Illinois State University

ISU ReD: Research and eData

Theses and Dissertations

7-14-2020

Determination Of The Summer Origins Of American Kestrels (Falco Sparverius) Wintering In Northern And Central Illinois

Taylor P. Joray

Illinois State University, taylorjoray@gmail.com

Follow this and additional works at: <https://ir.library.illinoisstate.edu/etd>

Part of the [Biodiversity Commons](#), and the [Biology Commons](#)

Recommended Citation

Joray, Taylor P., "Determination Of The Summer Origins Of American Kestrels (Falco Sparverius) Wintering In Northern And Central Illinois" (2020). *Theses and Dissertations*. 1293.

<https://ir.library.illinoisstate.edu/etd/1293>

This Thesis is brought to you for free and open access by ISU ReD: Research and eData. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of ISU ReD: Research and eData. For more information, please contact ISURed@ilstu.edu.

DETERMINATION OF THE SUMMER ORIGINS OF AMERICAN KESTRELS (*FALCO*
SPARVERIUS) WINTERING IN NORTHERN AND CENTRAL ILLINOIS

TAYLOR P. JORAY

83 Pages

The seasonal and interannual movements of the American Kestrel (*Falco sparverius*) are not fully understood. Although one of the most widespread and abundant raptors found in North America, information on where many populations summer and overwinter is lacking. We used stable hydrogen isotope values obtained from feathers ($\delta^2\text{H}_f$) of known origin to create age-specific calibration functions for juvenile and adult American Kestrels. We then used these calibration functions to determine the most likely summer origins of the American Kestrels that wintered in northern and central Illinois during 2015-16, classified these individuals as year-round residents or wintering migrants, and validated these predictions with a test dataset of known origin birds withheld from calibration function creation. The latitudinal band stretching from $\sim 44.20^\circ\text{N}$ to $\sim 48.00^\circ\text{N}$, which runs from central Wisconsin to northern Minnesota when considering areas north of the winter capture locations for the sampled individuals, contained areas that were consistently predicted as potential summer origins for those classified as migrants, suggesting the possibility of a northward shift in their wintering distribution. Our analyses also found that the ratio of residents to migrants in northern and central Illinois is between 1:1 and 3:2, suggesting that migrant individuals compose a considerable portion of the American Kestrels wintering in this region. This approach provided a robust methodology for assigning summer origins to both juveniles and adults, which previously has been unsuccessful.

Application of this approach allows for the monitoring of population level changes in annual movement patterns, which is essential to tracking future range shifts caused by land-use or climate change.

KEYWORDS: American Kestrel, *Falco sparverius*, stable isotopes, deuterium, origins, IsoMAP

DETERMINATION OF THE SUMMER ORIGINS OF AMERICAN KESTRELS (*FALCO*
SPARVERIUS) WINTERING IN NORTHERN AND CENTRAL ILLINOIS

TAYLOR P. JORAY

A Thesis Submitted in Partial
Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

School of Biological Sciences

ILLINOIS STATE UNIVERSITY

2020

© 2020 Taylor P. Joray

DETERMINATION OF THE SUMMER ORIGINS OF AMERICAN KESTRELS (*FALCO*
SPARVERIUS) WINTERING IN NORTHERN AND CENTRAL ILLINOIS

TAYLOR P. JORAY

COMMITTEE MEMBERS:

Angelo P. Capparella, Chair

Steven A. Juliano

John C. Kostelnick

R. Given Harper

ACKNOWLEDGMENTS

I would like to acknowledge all those who have helped with the completion of this thesis. Specifically, I would like to thank my advisor, Angelo P. Capparella, and my committee members, Steven A. Juliano, John C. Kostelnick, and R. Given Harper, for their continued support, guidance, and patience throughout this project. Without their assistance, this project would not have been accomplished. I would also like to thank the many people who helped me with fieldwork. The time spent in the field was truly a highlight of this project, and all those who assisted with fieldwork helped greatly. I would like to extend a special thanks to Gregory Tito, for joining me during countless hours in the field and for his continued encouragement. This thesis would not have been possible without the generous funding from the Illinois Ornithological Society and the Illinois State University School of Biological Sciences Collections Fund. Additionally, I would like to thank Jennifer L. Greenwood and Russell D. Dawson for providing access to data that was critical to the development of this project. Finally, I would like to thank my family and friends for their encouragement, motivation, and much needed laughs throughout this journey. Andrea I. Pacheco deserves a special thanks for her unwavering support and continuous assistance every step of the way.

T. P. J.

CONTENTS

	Page
ACKNOWLEDGEMENTS	i
CONTENTS	ii
TABLES	iv
FIGURES	v
CHAPTER 1: DETERMINATION OF THE SUMMER ORIGINS OF AMERICAN KESTRELS (<i>FALCO SPARVERIUS</i>) WINTERING IN NORTHERN AND CENTRAL ILLINOIS	1
Abstract	1
Lay Summary	2
Introduction	3
Animal Movement	3
Tracking Avian Movement	4
Intrinsic Markers as a Method of Studying Movement	8
The Use of Stable Hydrogen Isotopes in Avian Movement Studies	9
Assigning Geographic Origins from $\delta^2\text{H}$ Measurements	11
The Efficacy of $\delta^2\text{H}$ -based Avian Movement Studies	13
Movements of the American Kestrel	15
Methods	18
Capture of Live Birds and Field Data Collection	18
Sample Preparation and Isotopic Analysis	21
Statistical Analyses and Assignments of Geographic Origin	22

Results	37
Discussion	41
American Kestrels Wintering in Northern and Central Illinois	42
Conservation and Management Implications	47
Recommendations and Limitations	49
Acknowledgements	52
Literature Cited	52
Appendix	72
Tables	79
Figures	80

TABLES

Table	Page
1. Ratio of resident to migrant American Kestrels wintering in the Northern and Central Divisions of Illinois	79

FIGURES

Figure	Page
1. Location of feather clippings collected from P4 of a male and female American Kestrel	80
2. Juvenile ordinary least squares (OLS) regression modelling the relationship between $\delta^2\text{H}_p$ from our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape and $\delta^2\text{H}_f$ values of the known origin juvenile American Kestrels from the Lott and Smith (2006) dataset ($n = 41$) and a subset of the Greenwood and Dawson (2011) dataset ($n = 5$)	81
3. Likely summer origin for an individual American Kestrel based on the upper 20% of the grid cell values and refinements	82
4. The refined summer origin predictions for the migrant American Kestrels able to be aged definitively ($n = 21$) that wintered in the Northern and Central Divisions of Illinois during the 2015-16 winter	83

CHAPTER I: DETERMINATION OF THE SUMMER ORIGINS OF AMERICAN KESTRELS
(*FALCO SPARVERIUS*) WINTERING IN NORTHERN AND CENTRAL ILLINOIS

RESEARCH ARTICLE

Determination of the summer origins of American Kestrels (*Falco sparverius*) wintering in northern and central Illinois

Taylor P. Joray,^{1*} Angelo P. Capparella,¹ Steven A. Juliano,¹ John C. Kostelnick², R. Given Harper³

¹ School of Biological Sciences, Illinois State University, Normal, Illinois, USA

²Department of Geography, Geology, and the Environment, Illinois State University, Normal, Illinois, USA

³Department of Biology, Illinois Wesleyan University, Bloomington, Illinois, USA

* Corresponding author: taylorjoray@gmail.com

ABSTRACT

The seasonal and interannual movements of the American Kestrel (*Falco sparverius*) are not fully understood. Although one of the most widespread and abundant raptors found in North America, information on where many populations summer and overwinter is lacking. We used stable hydrogen isotope values obtained from feathers ($\delta^2\text{H}_f$) of known origin to create age-specific calibration functions for juvenile and adult American Kestrels. We then used these calibration functions to determine the most likely summer origins of the American Kestrels that wintered in northern and central Illinois during 2015-16, classified these individuals as year-round residents or wintering migrants, and validated these predictions with a test dataset of known origin birds withheld from calibration function creation. The latitudinal band stretching from ~44.20°N to ~48.00°N, which runs from central Wisconsin to northern Minnesota when

considering areas north of the winter capture locations for the sampled individuals, contained areas that were consistently predicted as potential summer origins for those classified as migrants, suggesting the possibility of a northward shift in their wintering distribution. Our analyses also found that the ratio of residents to migrants in northern and central Illinois is between 1:1 and 3:2, suggesting that migrant individuals compose a considerable portion of the American Kestrels wintering in this region. This approach provided a robust methodology for assigning summer origins to both juveniles and adults, which previously has been unsuccessful. Application of this approach allows for the monitoring of population level changes in annual movement patterns, which is essential to tracking future range shifts caused by land-use or climate change.

Keywords: American Kestrel, *Falco sparverius*, stable isotopes, deuterium, origins, IsoMAP

LAY SUMMARY

- Information on where many populations of American Kestrels summer and overwinter is lacking
- Stable hydrogen isotope ratios found in the feathers of wild-caught American Kestrels that were wintering in northern and central Illinois during 2015-16 were examined
- Migrants from areas farther north of Illinois composed a considerable portion of the American Kestrels sampled
- This approach provides a way to determine the summer origins of juvenile and adult American Kestrels from a feather sample, which was previously unsuccessful
- These methods can be used to track future range shifts caused by land-use or climate change

INTRODUCTION

Animal Movement

One of the most challenging aspects of understanding the life history of animals is effectively studying their movement. The daily, seasonal, or annual movement of animals is foundational to their life histories, and characterization of this movement is essential to conserve them (Hobson 1999). For research on movement, birds are among the most studied organisms on the planet, with a history of migration extending over millions of years (Hughes 2009). An estimated 4,000 species of birds migrate, with songbirds, waterfowl, waders, and shorebirds comprising a majority of this total (Hughes 2009). Although birds are the best-studied vertebrate taxon (Şekercioğlu 2006), details of the seasonal and interannual movements of many avian populations and species are still lacking (Webster and Marra 2005, Martin et al. 2007).

Sadly, current trends predict that by the year 2100, ~5-13% of all extant species will be extinct, and ~6-24% will be functionally extinct (Şekercioğlu et al. 2004). Since 1970, there has been a net loss of 2.9 billion breeding birds across North America (Rosenberg et al. 2019), and under a global climate change scenario with a global mean temperature rise of 3.0°C (5.4°F), nearly two-thirds (63%) of North American bird species will be vulnerable to extinction due to range loss by 2100 (Wilsey et al. 2019). In response to this loss of avian diversity, there will likely be a loss of many ecosystem services birds supply (Şekercioğlu et al. 2004), and thus, a great conservation challenge lies ahead of us. Protecting migratory species is difficult because it involves piecing together the geographically distinct events that occur over time so that fully formed pictures of their life histories are created (Martin et al. 2007). Thus, a sound understanding of the movement of migratory species and how that will be affected by climate

change is crucial to the development and implementation of successful conservation strategies (Webster and Marra 2005).

Tracking Avian Movement

Tracking avian movement is challenging, and a variety of techniques have been developed. The traditional method of studying the movement of individual birds, which has laid the foundation for our knowledge of migratory connectivity, involves the use of extrinsic markers and is often termed the mark/recapture method. This approach relies on our ability to capture a bird, place some sort of marker on the individual, and reencounter the bird subsequently, thus providing information on the bird's movement. Markers for this method include leg bands, neck collars, patagial tags, and plumage marking dyes (Hobson 1999). Although such extrinsic markers are inexpensive and have provided valuable insight regarding avian movement and migration, reencounter rates (the percentage of individuals found dead, recaptured, or resighted) are typically very low, limiting their efficacy. For example, the reencounter rate for North American passerines banded from 1955-2000 is regularly less than 1% (Hobson 2003), while the reencounter rate for North American raptors is equally poor as well, ranging from 1-5% for the four most commonly banded raptor species in the United States (U.S.) and Canada (Goodrich et al. 2012), which includes the American Kestrel. High reencounter rates are generally only seen with game species (Hobson 2003). For instance, waterfowl comprise ~1/3 of the bird species banded and registered in the U.S. under the United States Geological Survey (USGS) Bird Banding Laboratory each year, but due to regulated hunting seasons increasing the chance of hunters recovering banded birds, they account for ~87% of all reported band recoveries (Lament 2005). In addition to low reencounter rates, the use of extrinsic markers is typically geographically biased due to geographic variation in marking efforts, and the reencounter rates

are usually proportional to the number of birds banded at the various marking sites (Hobson et al. 2004).

