two decades. This trend is expected to continue as stable isotopes serve as valuable nonradioactive and nondestructive tracers (Dawson et al. 2002) of how organisms have interacted with and responded to their abiotic and biotic environment. Stable elemental isotopes, like carbon, nitrogen, sulfur, hydrogen and oxygen, occur naturally in several forms with differing nuclear masses. Isotope abundance varies in the environment because of a range of biological and biogeochemical processes and thus, stable isotopes are incorporated directly from diet into animal tissues (Rubenstein & Hobson 2004). They are measured with great precision as isotopic differences relative to international standards and reported as ratios in delta (δ) units as parts per thousand (‰) (Rubenstein & Hobson 2004; Peterson & Fry 1987) and can be utilized to study various ecological processes (Rubenstein & Hobson 2004).

Stable isotope methods have been featured in a variety of ecological studies including the studies of plants at the population and community levels. Most studies employ hydrogen, carbon, oxygen and nitrogen isotope data to provide key insights into biogeochemical interactions between plants, soils, and the atmosphere (Dawson et al. 2002). Stable isotope studies have also been extensively used to gain information on predator/prey distributions and trophic interactions. Many stable isotopes can provide a continuous measure of trophic position that integrates the assimilation of energy or mass flow through all the different trophic pathways ultimately leading to a singular point (Post 2002). Stable isotope measurements of animal tissues are also frequently used to quantify animal movement because biogeochemical information inherent in isotope values is transferred from the base of food webs to animal tissues (Tonra et al. 2014; Hache et al. 2012; Hobson & Wassenaar 2008). Up until recently, tracking animal movement has been done directly, by using some form of *extrinsic* marker (Hobson 1999). The ability to trace movement of individual animals is limited and biased toward a few conspicuous, larger species. Technological limitations related to the use of extrinsic markers also typically require the recovery of individuals as well. For example, tracking birds involves leg bands, neck collars, patagial tags, and plumage marking with dyes or picric acid. Remote sensing capabilities provide an improvement over mark-recapture techniques, but have only extended our ability to track organisms large enough to carry GPS or geolocators. Such methods are to date, impractical or expensive for tracking small or non-game animals (Hobson 1999). With the use of stable isotopes, movement can be tracked indirectly by inferring origins using *intrinsic* biogeochemical markers (Rubenstein & Hobson 2004). It also allows researchers to sample more individuals across a species' range in a relatively short time frame (Tonra et al. 2014).

Stable Hydrogen and Migratory Connectivity

Historic methods of tracking migratory birds such as banding has been informative for some avian groups such as shorebirds and waterfowl, but levels of band returns for migrant songbirds are often miniscule (Clegg et al. 2003; Berthold 2001). Radio and satellite tracking are valuable for determining movements of large-bodied migrants capable of carrying heavy transmitters (Hobson 1999), but cannot be applied to small passerines. The difficulty of applying these techniques to small songbirds has led to the use of intrinsic genetic and isotopic markers to track populations (Clegg et al. 2003; Hobson 2001a; Hobson 2001b; Hobson 1999; Hobson 1997). The stable isotope ratios of hydrogen ($^2H/^1H$; depicted as δ^2H) are particularly useful for assigning individuals to approximate location because the processes that create variance in these isotopes in the hydrosphere are relatively well understood at continental scales (Hache et al. 2012; Bowen et al. 2005). Thus, stable hydrogen isotopes permit studies that connect breeding and nonbreeding ranges of migratory birds, separated by thousands of miles, giving new understanding to migratory connectivity (Rushing et.al. 2014; Hobson, 2005a).

Hydrogen isotopes deteriorate systematically across ecosystems and geographical regions (Figure 1) (Bowen et al. 2010). In North America, the ratio of deuterium (^2H) to hydrogen (^1H), expressed as δD, in rainfall varies in a predictable, broad-scale geographic pattern (Bowen et al. 2005), as demonstrated in Figure 2. A precipitation signal, transferred through local food web and diet (Figure 3) (Hobson & Van Wilgenburg 2015; Hobson et al. 2012; Wassenaar & Hobson 1998; Hobson & Wassenaar 1997; Cormie et al. 1994), is incorporated into δD values of feathers both by juveniles growing their first set of feathers and by adults replacing molted feathers (Chamberlain et al. 1997, Hobson & Wassenaar 1997). In birds, these isotopic ratios of hydrogen are permanently fixed into the keratin of feathers, reflecting the local environment where the tissue was grown (Rushing et.al. 2014; Boone et.al 2010; Rubenstein et al. 2002; Wassenaar & Hobson 1998; Cormie et al. 1994).

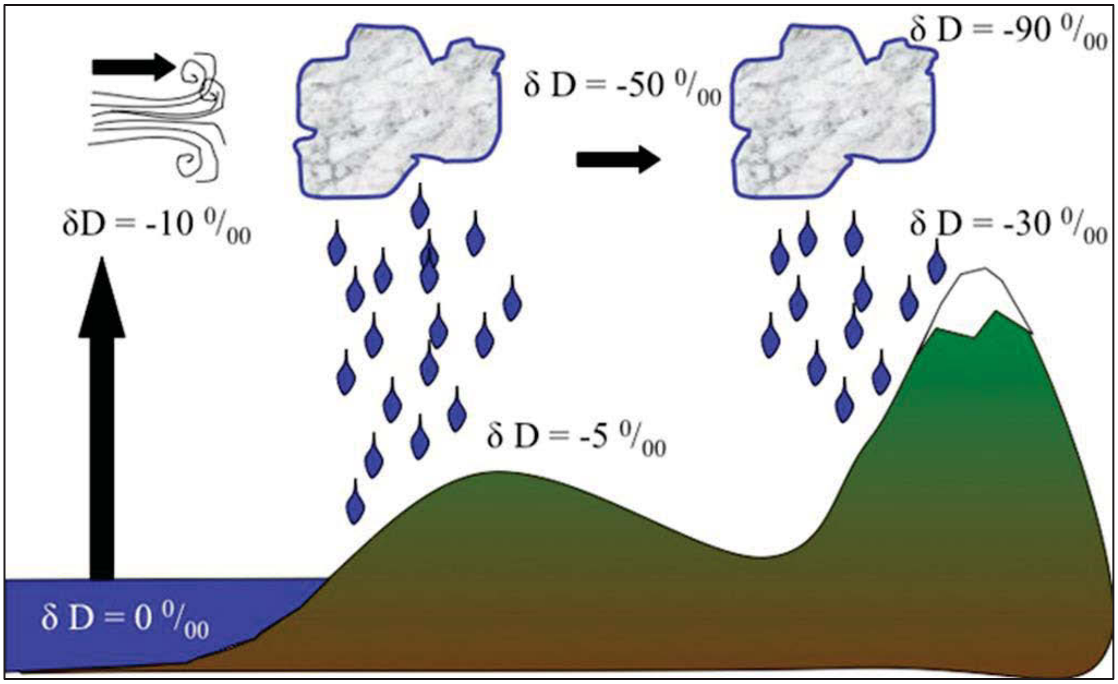


Figure 1: Global patterns in precipitation reflect evaporation off the oceans, fractionation of Hydrogen isotopes during precipitation events, as well as distance from the coast, elevation, and temperature (University of Oklahoma [Animal Migration Research, Jeff Kelly Lab])

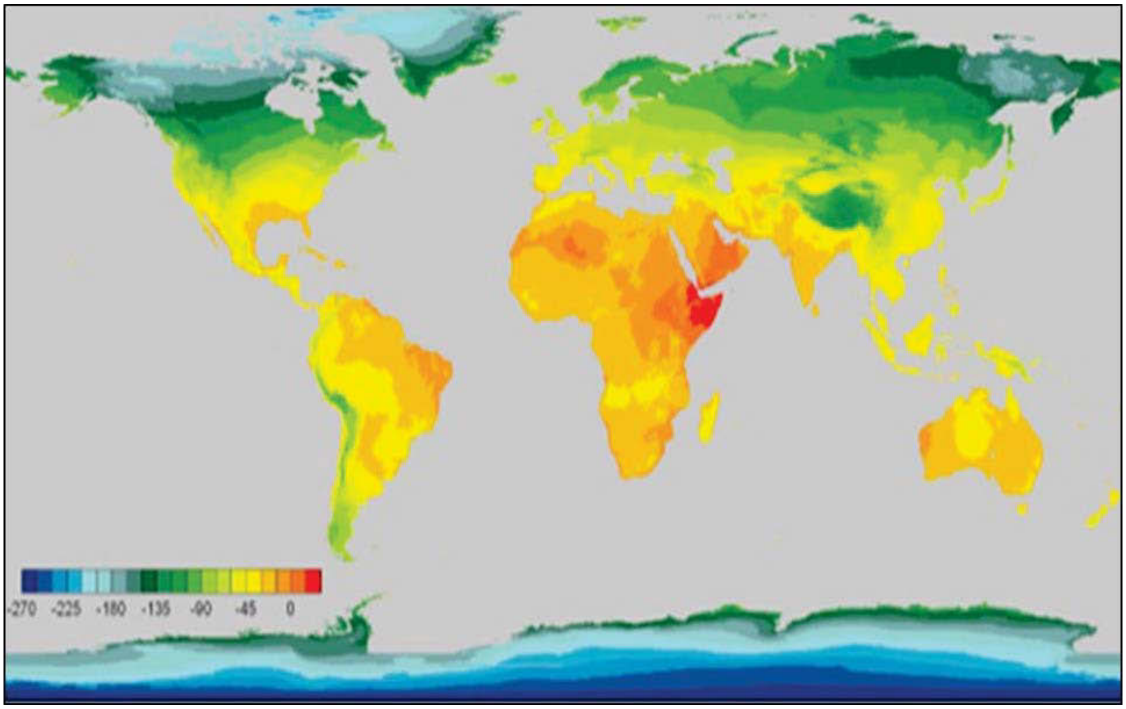


Figure 2: δD zones from precipitation (University of Oklahoma [Animal Migration Research, Jeff Kelly Lab])

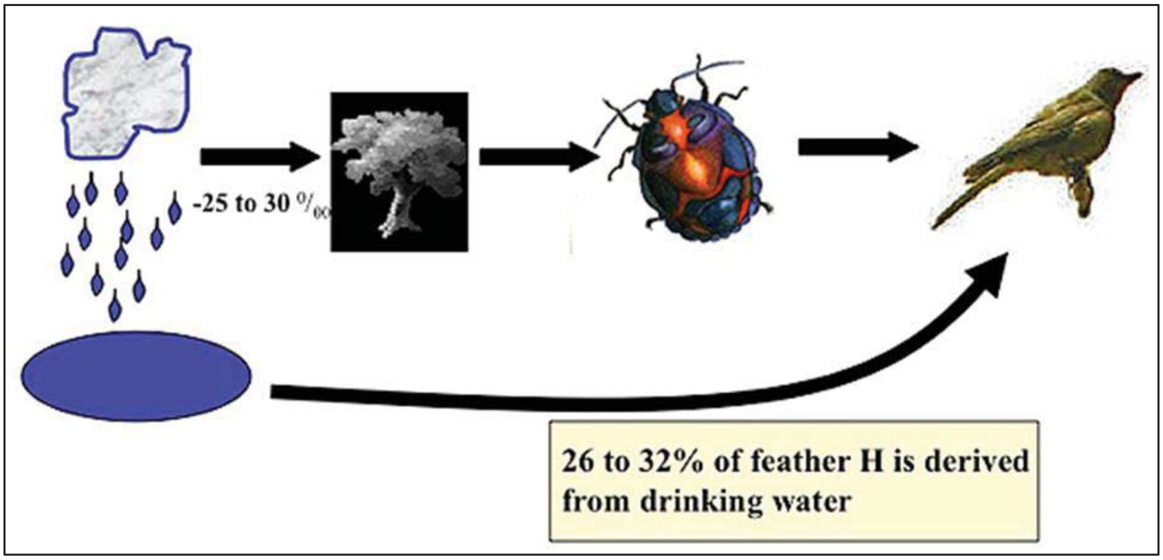


Figure 3: Hydrogen in a bird's feathers comes from the food they eat. In the summer, this food is a direct product of growing season precipitations. This relationship results in a strong causal relationship between the isotope ratio of local growing season precipitation and the isotope ratios in feathers of passerine birds that are grown in that location (University of Oklahoma [Animal Migration Research, Jeff Kelly Lab])

Annual variation can exist from year to year, but with long-term means (Tonra et al. 2014) stable hydrogen isotopes can be used to determine the relationships between and within breeding sites, stopover locations and wintering habitat of avian species (Veen 2013; Ambrosini et al. 2009; Webster et al. 2002;). For many migratory bird species in North America, a molt occurs on the breeding grounds (Pyle 1997) prior to migration. Therefore, the δ^2H value in a feather can be used to identify the geographic location where breeding occurred even if the feather is not obtained on the breeding ground (Hobson et al. 2014; Hache et al. 2012). For example, as shown in Figure 4, a feather collected at the wintering ground but grown at the breeding ground can be used to estimate where an individual bred (Veen 2013; Mazerolle & Hobson 2005). Known stable hydrogen isotope values from precipitation are used to derive probability isoscapes across North America using methods built on work by Wunder (2010). Probability that an individual's stable isotope signatures originate from a certain location can thus be calculated. These probabilities can then be positioned on a map to estimate the most likely region of breeding origin of an individual (Veen 2013).

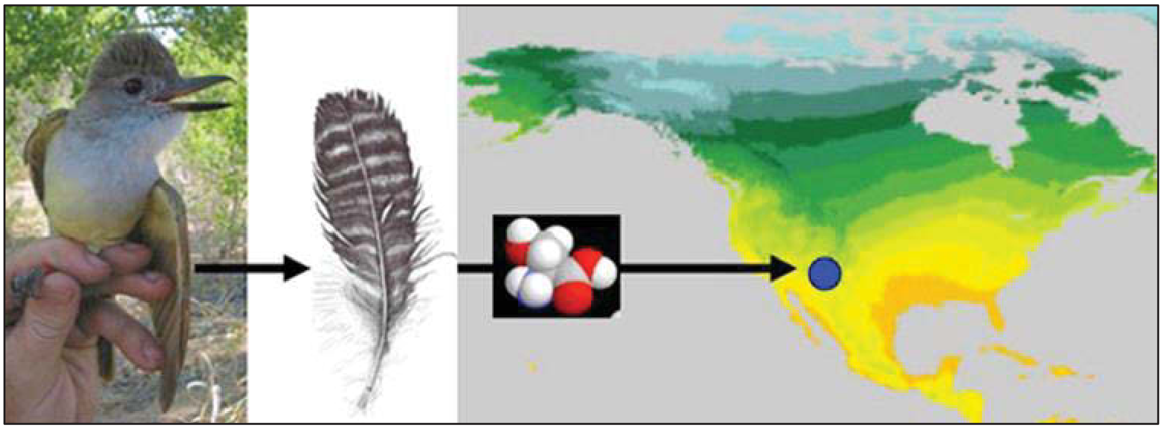


Figure 4: Feather connections in migratory birds to stable hydrogen isotope signatures from precipitation (University of Oklahoma [Animal Migration Research, Jeff Kelly Lab])

In order to properly place probabilities, isotope signatures must be adjusted for fractionation as stable hydrogen in passerine feathers is typically depleted in the heavy isotope compared to mean annual growing season δD in precipitation (Figure 3) (Wassenaar & Hobson 2000, Bowen et al. 2005). As Hobson (2012) demonstrates, short-distance migrants had more negative δ^2H values (-36.9%), followed by ground foraging resident species (-27.9%), non-ground foraging Neotropical migrant (-27.1%), ground foraging short-distance migrants (-23.0%), ground foraging Neotropical migrants (-17.6%), and finally by non-ground foraging resident species (-11.2%). Nevertheless, stable hydrogen has been used successfully to determine latitudinal zones of natal or breeding origin for several passerines (Kelly 2006) and nonpasserines (Wassenaar & Hobson 2000, Hobson & Wassenaar 2001, Kelly et al. 2002, Rubenstein et al. 2002, Hobson et al. 2004; Hobson et al. 2007)

The δD values in feathers decreases with increasing breeding latitude in the temperate North American breeding grounds. In some species, within the wintering range, δD values also decrease with increasing longitude (Rubenstein et al. 2002). These ‘intrinsic’ markers do not require the recapture of an individual and they do not degenerate over time. Stable isotope analyses are relatively inexpensive, and samples are relatively easy to obtain (Veen 2013). Thus, stable-hydrogen isotopes have slowly become a primary means for quantifying the movement ecology of migratory animals (Hobson 2005b; Kelly et al. 2002); however, stable isotope techniques have important limitations. First, the patterns of δ^{2}H in North America provide a strong latitudinal signal of origin but provide less resolution to delineating longitude of origin (Hobson & Van Wilgenburg 2015; Bowen et al. 2005). Second, numerous assumptions are made when using isotopes to assign birds to specific molting locations.

1. The underlying mean δ^{2}H corresponding to precipitation during the growing season from the long-term Global Network of Isotopes in Precipitation (GNIP) database (IAEA/WMO 2015) correctly models the variation in δ^{2}H (Hache et al 2012; Hobson 2008; Wunder et al. 2005).
2. All Individuals show the same δ^{2}H isotoptic signature if they grew their feathers in the same region.

Unravelling migratory patterns is extremely important for guiding conservation decisions (Veen 2013; Fraser et al. 2012) and the technique is inexpensive enough to be applied to large sample sizes across species’ ranges (Hobson et al. 2014). For example, Kelly et al. (2002) measured hydrogen stable-isotope ratios (δD) of feathers from breeding, migrating and wintering Wilson’s warblers. They revealed a pattern indicating Wilson’s warblers that bred furthest north migrated earliest in the autumn and birds that bred furthest north wintered furthest south. Hobson et al. (2014) also discovered black-and-white warblers captured in Mexico displayed a bimodal distribution of breeding origins, with birds coming from the extreme northern and southern portions of their breeding range. _In order to appropriately manage avian migrants it is important to understand the connectivity between the breeding and wintering range as the separation between the two makes conservation more challenging.

Range Change

In light of the observed and projected environmental changes that have coincided with anthropogenic human activities, many populations will have to acclimate, adapt or else perish (IPCC 2014; Vogel & Lazar 2010). Habitat fragmentation and the destruction of natural habitats through direct human activities are considered great threats to terrestrial biodiversity (Jetz et al. 2007; Opdam & Wascher 2003; Travis 2002). However, climate change is thought to be the most influential driver of range change and there is mounting evidence to support shifts in species' distributions as a result of recent climate warming (Hickling et al. 2006; Parmesan & Yohe 2003). To the extent that dispersal and resource availability allow, many species are expected to track the changing climate and likewise shift their distributions poleward in latitude or upward in elevation (Melles et al. 2011; Thomas 2010; Colwell et al. 2008; Sekercioglu et al. 2008; Franco et al. 2006; Precht & Aronson 2004; Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2002). Although many species have responded to climatic changes throughout evolutionary history, a primary concern for wild species and their ecosystems is the current rapid rate of change (Root et al. 2003).

The past century has recorded a nearly 1 °C rise in global average temperature, with up to 7 °C of warming predicted by 2100 (IPCC 2014). Global warming has already led to significant shifts in the distribution, phenology and behavior of organisms. Of

1,700 plant, insect, amphibian and bird species examined in a review by Parmesan and Yohe (2003), 80% had a poleward range shift of 6.1 km per decade, and 87% had an advancement in the timing of phenological events, such as breeding or flowering, of 2.3 days per decade (Sheridan & Bickford 2011).