In the early 1960s, the inception of very high frequency (VHF) radio telemetry provided a new technique for monitoring the movements of wildlife in a way not possible previously (Cochran and Lord 1963). In this approach, a transmitter that emits high frequency pulses (30 to 300 MHz) is placed on the animal, allowing it to be tracked in the field with the use of a specialized antenna and receiver (The Migratory Connectivity Project 2017b). This technique was monumental to the field of animal tracking because for the first time ever, animals were able to be tracked in real time (The Migratory Connectivity Project 2017b). Although VHF radio telemetry is relatively inexpensive and can be used to track a variety of animals, it is impractical for tracking over long distances or times in most circumstances. Unless a stationary antenna array is used, researchers must actively track the animal in the field each time a location is to be obtained, and in both scenarios, the subject must be within range for the receiver to pick up the transmitter's signal (Kingsbury and Robinson 2016). The Motus network, which pairs VHF telemetry with automated receiver stations, is working to overcome the need for in-the-field tracking, but inconsistent spatial coverage currently limits the efficacy of this approach (Taylor et al. 2017). Due to these factors, VHF radio telemetry is currently better suited for tracking localized movements as opposed to the longer distances traveled by migratory birds.

The advent of satellite telemetry has allowed researchers to track birds over a much longer distance and time period than was previously possible with VHF radio telemetry. Since the 1980s, transmitters called platform transmitting terminals (PTTs) have been used in conjunction with the Advanced Research and Global Observation Satellite (ARGOS) system, a global satellite system dedicated to monitoring and increasing our understanding of the planet's

environment (Seegar et al. 1996). PTTs periodically transmit radio signals to the satellites that comprise the ARGOS system, and once a satellite receives multiple hits from a PTT, the location of the tagged individual can be calculated using the Doppler Effect (Kingsbury and Robinson 2016). Locations calculated for PTTs are generally accurate to between a few hundred meters and tens of kilometers (Kingsbury and Robinson 2016) and can be relayed remotely, eliminating the need to recapture tagged individuals. Although the miniaturization of PTTs has progressed immensely since their initial application, with some now weighing less than 5 g, they are still too heavy for many small birds if following the 3% safety rule in relation to the transmitter/body weight ratio (Casper 2009).

Global Positioning Systems (GPS) tracking, another form of satellite telemetry, has provided the possibility for tracking even smaller birds. GPS tracking devices are equipped with small radio receivers that collect messages from NAVSTAR GPS satellites at pre-determined user defined intervals and can produce remarkably accurate location information to within a few meters (Kingsbury and Robinson 2016). Archival GPS data loggers as light as ~1 g are now available and have been used to track the entire migratory pathway of small songbirds (Hallworth and Marra 2015, Siegel et al. 2016, Fraser et al. 2017), but they must be retrieved to obtain the GPS fixes. Groupe Spécial Mobile (GSM) tags utilize GPS technology and can send GPS fixes to researchers remotely via cellular networks, but are heavier, typically within the 18-70 g range (Hallworth and Marra 2015). GPS receivers have also been combined with PTTs to incorporate the best of both devices: the highly accurate location data of the GPS system and the remote data transfer capabilities of the ARGOS system. There now exists such a device, referred to as a GPS ARGOS tag, which weighs only 3.5 g and can provide highly accurate location information over an entire migration (<https://www.lotek.com/products/pinpoint-gps-argos/>).

Overall, satellite telemetry devices suitable for use on birds are costly, with a minimum price generally around \$1,000 per device and some costing much more (Kingsbury et al. 2016). Thus, sample sizes for projects utilizing satellite telemetry devices may be dictated by budgetary restraints.

A less costly method for tracking long distance movements of small migratory birds exists in the form of archival light-level geolocators. Geolocators are tiny devices that regularly measure and store light-level data, which can then be used to determine estimates of latitude and longitude based on day length and the time of solar noon respectively (The Migratory Connectivity Project 2017a). The lightest devices weigh less than 1 g, which has enabled them to be used on a wide variety of avian species (Bridge et al. 2013). Unfortunately, geolocators must be retrieved to obtain the location data stored on-board, which requires the recapture of tagged individuals. Another problem with geolocators is that location accuracy is easily impaired by environmental conditions affecting light levels (e.g., cloud cover, vegetation), which has resulted in location errors well over 100 km (Fudickar et al. 2012).

Devices such as these have allowed researchers to track movements over the entire annual cycle and have revealed breeding locations (Kanai et al. 2002, Bustnes et al. 2010), migration routes (Fuller et al. 1998, Martell et al. 2001, Anker-Nilssen and Aarvak 2009), migration timing (Martell et al. 2001, Bustnes et al. 2010), stopover sites (Stutchbury et al. 2009), and non-breeding territories (Fuller et al. 1998, Martell et al. 2001, Hallworth and Marra 2015). Although these techniques have allowed researchers to study intricate details of avian movement in ways never before possible, one must consider the issues that arise when placing telemetry and bio-logging devices on birds. Barron et al. (2010) found that the attachment of transmitters and other similar devices negatively affected many aspects of bird behavior and

ecology, most notably an increase in energetic expenditure and a decrease in the likelihood of nesting, even when following weight limit guidelines for tracking devices. Equally as important as the weight of the tracking device is the aerodynamic interference it imposes. Bowlin et al. (2010) found that geolocators significantly increased drag during flight simulations in a wind-tunnel, and that the combination of the increased weight and drag of geolocators decreased the predicted flight range of migratory bird species in an avian flight model by up to ~20% in some circumstances. Altered behavior and vital rates are inherent risks when using tracking devices, which can ultimately jeopardize the quality of the data being collected and even put the animal itself in danger (McMahon et al. 2011).

Intrinsic Markers as a Method of Studying Movement

Due to the disadvantages of the aforementioned techniques, there has been a push to develop new methodologies to study the movement of birds and other mobile organisms. This has led to the use of intrinsic markers, notably stable isotopes. On our planet, several elements occur in more than one stable isotope, and although they are chemically equivalent, differences in numbers of neutrons produce different atomic masses, which in turn alters their behavior in physical processes and chemical reactions (Martinez del Rio and Wolf 2005). For instance, heavier isotopes generally create stronger bonds and have a slower molecular velocity, and thus a slower reaction rate than lighter isotopes (Sulzman 2007). Due to these bond energy and reaction rate differences, differences occur in the isotopic ratios of inorganic and organic compounds in discrete physical and biological reactions, a process referred to as isotopic fractionation (Ben-David and Flaherty 2012). Isotopic fractionation produces spatial and temporal variation in the ratios of heavy to light isotopes of element pools within natural systems and contributes to isotopic discrimination during the tissue formation of living organisms (Ben-David and Flaherty

2012). This natural variation in the abundance of isotopes in all ecosystems has served as an effective marker system utilized in studies of a multitude of ecological topics including animal movement (Ben-David and Flaherty 2012).

Among the first to use stable isotopes to track animal movement, Schell et al. (1988) examined carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) measurements taken from the baleen of western arctic Bowhead whales (*Balaena mysticetus*) to reconstruct their annual migration. A decade later, Chamberlain et al. (1997), Hobson and Wassenaar (1997), and Hobson et al. (1999b) paved the way for migration tracking of terrestrial species based on stable hydrogen, carbon, and strontium values found in keratinized tissue. Since these pioneering studies, the use of hydrogen stable isotopes has become an important tool in the tracking of avian movement (Hobson et al. 2004, Mazerolle et al. 2005, Hobson et al. 2007, Pérez and Hobson 2007, Hobson et al. 2009, Macías-Duarte and Conway 2014, Nelson et al. 2015, Asante et al. 2017, Smith et al. 2019).

The Use of Stable Hydrogen Isotopes in Avian Movement Studies

Avian movement studies utilizing stable hydrogen isotopes examine the ratio of the heavy hydrogen isotope deuterium (^2H or D) to the light hydrogen isotope (^1H) found in tissues ($^2\text{H}:^1\text{H}$ or $\delta^2\text{H}$). These studies depend on the widespread, systematic environmental variation in abundances of stable hydrogen isotopes in water (Dansgaard 1964, Rozanski et al. 1993, West et al. 2006). Large numbers of both ^2H and ^1H , enter the environment through precipitation. The distribution of these stable hydrogen isotopes in the environment is dependent on several factors, which are all largely temperature driven (Dansgaard 1964, West et al. 2006). The majority of water vapor on Earth originates in the tropics (Peixoto and Oort 1983) and is carried poleward, where it subsequently mixes with different air masses and atmospheric water. As water vapor moves away from the equator or is orographically lifted, the heavier molecules are shed first

during precipitation (Rozanski et al. 1993, Ben-David and Flaherty 2012), leaving less deuterium to be incorporated into precipitation as water vapor moves poleward. However, coastal locations often have higher deuterium levels in comparison to more inland locations regardless of their latitude relative to the tropics, due to the possibility of mixing with oceanic water vapor that is enriched in deuterium (Rozanski et al. 1993). The amount of rainfall in an area also affects isotopic compositions, with lower $\delta^2\text{H}$ in areas with high precipitation intensities (Rozanski et al. 1993, West et al. 2006). This “amount effect” is largely due to the higher probability of ^1H being incorporated into rainfall as the overall levels of D decrease in the area’s remaining water vapor. Together, these factors create consistent geographic patterns in the isotopic composition of precipitation, enabling us to generate precipitation isoscapes on continental scales (Bowen and Revenaugh 2003, Meehan et al. 2004, Bowen et al. 2005, West et al. 2006) that predict expected $\delta^2\text{H}$ values for specific geographic locations (Wunder 2010).

Stable hydrogen isotopes in the environment are then transferred to primary producers and to higher trophic levels via food and water consumption, where they are incorporated into growing animal tissues (Estep and Dabrowski 1980, Hobson et al. 1999a). Metabolically inert tissues such as feather keratin effectively fix the isotopic composition of non-exchangeable hydrogen atoms they incorporate during the period of growth (Hobson and Wassenaar 1997, Bowen et al. 2005), leaving an isotopic signature that can be used to estimate the geographic location of a bird during molt. The isotopic signature acquired by feather keratin is largely representative of the bird’s isotopic intake at the time of or shortly before (a few days to several weeks) tissue formation (Hobson and Clark 1992, Bearhop et al. 2002, Pearson et al. 2003, Becker et al. 2007, Inger and Bearhop 2008). Hobson and Wassenaar (1997) were among the first to demonstrate a strong link between the $\delta^2\text{H}$ of feather keratin (referred to as $\delta^2\text{H}_f$) and that

of precipitation (referred to as $\delta^2\text{H}_p$), while exploring the breeding and wintering grounds of several different Neotropical migrant songbird species. In their study, Hobson and Wassenaar (1997) found $\delta^2\text{H}_f$ to be strongly correlated with $\delta^2\text{H}_p$ in the areas where feather molt took place. Likewise, Chamberlain et al. (1997) found a strong correlation between the $\delta^2\text{H}_f$ of Black-throated Blue Warblers (*Setophaga caerulescens*) and American Redstarts (*Setophaga ruticilla*) and the $\delta^2\text{H}$ of surface and rain waters where the birds molted. Since then, other studies have demonstrated a connection between $\delta^2\text{H}_f$ and $\delta^2\text{H}_p$ (Wassenaar and Hobson 2000, Hobson et al. 2004, Lott and Smith 2006, Hobson et al. 2009). The link between $\delta^2\text{H}_f$ and $\delta^2\text{H}_p$ at the location of molt is the foundation for assigning geographic origins to birds of unknown origins.