Hundreds of species have already adapted to recent warming trends by expanding their ranges to higher latitudes or elevations (Melles et al. 2011; Thomas 2010; Colwell et al. 2008; Sekercioglu et al. 2008; Franco et al. 2006; Precht & Aronson 2004; Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2002). Meta-analyses have shown a clear effect of climatic change on recent northward movements of species' range boundaries (Parmesan & Yohe, 2003; Root et al., 2003). Latitudinal and elevational changes in range limits correlated with climate change as well as fluctuations in precipitation have been documented for a wide spectrum of temperate and subtropical species (Colwell et al. 2008; Hitch & Leberg 2006) including many insects and plant species (Hickling et al. 2006), birds (Thomas & Lennon 1999; Crick & Sparks, 1999), mammals (Sillett et al., 2000), and butterflies. Continued climate warming is expected to increase the ratio of extinctions at the southern warm range limit and colonizations at the northern cold range limit of species ranges which results in extensive range shifts for many species (Opdam & Wascher 2003; Honnay et al. 2002). However, recent studies have shown that climate-driven range expansions at high-latitude northern range boundaries are limited as some species are failing to expand northwards because of the loss and fragmentation of their northern habitats (Wilson et al. 2009; Franco et al. 2006; Thomas et al. 2004; Honnay et al. 2002).

Over the past few decades, land-use change has led to substantial range contractions and species extinctions (Jetz et al. 2007). Expansion beyond current species range margins may be inhibited by landscapes in which a lack of habitat leads to low rates of colonization and to high rates of extinction in populations that become temporarily established (Wilson et al. 2009). Worldwide changes to forests, farmlands, waterways and air are being driven by the need to provide food, fiber, water and shelter to the world's growing population (Foley et al. 2005). The pace, magnitude and spatial reach of human alterations of the Earth's land surface are unprecedented (Lambin et al. 2001)—whether converting natural landscapes for human use or changing management practices on human-dominated lands—humans have transformed a large proportion of the planet's land surface. By clearing tropical forests, intensifying farmland production, or expanding urban centers, human actions are changing the world's landscapes in pervasive ways (Foley et al. 2005) that, when aggregated globally, significantly affect key aspects of Earth System functioning (Lambin et al. 2001).

Landscapes with a dominant human land use will continue to change due to increasing mobility, economic activity, urbanization and agricultural development, causing a further decrease of spatial cohesion of habitat for species (Opdam & Wascher 2003). For example, 400–900 bird species are projected to have over 50% of their current range transformed to a different habitat by 2050. Even more dramatic environmental change is projected for this century (Jetz et al. 2007). Land-use activities, primarily for agricultural expansion and timber extraction, have already caused a net loss of 7 to 11 million km^2 of forest in the past 300 years (Foley et al. 2005). Fuel-wood collection, forest grazing and road expansion have also degraded forest ecosystem conditions in terms of productivity, biomass, stand structure and species composition. Land use can also degrade forest conditions indirectly by introducing pests and pathogens, changing fire-fuel loads, changing patterns and frequency of ignition sources, and changing local meteorological conditions (Foley et al. 2005). Many projections also state that 60% of the world's population will be urban by 2025 and, given that urban life-styles tend to raise consumption expectations and affects land change elsewhere through the transformation of urban-rural linkages—the urban ‘‘ecological footprint’’ is going to grow (Lambin et al. 2001).

Furthermore, the largest potential loss of range size occurs among specialist species that have restricted ranges, low colonization ability and poor dispersal (Jetz et al. 2007; Travis 2002). Many specialist species already have small population sizes and are exposed to a high risk of extinction from stochastic demographic processes (Jetz et al. 2007). Species with relatively wide ranges are perhaps unsurprisingly the most resilient to the effects of anthropogenic activities (Travis 2002). In general, species that live in the tropics tend to have narrower ranges than those living in temperate regions. Given similar rates of climate change in both tropical and temperate areas, we would expect those in the tropics to be most at risk of extinction (Travis 2002). However, climate change is projected to be strongest in the high latitudes of Siberia and North America. In contrast, human land-use change dominates lower latitudes, specifically in Central and South America, central Africa, and portions of India and China (Jetz et al. 2007).

Predicting extinction risks for populations in a world suffering simultaneously from several sources of anthropogenic change is a major challenge ecologists and conservation biologists face today (Travis 2002). There are difficulties in distinguishing between extinctions due to climate change and those due to habitat change; a species that spreads northwards (in the northern hemisphere) across an otherwise deteriorating landscape is almost certain to be responding to climate warming, but a species that declines at its southern boundary could equally be responding to habitat loss or to climate change (Franco et al. 2006), though compelling evidence typically links northward movements to climate change (McCarty 2001; Thomas & Lennon 1999). Nevertheless, predicting those species that will be able to shift their distributions in response to climate change and those that will require active conservation management due to habitat loss and fragmentation is becoming increasingly important (Wilson et al. 2009).

A more accurate estimate of global range change should evaluate the area of occupancy, which includes the occupied area within a species known, inferred or projected sites of present occurrence—excluding cases of vagrancy (Sekercioglu et al. 2008; IUCN). This is particularly critical given that geographical range size is a fundamental criterion for determining when a species faces a heightened risk of extinction. Small range size is the single best predictor of extinction risk for terrestrial species (Harris & Pimm 2007; Manne et al. 1999). Simply, with large-scale changes in land use (e.g., deforestation), it is easier to entirely eliminate a species with a small range than a large one. As such, estimates of changes in range size are used regularly to predict extinctions due to habitat loss or climate change (Sekercioglu et al. 2008; Thomas et al. 2004). It is important to utilize techniques that identify how species have already reacted to recent global change (Chen et al. 2011) so conservation can be adapted appropriately.

Neotropical Avian Migrants

Migration is the term used to describe the seasonal movements of bird populations north and south between breeding and wintering grounds. Birds typically move from areas of decreasing resources to areas of increasing resources. This can include the search for productive breeding ground which consists of ideal nesting locations and plenty of food in order to maximize fitness in a seasonal environment (Newton 2010; Alerstam et al. 2003; Berthold 2001). Neotropical migratory birds are specifically western hemisphere species that breed north of the Tropic of Cancer and winters south of that same latitude (Berthold 2001; Deinlein n.d.). There are about 200 species of neotropical migratory birds, about one third of all species in North America (Hobson et al. 2014), and the majority are songbirds such as warblers, thrushes, tanagers, and vireos. However, there are also shorebirds, raptors and a few waterfowl (Berthold 200l). However, migration distance can still vary greatly between species.

The shortest migrations are a few hundred miles. Some of the longest migrations are made by shorebirds that winter in the southern most parts of South America with a one-way distance of up to 10,000 miles. Others travel roughly 7,000 miles and migrate between Central and South America and Canada (Berthold 2001; Deinlein n.d.). For bird species at high latitudes there will be more excess resources available for breeding relative to the resource level during the survival (winter) period, giving room for larger clutch sizes than for species at equatorial latitudes (Newton 2010). Migration to a large degree serves as an adaptation for exploiting different habitats for survival and reproduction, and for combining these fractional niches into a complete basis of existence (Newton 2010; Alerstam et al 2003).

Birds perform many ecosystem services that benefit the human race, including their roles as predators, pollinators, scavengers, seed dispersers and ecosystem engineers (Whelan et al. 2008; Clout & Hay 1989). Furthermore, migrant species link ecosystem processes and fluxes that are separated by great distances and times (Whelan et al. 2008). The disruption of these ecological processes, such as seed dispersal and forest regeneration, in the wake of extinctions or reductions in population size could be considerable. Overall, 21% of bird species are currently extinction-prone and 6.5% are functionally extinct (Sekercioglu, Daily & Erhlich 2004), insignificantly contributing to ecosystem processes. Approximately one-quarter or more of frugivorous and omnivorous species and one-third or more of herbivorous, piscivorous, and scavenger species are extinction prone. Furthermore, projections indicate that by 2100, 6–14% of all bird species will be extinct, and 7–25% (28–56% on oceanic islands) will be functionally extinct (Sekercioglu, Daily & Erhlich 2004). Important ecosystem processes, particularly decomposition, pollination, and seed dispersal, will likely decline as a result. Concern about decline in avian species and the subsequent ecological services they provide was one of the factors that lead to the formation of Partners in Flight and other major conservation initiatives (Hobson & Van Wilgenburg 2015).

Migrants are key components of biological systems in high latitude regions, where the speed and magnitude of climate change impacts are greatest. They also rely on highly productive seasonal habitats that may become less food-rich and predictable in space and time with climate change, habitat loss and changes in land use (Robinson et al. 2009; Sillett & Holmes 2002). Migratory species represent a paradox in the assessment of risk posed by climate change to biodiversity (Robinson et al. 2009). Because they are mobile, and populations frequently exhibit multiple migratory strategies, they may track geographic changes of suitable environments across the globe. On the other hand, because migrants are dependent upon the availability of suitable habitat at multiple locations (in breeding, migration, and non-breeding areas), all of which may be affected by climate change in different ways, migrants have the increased potential for deleterious impacts at some point in their annual cycle (Parmesan & Yohe 2003; Root et al. 2003; Walther et al. 2002). Moving long distances exposes migrants to additional risks from climate change, but their ability to move long distances also provides potential for their survival. For example, breeding dispersal is on average greater for migrants than residents and those species with greater dispersal are better able to respond adaptively to warming temperatures. However, genetic or cultural constraints can limit the ability of a species to alter migratory journeys (Robinson et al. 2009).

Progress toward quantifying the effect and timing of climate change on neotropical migrants has been difficult because these species spend different parts of their annual cycle in diverse locations, often on different continents (Sillett, Holmes & Sherry 2000). The North American Breeding Bird Survey (BBS), an annual roadside survey of United States and Canadian birds, is currently the only quantitative source of information regarding regional changes in breeding populations of neotropical migrant birds. The BBS estimates are based on counts conducted each June along approximately 2000 randomly distributed roadside "routes" (Robbins et al. 1989).

Despite high interest in population trends of migratory passerines that breed in the North American boreal forest, most of these species are poorly monitored by the North American Breeding Bird Survey (BBS) because of limited road access across most of the habitat (Hobson & Van Wilgenburg 2015). Furthermore, events during one stage of the annual cycle are likely to influence populations in subsequent stages creating fluctuations in local populations (Figure 5) (Sillett, Holmes & Sherry 2000). A quantitative analysis of δ^2H in preserved specimens compared to δ^2H in current breeding birds could assist in the detection of range change over time for migratory passerines that breed primarily in the boreal forest and are otherwise poorly monitored by the North American Breeding Bird Survey (BBS) (Hobson & Van Wilgenburg 2015).

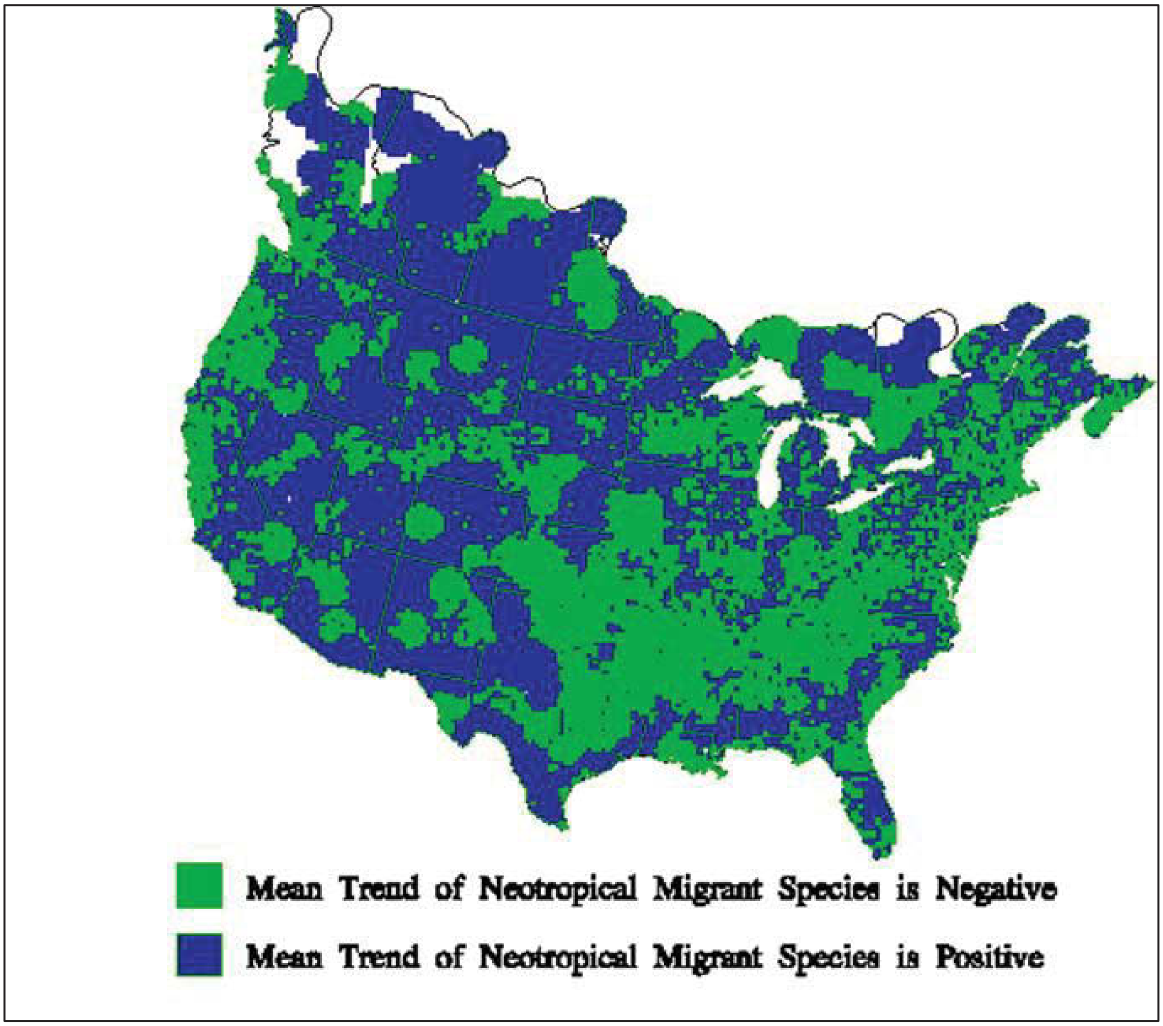


Figure 5: Trends in neotropical migrants determined by the North American Breeding Bird Survey (BBS)

The magnolia warbler

In order to determine whether analysis of stable hydrogen can be utilized to investigate range change it is important to choose a study specimen that is relatively stable in abundance. Since the magnolia warbler is listed as a species of least concern by the International Union for the Conservation of Nature (IUCN), any change that the model displays should not be related to a loss of species abundance.

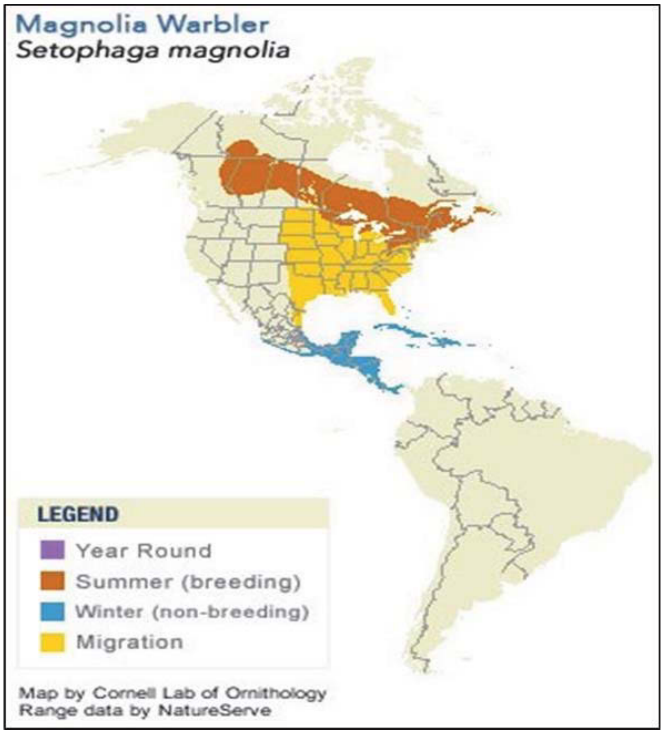


Figure 6: Traditional estimated range of the Magnolia warbler © allaboutbirds.com

The magnolia warbler is a small neotropical song bird in the wood warbler family *Parulidae*. It measures up to 13 centimeters in length and 20 centimeters across the wings (Pyle & Howell 1997). Body mass in adult birds can reach up to 12.6 grams (Pyle & Howell 1997). Magnolia warblers breed in boreal forests (Figure 7), where they can be found among the branches of densely packed coniferous trees. Their breeding range runs across the northern parts of Canada, such as in Saskatchewan, Manitoba, Ontario, and Quebec. However, they can also be found in the northern parts of the US at the southernmost limit of their range. During the winter, the warbler migrates through the eastern half of the United States to southern Mexico, Central America and the Caribbean (Dunn & Hall, 2010; Kaufman, 2001) therefore categorizing the magnolia warbler as a neotropical migrant (Figure 6).

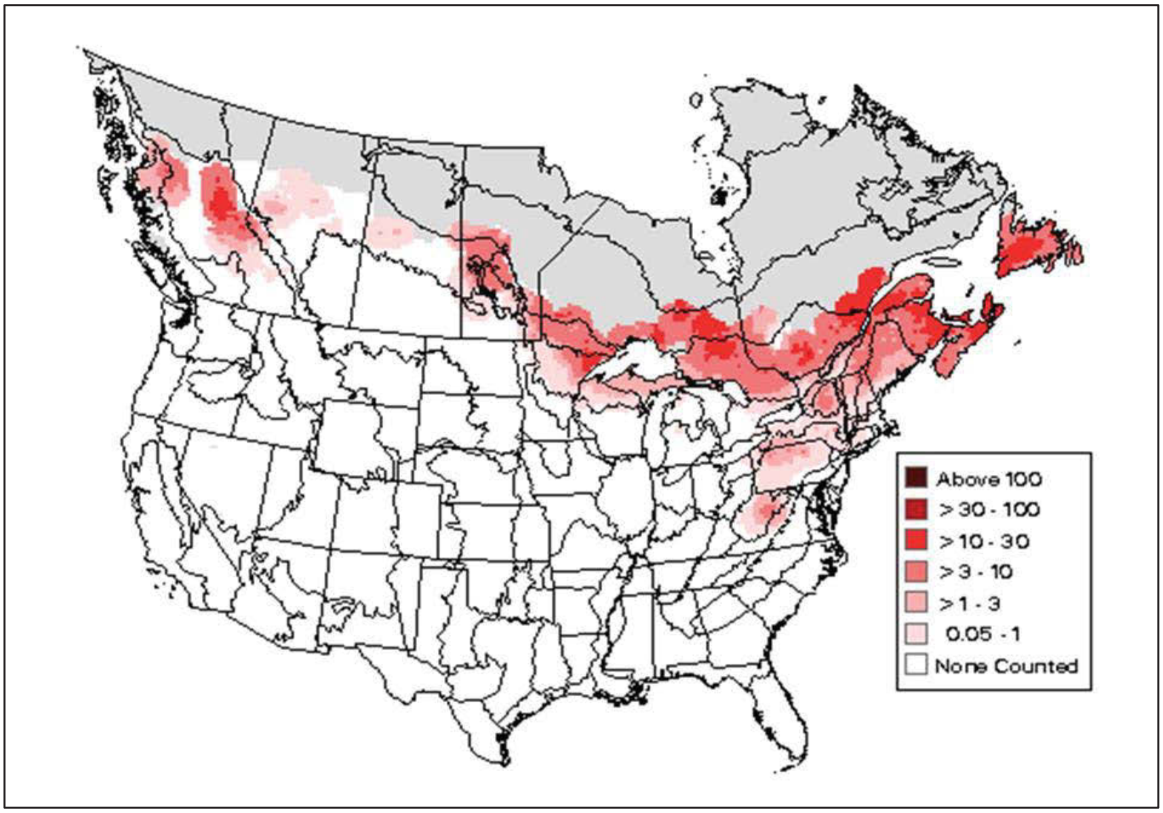


Figure 7:Magnolia warbler distribution according to the North American Breeding Bird Survey (BBS)

The magnolia warbler has a pre-alternate molt cycle and thus molts twice a year. As winter comes to a close, birds with a pre-alternate molt cycle shed some of their feathers on the wintering ground and grow the alternate plumage needed for attracting a mate. After they have reproduced, they replace all of their feathers with less brightly colored feathers for the winter. Figure 8 illustrates this annual molt cycle as it is applied to Magnolia warblers. When the magnolia warbler replaces all of its feathers on the breeding ground, those feathers contain an isotopic signature of δ^2H that correlates with the mean annual growing season δD in precipitation (Bowen et al. 2005; Wassenaar and Hobson 2000). However, since the magnolia warbler undergoes an incomplete molt on the wintering grounds, many of the feathers still contain an isotopic signature from the breeding grounds allowing for year round collection of prebasic feathers. In other words, a larger number of samples can be collected in a shorter period of time.