Assigning Geographic Origins from $\delta^2\text{H}$ Measurements

Isotope-based geographic assignments to birds of unknown origins are ultimately dependent upon models. The first and most important step to assigning model-based geographic origins to birds from stable hydrogen isotope measurements is to create a calibration function establishing the relationship between $\delta^2\text{H}_f$ and $\delta^2\text{H}_p$ using tissues of known origin (Wunder 2012). The calibration function draws a connection between geography and expected $\delta^2\text{H}_f$ and establishes an assumption that isotopic discrimination between local precipitation and keratinized tissue is predictable for all individuals (Wunder 2012). Although strong patterns generally exist between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ at the location of molt, the relationship is not perfectly predictable (Wunder 2012). Discrimination factors, which quantify the difference between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$, vary among taxonomic groups (Langin et al. 2007), including species (Rocque et al. 2006, Hobson et al. 2009), at a regional level (Lott and Smith 2006), and age-classes (Meehan et al. 2003, Haché et al. 2012). Deuterium ratios of feather keratin can vary among individuals of the same population foraging in the same general location (Wassenaar and Hobson 2006, Langin et al. 2007, Wunder

2012), and have even been shown to vary within different samples of the same tissue within individuals (Wassenaar and Hobson 2006). These observed variations in $\delta^2\text{H}_f$ are the result of a variety of factors from different drinking water sources and dietary inputs (Ben-David and Flaherty 2012) to different stressors and nutritional conditions during feather molt (McKechnie et al. 2004, Betini et al. 2009, Wunder 2012). The robustness of isotope inferred geographic assignments therefore relies on our ability to identify and incorporate these sources of variance into assignment models (Wunder 2012).

Wunder (2007) developed a continuous-surface assignment model to investigate the summer breeding grounds of Mountain Plovers (*Charadrius montanus*) wintering in California that allowed for the incorporation of multiple sources of variance. This model utilized a three-tiered hierarchical approach to estimate variances from: 1) analytical error (laboratory measurement error); 2) within and among feathers from the same individual; and 3) among individuals from the same location. The continuous-surface approach employed by Wunder (2007) covered all points in the defined geographic space and produced a probability of true origin for each point for each individual bird, while also incorporating all three sources of variance separately within the model. Other studies have utilized the continuous-surface approach while incorporating a single estimate of bulk variance obtained from the calibration function residuals (Nelson et al. 2015; see Wunder 2010 for a comparison of the two approaches for incorporating variance into models). Regardless of the specific approach used, the incorporation of variance is a key component to any isotope based geographic assignment model (Hobson et al. 2009, Wunder 2010, 2012).

The Efficacy of $\delta^2\text{H}$ -based Avian Movement Studies

Well planned and implemented stable hydrogen isotope-based studies can answer questions regarding avian movement that are impossible or impractical to answer via extrinsic based studies. Analytical costs for running stable isotope analyses on tissue samples are low in comparison to the costs of other techniques such as satellite telemetry, which allows for much larger sample sizes and ultimately provides a more realistic approach to making population-level inferences. Stable isotope analyses eliminate the need for the recapture of individuals, which led to Hobson's (2005) proclamation of "every capture is a recapture". Using keratinized tissue samples, all individuals of even the smallest species can be sampled (Hobson et al. 2003), as the size limitations associated with extrinsic tracking devices are irrelevant. The use of stable isotopes to infer geographic origins also provides a briefer and less stressful way of sampling individuals that avoids the issues that arise when placing telemetry and bio-logging devices on birds (Barron et al. 2010, Bowlin et al. 2010). Stable isotope analyses require such a small amount of tissue (<1 mg) that the effect on wild birds is thought to be minimal (Hobson et al. 2009).

The use of stable isotopes to study avian movement does have some weaknesses, but with proper planning, strategies can be implemented to minimize these disadvantages. Although not as precise as other extrinsic methods, likelihood-of-origin maps produced from stable isotope analyses can be overlaid with digital distribution information via Geographic Information Systems (GIS; Hobson 2007), combined with band recovery data (Van Wilgenburg and Hobson 2011), or utilized with multiple stable isotopes and genetic markers (Kelly et al. 2005) to reduce the geographic extent of the predicted origins for sampled individuals. Few studies have incorporated individuals of known origin from telemetry, banding, or other data to check

geographic assignments, which has led some to question the accuracy of stable isotope based geographic inferences. Caccamise et al. (2000) combined $\delta^{13}\text{C}_f$, $\delta^{15}\text{N}_f$, and $\delta^{34}\text{S}_f$ ratios to distinguish migrant Canada Geese (*Branta canadensis*) from residents. They utilized known origin feathers from three distinct groups (migrants, inland residents, and coastal residents) in a discriminant analysis and were able to correctly classify 92% of the sampled individuals. Wassenaar and Hobson (2000) tested whether $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values obtained from Red-winged Blackbirds (*Agelaius phoeniceus*) could determine their breeding locations across a transect stretching from Louisiana, USA to Saskatchewan, Canada. They were able to correctly assign 80% of the individuals when using the two isotopes together, while still correctly assigning 64% of the individuals when using $\delta^2\text{H}_f$ alone. Royle and Rubenstein (2004) also combined $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values and were able to correctly assign 62% of the Black-throated Blue Warblers in their study to the region of their breeding grounds. Unfortunately, combining 2 or more different stable isotopes to increase the accuracy of geographic assignments is only possible when isoscapes exist for each of the stable isotopes, which requires large sets of known origin tissue samples, preferably from the species of interest. More recently, Nelson et al. (2015) determined the accuracy of $\delta^2\text{H}_f$ based assignments for eight Golden Eagles (*Aquila chrysaetos*) with known summer origins obtained from telemetry and summer capture data. They found that when utilizing a generic raptor calibration function based on known origin feather samples from the Lott and Smith (2006) dataset, expected $\delta^2\text{H}_p$ values for the 8 known origin Golden Eagles were within the range of variation of the $\delta^2\text{H}_p$ values for the locations at which these birds summered.

Another disadvantage of stable isotope analyses is that the detailed views into entire migratory pathways provided by forms of satellite tracking are unobtainable. Despite this, well-timed and strategically planned stable isotope analyses can still provide valuable information on

migration timing, stopover sites, and migratory connectivity between breeding and non-breeding sites. Hobson et al. (2001) discovered several previously unknown breeding locations of Bicknell's Thrush (*Catharus bicknelli*) from $\delta^2\text{H}_f$ measurements taken on wintering grounds. Sarasola et al. (2007) found that flocks of Swainson's Hawks (*Buteo swainsoni*) wintering in Argentina consisted of individuals from a mixture of summering locales as opposed to individuals from discrete breeding populations, ultimately suggesting that high-wintering mortality is unlikely to have dire effects on any single breeding area in North America. Atkinson et al. (2005) combined $\delta^2\text{H}_f$ values with $\delta^{13}\text{C}_f$, $\delta^{15}\text{N}_f$, and $\delta^{18}\text{O}_f$ measurements from coastal-feeding Red Knots (*Calidris canutus*) and identified variation in their migratory strategies in addition to discovering three discrete wintering areas on the eastern seaboard of the Americas. Interestingly, Hobson et al. (2003) found that $\delta^2\text{H}_f$ and $\delta^{13}\text{C}_f$ measurements taken from the feathers of eight different hummingbird species in the Ecuadorian Andes illustrated distinct altitudinal levels over a 4,000-meter gradient, demonstrating the capability of examining altitudinal migration with stable isotopes. As is evident, $\delta^2\text{H}$ -based studies hold the potential to answering a diverse assortment of questions pertaining to avian movement for a plethora of avian species whose seasonal and interannual movements are not fully understood.

Movements of the American Kestrel

The American Kestrel (*Falco sparverius*) is one species whose seasonal and interannual movements are not fully understood and whose range is expected to shift significantly under climate change scenarios (National Audubon Society 2019). Among the smallest Nearctic falcon species, the American Kestrel is one of the most widespread birds of prey found in North America. During the summer months, American Kestrels breed throughout much of Canada, Alaska, and the lower 48 states, as well as in areas of Mexico, Central America, and on several

islands in the Caribbean. Then, from August through November, migratory movement of some to all individuals in certain North American Kestrel populations occurs (Smallwood and Bird 2002, Crossley et al. 2013).

The migratory behavior of the American Kestrel is complex, but in general, the tendency for individuals to migrate decreases from north to south (Smallwood and Bird 2002). American Kestrels in the northernmost stretches of their North American breeding range (north of $\sim 44^{\circ}\text{N}$) are completely migratory, and are thought to partake in “leap-frog” migration in which they leap over lower latitude winter populations composed of shorter distance migrants and resident birds, spending their winters in the southernmost wintering grounds (Smallwood and Bird 2002, Goodrich et al. 2012). For example, Kestrels banded in Pennsylvania and Maryland have frequently been recovered in a latitudinal stretch from North Carolina to Georgia (Roest 1957, Bird and Palmer 1988), while migrants from New England and southeastern Canada, often spend their winters farther south, from South Carolina to southern Florida (Roest 1957, Layne 1982, Bird and Palmer 1988). Some migrant American Kestrels from eastern Canada travel even farther south, spending their winters on Caribbean islands (Bird and Palmer 1988). Farther west, migrant American Kestrels from the south Canadian prairies east to the Great Lakes winter in Arkansas, Louisiana, and southern Texas (Roest 1957, Bird and Palmer 1988).

American Kestrels summering in middle latitudes ($\sim 44\text{--}36^{\circ}\text{N}$) are known to be partially migratory, with some birds engaging in seasonal migration and others resident in the general vicinity of the breeding grounds year-round (Bird and Palmer 1988). Illinois is within this middle latitudinal range, extending from $42.5\text{--}37^{\circ}\text{N}$, and is known to host both year-round residents and visiting migrants during the winter months (Enderson 1960). In this middle latitudinal range, the ratio of migratory Kestrels to resident Kestrels decreases from north to south (Bird and Palmer

1988), and at latitudes south of 35°N, Kestrels are thought to be largely resident (Bird and Palmer 1988, Smallwood and Bird 2002, Goodrich et al. 2012).

Hobson et al. (2009) examined the summer origins of Kestrels wintering in South Carolina and Tennessee and created a Kestrel-specific calibration function using the $\delta^2\text{H}_f$ values of known origin juvenile American Kestrels included in the Lott and Smith (2006) dataset. Hobson et al. (2009) reported that most nonresident Kestrels appeared to be from the northern mid-latitudes of the U.S., with a diminishing probability of birds originating from the northern extent of their range; they concluded that their findings were consistent with leap-frog migration. Hobson et al. (2009) also estimated that the percentage of residents was 13.1% for Tennessee and 9.3% for South Carolina. This has been the only stable isotope-based investigation into the breeding origins of wintering American Kestrels. Studies such as these have begun to elucidate the migratory connectivity of this species, but more studies from other parts of their range are needed. The present study is the first to investigate the summer origins of American Kestrels wintering in Illinois via stable isotope ($\delta^2\text{H}$) methods, which will allow the tracking of future range shifts due to climate change and provide improved techniques for obtaining annual location information for Kestrels that can better serve conservation efforts across North America. Our objectives were to determine the most likely summer origins of American Kestrels wintering in central and northern Illinois and to investigate the ratio of permanent residents to wintering migrants in that region.