	Winter	Sping	Summer	Fall	Winter
Year One			Bird Hatches - grows juvenile plumage	Bird goes through first prebasic molt prior to migration - incomplete	Bird winters
Year Two	Bird goes through first prealternate molt prior to migration - incomplete	Bird migrates north to breeding ground	Bird breeds	Bird goes through prebasic molt prior to migration - complete	Bird winters
Year Three	Bird goes through second prealternate molt prior to migration - incomplete	Bird migrates north to breeding ground	Bird breeds	Bird goes through prebasic molt prior to migration - complete	Bird winters

Figure 8: The molt cycle of avian species with a pre-alternate molt expressed by season © Annie Crary, 2014

The breeding, or pre-alternate, plumage of breeding males (Figure 9) can be recognized by distinctive black streaking on the breast and a black mask around the eye. There is a mixture of white, gray, and black on their backs with yellow on the sides and stomachs (Stephenson & Whittle 2013; Dunn & Hall, 2010; Kaufman, 2001; Pyle & Howell 1997). They also have black tails with white spots in the center of all but two tail feathers and defined white patches on their wings, called wing bars. Breeding females typically have the same coloration as the males, but they lack the black mask and are much duller and drab. Immature individuals have similar coloration to the adult females (Stephenson & Whittle 2013; Dunn & Hall, 2010; Kaufman, 2001; Pyle & Howell 1997). Nonbreeding plumage or basic plumage is much duller in all individuals with reduced streaking and more olive-green tones. Males lose their black mask in favor of a gray face with a white eyebrow (Stephenson & Whittle 2013).

Figure 9: The pre-alternate plumage of an adult male magnolia warbler © Powdermill Nature Reserve

Progress toward quantifying range change in neotropical migrants has been difficult. Since the magnolia warbler is relatively stable in abundance, has a partial pre-alternate molt cycle and is classified as a neotropical migrant, it is an ideal study species. Successful application of a temporal δ^2H comparison in magnolia warblers could be used to identify how threatened or endangered neotropical migrants have responded to recent global change so conservation can be adapted appropriately.

Hypothesis and Objectives

When breeding latitudes of the magnolia warbler, determined by analyzing stable hydrogen, are compared between two distinct time periods, changes in range use will be distinguishable.

Objectives:

1. Determine breeding zones by comparing δD from feather samples to interpolation of δD from precipitation.
2. Determine if Magnolia warblers are experiencing a shift within natural range or a change in distribution on the breeding ground by comparing a historic representation of the breeding ground to a current representation.
3. Evaluate the success of using Geographic Information Systems (GIS) and δD from feather samples to evaluate spatial change over time

Materials & Methods

Field Sampling

In order to create a data set that would represent the current breeding latitudes using stable hydrogen isotopes, prebasic feathers (Figure 10) from transient magnolia warblers were collected by the Powdermill Avian Research Center (PARC) during the spring and fall migrations of 2014. PARC is operated under a master banding license as a part of Carnegie Museum of Natural History's Powdermill Nature Reserve located in the Laurel Highlands of Westmoreland County, Pennsylvania. The PARC facility is 10-hectares comprised of old fields, hedgerows, and marshy ponds, along with alder and willow-lined streams. The area is bound by a mixed deciduous forest along the Laurel Ridge to the east and by low intensity agricultural areas in the Ligonier Valley to the west. Birds were captured using up to 70 mist nets that are 12 meters long and 2.5 meter high (30 mm mesh). Nets were placed singly or in series of up to eight connected nets in hedgerow gaps and along habitat edges, mostly where adjacent vegetation is not much higher than the nets themselves. To maintain the efficiency of the net locations for catching birds, habitat management is performed to remove tall woody vegetation from the vicinity of net lanes. The nets were opened 30 min before sunrise, checked every 30 to 40 minutes as conditions allow, and operated 6 hours per day for 5-6 days a week mid-April through May and mid-August through October.

Figure 10: Prebasic plumage of a Magnolia warbler during fall migration © Jim Burns

Upon capture, each bird was placed in a small drawstring, breathable, cloth bag for transfer back to the banding station. Once in the lab, each magnolia warbler was banded with a U.S. Geological Survey aluminum leg band or reprocessed if they had been banded previously. Individuals were aged as either hatch year, after hatch year, second year or after second year by rectrice shape, feather wear, and molt limits within wing coverts (Mulvihill 1993; Pyle & Howell 1997) and sexed by plumage characteristics (Pyle & Howell 1997). Wing chord and body mass were also measured to the nearest 0.1 g. Due to the volume of birds that go through the banding station, feathers could not be collected from every magnolia warbler that come through. However, samples for stable-isotope analyses were sub-sampled to create an even representation of sex and age classes. Sub-samples included one hundred (n=100) birds, with sub categories as close as possible to twenty-five (n=25) young males, twenty-five (n=25) young females, twenty-five (n=25) adult males, and twenty-five (n=25) adult females. Each sub-category (young male; young female; adult male; adult female) was also sampled evenly across the migration season as best as possible. During spring migration, 203 magnolia warblers came through the Powdermill Avian Research Center and of those, 110 had feathers collected. The fall migration season saw 331 magnolia warblers and roughly 300 had feathers collected.

The two outer most retrices (n = 2 feathers), highlighted in Figure 11, were pulled from magnolia warblers as they went through the banding station. Feathers were stored in small envelopes labeled with the bird's band number, date, age and sex for delivery to Youngstown State University. Since the magnolia warbler undergoes an incomplete molt on the wintering grounds and thus the tail feathers (Pyle & Howell 1997) retain the isotopic

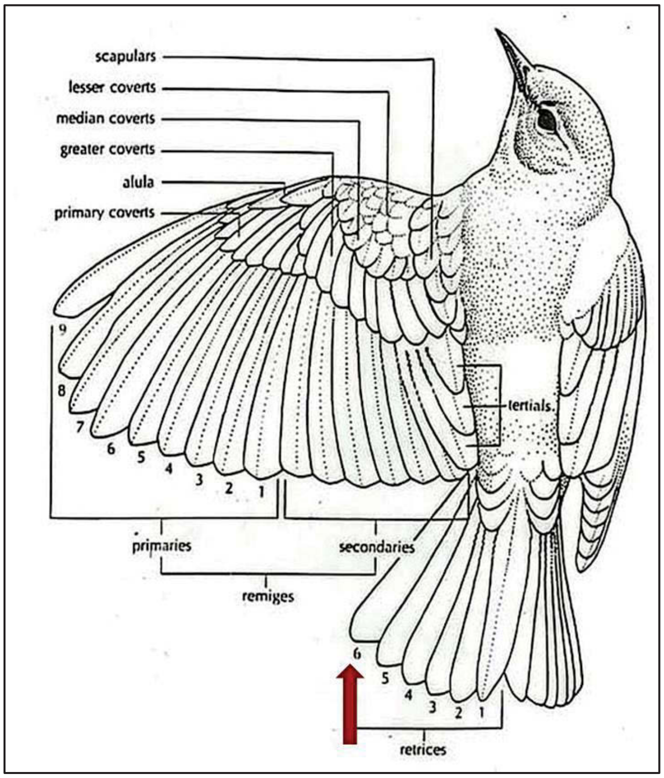


Figure 11: A diagram illustrating feather classification on a passerine species with special emphasis on the outer retrice, number 6

signature of the breeding grounds from the previous year, feathers collected during spring migration in 2014 were used to represent the breeding latitudes from 2013. Feathers collected during the fall migration of 2014 however were used to create a data set representing the breeding latitudes from 2014 as the magnolia warbler undergoes a complete molt on the breeding grounds and thus replaces all of its feathers (Pyle & Howell 1997) which incorporate the isotopic signature of the breeding latitudes.

Museum Sampling

The Carnegie Museum of Natural History has a bird database containing 205,720 records of specimens catalogued into the collection. However, more than 15,000 of those specimens have been exchanged and an additional number have been given away or discarded. As a result, the museum currently holds roughly 188,000 specimens. The majority are standard study skins with roughly 154,000 of this type of specimen representing around 5,700 different species. The collection is also completely digitized and maintained in a Microsoft Access format (http://www.carnegiemnh.org/birds/collection.html). There were a total of 327 magnolia warbler specimens in the database and eighty-eight (n=88) specimens were sampled based on date, geographic location of original collection and availability, as not all 327 specimens were housed in the

Figure 12: Counties of Ohio, Pennsylvania, and West Virginia that surround Powdermill Avian Research Center, located in Westmoreland County, PA

museum. The eighty-eight (n=88) specimens were originally collected and preserved between 1895 and 1985 and originally collected within the same geographic region as PARC, including Allegheny, Armstrong, Beaver, Blair, Cambria, Centre, Clearfield, Somerset and Westmoreland counties in Pennsylvania as well as Mahoning county in Ohio (Figure 12). In order to preserve specimen integrity, prebasic body feathers were pulled, using tweezers, from under the wing (Figure 13) instead of tail feathers. Body feathers were stored in small envelopes with the specimens ID number and intake date and delivered to the Stable Isotope Laboratory at Cornell University for analysis of stable hydrogen.

Figure 13: Magnolia warbler © Hilton Pond Center for Piedmont Natural History

Isotope Analysis

Feathers were analyzed by the Cornell University Stable Isotope Laboratory, following methods demonstrated in Kelly et al. (2002), Clegg et al. (2003), and Hobson et al. (2007). Feathers were washed and rinsed thoroughly with acetone to remove oil, dirt and were then dried. A small piece of the distal end of a feather was then removed and encapsulated in silver. The capsule was dropped into Temperature Conversion elemental analyzer interfaced into an isotope-ratio mass spectrometer (C/EA-IRMS). To ensure accuracy and precision, standards were analyzed every tenth sample. Isotope corrections were performed using two established standards (Wassenaar and Hobson, Environmental Canada, CBS and KHS). The ratio of stable hydrogen isotopes (^{2}H/ ^{1}H) in a sample is expressed as the parts per thousand (%) deviation from standard mean ocean water (vSMOW = 0%). This data is returned in a spreadsheet with the deviation in delta notation (δD), calculated as δD = ((Hydrogen Isotope Ratio Sample/ Hydrogen Isotope Ratio Standard) - 1) x 1000 (Clegg et al. 2003; Kelly 2000; Peterson & Fry 1987). This data can then be used to create a GIS model of probable breeding latitude within the species natural range as higher values of δD correspond with heavier isotope composition and lower latitudes.

Interpolating δD

The data needed to estimate geospatial distribution of stable hydrogen isotopes in precipitation is drawn from a continuous data set maintained by the International Atomic Energy Association (IAEA) and World Meteorological Organization (WMO). Together they established the Global Network for Isotopes in Precipitation (GNIP) during the early 1960s, which is a worldwide network of precipitation-monitoring stations that continues to evolve today. The GNIP has gathered water isotope data at a monthly time resolution at almost 400 stations (Figure 14) worldwide and contains stable hydrogen and oxygen isotope measurements from rainwater and snowfall collected at several hundred

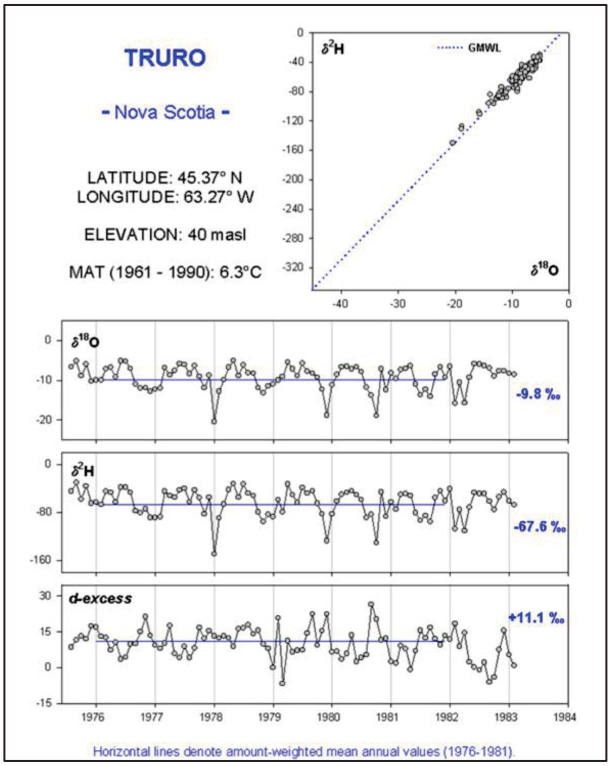
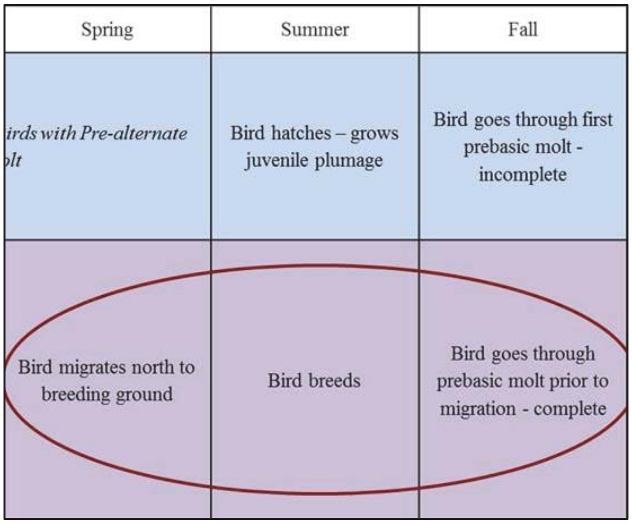


Figure 14: Graphical representations of oxygen and hydrogen isotopes measurements from 1976-1981 in Truro, Nova Scotia © Canadian Network for Isotopes in Precipitation

additional sites (IAEA/WMO, 2015). In the past, complex spatial interpolation schemes needed to be applied to meteorological data from the GNIP data set in order to produce global and regional, annual and monthly average precipitation water isotope maps. But, Bowen & Wilkinson (2002) developed an advanced approach of spatial estimation methods known as detrended interpolation. It provided improvement through the use of additional independent variables to describe predictable variation in isotope ratios. In practice, their method involves fitting parameters of an empirical model to stable isotope data using multiple regression, and applying the model to a global grid to produce first-pass estimates of water isotope compositions. A spatial interpolation method is then applied to the residuals of this model to create a second-pass model correction that accounts for regional isotopic variability not otherwise represented in the model. Bowen & Revenaugh (2003) continued to refine this method by improving the mathematics of the model for the estimation of the stable isotope composition of precipitation and demonstrating that this model reduces the average error of estimates by 10-20% relative to the other models tested.

Bowen provides global and regional grids of average monthly and annual hydrogen and oxygen isotope composition of precipitation in ArcGrid raster format on his website waterisotopes.org (Bowen 2015). Updated versions using the spatial estimation methods described in Bowen & Revenaugh (2003) are available for download. However, with the incorporation of larger data sets, the level of clustering has increased to problematic levels; therefore, the most recent mapping efforts use Kriging, rather than inverse distance interpolation, to better handle clustering (Bowen 2015).



Spring	Summer	Fall
irds with Pre-alternate lt	Bird hatches – grows juvenile plumage	Bird goes through first prebasic molt - incomplete
Bird migrates north to breeding ground	Bird breeds	Bird goes through prebasic molt prior to migration - complete

Figure 15: A portion of the molt cycle of avian species with a pre-alternate molt © Annie Crary, 2014

Hydrogen isotope ratios from precipitation during the growing season (δ^2H) show predictable patterns in local food webs (Hobson & Van Wilgenburg 2015; Hobson et al. 2012; Hobson & Wassenaar 1997) and birds incorporate these ratios into their feathers (Figure 15). In North America, the growing season is typically April through October; so ArcGrid rasters of North America representing each month's mean hydrogen isotope composition were downloaded from waterisotopes.org (Bowen 2015). Those raster files were then averaged using the map algebra function in ArcMap10.2 to create a single GIS model of average expected growing-season δ^2H in precipitation in North America (δ^2H_p).

The GIS model of expected growing-season δ^2H in precipitation (δ^2H_p) (Bowen et al. 2005) needs to be converted into a model of expected feather δD surface that accounts for fractionation of δ^2H (δ^2H_f). The magnolia warbler is a non-ground foraging neotropical migrant as it feeds on insects in tree leaves (Dunn & Hall, 2010; Kaufman, 2001). According to Hobson (2012), this translates to fractionation value of -27.1%. Map algebra was used once more to apply the algorithm, $\delta2H_f = -27.1 + 0.95\ \delta2H_p$, relating the variation in δ^2H in feathers to variation in δ^2H in precipitation (Hobson et al. 2014; Hobson et al. 2012). The final GIS model (δ^2H_f) thus represents geospatial variation in

δ^2H in feathers and can be used in conjunction with δ^2H values from collected samples to predict breeding latitudes similar to the methods seen in Hobson et.al (2007).

Statistical Analysis and GIS

All three sample sets – spring 2014, fall 2014, and museum – had basic descriptive statistics calculated, including mean and standard deviation. Every sample was tested for normality using the Shapiro-Wilkes test in the statistical program R as well. The spring and fall 2014 sample sets were combined to a single sample set, the Field sample, in order to remove annual variation in δ^2H as longer-term means assign birds more precisely (Tonra et al. 2014). The field sample and the museum sample were also broken into subsets; museum males, museum immatures, specimens from 1895-1910, specimens from 1963-1984, field males and field immatures. The subsets also had descriptive statistics calculated and were tested for normality.

Statistical tolerance limits of the δD data from the feather samples were also calculated to delineate probable origins. In contrast to confidence intervals, which express the confidence around the estimation of a parameter, such as the mean, tolerance limits represent the limits within which a specified proportion of the population will fall at an expressed level of confidence (Young 2010). However, the structure of the data and the assumptions made affect the calculations of the tolerance intervals. For example: the structure of the data may be univariate or multivariate, assumed to follow a certain distribution or no distribution at all, or the data may consist of a dependent variable which is to be modeled as a function of one or more independent variables. There are a variety of tolerance intervals for different settings and Young (2010) developed a tolerance package within the R statistical environment which provides estimation and plotting capabilities of different tolerance intervals.