METHODS

Capture of Live Birds and Field Data Collection

American Kestrels were trapped from December 2015 through February 2016, in northern Illinois (from 42.50°N to 40.92°N) and central Illinois (from 41.73°N to 39.00°N), USA. Our objective was to sample birds that had reached their wintering grounds in Illinois, while avoiding migrating individuals. Migration timing data from several long-term (count data covering >5 years) hawkwatch sites in Illinois indicate that fall American Kestrel migration within the state peaks from mid-September through mid-October, levels off by November, and thus concludes prior to December (Hawk Migration Association of North America 2019). Unfortunately, none of these Illinois hawkwatch sites are active during the spring migration season, so data pertaining to the timing of spring migration were obtained from alternative sources. Spring American Kestrel migration is more dispersed in comparison to the more concentrated fall migration and primarily occurs from late March through early May (Smallwood and Bird 2002, Crossley et al. 2013). Enderson (1960) monitored the American Kestrel population in a 43 square mile study area in east-central Illinois from December 1958 to July 1959 and found that the number of Kestrels observed remained relatively level from December through February, began to increase in early March, and peaked from mid-March to Mid-April. These data suggest that spring Kestrel migration through Illinois occurs post-February. Spring migration data collected in nearby states also seem to support this. Spring migration count data available from four hawkwatch sites in Michigan that have collected data ranging from nine to sixteen consecutive years and covering the latitudinal span from 43.10°N to 47.46°N, consistently show count totals that are level throughout March and that peak from mid-April to early May (Hawk Migration Association of North America 2019). A hawkwatch site that collected spring migration data in Ashland, WI

(46.58°N) from 2003 to 2004 also had count totals that remained level throughout March and peaked in April (Hawk Migration Association of North America 2019). The spring migration timing depicted by these data supports the inferred post-February spring Kestrel migration through Illinois.

All Kestrels sampled were caught using a bal-chatri trap lured with a House Mouse (*Mus musculus*). Bal-chatri traps are small metal cages that use monofilament nylon tied to the top of the trap in the form of self-tightening nooses (Bub 1991). When a Kestrel is spotted, often perched on rural utility wires or utility poles, the bal-chatri trap containing the lure mouse is placed in a safe location (e.g., on the shoulder or grassy edge of a non-busy road) unobstructed from the Kestrel's line of sight. The lure mouse housed within the trap attracts the Kestrel, which flies down to retrieve its intended prey. However, instead of capturing the rodent, the bird's foot gets caught in the monofilament nooses, thus preventing it from flying away. Once caught, all Kestrels were promptly removed from the trap, immediately processed, and then released at the site of capture.

Feather samples were obtained from each bird by cutting a small piece of the vane from the second white spot proximal to the feather tip on the fourth primary feather (P4; Figure 1) of the right wing, in accordance with the recommendation of Hobson et al. (2009). Hobson et al. (2009) emphasize the importance of choosing a feather that holds a high probability of being molted at the area of interest (e.g., the breeding or summering grounds), thus incorporating a distinct isotopic signature from this area. Each year, American Kestrels undergo a prebasic molt that overlaps extensively with breeding (Willoughby and Cade 1964, Smallwood 1989, Howell 2010). Once eggs are laid, both sexes may begin their wing molt (Howell 2010). Females frequently begin primary molt at the onset of incubation, likely because they have a lower

energetic expenditure during the incubation and brooding period in comparison to males (Balgooyen 1976, Smallwood 1988). Conversely, males typically suspend their primary molt until later during the breeding season because they are the primary provider of food for the female and nestlings during this time (Sherman 1913, Roest 1957, Willoughby and Cade 1966, Balgooyen 1976). Regardless of sex, primary feather molt begins with P4 and then progresses both inward and outward simultaneously (Willoughby 1966, Howell 2010). Because P4 is the first primary feather to be molted, it holds the highest probability of being grown on or near the breeding grounds in adult birds, maximizing the likelihood of providing insight to the summer origins via a stable isotope approach. All juvenile primary feathers are grown simultaneously while in the nest, prior to fledging, and are retained until their second summer (Howell 2010), thus providing insight to their natal grounds. All feather samples were then stored in paper envelopes until they were prepared for isotopic analysis.

All individuals were also sexed, aged, and photographed before being released at the capture location. Aging was performed using the revised key produced by Smallwood (1989), which is based on body plumage and flight feather characteristics such as the presence and arrangement of fault bars, flight feather wear, evidence of molt (e.g., retained flight feathers), and the width of the sub-terminal band in comparison to the other proximal bands on female rectrices. Individuals were assigned as a juvenile, adult, or with an unknown age if they did not possess age-defining characteristics (i.e. lack of fault bars, no retained flight feathers). A juvenile was defined as an individual that had completed its first prebasic, or prejuvenile, molt, acquiring its first “real”, non-downy feathers, but had not yet undergone the second prebasic molt (Howell 2010). An adult was defined as an individual that had completed a second or subsequent prebasic

molt, and thus no longer carried its juvenile remiges or rectrices acquired by the prejuvenile molt (Howell 2010).

Sample Preparation and Isotopic Analysis

The two-step cleaning protocol recommended by Paritte and Kelly (2009) was utilized to clean all feather samples prior to analysis. Paritte and Kelly (2009) found that by first cleaning feather samples of Japanese Quail (*Coturnix japonica*) in a detergent solution and then with a chloroform:methanol solution, variation in the measured stable isotope ratios of the feathers was reduced. First, feather samples were soaked in a 1:30 detergent:deionized water solution for 5 minutes. Samples were then rinsed with deionized water until all suds were gone. Then, feather samples were rinsed with a 2:1 chloroform:methanol solution for five minutes, and the solution was then vacuumed. Samples were soaked in the 2:1 chloroform:methanol solution two more times for five minutes each and were then rinsed five to eight times with deionized water to remove any trace of the 2:1 chloroform:methanol solution. Feather samples were then carefully transferred to a clean surface in a fume hood and allowed to air dry for at least twenty-four hours. Once feathers were completely dry, they were placed in microcentrifuge tubes and then into paper coin envelopes for shipping to the UW Stable Isotope Facility at the University of Wyoming.

Once samples were received by the UW Stable Isotope Facility, a modification of the comparative equilibration technique detailed by Wassenaar and Hobson (2003) was utilized to measure the $\delta^2\text{H}$ of nonexchangeable hydrogen in the samples. Approximately 0.2 mg of each cleaned sample, international standards (USGS42 and USGS43; Coplen and Qi 2012), and the lab's internal keratin standard (turkey feather keratin; UWSIF33) was placed in a silver capsule slightly crimped at the top and was allowed to equilibrate with ambient water vapor in the lab for

3 weeks prior to deuterium isotope analysis so that the $\delta^2\text{H}$ value of exchangeable hydrogen could be calculated. All samples and standards were then dried for at least twelve hours under vacuum at room temperature to remove any absorbed water. A Thermo temperature conversion elemental analyzer (TC/EA) connected to a Thermo Delta-V isotope ratio mass spectrometer (IRMS) was then used to measure $\delta^2\text{H}_f$. The $\delta^2\text{H}$ data are reported in per mil (‰) relative to the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale using a 2-point normalization curve with USGS42 (Tibetan hair) and USGS43 (Indian hair; Coplen and Qi 2012), whose $\delta^2\text{H}$ values of nonexchangeable hydrogen are -78.5‰ and -50.3‰ respectively. The among-run analytical precision (1σ) of the internal keratin standard (UWSIF33) analyzed along with the samples was 2.67‰, while the among-run analytical precision (1σ) of the international standards, USGS42 and USGS43 (Coplen and Qi 2012), was 1.79‰ and 1.29‰ respectively.

Statistical Analyses and Assignments of Geographic Origin

Previous studies have used amount-weighted $\delta^2\text{H}_p$ values of growing-season (months with a mean daily temperature $>0^\circ\text{C}$) precipitation in the creation of their calibration functions (Hobson et al. 2007, Hobson et al. 2009, Van Wilgenburg and Hobson 2011, Haché et al. 2012). However, the months of rainfall that hold the strongest influence on the $\delta^2\text{H}$ values within the food webs of local ecosystems, which in turn largely influences the $\delta^2\text{H}_f$ values obtained during feather growth, remains uncertain (Hobson 2011, Hobson et al. 2012). Thus, others have used models of amount-weighted mean annual $\delta^2\text{H}_p$ values instead of growing-season precipitation $\delta^2\text{H}_p$ values (Macías-Duarte and Conway 2015). Due to its complex nature, the isotopic flow of $\delta^2\text{H}$ from the environment to an American Kestrel, or any other living organism, likely incorporates many different precipitation events spread across a wide time frame (Hobson 2011). For these reasons,

a geostatistical model of amount-weighted mean annual $\delta^2\text{H}_p$ values for North America was created using the online workspace IsoMAP (Bowen et al. 2014). IsoMAP is a web accessible tool that allows users to model $\delta^2\text{H}_p$ values found in the environment across a specified geographic and temporal extent using data collected by the Global Network of Isotopes in Precipitation (GNIP; Bowen et al. 2014, Bowen et al. 2019). IsoMAP also gives users the ability to utilize a semi-parametric Bayesian framework developed by Wunder et al. (2005) to make geographic assignments based on $\delta^2\text{H}$ values from samples of unknown origin (Bowen et al. 2014). The model we created incorporated environmental data spanning from 1960 to 2010 that were collected from 119 unique monitoring stations. Elevation (e) and latitude (l^2) were included as independent variables in the model due to their influence on $\delta^2\text{H}_p$ values in North America (Dansgaard 1964, Rozanski et al. 1993, Bowen 2010) and their statistically significant contribution to the model. The model and map for our mean annual $\delta^2\text{H}_p$ isoscape are published as jobs 73439 and 73636 at <https://isomap.rcac.purdue.edu/isomap/>, and the model summary is presented in Appendix Table 2.

Age-related discrepancies in $\delta^2\text{H}_f$ values have been documented in multiple avian families (Meehan et al. 2003, Smith and Dufty Jr. 2005, Langin et al. 2007, Greenwood and Dawson 2011, Haché et al. 2012, Marquiss et al. 2012, Studds et al. 2012, van Dijk et al. 2014). Several non-exclusive hypotheses have been proposed to explain the observed age-related differences, which typically involve adults with enriched $\delta^2\text{H}_f$ values in comparison to nestlings and immature birds with retained feathers molted during the nestling stage. The hypotheses include differences in hydrogen budgets owing to variation in diet, the use of endogenous reserves accumulated prior to the nesting season, contrasting feather growth rates, and distinct

exposure levels to heat stress resulting from varying microenvironments and activity levels during feather molt (Meehan et al. 2003, Langin et al. 2007, Haché et al. 2012).

Age-related differences in $\delta^2\text{H}_f$ values between adult and nestling raptors in the families Accipitridae and Falconidae have been observed and are substantially more pronounced than those of other avian families (Meehan et al. 2003, Smith and Dufty Jr. 2005, Greenwood and Dawson 2011). Meehan et al. (2003) first revealed this discrepancy when they found that the feathers of adult Cooper's Hawks (*Accipiter cooperii*) in Wisconsin, North Dakota, and British Columbia, Canada exhibited highly enriched $\delta^2\text{H}_f$ values when compared to those of their nestlings. Smith and Dufty Jr. (2005) and Greenwood and Dawson (2011) also found that adults exhibited highly enriched $\delta^2\text{H}_f$ values when compared to nestlings in their studies on Northern Goshawks (*Accipiter gentilis*) in western North America and American Kestrels in Saskatchewan, Canada respectively. Meehan et al. (2003) proposed three nonexclusive hypotheses to explain the highly enriched $\delta^2\text{H}_f$ values exhibited by the adult Cooper's Hawks in their study. First, there is the possibility that adults consume migrant prey with tissues that are more enriched than those of local prey. Second, if the adults themselves are migratory, their feathers could be incorporating endogenous reserves collected at lower latitudes or elevations (Bearhop et al. 2002, Inger and Bearhop 2008). Third, evaporative cooling from the upper respiratory tract and cutaneous body surfaces may result in enriched body water in adult birds (Wolf and Martínez del Río 2000, Wolf and Martínez del Río 2003, McKechnie et al. 2004).