The data were assumed to be either normally distributed or nonparametric. The formulas for estimating lower (L) and upper (U) tolerance limits for normally distributed data are

$$L = \hat{\mu} - k\hat{\sigma} \text{ and } U = \hat{\mu} + k\hat{\sigma}$$

where $\hat{\mu}$ is the mean, $\hat{\sigma}$ is the standard deviation and k is determined so intervals cover a proportion of the population (ρ) with confidence γ. The calculation for k is:

$$k = \sqrt{\frac{(N-1)\left(1+\frac{1}{N}\right) z^2_{(1-\rho)/2}}{\chi^2 \gamma, N-1}}$$

$\chi^2 \gamma, N-1$ is the critical value of the chi-square distribution with degrees of freedom, N – 1, that is exceeded with probability γ, and $z^2_{(1-\rho)/2)}$ is the critical value of the normal distribution that is exceed with probability $(1-\rho)/2$ for the desired confidence level (Young 2010; Hobson et al. 2007). The basic form [100 X (1 – α)%] / [100 X P%] for estimating lower (L) and upper (U) nonparametric tolerance limits is

$$L = \chi_{(r)} \text{ and } U = \chi_{(s)}$$

Computing nonparametric tolerance intervals involved finding the appropriate r and s values. The Wilks method was used for computing r and s, which estimates based on a beta distribution to omit a certain number of observations from either side. In this instance, two-sided tolerance intervals were calculated symmetrically about the center of the observed data. Tolerance limits were computed within the statistical program R to encompass 50%, 75%, and 90% of the population, at a 95% confidence level. This should be interpreted as having 95% confidence that 50%, 75%, and 90% of the population, respectively, come from within the calculated limits.

Tolerance limits were mapped by reclassing the δ^2H_f raster model. Locations on the raster falling within the 50%, 75%, and 90% limits can be selected as potential origins during the reclassification. Cells outside the tolerance limits can be classified as containing no data and cells falling within the calculated tolerance limits are assigned values of 50%, 75%, and 90% accordingly. Potential origins are further limited by using ArcGIS to restrict the expected origins to those areas only falling within the well-established breeding range of each species using a georeferenced species distribution map. The final GIS model for each sample should resemble the model shown in Figure 16, designed by Hobson et al. (2007) using the aforementioned methods. In ArcMap10.2 the reclassified tolerance limits can be converted to a polygon shapefile and separated by attribute so that the tolerance limits for one sample or subset can be overlaid and compared to another. The field sample δ^2H_f raster layer and subsets were converted so that they could be overlaid with the museum sample and subsets. Finally, an anova test was applied to the latitudes and longitudes

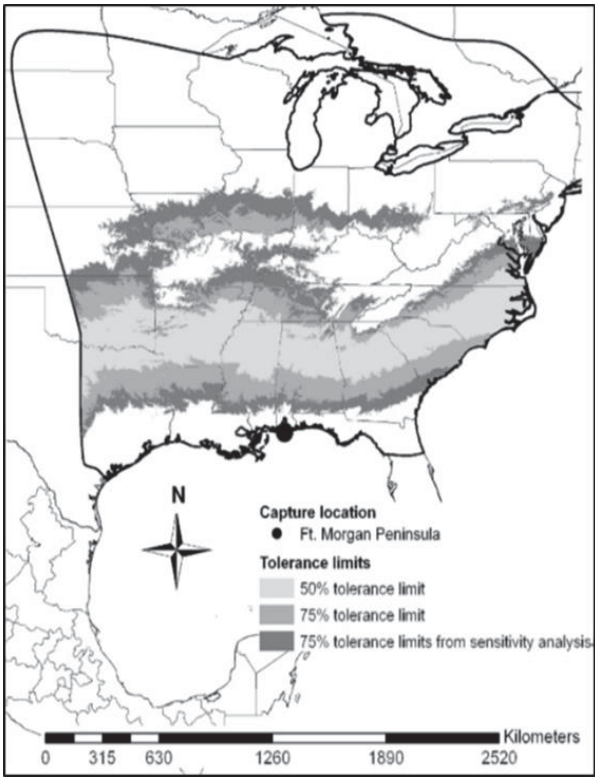


Figure 16: Probable breeding origins of Wood Thrushes migrating through stopover site at Ft. Morgan Peninsula, Alabama, 2000–2002, based on 50% and 75% tolerance limits of the feather δD distribution (Hobson et al. 2007)

occupied by the 50% and 75% tolerance limits in order to detect significant changes between different time periods.

Results

Figure 17 below shows the final GIS model (δ^2H_f) and represents geospatial variation in δ^2H in feathers. This model was restricted using the georeferenced breeding distribution map for the magnolia warbler seen in Figure 18 before being reclassified to display statistical tolerance limits.

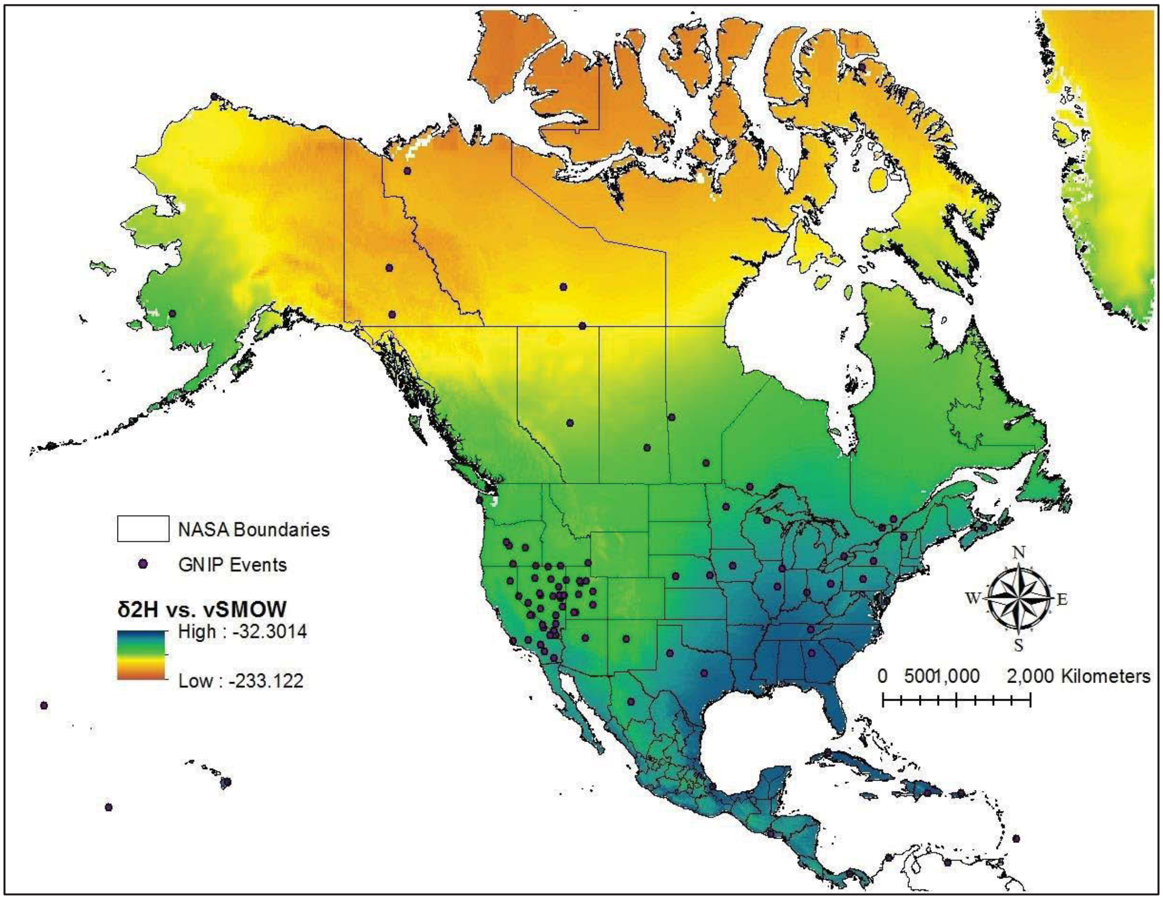


Figure 17: Geospatial variation in δ^2H from feathers vs. deviation from standard mean ocean water (vSMOW) (δ^2H_f)

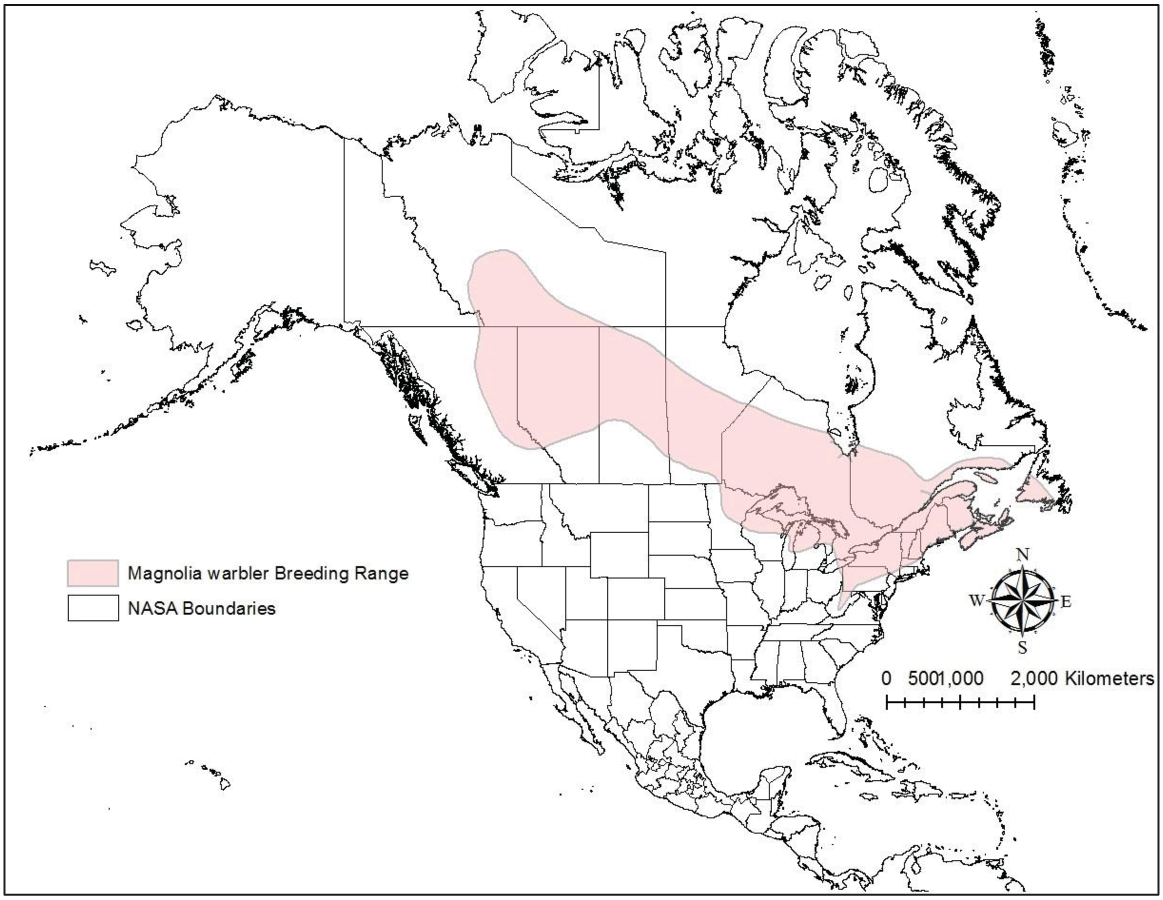


Figure 18: A georeferenced breeding distribution map for the magnolia warbler

Table 1.0 below summarizes the statistics for each sample and subset including count, mean, standard deviation, the Shapiro-Wilkes p-value and the 50%, 75%, and 90% tolerance limits. At first glance, the annual variation discussed by Tonra et al. (2014) is visible between the spring 2014 and fall 2014 which represent the 2013 breeding grounds and 2014 grounds respectively supporting the decision to combine them into a field sample that demonstrates longer-term means so birds can be assigned to probable origins more precisely. The Shapiro-Wilkes p-values demonstrate that the fall 2014 sample was the only normally distributed sample, everything else is considered nonparametric. The mean for the 1895-1910 sample is significantly lower than the mean for the combination sample as well. Finally, the total number of museum specimens is reduced by one (n=87) due to analysis error. The δ^2H_f raster model, shown in Figure 16 was reclassified for each sample set listed in Table 1 to create a geospatial representation of each sample's tolerances limits (Figures 19-28).

Table 1: Statistical Analysis of the δ^2H samples and subsets

Sample	N	Mean	Standard Deviation	Shapiro-Wilkes p-value	Tolerance Interval				Figure Number
Spring 2014	100	-98.23	18.56	1.70E-05	90%	-127.32	to	-44.85	19
					75%	-118.87	to	-64.04	
					50%	-111.91	to	-86.67	
Fall 2014	100	-108.60	12.78	0.351	90%	-132.55	to	-84.65	20
					75%	-125.35	to	-91.85	
					50%	-118.42	to	-98.78	
Field Sample	200	-103.42	16.72	7.02E-08	90%	-128.96	to	-60.04	21
					75%	-121.70	to	-81.82	
					50%	-115.95	to	-94.01	
Field Males	105	-102.48	18.89	2.90E-05	90%	-129.33	to	-55.58	22
					75%	-123.14	to	-67.85	
					50%	-117.24	to	-92.48	
Field Immatures	93	-104.09	17.62	3.00E-06	90%	-130.63	to	-44.85	23
					75%	-124.30	to	-74.13	
					50%	-117.73	to	-95.71	
Museum	87	-94.47	19.63	1.21E-03	90%	-145.99	to	-59.77	24
					75%	-115.25	to	-65.47	
					50%	-109.16	to	-73.09	
1895 - 1910	29	-85.31	22.36	6.78E-03	90%	-156.69	to	-58.54	25
					75%	-121.66	to	-59.77	
					50%	-105.33	to	-65.47	
1963 - 1984	57	-99.33	16.49	1.06E-03	90%	-145.99	to	-60.73	26
					75%	-117.35	to	-68.01	
					50%	-111.30	to	-82.35	
Museum Males	56	-91.40	21.29	0.01033	90%	-156.69	to	-58.54	27
					75%	-117.62	to	-62.50	
					50%	-111.04	to	-69.20	
Museum Immatures	41	-97.89	17.17	0.03331	90%	-145.99	to	-60.73	28
					75%	-117.62	to	-67.21	
					50%	-112.24	to	-78.90	

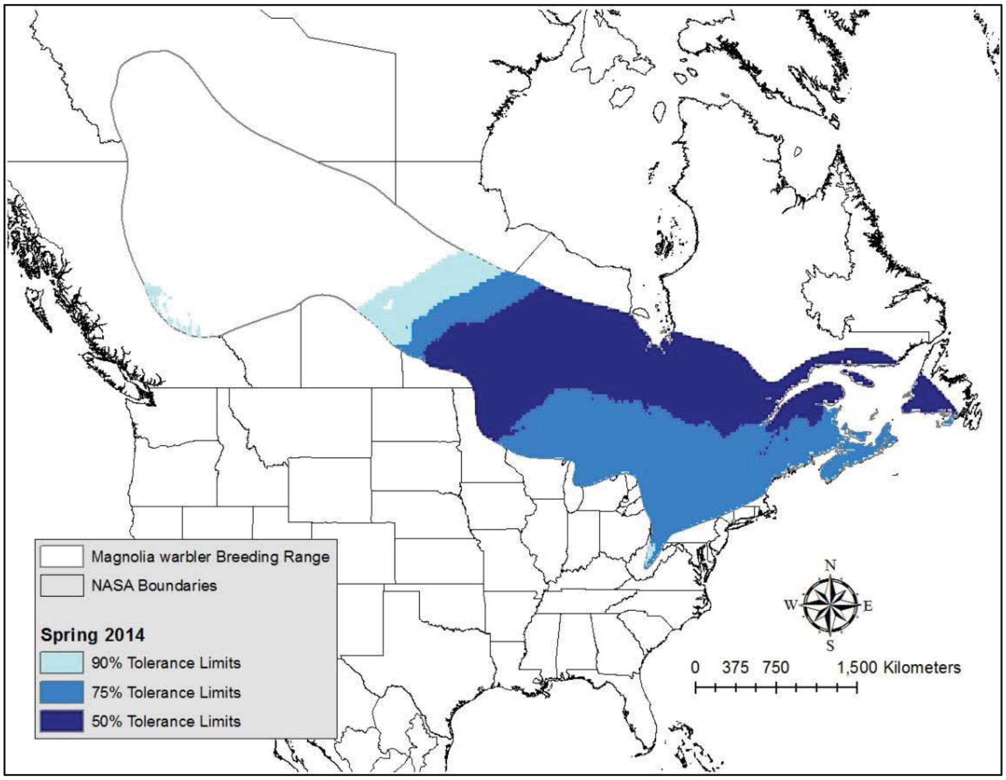


Figure 19: Probable breeding origins for the 2013 breeding season based on 50%, 75%, and 90% tolerance limits of the spring 2014 sample

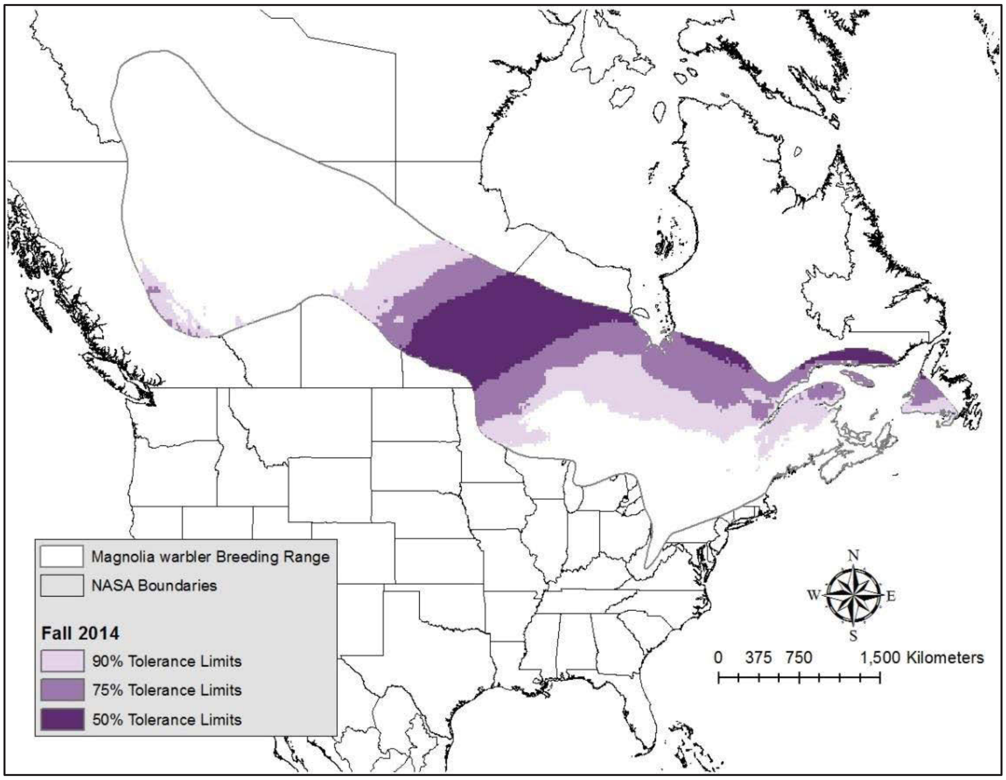


Figure 20: Probable breeding origins for the 2014 breeding season based on 50%, 75%, and 90% tolerance limits of the fall 2014 sample