Meehan et al. (2003) and Smith and Dufty Jr. (2005) provide examples that contest the first two hypotheses, but Greenwood and Dawson's (2011) findings corroborate the evaporative cooling hypothesis. Molt in North American raptors often overlaps with breeding activities such as incubation, brooding, and food provisioning (Howell 2010). Each of these activities can

increase the metabolism and body temperature of adult birds (Williams 1996, Thomson et al. 1998, Gill 2007, Langin et al. 2007). Furthermore, during the incubation period, adults must maintain a strict body temperature range to keep the eggs close to the optimum temperature for development (Gill 2007). If the nest temperature becomes too high, egg cooling can be achieved through contact with the adult's body, which is kept cool through increased evaporative cooling (Walsberg and Voss-Roberts 1983). Together, these factors increase the likelihood and frequency of evaporative water loss during the period of feather molt. During periods of increased evaporative water loss, body water levels can become deuterium enriched, as water molecules incorporating the lighter hydrogen isotope (protium) evaporate more readily than those composed with deuterium (McKechnie et al. 2004). Hobson et al. (1999a) demonstrated that approximately 26-32% of the nonexchangeable hydrogen in feather keratin originates from the body water pool, illustrating how evaporative water loss leading to a deuterium enriched body water pool could result in enriched feathers. If the extensive $\delta^2\text{H}_f$ discrepancy between adult and nestling raptors at similar geographic locations is due to the overlap between breeding and feather molt in adult birds, it could clarify why the phenomenon is less pronounced in other bird species (Powell and Hobson 2006, Langin et al. 2007, Marquiss et al. 2012, Studds et al. 2012, van Dijk 2014), which undergo molt post-breeding (Howell 2010).

Regardless of the underlying mechanism, age-related differences in the $\delta^2\text{H}_f$ values of juvenile and adult raptors are substantial and need to be accounted for when making isotope-based geographic assignments. Prior studies utilizing calibration functions created from tissue samples of known origin obtained from nestling and juvenile raptors on or near their natal grounds have produced questionable, and ultimately unreliable, geographic assignments for adult raptors of unknown origin (Hobson et al. 2009, De Ruyck et al. 2013, Wittenberg et al. 2013).

Consequently, separate age-specific calibration functions were created to produce geographic assignments for juvenile and adult American Kestrels. The juvenile calibration functions were created using known origin juvenile American Kestrel $\delta^2\text{H}_f$ values from the Lott and Smith (2006) dataset ($n = 41$) and a limited portion of the Greenwood and Dawson (2011) dataset ($n = 5$). Estimates of $\delta^2\text{H}_p$ values for the feather sample locations of the Lott and Smith (2011) juveniles were obtained using a modification of their recommended approach with our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape that was created in IsoMAP. Because there was no standardized protocol for reporting location information for each bird, and because most locations were somewhat inexact (e.g., the name of a city or the name of a geographic feature such as a lake, creek, or bay), our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape and the geographic coordinates for the 41 known origin juvenile American Kestrels reported in the Lott and Smith (2006) dataset were imported into ArcMAP 10.7© (henceforth as ArcMAP), and circular buffers with a 10-km radius were created around the geographic coordinates for each bird. The mean $\delta^2\text{H}_p$ value for each buffer was then obtained using the Zonal Statistics as Table tool in ArcMAP and was utilized for these birds. Exact geographic coordinates of the occupied Kestrel nest boxes in the Greenwood and Dawson (2011) dataset were available, so the geographic coordinates for the nest boxes used by these birds were imported onto our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape in ArcMAP, and the $\delta^2\text{H}_p$ value at each of these points was used for the corresponding birds.

The appropriate regression technique for defining a line of best fit for a bivariate relationship with uncertainty in both variables is ambiguous (Smith 2009). While neither technique is perfect for modelling the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$, both the reduced major axis (RMA) regression and the ordinary least squares (OLS) regression have been used in

calibration function development (Lott and Smith 2006, Hobson et al. 2009, van Dijk et al. 2014, Nelson et al. 2015). RMA regression creates a line of best fit that minimizes the sum of the product of the horizontal and vertical deviations, and thus the area of the right triangles formed when straight lines are drawn from the data points to the resulting regression line, and is often utilized to model the data when there is uncertainty in both the X-axis and Y-axis variables (Smith 2009). On the other hand, OLS regression creates a line of best fit that minimizes the sum of the squared vertical deviations (Smith 2009) and is often used when there is thought to be uncertainty in only the Y-axis variable (Smith 2009). Biologically, $\delta^2\text{H}_p$ largely determines $\delta^2\text{H}_f$ because precipitation events directly impact the distribution of available stable hydrogen isotopes found in environmental water throughout natural systems (Dansgaard 1964, Rozanski et al. 1993, West et al. 2006). Therefore, linear functions have typically been utilized with $\delta^2\text{H}_p$ as the independent variable and $\delta^2\text{H}_f$ as the dependent variable, producing calibration functions in the form of $\delta^2\text{H}_f = \beta_0 + \beta_1 * \delta^2\text{H}_p$, where β_0 is the y-intercept and β_1 is the slope. Smith (2009) argues that in biological situations such as this, in which one variable is dependent on the other (asymmetrical relationship between variables), the data should be modeled with OLS regression, even when there is error present in both the X-axis and Y-axis variables. Ultimately, both an RMA regression-based and OLS regression-based calibration function were created utilizing $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ values for the 46 known origin juvenile American Kestrels described above. Both regressions were run in SAS 9.4©.

Ideally, an adult American Kestrel calibration function would be developed with a large sample size of known origin adults spread across their North American breeding range, but such a dataset does not currently exist. Therefore, to create the RMA regression-based and OLS regression-based adult American Kestrel calibration functions, we established an age-related

$\delta^2\text{H}_f$ adjustment factor that could be used to adjust the juvenile calibration functions we created. Greenwood and Dawson (2011) were able to obtain $\delta^2\text{H}_f$ values from adult American Kestrels and their nestlings at 12 distinct nest boxes spread throughout their study area. Using the $\delta^2\text{H}_f$ values from the adults and corresponding nestlings at these 12 nest boxes, the mean difference in $\delta^2\text{H}_f$ values between adults and nestlings was calculated and utilized as the age-related $\delta^2\text{H}_f$ adjustment factor. Each juvenile calibration function was then adjusted by subtracting the age-related $\delta^2\text{H}_f$ adjustment factor from $\delta^2\text{H}_f$. Isolating $\delta^2\text{H}_f$ on one side of the functions altered the y-intercept for each, effectively shifting the regression lines upwards and creating an RMA regression-based and OLS regression-based adult American Kestrel calibration function. This calibration function adjustment is made under the assumption that there is no substantial geographic variation in the magnitude of the difference in $\delta^2\text{H}_f$ values between juvenile and adult American Kestrels, which may not be valid (Meehan et al. 2003). Meehan et al. (2003) witnessed geographic variation in the magnitude of the difference in $\delta^2\text{H}_f$ values between juvenile and adult Cooper's Hawks at the same location. However, Smith and Dufty Jr. (2005) observed that temporal patterns in $\delta^2\text{H}_p$ seem to explain much of the geographic variation witnessed by Meehan et al. (2003), and that when compensated, the age-related discrepancy in $\delta^2\text{H}_f$ values is comparable for Cooper's Hawks and Northern Goshawks across regions. Smith and Dufty Jr. (2005) also noted that geographic variation in the $\delta^2\text{H}_f$ discrepancy between age classes is much more apparent when comparing values between geographic locations with pronounced differences in seasonal $\delta^2\text{H}_p$ patterns (e.g., coastal vs. inland sites).

Prior to producing geographic assignments for the 78 Kestrels of unknown origin sampled in our study, model performance was examined using a test dataset of 54 birds to determine the actual calibration functions (RMA-based or OLS-based) that would be used.

Observed $\delta^2\text{H}_f$ values were regressed against predicted $\delta^2\text{H}_f$ values for 31 juvenile and 23 adult American Kestrels of known origin (location of feather molt known for the feathers that were sampled). Twenty-eight of the juvenile Kestrels and 21 of the adult Kestrels were part of the Greenwood and Dawson (2011) dataset, while the remaining 3 juveniles and 2 adults were specimens belonging to Illinois State University's John Wesley Powell-Dale Birkenholz Natural History Collections (hereafter referred to as ISU Collections). The same two-step cleaning protocol recommended by Paritte and Kelly (2009) was also used to clean the feathers of the 5 known origin Kestrels obtained from the ISU Collections. None of these 54 individuals were included in calibration function creation. Predicted $\delta^2\text{H}_f$ values were obtained by plugging $\delta^2\text{H}_p$ values pulled from our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape into the appropriate age-specific calibration functions. For the individuals that had exact location information ($n = 50$; e.g., nest-box locations), $\delta^2\text{H}_p$ values were obtained from specific geographic coordinates. For the remaining Kestrels with inexact information pertaining to the geographic area of feather molt (i.e. the name of a city; $n = 5$), circular buffers with a 10-km radius were created around the center of the city/town/county these birds originated from. The mean $\delta^2\text{H}_p$ value for each buffer was then utilized for these birds. These 5 birds were assumed to be on or near their breeding grounds, and thus likely near the location of feather molt, as their collection dates coincided with or were shortly after the North American Breeding Bird Survey window for their respective locations (USGS Patuxent Wildlife Research Center 2018). The resulting slope and y-intercept values of the model performance regressions were compared and examined for a measure of bias and predictive ability. In an additional effort to examine the predictive ability of the calibration functions, the mean difference between the observed $\delta^2\text{H}_f$ values and the predicted $\delta^2\text{H}_f$ values was compared for the RMA and OLS regression-based calibration functions, as well as the

frequency in which the RMA and OLS regression-based calibration functions produced more accurate predictions of $\delta^2\text{H}_f$ (predicted $\delta^2\text{H}_f$ value closer to the observed $\delta^2\text{H}_f$ value). Both the juvenile and adult OLS regression-based calibration functions exhibited a superior predictive ability and less bias than the RMA regression-based calibration functions, so they were used for all further geographic assignments and are henceforth referred to simply as calibration functions.

IsoMAP was designed to produce geographic assignments based on water isoscapes (Bowen et al. 2014); thus, $\delta^2\text{H}_f$ values were converted to $\delta^2\text{H}_p$ values utilizing the age-specific calibration functions. In addition to incorporating a spatially varying component of uncertainty in geographic assignments correlated with $\delta^2\text{H}_p$ isoscape estimates, IsoMAP also includes a spatially invariant component of uncertainty associated with the many processes affecting the relationship between $\delta^2\text{H}_p$ and the $\delta^2\text{H}$ value of a sample (Bowen et al. 2014). To include this spatially invariant component of uncertainty in geographic assignments, IsoMAP users are required to input a rescaled version of the calibration function variance, obtained by dividing the standard deviation of the regression residuals by the slope of the regression line (Bowen et al. 2014). Because the adult calibration function was created by adjusting the juvenile calibration function rather than utilizing a distinct dataset of known origin birds, the standard deviation of the regression residuals from the juvenile calibration function was used to estimate the variance in the relationship between $\delta^2\text{H}_p$ values and the $\delta^2\text{H}_f$ values of adults. Geographic assignments were then made for all individuals using the IsoMAP Assignment Model tool in combination with our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape. All individuals that were able to be aged solely on the body plumage and flight feather characteristics outlined by Smallwood (1989; $n = 48$) or leg band information ($n = 1$) were assigned utilizing the appropriate age-specific calibration function. Three additional birds were aged as adults based on a combination of

supportive, but nondefinitive, body plumage and flight feather characteristics and their measured $\delta^2\text{H}_f$ value (see Appendix for explanation). Geographic assignments for the remaining 26 birds of unknown age were made using both the juvenile and adult calibration functions, and the differences in their predicted summer origins were compared. Geographic assignments were also produced for the 54 birds of known origin that composed the test dataset.

The IsoMAP Assignment Tool produced a 5-arc minute resolution probability of origin surface for each bird, where each individual grid cell within the selected spatial range presents a probability of origin value, and the sum of the probability values for the grid cells is equal to 1. We then examined where the grid cell values that encompassed the actual summer origins of the known origin test dataset birds fell within the range of the cell values produced for their respective probability of origin surfaces and determined the accuracy of the geographic assignments for the test dataset birds at several distinct thresholds (i.e. only including the upper 30%, 20%, and 10% of grid cell values as likely summer origins). This was done by recoding the upper 30%, 20%, and 10% of grid cell values of the estimated “probabilities of origin” for each individual bird of known origin in the test dataset as 1 and all other grid cells as 0. Accuracy was quantified by calculating the percentage of the known origin test dataset birds withheld from calibration function creation with actual summer origins contained within the likely summer origins produced by their respective binary maps. Based on the accuracy levels observed under these distinct scenarios, the grid cells that represented the upper 30% and the upper 20% of the estimated “probabilities of origin” for each individual bird of unknown origin were then separately recoded as 1, and all other grid cells were recoded as 0 and were no longer considered as likely summer origins. This effectively created two binary maps per assigned individual (four

for individuals of unknown age), representing that bird's likely summer origins under two different scenarios with distinct levels of accuracy and precision.

We then further refined our maps of likely origin by only including geographic areas within the North American breeding range of the American Kestrel, by removing grid cells containing unlikely breeding habitat, and by excluding grid cells representing unlikely summer origins based on movement patterns revealed by banding data. A breeding range map for the American Kestrel was produced by Fink et al. (2019a) using an ensemble of boosted regression tree models built using occurrence data retrieved from eBird (Sullivan et al. 2009) and three classes of predictor variables (observation-effort, temporal, and environmental) and was obtained from <https://ebird.org/science/status-and-trends/download-data>. For an example of this approach using the Wood Thrush, see Fink et al. (2019b). A species' range was defined as the areas where the species is expected to occur on at least five percent of the predicted hypothetical eBird checklists in a given week (Fink et al. 2019a). The raw 2.96 km resolution breeding range map was downloaded, imported into ArcMap, and was converted to a raster with a resolution of 2.96 km. The breeding range map was then projected into the North America Albers Equal Area Conic projection (NAD83 datum), clipped to the North American extent of the American Kestrel's breeding range, and was resampled to a 1 km resolution to arrive at a common spatial resolution given the different resolutions of the datasets. A 1 km resolution was chosen because 1 km² is within the range of the breeding territory size of the American Kestrel, which is thought to vary with food and nest-site availability (Bird and Palmer 1988, Smallwood and Bird 2002).

Grid cells containing unlikely summering habitat were then removed from the breeding range map. During the breeding season, American Kestrels occupy a wide variety of habitats that are dominated by open space with short ground vegetation and little taller woody vegetation

(Bird and Palmer 1988). When nest boxes are made available, occupancy rates by American Kestrels are lower in areas with a higher density of woody vegetation and are highest in the most open habitats (Rohrbaugh Jr. and Yahner 1997, Smallwood and Wargo 1997). Thus, grid cells composed largely of woody vegetation were deemed as unlikely summering habitat for American Kestrels and were removed from the breeding range map. To accomplish this, percent tree cover (PTC) data for North America were obtained from the Terra MODIS Vegetation Continuous Field (VCF) product (available as MOD44B v006 <https://lpdaac.usgs.gov/products/mod44bv006/>). The PTC layers available in the MOD44B v006 data product provide a global, quantitative estimation (values ranging from 0 to 100) of the PTC in a 250 m resolution grid cell format. Because of the magnitude of the entire dataset, the global PTC data are broken down into smaller tiles that can be downloaded individually and mosaicked together to depict PTC coverage for a target geographic area during the years 2000 to 2017. Tiles covering North America were downloaded and mosaicked together in ArcMAP for each year during the 2000 to 2017 timespan. The PTC grid cell layers were then projected in the North America Albers Equal Area Conic projection and resampled to a 1 km resolution.

Summer occurrence records were then obtained from eBird (Sullivan et al. 2009). A “Date Range” filter was activated so that only June and July occurrence records were displayed, presumably characterizing the types of areas most likely occupied during the period of breeding and/or molt based on the known phenology of these activities (Smallwood and Bird 2002). Occurrence records were not constrained by year. Occurrence records were then manually screened to locate those with the highest precision and accuracy possible. This involved manually searching for occurrence records that included the GPS coordinates of the sighting location, indicating that the observation pin was placed on or near to the sighting (e.g., nest box

locations, stationary counts, addresses), or that provided enough detail in the “location” and/or “details” to decipher precise and accurate location information. A total of 470 unique occurrence records ranging from 1990 to 2019 were drawn from 48 U.S. states and 10 Canadian provinces. Google Earth Pro (WGS84 datum) was then used to manually obtain GPS coordinates for the occurrence records that did not already have them included with their eBird submission. This was done by matching the eBird submission pin or the area described in the observation details with the matching geographic location in Google Earth Pro and retrieving the latitude and longitude GPS coordinates.

The GPS coordinates for the 470 summer occurrence records were then imported into ArcMAP and plotted on top of the PTC grid cell layers. Occurrence records from the years 2000 to 2017 were plotted on the corresponding year’s PTC layer, while all occurrence records prior to the year 2000 were plotted on the 2000 PTC layer, and all occurrence records after 2017 were plotted on the 2017 PTC layer. The underlying PTC grid cell value for each of the summer occurrence records was extracted, and a highest presence threshold was determined based on the highest PTC value for a cell occupied by a summering Kestrel. The highest presence threshold was determined to be 62%, so all grid cell values $>62\%$ were removed from the 2015 PTC layer, which depicts PTC coverage for the time period of interest for the 78 Kestrels of unknown origin we sampled during the winter of 2015-16. The raster calculator tool in ArcMAP was then used to add the North American breeding range raster with the edited 2015 PTC raster, and a new grid cell raster layer composed of only cells that were both within the North American breeding range and that had a PTC value $\leq 62\%$ was created (henceforth referred to as the BR ≤ 62 raster).

Grid cells representing unlikely summer origins based on known movement patterns were then removed from the BR ≤ 62 raster. American Kestrels concentrate into 4 major flight

corridors during fall migration: along the Atlantic Coast, Appalachian ridges, Great Lakes coastlines, and western mountains (Smallwood and Bird 2002). These flight corridors ultimately seem to influence where migratory American Kestrels winter. Based on band recovery data, American Kestrels summering east of the Appalachian Mountains also tend to winter east of the Appalachians, while Kestrels summering west of the Continental Divide remain west for the winter (Roest 1957, Layne 1982, Bird and Palmer 1988). Thus, all grid cells lying east of the Appalachian Mountains and west of the Continental Divide were removed from the $BR \leq 62$ raster. Furthermore, all grid cells south of $\sim 39.52^\circ\text{N}$ (the southernmost limit of the boundary line of Morgan County, IL, the southernmost county Kestrels were sampled from during the winter of 2015-16) were removed from the $BR \leq 62$ raster. Although band recovery data indicate that recently fledged birds and post-breeders may disperse in any direction following fledging/nesting, this movement occurs prior to their fall migration southward (Roest 1957, Bird and Palmer 1988), and we did not expect Kestrels to winter north of their summering location.

Following this, each of the binary maps produced for the 78 Kestrels of unknown origin was projected in the North America Albers Equal Area Conic projection and resampled to a 1 km resolution. The raster calculator tool in ArcMAP was then utilized to add each binary map with the newly created raster described above, creating two refined binary maps for each bird (four for the birds that were unable to be aged) that represents that individual's likely summer origins based on the combination of its $\delta^2\text{H}_f$ value and the refinements made by only including geographic areas within the North American breeding range of the American Kestrel, by removing grid cells containing unlikely breeding habitat, and by excluding grid cells representing unlikely summer origins based on known movement patterns (Figure 3). The

precision of our geographic assignments was quantified as the mean number of grid cells ($\pm$ SD; equivalent to km²) that were predicted as summer origins in our refined binary maps.

Using the likelihood-based approach established by Van Wilgenburg et al. (2012) and employed by Asante et al. (2017), individuals were then classified as locals or migrants using the relationship between their observed $\delta^2\text{H}_f$ value and the expected mean $\delta^2\text{H}_f$ value for a bird at their wintering location. Expected mean $\delta^2\text{H}_f$ values were obtained by creating juvenile and adult American Kestrel $\delta^2\text{H}_f$ surfaces by converting our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape to juvenile and adult expected mean $\delta^2\text{H}_f$ isoscapes (Appendix Figures 5 and 6) using the respective calibration functions. Expected mean $\delta^2\text{H}_f$ values were extracted from the appropriate $\delta^2\text{H}_f$ surfaces, and these values were compared to the observed $\delta^2\text{H}_f$ values of the 78 Kestrels of unknown origin. Under the assumption that the $\delta^2\text{H}_f$ values of feathers grown at a specific locality follow a normal distribution, a normal probability density function was used to estimate the likely distribution of potential $\delta^2\text{H}_f$ values of feathers grown at a locality. Probability densities were estimated by utilizing the expected mean $\delta^2\text{H}_f$ value as the mean $\delta^2\text{H}_f$ value for the normal distribution at a locality, and by using the standard deviation of the regression residuals (SD = 23.27‰) from our calibration function as the estimated standard deviation for the $\delta^2\text{H}_f$ values of that locality. Individual birds were then assigned as locals or migrants based on whether or not their observed $\delta^2\text{H}_f$ value was within 23.27‰ of the expected mean $\delta^2\text{H}_f$ value at the location at which they were wintering. Based on these assumptions, this effectively established a 2:1 odds ratio (~68% chance) that an individual's $\delta^2\text{H}_f$ value was grown at that locality (Boslaugh 2013). The ratio of residents to migrants was then summarized for the Kestrels wintering in the Northern and Central Divisions of Illinois (Gault et al. 1922). The Northern Division runs from 42.50°N at its northernmost point to 40.92°N at its southernmost

point, while the northernmost and southernmost points of the Central Division are at 41.73°N and 39.00°N, respectively. The test dataset birds withheld from calibration function creation were also classified as residents or migrants to determine whether the likelihood-based approach used would correctly classify them as originating from their known summering locations.

The refined binary maps of likely summer origins for the migrant Kestrels were then summed using the raster calculator in ArcMAP. This allowed us to effectively visualize the most likely summer origins of the migrant Kestrels that wintered in the Northern and Central Divisions of Illinois during 2015-16. This was first done solely with the migrant Kestrels that were able to be aged and was then also done including individuals of an unknown age that were classified as migrants when all of the unknown age individuals were treated as juveniles or adults.

Finally, using SAS 9.4©, a two-tailed two-sample Welch's t-test and a two-tailed Wilcoxon rank sum test were performed on the migrants that were able to be aged to determine if there was a sex effect on $\delta^2\text{H}_f$ values. Prior to performing the tests, $\delta^2\text{H}_f$ values of the adult birds were adjusted using the age-related $\delta^2\text{H}_f$ adjustment factor (i.e. 58.55% was subtracted from each adult $\delta^2\text{H}_f$ value), which allowed for a direct comparison of the $\delta^2\text{H}_f$ values of male and female migrants regardless of age. Before performing the two-sample t-test, the normality assumption and the assumption of homogeneity of variance were checked using the Shapiro-Wilk test and the *F*-test of Equality of Variances respectively.

RESULTS

A total of 78 American Kestrels were captured and sampled during the winter of 2015-16 (Appendix Table 3). When combining the American Kestrels sampled from both northern and central Illinois, 50% were males and 50% were females. When considering only the American

Kestrels sampled in northern Illinois ($n = 11$), ~82% were males, while only ~18% were females. When considering only the American Kestrels sampled in central Illinois, ~45% were males and ~55% were females. Measured $\delta^2\text{H}_f$ values ranged from -76.20‰ to 39.63‰. When using $\delta^2\text{H}_p$ values from our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape and $\delta^2\text{H}_f$ values of the known origin juvenile American Kestrels from the Lott and Smith (2006) dataset ($n = 41$) and a subset of the Greenwood and Dawson (2011) dataset ($n = 5$), the juvenile OLS calibration function characterizing the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ was: $\delta^2\text{H}_f = 20.74 + 1.05 * \delta^2\text{H}_p$ ($F = 81.04$, $df = 1$ and 44 , $P < 0.001$, $r^2 = 0.65$; Figure 2). The standard deviation of the regression residuals was 23.27‰. The age-related $\delta^2\text{H}_f$ adjustment factor that was used to adjust the juvenile OLS calibration function we created was 58.55‰ ($\pm$ SD 15.30‰), and the resulting adult OLS calibration function was: $\delta^2\text{H}_f = 79.29 + 1.05 * \delta^2\text{H}_p$. The juvenile RMA calibration function, created using the same amount-weight mean annual $\delta^2\text{H}_p$ isoscape and $\delta^2\text{H}_f$ values from the known origin juvenile American Kestrels, and the adult RMA calibration function created using the same age-related $\delta^2\text{H}_f$ adjustment factor can be found in the Appendix.