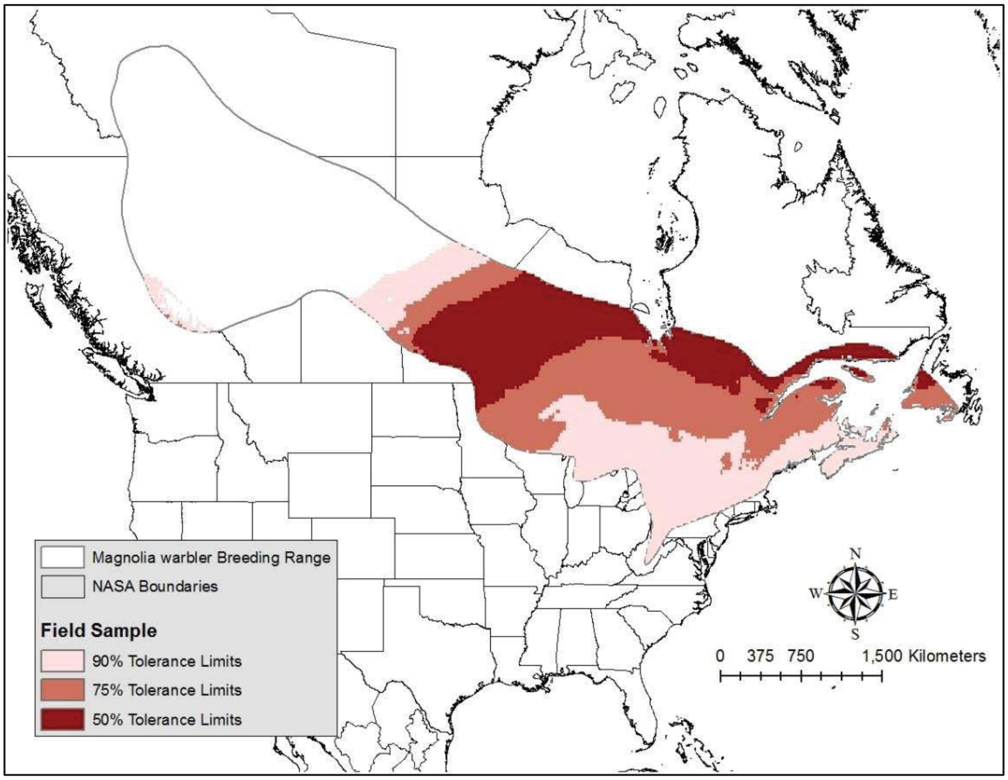


Figure 21: A representation of the current breeding latitudes based on 50%, 75%, and 90% tolerance limits of the combined 2013-2014 breeding season data

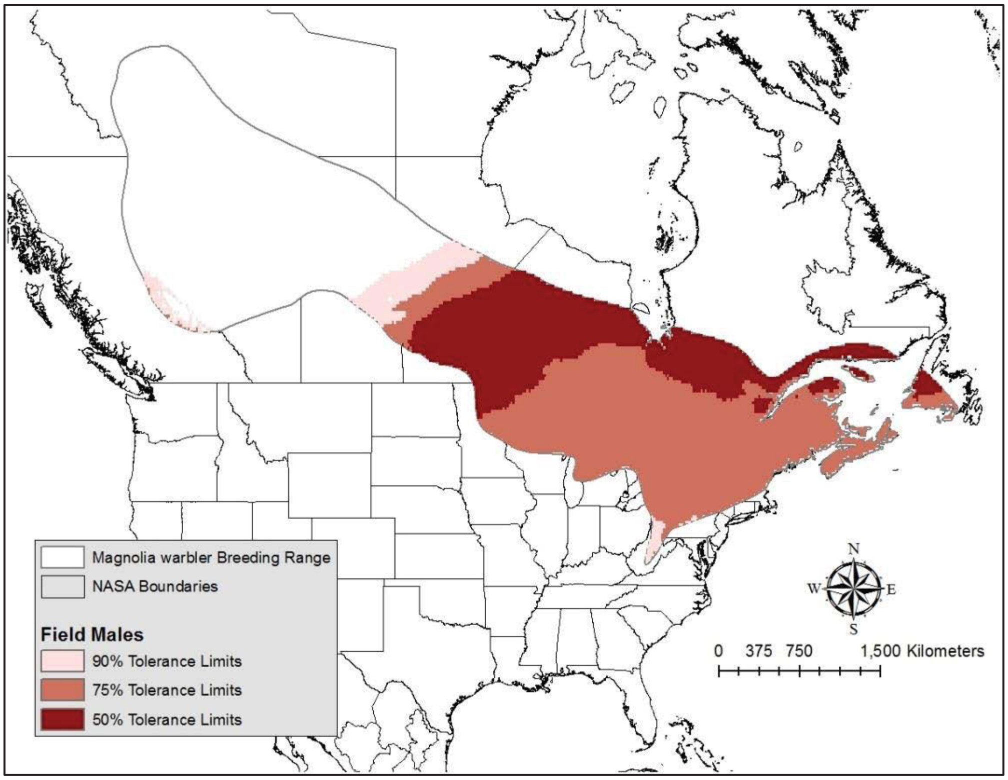


Figure 22: A representation of the current breeding latitudes for males based on 50%, 75%, and 90% tolerance limits of the combined 2013-2014 breeding season data

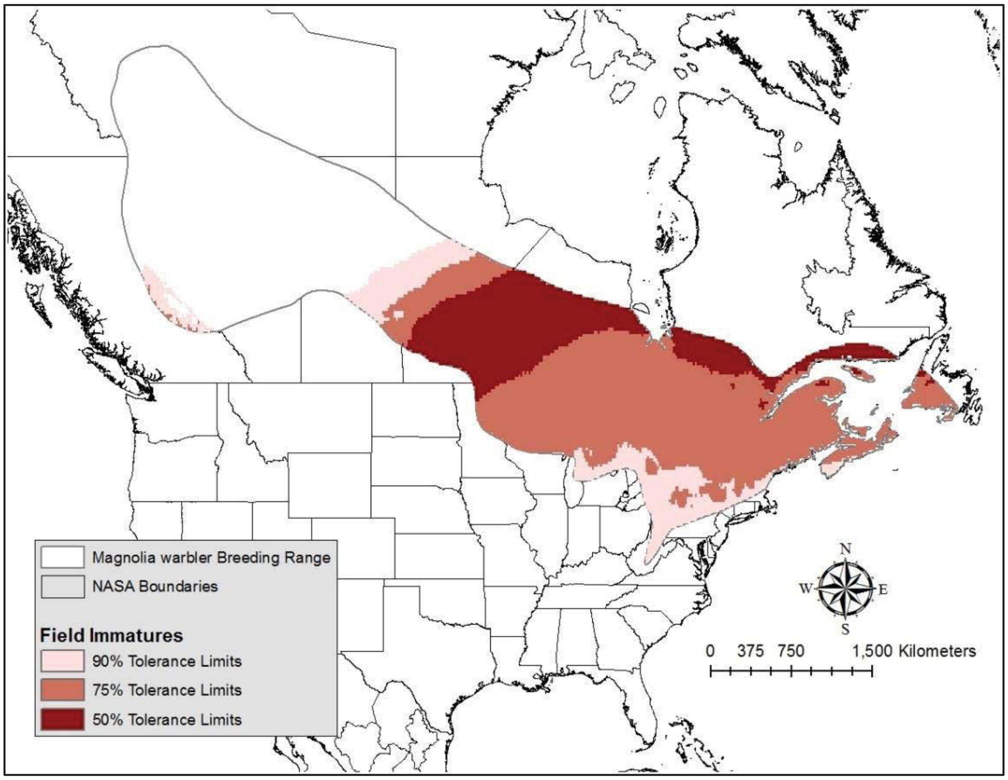


Figure 23: A representation of the current breeding latitudes for immatures based on 50%, 75%, and 90% tolerance limits of the combined 2013-2014 breeding season data

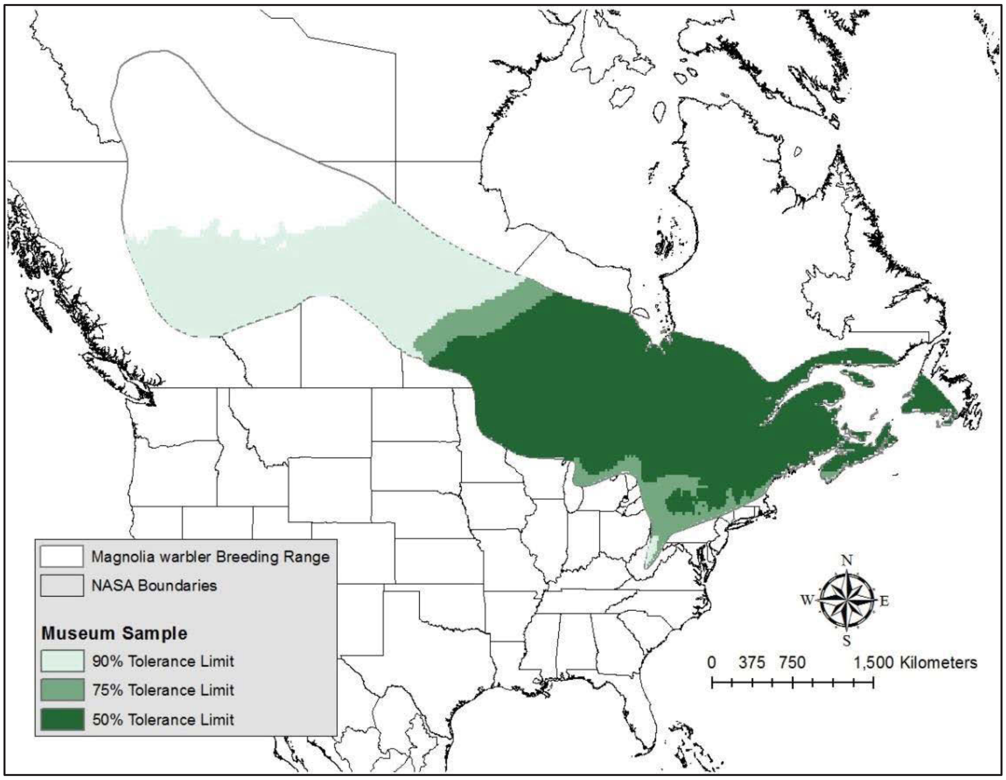


Figure 24: A representation of the average breeding latitudes from 1895-1984 based on 50%, 75%, and 90% tolerance limits of the museum specimens

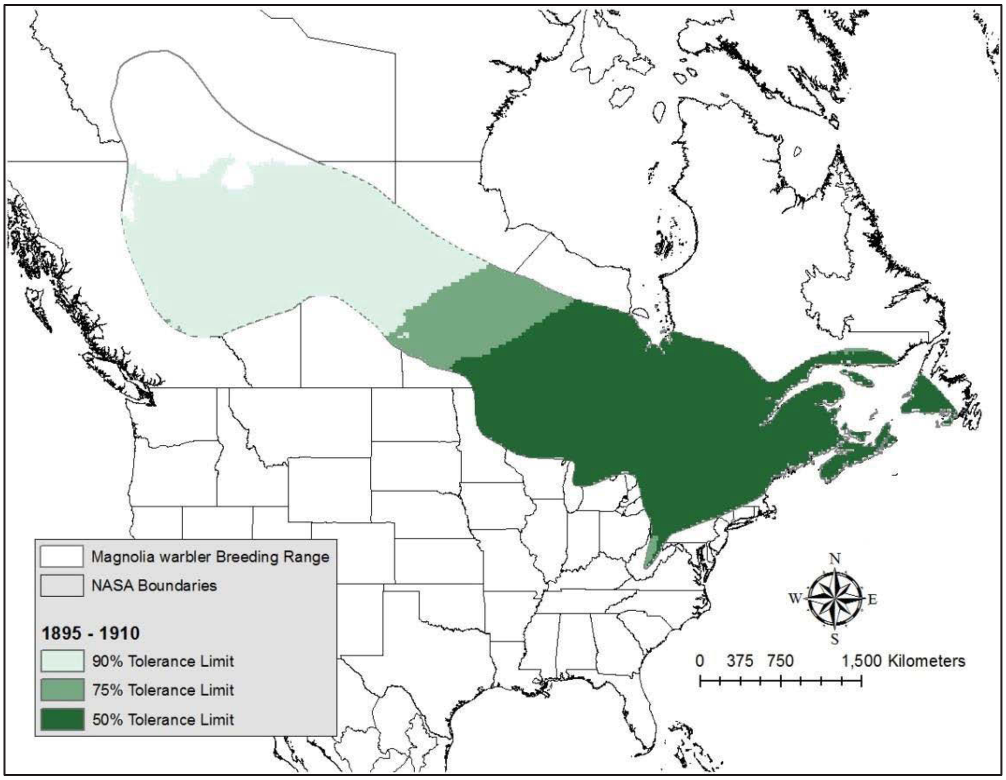


Figure 25: A representation of the average breeding latitudes from 1895-1910 based on 50%, 75%, and 90% tolerance limits of the museum specimens

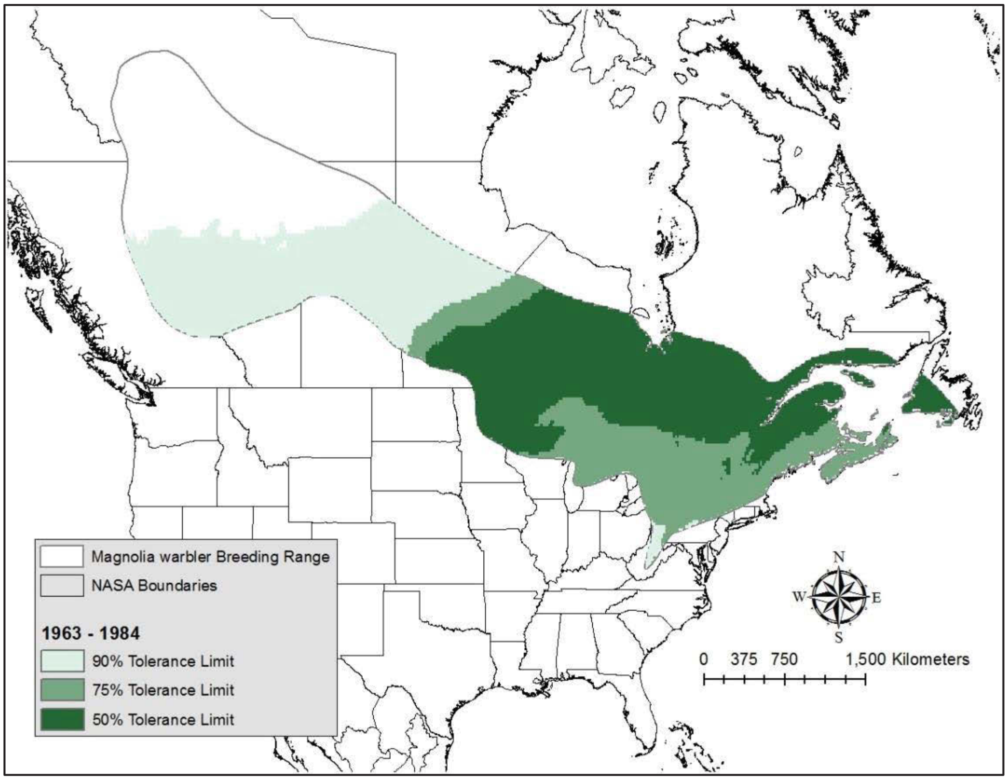


Figure 26: A representation of the average breeding latitudes from 1963-1984 based on 50%, 75%, and 90% tolerance limits of the museum specimens

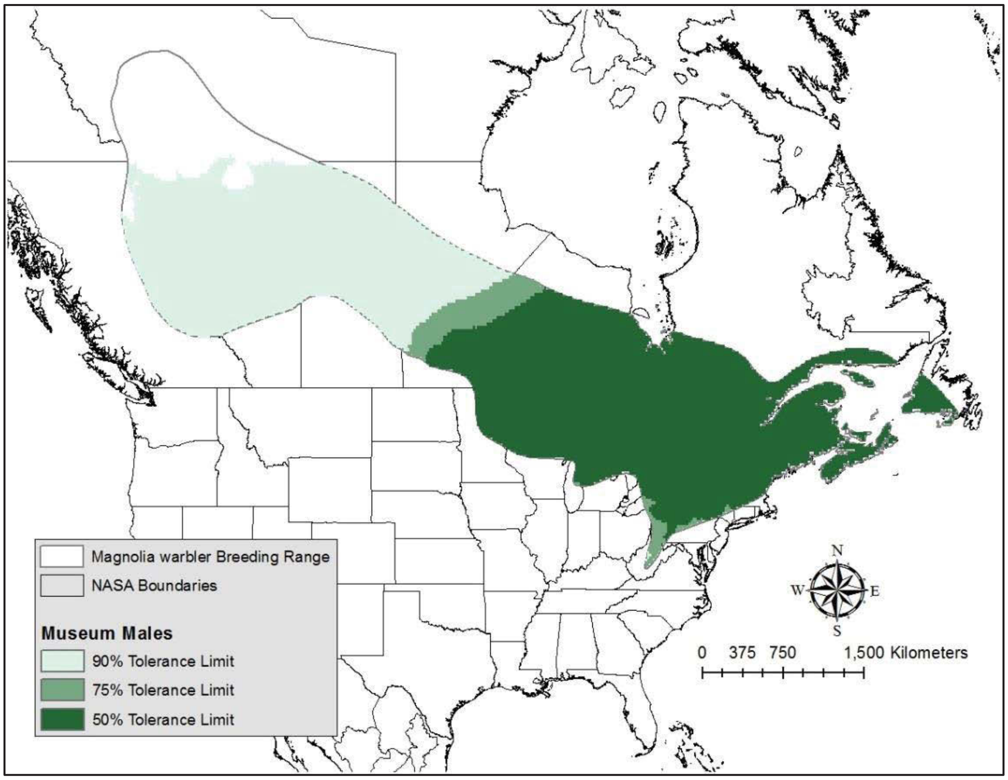


Figure 27: A representation of the average breeding latitudes of males from 1895-1984 based on 50%, 75%, and 90% tolerance limits of the museum specimens

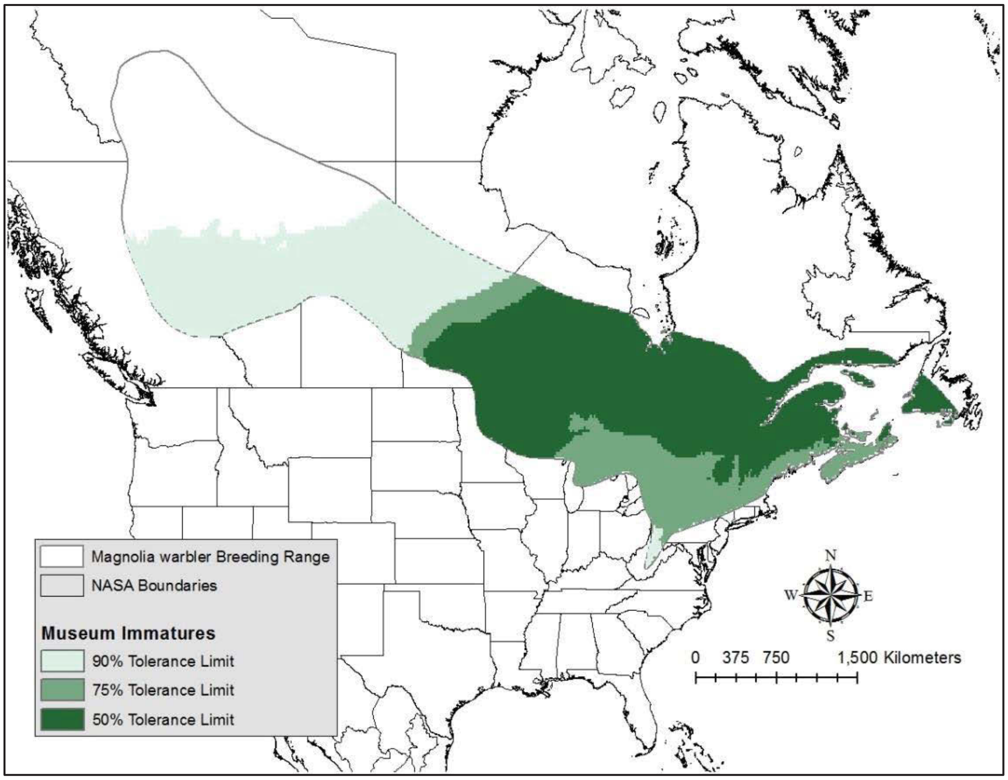


Figure 28: A representation of the average breeding latitudes of immatures from 1895-1984 based on 50%, 75%, and 90% tolerance limits of the museum specimens

Figure 29 shows a comparison of the geospatial tolerance limits of the spring 2014 sample to the geospatial tolerance limits of the fall 2014 sample which represent the 2013 breeding grounds and 2014 grounds respectively. The fall 2014 sample has tighter tolerance limits than the spring 2014 sample and is shifted farther north within the breeding range as well. The lower limit of 90% for the fall 2014 sample is nearly aligned with the lower limit of 50% for the spring 2014 sample. An anova test demonstrates that there is a statistical difference between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the 2013 breeding season and the 2014 breeding season (Table 2). The F ratio is greater than the F-critical value and the p-values are all less than 0.05 meaning the variation between the two time periods is significant. Part of this variation could be a result of statistical distribution, as the spring 2014 is nonparametric and the fall 2014 sample is normally distributed. The variation is also likely a result of annual variation in this system as a result of food web or individual level processes discussed by Tonra et al. (2014). These samples were combined into the field sample to remove the significant annual variation so that birds could be assigned to probable origins more precisely. The recalculated tolerance limits can be seen in Figure 21.