Regression of observed vs. predicted $\delta^2\text{H}_f$ values for the test dataset composed of Kestrels of known origin withheld from calibration function creation ($n = 54$) suggested that the OLS-based calibration functions had a superior predictive ability and exhibited less bias than the RMA-based calibration functions. Regression of observed vs. predicted $\delta^2\text{H}_f$ values for the juvenile American Kestrels of known origin in the test dataset ($F = 248.0$, $df = 1$ and 29 , $P < 0.001$, $r^2 = 0.90$) produced regression equations of:

$$\text{OLS: observed } \delta^2\text{H}_f = -4.68 (6.58 \text{ SE}) + 0.91 (0.06 \text{ SE}) * \text{predicted } \delta^2\text{H}_f \quad (1)$$

$$\text{RMA: observed } \delta^2\text{H}_f = -18.94 (5.71 \text{ SE}) + 0.73 (0.05 \text{ SE}) * \text{predicted } \delta^2\text{H}_f \quad (2)$$

Regression of observed vs. predicted $\delta^2\text{H}_f$ values for the adult American Kestrels of known origin in the test dataset ($F = 148.5$, $df = 1$ and 21 , $P < 0.001$, $r^2 = 0.88$) produced regression equations of:

$$\text{OLS: observed } \delta^2\text{H}_f = -7.19 (3.98 \text{ SE}) + 0.82 (0.07 \text{ SE}) * \text{predicted } \delta^2\text{H}_f \quad (3)$$

$$\text{RMA: observed } \delta^2\text{H}_f = -10.68 (3.73 \text{ SE}) + 0.66 (0.05 \text{ SE}) * \text{predicted } \delta^2\text{H}_f \quad (4)$$

In both instances, the OLS-based calibration functions exhibited less proportional bias in relation to their slopes and less fixed bias as evident by their y-intercepts. The mean difference between the observed and the predicted $\delta^2\text{H}_f$ values for the juvenile Kestrels in the test dataset was 8.72‰ when using predicted values produced with the juvenile OLS-based calibration function, and 15.66‰ when using predicted values produced by the juvenile RMA-based calibration function. The mean difference between the observed and the predicted $\delta^2\text{H}_f$ values for the adult Kestrels in the test dataset was 8.87‰ when using predicted values produced with the adult OLS-based calibration function and 15.39‰ when using predicted values produced by the adult RMA-based calibration function. The juvenile OLS-based calibration function produced a more accurate prediction of $\delta^2\text{H}_f$ 87.10% of the time, while the adult OLS-based calibration function produced a more accurate prediction of $\delta^2\text{H}_f$ 82.61% of the time.

When considering all individuals from the test dataset of known origin birds withheld from calibration function creation ($n = 54$), 98.15% had actual summer origins that were within the likely summer origins predicted when only including the upper 30% of grid cell values produced for their respective probability of origin surfaces, while 90.74% had actual summer origins that were within the likely summer origins predicted when only including the upper 20% of grid cell values. These percentages represent accuracy estimates for the binary maps produced using the upper 30% and 20% of grid cell values. Comparatively, only 55.55% of the known

origin test dataset birds had actual summer origins that were within the likely summer origins predicted when only including the upper 10% of grid cell values. The mean precision for the predicted summer origins of the 78 Kestrels of unknown origin was $\sim 1,000,000 \text{ km}^2$ when utilizing the upper 20% of grid cells and $\sim 1,400,000 \text{ km}^2$ when utilizing the upper 30% of grid cells. On average, there was a $\sim 22\%$ improvement in precision when creating maps of predicted summer origins with the upper 20% of grid cell values as opposed to the upper 30% of grid cell values (Appendix Figure 7).

Depending on the scenario considered, the ratio of resident to migrant American Kestrels sampled in Illinois during the winter of 2015-16 was anywhere from $\sim 2:3$ to $8:3$ (Table 1). When only considering birds that were able to be aged, the percentage of residents is consistently $\sim 60\%$ for both the Northern and Central Divisions individually and when combined. All 54 test dataset birds withheld from calibration function creation were correctly assigned as “residents” using the likelihood-based approach established by Van Wilgenburg et al. (2012), which means they were correctly classified as originating from their known summering locations.

The predicted summer origins for the American Kestrels classified as migrants were largely contained within a band stretching from $\sim 42.00^\circ\text{N}$ to $\sim 51.50^\circ\text{N}$ and from $\sim 108.00^\circ\text{W}$ to $\sim 70.00^\circ\text{W}$ (Figure 4). When considering areas north of the winter capture locations for the migrant Kestrels sampled, this band covers the northernmost areas of Illinois up to southern Ontario. The latitudinal band from $\sim 44.20^\circ\text{N}$ to $\sim 48.00^\circ\text{N}$, which runs from central Wisconsin to northern Minnesota, contains grid cells that were consistently predicted as potential summer origins for the migrant Kestrels. When considering only the migrant Kestrels that were able to be aged, grid cells within this latitudinal stretch were predicted as summer origins for 16 to all 21 individuals, regardless of whether the upper 20% or 30% of grid cells were used as the base prior

to map refinements. When including unknown age birds treated as juveniles, the predicted summer origins for the migrant Kestrels were virtually identical to the summer origins predicted for the aged individuals. Similarly, the latitudinal band from $\sim 44.20^{\circ}\text{N}$ to $\sim 48.00^{\circ}\text{N}$ contained grid cells that were predicted as summer origins for most of the Kestrels, with grid cells that were predicted summer origins for as many as 21 to all 27 of the migrant Kestrels. When including all of the unknown age individuals treated as adults, the predicted summer origins for the migrant Kestrels were substantially more dispersed, extending much farther to the north. Under this scenario, the predicted summer origins for one individual included grid cells as far north as the southern portion of the Northwest Territories.

The male migrants ($n = 7$) satisfied the Shapiro-Wilk test for normality ($W = 0.94$, $P > 0.05$), however the female migrants ($n = 14$) narrowly missed satisfying the normality assumption when $\alpha = 0.05$ ($W = 0.87$, $P = 0.048$). Male and female migrants had unequal variances according to the F -test for Equality of Variance ($F = 4.01$, $df = 6$ and 13 , $P < 0.05$). Both the two-tailed two-sample Welch's t -test ($t_{7.5} = 1.13$, $P > 0.05$) and the Wilcoxon rank sum test under the exact test ($z = -1.01$, $P > 0.05$) did not find a significant sex effect on the $\delta^2\text{H}_f$ values of the migrant Kestrels that were able to be aged ($n = 21$).

DISCUSSION

This study is the first to predict the summer origins of a raptor species using age-specific calibration functions characterizing the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$. We developed a new juvenile American Kestrel calibration function using $\delta^2\text{H}_f$ values from known origin individuals (Lott and Smith 2006, Greenwood and Dawson 2011) in combination with our amount-weighted mean annual $\delta^2\text{H}_p$ model, which differs from the American Kestrel calibration established by Hobson et al. (2009). Then, using the age-related $\delta^2\text{H}_f$ adjustment factor we developed by

quantifying the difference in $\delta^2\text{H}_f$ values between adult and juvenile American Kestrels at the same locality, we created an adult American Kestrel calibration function via an adjustment of our juvenile American Kestrel calibration function. Using these age-specific calibration functions, we produced maps of likely summer origins that were validated with a test dataset of known origin Kestrels withheld from calibration function creation, producing accuracy estimates of ~90% and ~98%, depending on the threshold value used when converting continuous surfaces to binary maps. This approach provided a methodology for assigning summer origins to both juvenile and adult American Kestrels, which previously has been unsuccessful for adults when utilizing calibration functions derived from known origin juveniles.

American Kestrels Wintering in Northern and Central Illinois

Based on our stable isotope analyses, the American Kestrels that wintered in the Northern and Central Divisions of Illinois during 2015-16 are composed of both residents and migrants from farther north. Depending on the scenario being considered, the ratio of residents to migrants ranged from ~2:3 to 8:3, suggesting that a considerable portion of the Kestrels wintering in northern and central Illinois are migrants. When considering only individuals that were able to be aged, the percentage of residents was consistently ~60%, and if we consider the two alternative scenarios presented in Table 1 as extremes unlikely to represent the true ratio of residents to migrants, a more accurate estimate of the ratio can be obtained from the average of these two extremes. When using the likelihood-based approach we used, the ratio of residents to migrants in the Northern and Central Divisions of Illinois is somewhere between 1:1 and 3:2, but we advise caution when using this approach to identify individual Kestrels as residents or migrants. The number of migrant American Kestrels classified using this approach is almost certainly underestimated due to the substantial variation in the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$.

documented in American Kestrels. Under this classification scheme, the difference between the observed $\delta^2\text{H}_f$ value and the expected mean $\delta^2\text{H}_f$ value at the location at which an individual was wintering had to be in excess of 23.27‰ for American Kestrels to be classified as migrants. If individuals had a $\delta^2\text{H}_p$ - $\delta^2\text{H}_f$ relationship similar to those established by our calibration functions, this would equate to ~375 km (~233 mi.) of latitudinal movement in some circumstances, without being classified as a migrant. Additionally, several of the Kestrels we sampled during the winter of 2015-16 were members of a male-female pair, evidently occupying the same winter territory, and in some circumstances, we were able to catch and sample both individuals of these pairs. In one instance, the male Kestrel of the pair narrowly missed being classified as a migrant (by 0.01‰), and was thus classified as a resident, while the female member of the pair was classified as a migrant, even though her $\delta^2\text{H}_f$ was within ~4‰ of her male counterpart. We find it very unlikely that one member of a pair was a migrant, and the other was a resident. Cade (1955) documented male-female pairs sharing winter territories, but this was only observed in nonmigratory mated pairs in southern California. Interestingly, in the other two instances in which members of a wintering pair were sampled, the individual female and both the male and female were classified as migrants, which suggests the possibility of male-female pairs migrating and ultimately wintering together. This phenomenon has also been documented in Golden Eagles, where a male and female bred in northern Manitoba and then migrated separately over 1,600 miles south, where they ultimately reunited and wintered together in Kentucky (Berry 2019).

Our analysis indicated that the predicted summer origins for the American Kestrels classified as migrants in northern and central Illinois were largely contained within a latitudinal band stretching from ~42.00-51.50°N. However, even after refining our isotopic predictions by

only including areas within the American Kestrel's breeding range, eliminating grid cells containing unsuitable habitat based on PTC data, and excluding areas containing unlikely summer origins based on known movement patterns, assignment bands still covered a large east-west distance (regularly from ~ 108.00 - 70.00°W) with a precision often lower than 1,000,000 km^2 . After the predicted summer origins for the migrant Kestrels were summed, they spanned 10 Bird Conservation Regions across North America (NABCI 2020). This lack of longitudinal precision, which is inherent when using the stable hydrogen isotope-based approach, makes more fine inferences on the summer origins of these birds difficult to make. If we consider areas directly north of where the Kestrels were sampled during the winter, the predicted summer origins include the northernmost areas of Illinois up to southern Ontario. The latitudinal band from ~ 44.20 - 48.00°N , which runs from central Wisconsin to northeastern Minnesota, contains grid cells that were predicted as summer origins for a large majority of the migrant Kestrels. American Kestrels in the latitudinal band from ~ 36.00 - 44.00°N are thought to be partially migratory, regularly moving short distances due to winter weather events, so there is a high probability that the migrant Kestrels wintering in the Northern and Central Divisions of Illinois fit into this category and have summer origins in the northern one-third of Illinois and southern one-third of Wisconsin.