Table 2: Partial anova results of a comparison between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the 2013 breeding season and the 2014 breeding season

	Latitude			**Longitude**		
	F Ratio	*F Crit*	*P=value*	*F Ratio*	*F Crit*	*P-value*
50% Tolerance Limit	16.61	3.95	0.0001	13.35	3.86	0.0003
75% Tolerance Limit	48.36	3.91	0.00	8.70	3.86	0.0033

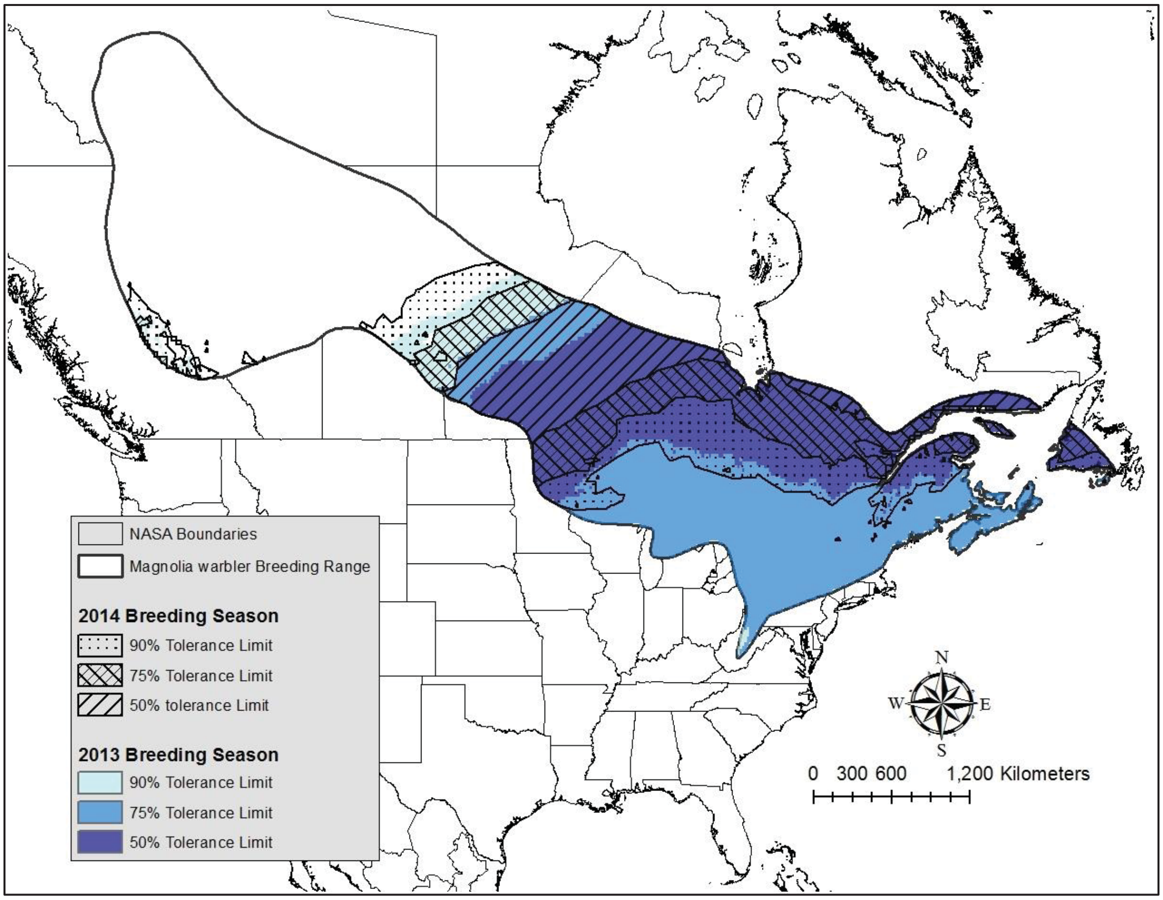


Figure 29: A visual comparison of the 50%, 75%, and 90% tolerance limits for the 2013 breeding season (Spring 2014) and the 2014 breeding season (Fall 2014)

Figure 30 is the comparison of the field sample to the oldest (1895-1910) museum specimens. Differences in probable origin within the breeding range between the 1895-1910 sample and the field sample were observed. The 50% geospatial tolerance limit for the 1895-1910 sample extends throughout the southernmost portions of the breeding range. In addition, the upper limit of 50% for the 1895-1910 sample only aligns with the lower portion of 50% for the field sample. An estimate of the distance between the upper limit of 50% for 1895-1910 and the upper limit of 50% for the field sample using the ArcMap measure tool indicates there is about 400-550 kilometers between the two. However, the upper portion of 90% for the 1895-1910 sample reaches much farther north within the breeding range than the upper portion of 90% for the field sample. The wider tolerance intervals may be a result of sample size. At 29, the 1895-1910 is the smallest sample size and at 200, the field sample is the largest. Notably, both had nonparametric distributions. The anova test shows that there is a statistical difference between the areas occupied at the 50% tolerance limit for the 1895-1910 sample and the field sample (Table 3). The F ratio is greater than the F-critical value and the p-values are less than 0.05 meaning the variation at the 50% tolerance limit between the two time periods is significant. However, while the change in longitude at the 75% tolerance limit is significant, the change in latitude is not. At the 75% tolerance limit, the p-value for latitude is greater than 0.05 meaning there is not a significant shift north. Nevertheless, the shifts between the 50% tolerance limits are significant, indicating there are differences in the area of occupancy between the two time periods.

Table 3: Partial anova results of a comparison between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the field sample and the 1895-1910 sample

	Latitude			**Longitude**		
	F Ratio	*F Crit*	*P-value*	*F Ratio*	*F Crit*	*P-value*
50% Tolerance Limit	53.12	3.91	0.00	7.43	3.86	0.0066
75% Tolerance Limit	0.69	3.93	0.4085	47.00	3.87	0.00

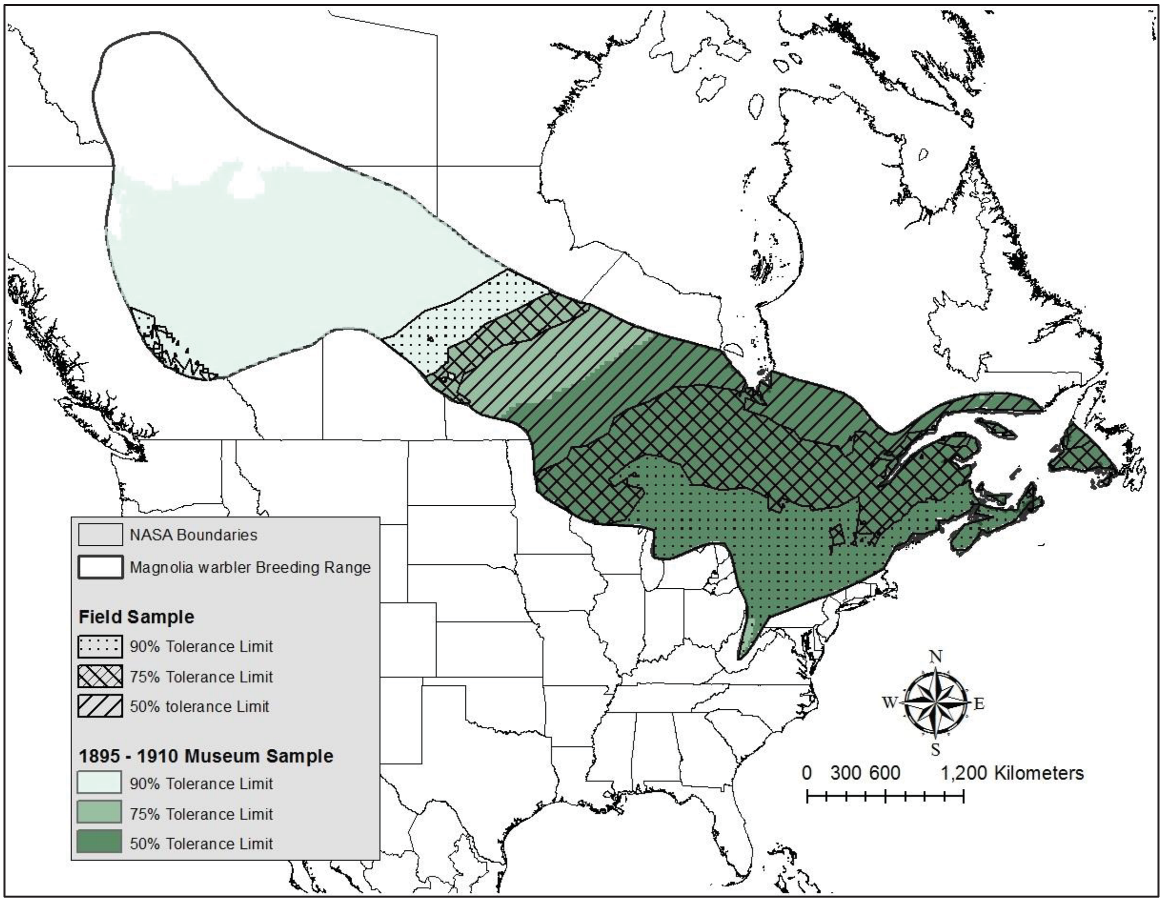


Figure 30: A visual comparison of the 50%, 75%, and 90% tolerance limits for the current breeding latitudes (field sample) and the average breeding latitudes from 1895-1910

Figure 31 is the comparison of the field sample to the 1963-1984 museum specimens. The changes in probable origins within the breeding range between the 1963-1984 sample and the field sample are significantly less. The distance between the upper limit of 50% for 1963-1984 is only about 250 kilometers away from the upper limit of 50% for the field sample. The lower limit of the 50% geospatial tolerance limit for the 1963-1984 aligns with the lower limit of 75% for the field sample. In addition, the upper limit of 50% for the field sample is only slightly north of the upper limit of 50% for the 1963-1984 sample and closely aligns with the upper limit of 75% for the 1963-1984 sample. Again, the upper portion of 90% for the 1963-1984 sample reaches much farther north within the breeding range than the upper portion of 90% for the field sample, but the sample size was 200 and 57 for the field sample and the 1963-1984 sample respectively, resulting in tighter tolerance limits for the field sample. Both of these samples were also nonparametric. An anova test reveals that the differences in latitude are significant but the differences in longitude are not (Table 4). The latitudes within the 50% tolerance limit and the 75% tolerance limit have p-values that are less than 0.05 and F ratios that are greater than the F critical value indicating there is a statistical difference between the field sample and the 1963-1984 sample. The p-values for the longitudes within the 50% tolerance limit and the 75% tolerance limit are both greater than 0.05 though. There is not a significant difference in longitude between the field sample and the 1963-1984 sample. The anova results indicate that the apparent shifts are weaker, as only the change in latitude is statistically significant.

Table 4: Partial anova results of a comparison between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the field sample and the 1963-1984 sample

	Latitude			**Longitude**		
	F Ratio	*F Crit*	*P-value*	*F Ratio*	*F Crit*	*P-value*
50% Tolerance Limit	14.10	3.93	0.0003	3.21	3.86	0.0739
75% Tolerance Limit	17.79	3.90	0.00	0.02	3.86	0.8826

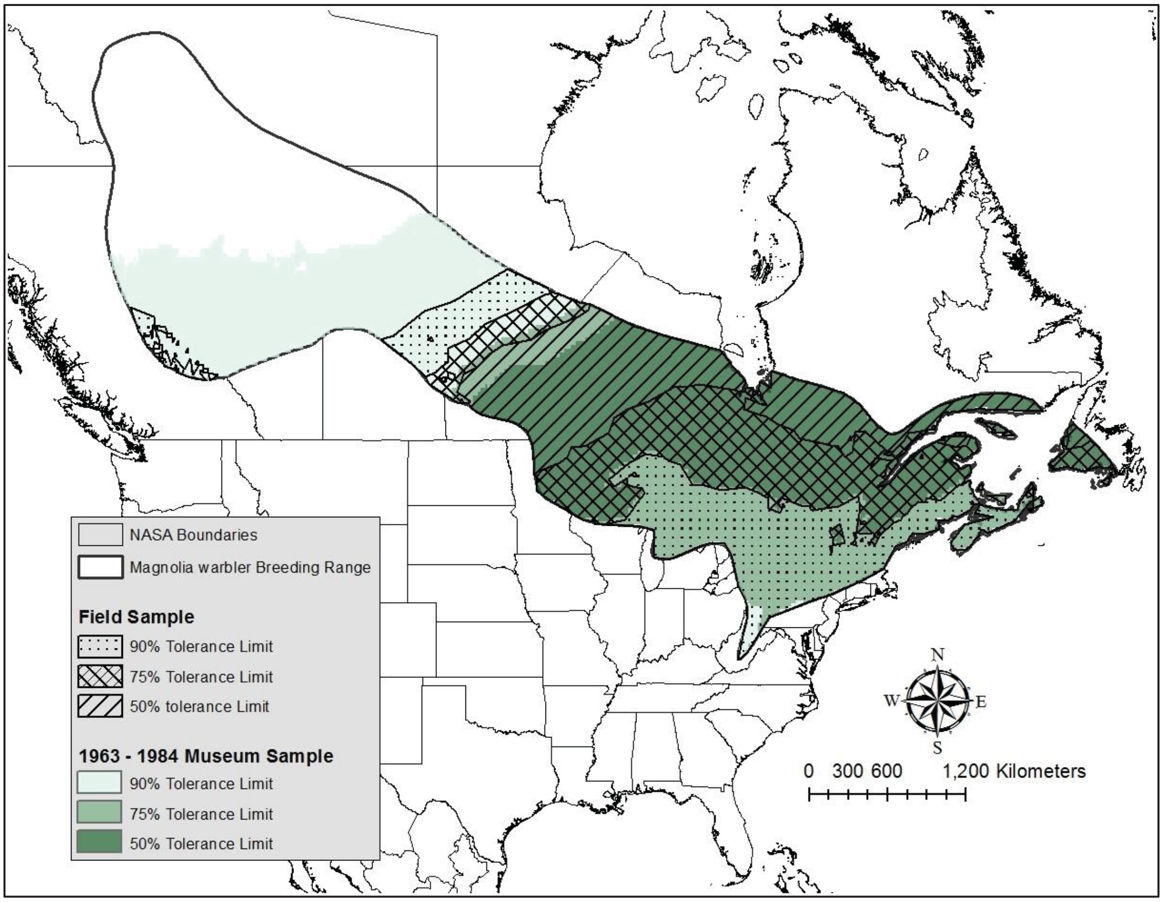


Figure 31: A visual comparison of the 50%, 75%, and 90% tolerance limits for the current breeding latitudes (field sample) and the average breeding latitudes from 1963-1984

Figure 32 compares the males in the field sample to the males in the museum sample (1895-1984). Similar to Figure 31, the upper limit of 50% for the field males is only slightly north of the upper limit of 50% for the museum males and closely aligns with the upper limit of 75% for the museum males. However, the 50% geospatial tolerance limit for the museum males extends throughout the southernmost portions of the breeding range and the lower limit closely aligns with the lower limit of 75% for the field males. Again, both the field males and the museum males had nonparametric distributions and sample sizes of 200 and 56 respectively. The anova test indicates that the differences in latitude are significant but the differences in longitude within the 50%

tolerance limit are not (Table 5). The latitudes within the 50% tolerance limit and the 75% tolerance limit both have p-values that are less than 0.05 and F ratios that are greater than the F critical value indicating there is a statistical difference in latitude between the field males and the museum males. However, while the p-value for the longitudes within the 50% tolerance limit is greater than 0.05, the p-value for the longitudes within the 75% tolerance limit are less than 0.05. In other words, the difference in longitudes at the 50% tolerance limit between the field males and museum males is not statistically significant but the differences in longitudes at the 75% tolerance limits are significant. The shift at the 50% tolerance limit between field male and museum males is thus weaker than the shifts at the 75% tolerance limit.

Table 5: Partial anova results of a comparison between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the field males and the museum males

	Latitude			**Longitude**		
	F Ratio	*F Crit*	*P-value*	*F Ratio*	*F Crit*	*P-value*
50% Tolerance Limit	34.38	3.91	0.00	2.87	3.86	0.0907
75% Tolerance Limit	1.09	3.90	0.30	41.62	3.86	0.00

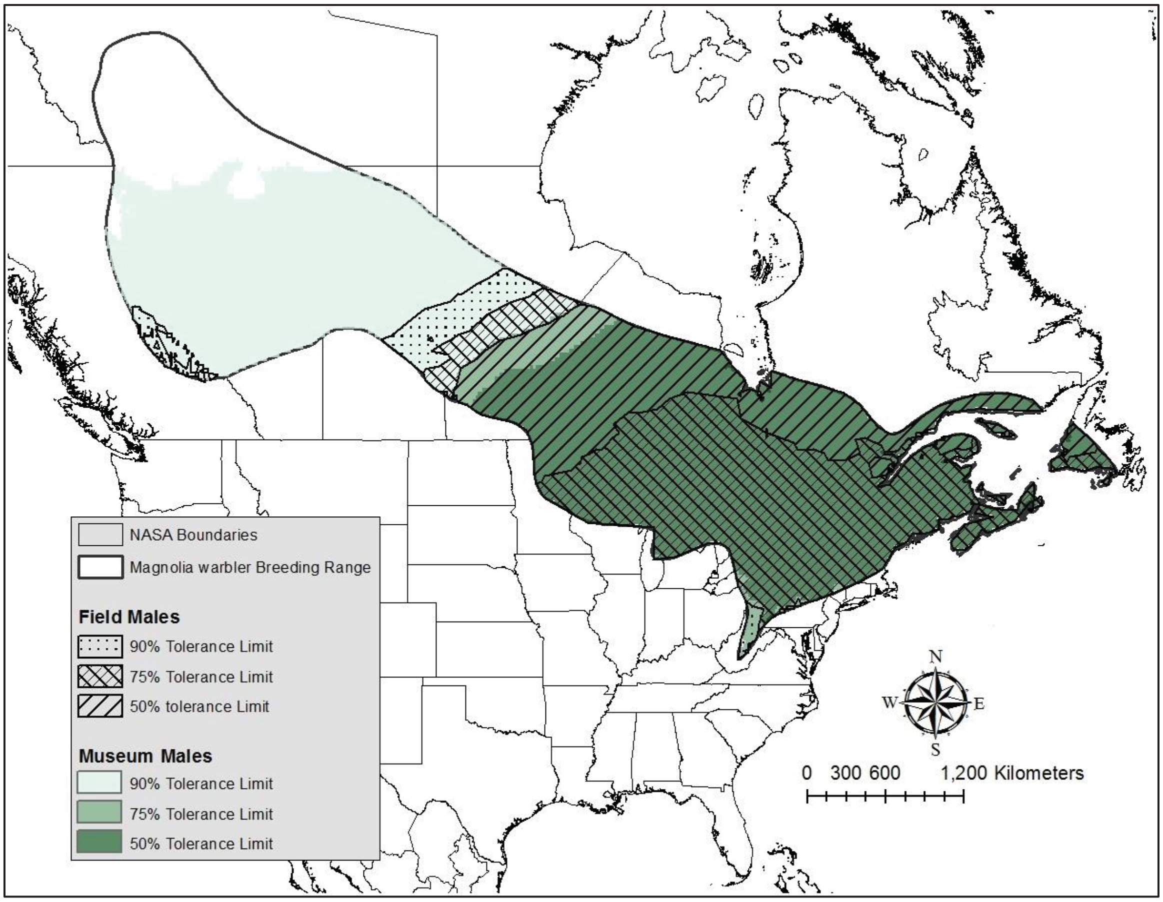


Figure 32: A visual comparison of the 50%, 75%, and 90% tolerance limits for the current breeding latitudes of males (field males) and the average breeding latitudes of males from 1895-1984 (museum males)

Figure 33 compares the immature individuals in field sample to the immature individuals in the museum sample (1895-1984). Similar to Figure 31 and 32, the upper limit of 50% for the field immature is only slightly north of the upper limit of 50% for the museum immature and almost perfectly aligns with the upper limit of 75% for the museum immature. However, the 50% geospatial tolerance limit for the museum immature extends past the lower limit of 50% for the field immature but does not quite reach the lower limit of 75% for the field immature. Both the field immature and the museum immature had nonparametric distributions and sample sizes of 200 and 41 respectively. The anova test demonstrates that the differences in latitude are significant but the differences in longitude within the 75% tolerance limit are not. The latitudes within the 50% tolerance limit and the 75% tolerance limit both have p-values that are less than 0.05 and F ratios that are greater than the F critical value indicating there is a statistical difference in latitude between the field immature and the museum immature. However, while the p-value for the longitudes within the 50% tolerance limit is less than 0.05, the p-value for the longitudes within the 75% tolerance limit are greater than 0.05. In other words, the difference in longitudes at the 50% tolerance limit between the field immature and the museum immature are statistically significant but the differences in longitudes at the 75% tolerance limits are not. The shift at the 50% tolerance limit between the field immature and the museum immature is thus stronger than the shifts at the 75% tolerance limit. There were not enough individual females and adults within the museum sample to successfully calculate tolerance limits so they were not compared to the field sample.

Table 6: Partial anova results of a comparison between the areas occupied at the 50% tolerance limit and the 75% tolerance limit for the field immature and the museum immature

	Latitude			**Longitude**		
	F Ratio	*F Crit*	*P-value*	*F Ratio*	*F Crit*	*P-value*
50% Tolerance Limit	20.41	3.93	0.00	4.51	3.86	0.0342
75% Tolerance Limit	8.19	3.90	0.00	0.27	3.86	0.604

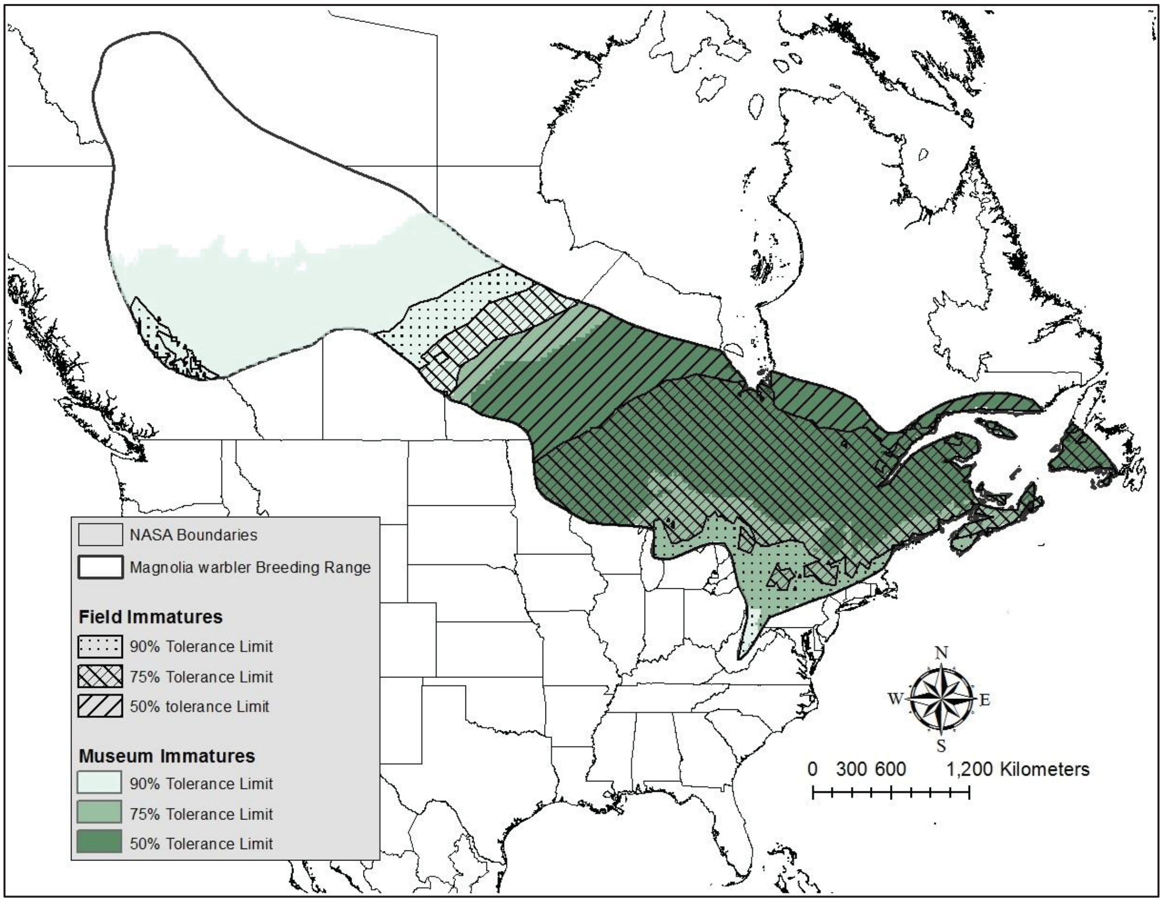


Figure 33: A visual comparison of the 50%, 75%, and 90% tolerance limits for the current breeding latitudes of immature (field immature) and the average breeding latitudes of immature from 1895-1984 (museum immature)

Discussion

Overall, probable breeding zones were successfully calculated using tolerance limits for several data sets encompassing the past 120 years. The probable breeding zones discerned from δ^2H values in the magnolia warbler feathers indicate that the species is breeding within the expected range as well. This supports conclusions from similar studies (Boone et al. 2010; Bowen et al. 2005; Clegg et al. 2003; Chamberlain et al. 1997; Cormie et al. 1994) and continues to validate the use of δ^2H as a tool for tracking probable breeding latitudes.

However, it is important to remember the assumptions made when using isotopes to assign birds to specific breeding and molting locations. The Global Network of Isotopes in Precipitation (GNIP) database (IAEA/WMO 2015) is assumed to correctly model δ^2H, but a lack of sampling locations in specific geographic regions (e.g. coastal regions), may skew the overall model (Hache et al. 2012; Hobson 2008; Wunder et al. 2005). The use of δ^2H does not account for differential timing in feather growth either. It assumes there is no difference in δ^2H for individuals in the same part of the breeding range and all individuals of a species show the same isotoptic signature if they grew their feathers in the same region. It does not account for differences that might occur between adults and juveniles or males and females (Hache et al. 2012).

Other factors to consider include feather availability and error in feather origin. Feather availability can be extremely limiting, making it difficult to include one hundred (n=100) birds, with sub categories at twenty-five (n=25) young males, twenty-five (n=25) young females, twenty-five (n=25) adult males, and twenty-five (n=25) adult females, sampled evenly across the migration season. For example, during spring migration in 2014, only 203 magnolia warblers came through the Powdermill Avian Research Center and only 110 had feathers pulled. In comparison, the fall 2014 migration season saw 331 magnolia warblers and 300 had feathers pulled. Sampling should be done regularly and consistently in order to ensure enough feathers are collected for stable-isotope analyses. There could be error that stems from the assumption that all the feathers collected were truly grown on the breeding ground as well. There is a possibility that individuals undergo an advantageous molt if they damage or lose feathers in an accident or predator attack. If an individual undergoes an advantageous molt, then the isotopic signature within the feather will correlate with the location of the advantageous molt instead of the breeding ground. While prebasic feathers can be collected during both spring and fall migration, it is recommended sampling is restricted to fall migration. It is much less likely that bids will undergo an advantageous molt after leaving the breeding grounds as they migrate south, reducing the possibility for error.

Nevertheless, a statistical comparison of the museum feathers to current field feathers suggests that the area of occupancy has significantly shifted through time. An anova test was applied to the latitudes and longitudes occupied by the 50% and 75% tolerance intervals in order to detect significant changes between different time periods. A significant difference in both latitude and longitude indicates a stronger shift between time periods as the area of extent for the magnolia warbler moves northwest through Canada. The anova comparison of the 50% tolerance interval for the 1895-1910 sample and the field sample indicated that there was a significant difference in both latitude and longitude. Therefore the change between the two time periods at the 50% tolerance interval is stronger. Yet the anova of the 75% tolerance interval demonstrated the difference in longitude was significant and the change in latitude was not, suggesting the change between the two time periods at the 75% tolerance interval is weaker. The anova comparison of the 50% tolerance interval for the 1963-1984 sample and the field sample revealed that there was a significant difference in latitude but not in longitude. The anova of the 75% tolerance limit also indicated the difference in latitude was significant and the difference in longitude was not. Therefore the change between these two time periods at both the 50% and 75% tolerance interval is weaker.

The anova comparison of the 50% tolerance interval for the 1895-1984 museum males and the field males indicated that there was a significant difference in latitude but not in longitude. Therefore the change between the two time periods at the 50% tolerance interval is weaker. In addition, the anova of the 75% tolerance interval demonstrated the difference in longitude was significant and the difference in latitude was not, suggesting the change between the two time periods at the 75% tolerance interval is also weaker. The anova comparison of the 50% tolerance interval for the 1895-1984 museum immature and the field immature indicated that there was a significant difference in both latitude and longitude. Therefore the change between the two time periods at the 50% tolerance interval is stronger. Meanwhile, the anova of the 75% tolerance interval revealed the difference in latitude was significant and the difference in longitude was not, suggesting the change between the two time periods at the 75% tolerance interval is weaker. However, the anova tests applied to sub-categories have lower confidence in the comparisons as the museum specimens occur between a larger time period, 1895-1984, due to sample size constraints. Overall, these results suggest that the greatest change has occurred over the longest period of time though.

The reasons for change seen at the northern and southern boundaries may vary or be the result of multiple factors working in combination. Over the years, southeast Canada and New England in the United States have experienced dramatic changes in land use which has degraded and fragmented breeding habitat (Rustad et al. 2012). Between urbanization and land conversion for agriculture, the magnolia warbler may be experiencing varying levels of habitat loss along its southern breeding boundary. However, some of the changes seen along the northern boundaries of probable origin more likely reflect northern colonization in response to climate warming. Climate change is projected to be strongest in the high latitudes of Siberia and North America. In contrast, human land-use change dominates lower latitudes (Jetz et al. 2007). It is difficult to conclude the exact cause of range change taking all of these factors into consideration. Nevertheless, this unique approach to assessing species response to human induced stressors, such as climate change and habitat loss, has shown varying degrees of change in the area of occupancy within the extent of the breeding range over time.

Generally, this novel approach of assessing species range response to climate change and habitat loss over time is considered successful. The effective comparison of preserved museum specimens to current breeding birds provided useful information that could allow wildlife managers to adapt management strategies in response to species movements. The largest potential loss of range size occurs among specialist species that have restricted ranges, low colonization ability and poor dispersal (Jetz et al. 2007; Travis 2002). Analysis of temporal movement in specialist species could be utilized to assess extinction risk. Generalist species with relatively wide ranges are perhaps more resilient to the effects of anthropogenic activities (Travis 2002), but it would still be useful to understand their range change over time so habitats could be conserved for future use.

Birds perform many ecosystem services that benefit the human race, including their roles as predators, pollinators, scavengers, seed dispersers and ecosystem engineers (Whelan et al. 2008; Clout & Hay 1989). Projections indicate that by 2100, 6–14% of all bird species will be extinct, and 7–25% will be functionally extinct (Sekercioglu, Daily & Erhlich 2004). Many of the important avian ecosystem processes, particularly decomposition, pollination, seed dispersal and forest regeneration will likely decline as a result, increasing the cost of sustaining these services. It is important to utilize new methods in order to create conservation plans that mitigate species extinctions, preserve avian ecosystem services and maintain a balance in nature.

This quantitative analysis of δ^2H in preserved specimens compared to δ^2H in current breeding birds will contribute to an understanding of temporal change in the area of occupancy. Without the unique integration of preserved museum specimens, it would not have been possible to statistically conclude that the current area of occupancy has changed. Moreover, older feathers can be used to project a rate of change into the future. This new methodology has the potential to help predict which threatened or endangered species might be suffering from extensive range change due to anthropogenic impacts. Specialized conservation plans could go a long way to mitigating the number of species threatened with extinction. This method should continue to be refined and applied to other neotropical avian migrants, both threatened and endangered, so future strategic conservation can be constructed around known temporal range change.

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Appendix

Table 7: Feathers collected during spring migration in 2014 representing the 2013 breeding season

Sample Number	Band Prefix	ID Number	Sex	Age	Date Captured	Weight (mg)	H2 Amp	%H	δ2H vs. VSMOW
1	268050	059T	F	ASY		0.460	2774	5.52	-109.60
2	268050	238T	F	ASY		0.410	2472	5.53	-95.11
3	268050	301T	F	ASY		0.362	2135	5.47	-107.67
4	268050	313T	F	ASY		0.428	2567	5.41	-59.60
5	268050	316T	F	ASY		0.498	3010	5.47	-119.25
6	268050	359T	F	ASY		0.392	2520	5.77	-127.32
7	268050	389T	F	ASY		0.393	2478	5.74	-96.33
8	268050	392T	F	ASY		0.376	2212	5.48	-78.99
9	268050	400T	F	ASY		0.441	2655	5.49	-94.54
10	268050	429T	F	ASY		0.469	2966	5.68	-102.26
11	268050	441T	F	ASY		0.368	2210	5.58	-104.79
12	268050	444T	F	ASY		0.299	1785	5.51	-110.26
13	268050	445T	F	ASY		0.317	1987	5.76	-97.93
14	268050	446T	F	ASY		0.342	2101	5.72	-128.96
15	268050	465T	F	ASY		0.376	2211	5.40	-94.04
16	268050	469T	F	ASY		0.374	2265	5.56	-107.61
17	268050	477T	F	ASY		0.454	2676	5.39	-103.75
18	268050	478T	F	ASY		0.328	1968	5.53	-108.02
19	268050	504T	F	ASY		0.362	2222	5.44	-108.02
20	268050	508T	F	ASY		0.395	2907	5.71	-93.22
21	268050	512T	F	ASY		0.371	2561	5.42	-77.16
22	268050	513T	F	ASY		0.311	2220	5.60	-101.42
23	268050	523T	F	ASY		0.383	2591	5.18	-116.57
24	268050	528T	F	ASY		0.395	2813	5.52	-107.83
25	268050	601T	F	ASY		0.303	2281	5.82	-107.03
26	268050	628T	F	ASY		0.356	2666	5.72	-107.50
27	268050	648T	F	ASY		0.372	2006	4.98	-104.37
28	268050	659T	F	ASY		0.434	2568	5.45	-111.75
29	268050	714T	F	ASY		0.355	2153	5.56	-102.53
30	268050	416T	F	SY		0.346	2384	5.39	-96.67
31	268050	470T	F	SY		0.332	2378	5.64	-64.04
32	268050	485T	F	SY		0.326	2397	5.77	-81.82
33	268050	490T	F	SY		0.317	2394	5.87	-74.13
34	268050	495T	F	SY		0.368	2448	5.27	-98.48
35	268050	540T	F	SY		0.363	2591	5.61	-101.65
36	268050	604T	F	SY		0.343	2422	5.59	-107.05
37	268050	608T	F	SY		0.380	2793	5.71	-103.02
38	268050	609T	F	SY		0.332	2323	5.50	-63.11
39	268050	614T	F	SY		0.355	2525	5.60	-86.67
40	268050	623T	F	SY		0.392	2853	5.68	-113.77
41	268050	630T	F	SY		0.350	2502	5.64	-89.38
42	268050	631T	F	SY		0.391	2968	5.91	-102.36
43	268050	641T	F	SY		0.350	2578	5.81	-102.18
44	268050	644T	F	SY		0.353	2515	5.58	-103.27
45	268050	650T	F	SY		0.355	2535	5.63	-121.39

46	268050	066T	M	ASY		0.332	2243	5.30	-103.24
47	268050	071T	M	ASY		0.326	2224	5.39	-76.44
48	268050	075T	M	ASY		0.337	1968	5.33	-97.94
49	268050	100T	M	ASY		0.388	2347	5.46	-118.88
50	268050	193T	M	ASY		0.396	2364	5.44	-94.01
51	268050	245T	M	ASY		0.291	1689	5.35	-117.73
52	268050	256T	M	ASY		0.308	1764	5.28	-96.79
53	268050	257T	M	ASY		0.330	1920	5.35	-93.79
54	268050	258T	M	ASY		0.418	2442	5.34	-62.44
55	268050	260T	M	ASY		0.405	2559	5.64	-85.96
56	268050	262T	M	ASY		0.529	3177	5.38	-55.58
57	268050	263T	M	ASY		0.414	2543	5.55	-122.26
58	268050	268T	M	ASY		0.373	2212	5.40	-66.39
59	268050	271T	M	ASY		0.440	2625	5.44	-93.47
60	268050	278T	M	ASY		0.351	2039	5.31	-104.04
61	268050	284T	M	ASY		0.475	2848	5.44	-123.14
62	268050	289T	M	ASY		0.312	1833	5.36	-92.61
63	268050	292T	M	ASY		0.328	1984	5.54	-96.66
64	268050	295T	M	ASY		0.359	2169	5.49	-89.86
65	268050	308T	M	ASY		0.440	2585	5.27	-109.83
66	268050	314T	M	ASY		0.385	2015	4.82	-118.51
67	268050	384T	M	ASY		0.380	2228	5.28	-106.15
68	268050	394T	M	ASY		0.441	2456	5.05	-117.24
69	268050	395T	M	ASY			3745		-103.59
70	268050	411T	M	ASY		0.383	2298	5.37	-65.27
71	268050	428T	M	ASY		0.428	2508	5.31	-114.26
72	268050	436T	M	ASY		0.436	2510	5.30	-60.04
73	268050	649T	M	ASY		0.428	2526	5.40	-93.71
74	268050	062T	M	SY		0.366	2691	5.61	-84.88
75	268050	241T	M	SY		0.348	2529	5.47	-67.85
76	268050	327T	M	SY		0.334	2462	5.65	-94.06
77	268050	341T	M	SY		0.365	2631	5.52	-95.71
78	268050	372T	M	SY		0.341	2460	5.56	-111.91
79	268050	379T	M	SY		0.391	2883	5.66	-106.72
80	268050	380T	M	SY		0.355	2632	5.69	-102.14
81	268050	381T	M	SY		0.324	2390	5.68	-103.56
82	268050	386T	M	SY		0.322	2336	5.68	-111.37
83	268050	403T	M	SY		0.383	2835	5.69	-99.42
84	268050	417T	M	SY		0.363	2631	5.54	-59.65
85	268050	418T	M	SY		0.309	2375	5.98	-95.89
86	268050	488T	M	SY		0.365	2074	5.21	-44.85
87	268050	492T	M	SY		0.417	2581	5.63	-81.87
88	268050	496T	M	SY		0.309	1704	5.12	-115.23
89	268050	500T	M	SY		0.325	2284	5.54	-124.57
90	268050	502T	M	SY		0.331	2412	5.71	-41.85
91	268050	503T	M	SY		0.330	2417	5.67	-109.53
92	268050	516T	M	SY		0.370	2720	5.69	-114.49
93	268050	517T	M	SY		0.359	2627	5.66	-109.00
94	268050	577T	M	SY		0.365	2541	5.44	-116.30
95	268050	589T	M	SY		0.382	2710	5.47	-118.87
96	268050	602T	M	SY		0.371	2622	5.47	-87.60
97	268050	610T	M	SY		0.320	2313	5.60	-109.19
98	268050	621T	M	SY		0.359	2614	5.69	-111.28
99	268050	636T	M	SY		0.329	2375	5.66	-118.19
100	268050	655T	M	SY		0.351	2535	5.65	-114.89

Table 8: Feathers collected during fall migration in 2014 representing the 2014 breeding season

Sample Number	ID Number	Age	Sex	Date Captured	Weight (mg)	H2 Amp	%H	δ2H vs. VSMOW
1	205F14	AHY	F	9/8/2014	0.349	2156	5.66	-111.01
2	221F14	AHY	F	9/9/2014	0.378	2206	5.35	-112.39
3	241F14	AHY	F	9/10/2014	0.363	2124	5.38	-107.33
4	282F14	AHY	F	9/12/2014	0.362	2152	5.44	-111.80
5	341F14	AHY	F	9/13/2014	0.357	2176	5.58	-85.93
6	372F14	AHY	F	9/14/2014	0.320	1862	5.36	-95.36
7	398F14	AHY	F	9/16/2014	0.444	2829	5.78	-125.04
8	522F14	AHY	F	9/16/2014	0.413	2617	5.76	-110.14
9	553F14	AHY	F	9/17/2014	0.425	2625	5.60	-103.91
10	581F14	AHY	F	9/18/2014	0.419	2622	5.70	-93.76
11	603F14	AHY	F	9/19/2014	0.347	2106	5.56	-103.56
12	624F14	AHY	F	9/20/2014	0.386	2302	5.47	-113.54
13	645F14	AHY	F	9/21/2014	0.400	2396	5.45	-111.96
14	664F14	AHY	F	9/23/2014	0.302	1875	5.66	-120.28
15	680F14	AHY	F	9/24/2014	0.480	3035	5.77	-92.52
16	701F14	AHY	F	9/25/2014	0.403	2478	5.65	-114.79
17	723F14	AHY	F	9/26/2014	0.341	2068	5.56	-110.74
18	754F14	AHY	F	9/28/2014	0.448	2697	5.48	-99.68
19	770F14	AHY	F	9/28/2014	0.345	2113	5.60	-110.45
20	792F14	AHY	F	9/30/2014	0.403	2522	5.72	-125.48
21	906F14	AHY	F	10/1/2014	0.330	2328	5.45	-100.30
22	930F14	AHY	F	10/4/2014	0.356	2659	5.75	-86.51
23	950F14	AHY	F	10/5/2014	0.354	2094	5.50	-90.78
24	963F14	AHY	F	10/7/2014	0.348	2045	5.43	-123.04
25	996F14	AHY	F	10/9/2014	0.429	2431	5.35	-112.20
26	024F14	HY	F	8/26/2014	0.367	2255	5.63	-107.01
27	056F14	HY	F	8/28/2014	0.358	2241	5.66	-112.44
28	081F14	HY	F	8/29/2014	0.293	1871	5.88	-97.36
29	107F14	HY	F	41881.00	0.347	2164	5.75	-105.73
30	122F14	HY	F	9/2/2014	0.420	2640	5.81	-111.26
31	159F14	HY	F	9/3/2014	0.359	2262	5.69	-122.04
32	175F14	HY	F	9/5/2014	0.384	2272	5.46	-113.77
33	192F14	HY	F	9/6/2014	0.336	2032	5.56	-115.95
34	215F14	HY	F	9/8/2014	0.376	2315	5.57	-84.77
35	232F14	HY	F	9/9/2014	0.357	2292	5.99	-104.99
36	251F14	HY	F	9/10/2014	0.323	2426	5.91	-121.20
37	261F14	HY	F	9/11/2014	0.345	2466	5.56	-110.09
38	301F14	HY	F	9/12/2014	0.324	2296	5.70	-118.33
39	344F14	HY	F	9/13/2014	0.314	2236	5.64	-118.40
40	375F14	HY	F	9/14/2014	0.328	2347	5.67	-107.67
41	400F14	HY	F	9/16/2014	0.349	2112	5.57	-130.84
42	561F14	HY	F	9/18/2014	0.329	1987	5.59	-109.04
43	597F14	HY	F	9/19/2014	0.373	2271	5.60	-121.70
44	639F14	HY	F	9/21/2014	0.377	2341	5.66	-109.28
45	694F14	HY	F	9/25/2014	0.373	2070	5.04	-112.82
46	744F14	HY	F	9/27/2014	0.311	1888	5.50	-109.42
47	778F14	HY	F	9/28/2014	0.369	2157	5.57	-97.09
48	785F14	HY	F	9/30/2014	0.342	2034	5.50	-124.69
49	923F14	HY	F	10/4/2014	0.371	2160	5.52	-88.87
50	955F14	HY	F	10/7/2014	0.340	2060	5.62	-102.83

51	104F14	AHY	M	8/30/2014	0.308	2028	5.19	-74.57
52	196F14	AHY	M	9/8/2014	0.319	2030	4.92	-95.12
53	287F14	AHY	M	9/12/2014	0.334	2245	5.37	-109.24
54	351F14	AHY	M	9/14/2014	0.315	1665	4.90	-96.56
55	368F14	AHY	M	9/14/2014	0.400	2313	5.28	-92.48
56	380F14	AHY	M	9/16/2014	0.327	1769	5.01	-103.94
57	511F14	AHY	M	9/18/2014	0.318	1793	5.18	-110.92
58	535F14	AHY	M	9/18/2014	0.327	1814	5.15	-84.74
59	560F14	AHY	M	9/18/2014	0.320	1863	5.40	-113.07
60	573F14	AHY	M	9/18/2014	0.344	1963	5.29	-140.83
61	583F14	AHY	M	9/18/2014	0.364	1899	4.80	-104.22
62	602F14	AHY	M	9/19/2014	0.349	2044	5.38	-122.17
63	623F14	AHY	M	9/20/2014	0.322	1892	5.34	-126.29
64	647F14	AHY	M	9/21/2014	0.327	1877	5.31	-120.04
65	660F14	AHY	M	9/23/2014	0.340	2090	5.65	-111.45
66	688F14	AHY	M	9/24/2014	0.319	2240	5.59	-116.97
67	699F14	AHY	M	9/25/2014	0.376	2630	5.47	-113.82
68	714F14	AHY	M	9/26/2014	0.349	2122	4.91	-114.44
69	736F14	AHY	M	9/27/2014	0.331	2257	5.38	-81.13
70	763F14	AHY	M	9/28/2014	0.347	2268	5.02	-116.51
71	796F14	AHY	M	9/30/2014	0.323	2139	5.20	-104.52
72	921F14	AHY	M	10/4/2014	0.318	2429	6.01	-98.57
73	945F14	AHY	M	10/5/2014	0.325	2054	4.99	-90.58
74	965F14	AHY	M	10/7/2014	0.329	2098	5.09	-104.59
75	987F14	AHY	M	10/9/2014	0.311	2009	5.10	-120.08
76	009F14	HY	M	8/22/2014	0.366	2858	6.18	-124.30
77	085F14	HY	M	8/29/2014	0.347	3041	6.86	-114.82
78	126F14	HY	M	9/2/2014	0.314	1881	4.77	-100.72
79	155F14	HY	M	9/3/2014	0.345	2262	5.17	-99.30
80	165F14	HY	M	9/4/2014	0.352	2592	5.78	-101.52
81	194F14	HY	M	9/8/2014	0.367	2470	5.28	-105.06
82	236F14	HY	M	9/9/2014	0.319	1950	4.90	-116.07
83	266F14	HY	M	9/11/2014	0.353	2396	5.34	-109.69
84	281F14	HY	M	9/12/2014	38.000	2508	0.05	-120.50
85	316F14	HY	M	9/13/2014	0.368	2227	4.85	-117.73
86	355F14	HY	M	9/14/2014	0.331	2187	5.22	-70.83
87	396F14	HY	M	9/16/2014	0.372	2570	5.44	-99.09
88	550F14	HY	M	9/17/2014	0.356	2318	5.21	-103.63
89	575F14	HY	M	9/18/2014	0.345	2056	4.74	-101.91
90	598F14	HY	M	9/19/2014	0.326	2182	5.35	-119.45
91	644F14	HY	M	9/21/2014	0.386	2392	5.67	-129.33
92	659F14	HY	M	9/23/2014	0.330	2048	5.70	-116.68
93	667F14	HY	M	9/24/2014	0.458	2830	5.53	-91.85
94	713F14	HY	M	9/26/2014	0.334	2015	5.55	-126.71
95	734F14	HY	M	9/27/2014	0.321	1928	5.41	-108.50
96	769F14	HY	M	9/28/2014	0.420	2554	5.55	-112.65
97	784F14	HY	M	9/30/2014	0.330	1978	5.48	-109.66
98	908F14	HY	M	10/1/2014	0.336	2043	5.59	-128.98
99	952F14	HY	M	10/5/2014	0.361	2214	5.61	-130.63
100	991F14	HY	M	10/9/2014	0.344	2121	5.61	-103.53

Table 9: Feathers collected from the Carnegie Museum of Natural History

Catalog Number	County	Sex	Age	Date Collected	Weight (mg)	H2 Amp	%H	δ2H vs. VSMOW
2355	Beaver	M		5/8/1898	0.458	4295	5.14	-79.88
2405	Beaver	M		5/16/1898	0.375	3624	5.32	-59.77
2458	Westmoreland	F		6/6/1898	0.422	4160	5.41	-66.87
2463	Westmoreland	M		6/9/1898	0.368	3502	5.26	-62.50
2639	Allegheny	M		5/11/1895	0.554	5362	5.26	-156.69
2640	Allegheny	F		5/11/1895	0.464	4407	5.25	-105.33
2774	Centre	M		6/9/1898	0.435	4003	5.06	-71.55
2780	Centre	M		6/10/1898	0.444	4118	5.20	-71.53
2843	Cambria	M		6/10/1898	0.462	4227	5.05	-40.85
2979	Blair	M		6/8/1898	0.402	3700	5.09	-65.47
2982	Blair	M		6/8/1898	0.403	3460	4.84	-77.90
3007	Cambria	M		6/10/1898	0.328	3222	5.54	-63.07
3315	Somerset	M		7/22/1898	0.381	3377	4.97	-73.60
3321	Somerset	M		7/23/1898	0.360	3334	5.25	-76.20
3841	Beaver	M		5/17/1899	0.312	2797	5.01	-90.15
3848	Beaver	M		5/20/1899	0.403	3704	5.18	-76.56
4070	Clearfield	M		6/10/1899	0.467	4251	5.06	-69.20
4164	Armstrong	M		7/1/1899	0.422	3997	5.28	-70.84
4422	Beaver	M	IMMATURE	9/7/1899	0.445	4080	5.11	-92.91
4430	Beaver	F	IMMATURE	9/11/1899	0.393	3803	5.41	-81.88
4434	Beaver	F	IMMATURE	9/12/1899	0.366	3383	5.28	-67.21
7133	Beaver	M	IMMATURE	8/31/1900	0.359	3076	4.84	-99.04
31471	Beaver	F	IMMATURE	8/30/1909	0.469	4479	5.31	-113.67
34370	Beaver	F	IMMATURE	9/7/1910	0.393	3651	5.36	-98.20
34374	Beaver	M	IMMATURE	9/10/1910	0.449	4310	5.44	-121.66
114499	Allegheny	M		5/7/1908	0.422	4324	5.75	-110.71
114508	Allegheny	F		5/9/1908	0.392	3635	5.22	-101.34
114591	Allegheny	M		5/4/1909	0.381	3499	5.31	-103.96
114637	Allegheny	M		9/22/1910	0.383	3604	5.27	-87.63
133954	Allegheny	M		5/17/1950	0.387	3415	4.96	-83.24
140458	Allegheny	U		9/5/1963	0.390	3120	4.52	-96.19
141840	Westmoreland	M		5/9/1964	0.367	2616	4.05	-103.73
142464	Allegheny	M		10/5/1966	0.380	3617	5.33	-128.02
142480	Westmoreland	M	IMMATURE	8/6/1966	0.461	3753	4.59	-60.73
144946	Westmoreland	F	IMMATURE	9/4/1972	0.393	3869	5.50	-97.13
149657	Allegheny	M		5/17/1973	0.364	3541	5.46	-114.93
149675	Westmoreland	M		5/19/1973	0.442	4183	5.28	-111.64
150539	Allegheny	U	IMMATURE	10/11/1975	0.402	3223	4.55	-95.64
150656	Mahoning	F	ADULT	9/25/1975	0.450	4247	5.25	-102.79
150974	Allegheny	M		9/14/1976	0.390	4006	5.74	-110.14
151035	Westmoreland	M	IMMATURE	9/12/1976	0.368	3377	5.23	-92.05
151267	Allegheny	F		5/11/1977	0.398	3554	5.06	-101.79
152008	Mahoning	M		9/13/1978	0.370	3758	5.71	-66.91
152217	Allegheny	Possible F	IMMATURE	9/28/1978	0.374	3652	5.54	-102.17
152342	Westmoreland	M		9/1/1979	0.359	3370	5.36	-108.15
152346	Westmoreland	M	IMMATURE	9/21/1979	0.397	3694	5.27	-102.40
152487	Allegheny	M	IMMATURE	9/1/1979	0.459	4052	5.01	-112.24
152917	Westmoreland	M		9/27/1980	0.406	3720	5.25	-73.13
152979	Mahoning	M		5/12/1980	0.416	3845	5.27	-73.06
152981	Mahoning	F		5/13/1980	0.435	3823	5.04	-73.09
153019	Mahoning	M	IMMATURE	9/18/1980	0.370	3548	5.55	-117.62
153020	Mahoning	M	IMMATURE	9/18/1980	0.420	3644	5.03	-99.18
153117	Allegheny	F	IMMATURE	10/1/1980	0.430	4355	5.81	-145.99
153129	Allegheny	M	IMMATURE	10/10/1980	0.364	2930	4.78	-78.90
154196	Allegheny	U	IMMATURE	9/9/1981	0.369	3355	5.29	-114.84
154243	Mahoning	F		10/8/1981	0.394	3477	5.16	-106.88

154439	Westmoreland	M	IMMATURE	8/31/1982	0.409	3591	5.37	-68.17
154668	Allegheny	F	IMMATURE	9/15/1983	0.389	3508	5.33	-95.28
154755	Westmoreland	F	IMMATURE	9/14/1983	0.378	3535	5.42	-108.85
154757	Westmoreland	F (Probable)	IMMATURE	9/18/1983	0.362	3258	5.34	-98.70
166765	Mahoning	M	ADULT	9/25/1982	0.390	3553	5.41	-97.16
166766	Mahoning	M	ADULT	9/25/1982	0.376	3134	5.00	-109.16
166767	Mahoning	M	IMMATURE	9/26/1982	0.434	3534	4.89	-77.29
166768	Mahoning	F (Probable)	IMMATURE	9/26/1982	0.375	3259	5.19	-102.40
166769	Mahoning	M	IMMATURE	9/26/1982	0.410	3709	5.40	-101.68
166770	Mahoning	M	ADULT	9/26/1982	0.417	3546	5.12	-115.25
166771	Mahoning	F	IMMATURE	9/26/1982	0.398	3295	5.00	-103.66
166772	Mahoning	M	IMMATURE	9/26/1982	0.411	3684	5.29	-103.97
166773	Mahoning	F	ADULT	9/26/1982	0.444	4154	5.57	-117.35
166774	Mahoning	M	IMMATURE	9/26/1982	0.413	3382	4.95	-114.19
166775	Mahoning	F (Probable)	IMMATURE	9/26/1982	0.363	3080	5.11	-101.45
166776	Mahoning	M	ADULT	9/27/1982	0.417	2905	4.22	-107.61
166777	Mahoning	F	IMMATURE	9/27/1982	0.376	3251	4.93	-105.60
166778	Mahoning	M	IMMATURE	9/28/1982	0.420	4192	5.61	-102.15
166779	Mahoning	M	IMMATURE	9/28/1982	0.412	3855	5.27	-111.30
166841	Mahoning	M	IMMATURE	9/12/1983	0.418	4217	5.65	-105.41
166842	Mahoning	F	IMMATURE	9/12/1983	0.403	3878	5.27	-104.10
166888	Allegheny	F	IMMATURE	8/28/1984	0.410	4613	6.10	-82.35
166925	Westmoreland	F	ADULT	5/14/1984	0.408	4294	5.67	-99.59
167115	Mahoning	M		9/15/1984	0.372	3739	5.43	-99.28
167163	Mahoning	M	IMMATURE	9/27/1984	0.366	4043	5.95	-68.01
167164	Mahoning	M	IMMATURE	9/27/1984	0.429	4597	5.75	-86.80
167165	Mahoning	F	ADULT	9/27/1984	0.354	3432	5.25	-99.66
167166	Mahoning	F	ADULT	9/27/1984	0.388	3771	5.27	-107.04
167167	Mahoning	M	IMMATURE	9/27/1984	0.393	4098	5.55	-111.04
167168	Mahoning	F	IMMATURE	9/27/1984	0.374	3311	4.77	-103.11
167169	Mahoning	M	IMMATURE	9/27/1984	0.376	3614	5.12	-64.63
169399	Mahoning	M		5/13/1904	0.365	3618	5.30	-58.54

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