Based on band recovery data, Kestrels north of $\sim 44.00^{\circ}\text{N}$ regularly migrate farther south, eventually wintering in the southern portions of the United States, most often south of $\sim 36.00^{\circ}\text{N}$ (Roest 1957, Layne 1982, Goodrich et al. 2012). Kestrels banded during the summer in central Wisconsin have been recovered wintering in Mississippi, Missouri, Arkansas, and northern Louisiana (J. E. Eschenbauch personal communication). Therefore, if accurate, the predicted summer origins north of $\sim 44.00^{\circ}\text{N}$ potentially depict a northward shift in the winter distribution

of the American Kestrel, which has been suggested by Goodrich et al. (2012), Heath et al. (2012), Groves et al. (2013), and Paprocki et al. (2014). Northward shifts in the winter distribution of several other North American raptor species have also been documented over the past several decades and are potentially being caused by climate change, land-use change, or a combination of both (Goodrich et al. 2012, Groves et al. 2013, Paprocki et al. 2014, Paprocki et al. 2017).

Additionally, the finding that the grid cells in the latitudinal band from ~44.20-48.00°N were predicted as summer origins for a majority of the migrant Kestrels, with a decrease in the number of overlapping extents north of this band, lends support to leapfrog migration in American Kestrels, where birds breeding in the northernmost parts of the species' range winter the farthest south. In addition to band recovery data, which suggests that American Kestrels partake in leapfrog migration (Goodrich et al. 2012), Hobson et al. (2009) provided evidence of leapfrog migration in their stable isotope analysis on Kestrels wintering in Tennessee and South Carolina. We find it unlikely that the northernmost predictions for the unknown age Kestrels classified as migrants when treated as adults are accurate. When only considering individuals that were able to be aged, predicted summer origins this far north into Canada are absent, so most likely, these are truly juvenile birds with inaccurately predicted northern summer origins when treated as adults.

When examining the $\delta^2\text{H}_f$ values of the male and female migrant American Kestrels, we did not find support for differential sex migration, which has been documented by Willoughby and Cade (1964) and Goodrich et al. (2012) and suggested by Groves et al. (2013). Male American Kestrels have been documented wintering farther north than female Kestrels departing from similar summer latitudes (Willoughby and Cade 1964, Goodrich et al. 2012), so we

expected to observe more depleted $\delta^2\text{H}_f$ values in the female migrants wintering in northern and central Illinois than the males, but this was not the case. It is unclear whether this is representative of what is truly occurring, is an effect of our sample size, or is the result of some other factor (e.g., inter-individual variation in the $\delta^2\text{H}_p$ - $\delta^2\text{H}_f$ relationship). Groves et al. (2013) observed a male-biased sex ratio in the American Kestrels wintering in northern and central Illinois from 2004 to 2009, in which 64% of the American Kestrels identified to sex were males and 36% were females. Their study attributed the male-biased sex ratio to differential sex migration affecting the sex ratio at the northern boundaries of the American Kestrel's winter range. A northward shift in the winter distribution of the American Kestrel in recent years could account for the more even sex ratio we observed when combining all of the American Kestrels we sampled in both the Northern and Central Divisions of Illinois (50% males, 50% females), but it does not explain the lack of support we observed for differential sex migration in the migrant American Kestrels wintering in northern and central Illinois. When only considering the American Kestrels in the Northern Division of Illinois ($n = 11$), a male-biased sex ratio (~82% males) was observed, but this was not the case when only considering the individuals sampled in the Central Division of Illinois (~45% males). This difference in the sex-ratios observed between the individuals sampled in the Northern and Central Divisions of Illinois provides further support of a northward shift in the winter distribution of the American Kestrel, as male-biased sex ratios are only expected at the northernmost portions of their wintering range. If differential sex migration is occurring with the American Kestrels in this region, inter-individual variation in the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ may create difficulty in observing a sex effect on $\delta^2\text{H}_f$ values because these birds are thought to be short distance migrants (i.e. birds from different summering locations within the region may exhibit overlapping $\delta^2\text{H}_f$ values). Additionally, if the migrants

wintering in northern and central Illinois are birds that summered in the northernmost areas of Illinois and southernmost areas of Wisconsin, differential sex migration may not occur as it does with birds migrating farther distances south to winter in the southern United States, Latin America, and the Caribbean.

One of the Kestrels caught and sampled during the winter of 2015-16 had a USGS aluminum leg band placed on it during the previous winter, where it was caught wintering in the same location. This individual was classified as a migrant, which provides further support for winter site fidelity among some migrant Kestrels, which has been documented by Layne (1982) and Hinnebusch et al. (2010).

Conservation and Management Implications

American Kestrel populations appear to be experiencing long-term declines across much of North America (Farmer and Smith 2009, Smallwood et al. 2009, American Kestrel Partnership 2012, Paprocki et al. 2014, Sauer et al. 2014, McClure et al. 2017). Many potential causes for the declines have been suggested, including habitat loss (Farmer and Smith 2009, Smallwood et al. 2009), pesticides and other pollutants (Farmer and Smith 2009, Bird 2009), climate change (Steenhof and Peterson 2009), competition with non-native European Starlings (*Sturnus vulgaris*) for nesting cavities (Bird 2009), predation by Cooper's Hawks (Farmer and Smith 2009, Smallwood et al. 2009), and West-Nile Virus (Farmer and Smith 2009, Smallwood et al. 2009); however, a lack of supporting evidence for these causes (Farmer et al. 2006, Smallwood et al. 2009, McClure et al. 2017) has hindered conservation measures. Declines in American Kestrel populations across North America have been indicated by USGS Breeding Bird Surveys (Smallwood et al. 2009, Sauer et al. 2014), nest-box monitoring programs (Bird 2009, Smallwood et al. 2009), migration counts (Farmer and Smith 2009), and by National Audubon

Society Christmas Bird Counts (Paprocki et al. 2014), yet conflicting trends produced from these monitoring approaches have complicated efforts aimed at determining the contributing factors of the declines (McClure et al. 2017). Conflicting trends among population indices produced from different monitoring techniques may be the result of changes in the biology of American Kestrels induced by climate change and land-use change (Heath et al. 2012, Paprocki et al. 2014, Paprocki et al. 2017, McClure et al. 2017), the methodology of the monitoring techniques (McClure et al. 2017), or a combination of these factors, which in turn can cause disparate relationships between the population indices and actual population trends (McClure et al. 2017). Studies such as this, which investigate the annual movements of American Kestrels in North America and can provide details regarding migratory connectivity, are imperative for gaining a clearer picture of what's occurring (McClure et al. 2017, Zigler 2017) so that appropriate conservation measures can be taken. Approaches that can be utilized to monitor population level changes in annual movement patterns are necessary, especially since the American Kestrel's North American range is predicted to shift significantly under climate change scenarios (National Audubon Society 2019). Under a global climate change scenario with a global mean temperature rise of 3.0°C, the American Kestrel is predicted to lose 11% of its current summer range in North America by 2080, while gaining an additional 32% towards its summer range in areas not currently predicted as climatically suitable (National Audubon Society 2019). Under this same scenario, the American Kestrel's winter range is predicted to expand substantially, with an additional gain of 40% across North America (National Audubon Society 2019). If this climate change scenario is accurate, ~50% of the American Kestrel's summer range in Illinois will no longer be climatically suitable by 2080 (National Audubon Society 2019).

Recommendations and Limitations

IsoMAP provides a standardized and accessible tool that can be utilized to make isotope-based geographic assignments using a semi-parametric Bayesian framework that incorporates uncertainty stemming from $\delta^2\text{H}_p$ isoscape estimates and the processes affecting the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ (Bowen et al. 2014). As long as a calibration function linking $\delta^2\text{H}_p$ and the $\delta^2\text{H}_f$ exists for the species of interest (or for a closely related species thought to exhibit a similar relationship), IsoMAP is a powerful tool that we recommend for producing isotope-based maps of probable origins.

Additional steps can be taken to increase standardization and reduce variation in $\delta^2\text{H}_f$ based geographic assignments. Between-feather variation in the $\delta^2\text{H}_f$ values of several raptor species has been documented between primary feathers, greater primary coverts, and contour feathers (Smith and Dufty Jr. 2005, Smith et al. 2008). Smith et al. (2008) proposed isotopic fractionation associated with feather growth rates as an explanation for the observed differences in $\delta^2\text{H}_f$ values between feather types. Due to variation in $\delta^2\text{H}_f$ values between feather types, calibration functions constructed with feathers of known origin should ideally be built using the same feather type that is to be sampled from individuals of unknown origin. In our case, a small subset of the known origin feathers used to build our calibration functions was composed of the same feather we sampled from the American Kestrels during the winter of 2015-16 (P4; Greenwood and Dawson 2011), but a majority of the known origin feather samples originated from the Lott and Smith (2006) dataset, which was based on contour feathers. This difference in feather types could have introduced uncertainty in our characterization of the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$, ultimately reducing the precision of our geographic assignments.

Furthermore, we believe both the juvenile and adult American Kestrel calibration functions presented in this study can be improved. Although the juvenile calibration function was created using a diverse dataset of feather samples from juvenile American Kestrels spread across North America, its sample size ($n=46$) is lacking. An increased sample size could help better characterize the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ values from juvenile Kestrels across the continent. Although our adult calibration function provided geographic assignments as accurate as those produced for juvenile Kestrels with the juvenile calibration function, an adult American Kestrel calibration function should be built using a large, geographically diverse dataset of known origin feathers from adult Kestrels, as the discrepancy between the $\delta^2\text{H}_f$ values of adult and juvenile Kestrels may actually vary geographically. Additionally, a more geographically diverse test dataset of known origin birds withheld from calibration function creation should be utilized to check the accuracy of geographic assignments. Our test dataset was limited to individuals from Saskatchewan and Illinois, because to our knowledge, these were the only additional $\delta^2\text{H}_f$ values from American Kestrels of known origin in North America available. Accuracy estimates may prove different if a more geographically diverse test dataset is used, as our calibration functions may produce more or less accurate predictions for Kestrels that underwent molt in different regions of North America.

Due to the many processes that introduce variation in $\delta^2\text{H}_f$ values (Lott and Smith 2006, Wassenaar and Hobson 2006, Langin et al. 2007, Wunder 2012), $\delta^2\text{H}_f$ -based geographic assignments will likely never be as precise as origins produced using transmitters, but they are currently much less costly (Kingsbury et al. 2016), making them more suitable for making population-level inferences, and less stressful than when placing transmitters and bio-logging devices on birds (Barron et al. 2010, Bowlin et al. 2010). If possible, the precision of isotope-

based geographic assignments can be improved by combining them with genetic markers (Chabot et al. 2012). When using DNA microsatellites as priors in their Bayesian framework, Chabot et al. (2012) were able to reduce the size of the predicted area of likely feather origin by three to five times on average, and up to ten times in some instances. Combining genetic markers with stable isotope values to make geographic inferences requires that a genoscape, or a map of genetically distinct markers associated with distinct geographic populations (American Kestrel Partnership 2017), exists for the species of interest. The Full Cycle Phenology Project, a collaboration between the American Kestrel Partnership, HawkWatch International, Boise State University, St. Mary's University, the Environmental Laboratory of the U.S. Army Engineer Research and Development Center, and the University of California, Los Angeles, is currently underway on a North American genoscape for the American Kestrel. Based on the methodology employed by Ruegg et al. (2014), the Full Cycle Phenology Project is aiming to build a genoscape for breeding American Kestrel populations using single nucleotide polymorphisms obtained from feather samples so that summer origins can be inferred from feather samples taken from all individuals at any time during the annual cycle (American Kestrel Partnership 2017). The goal of the Full Cycle Phenology Project is to “find out more about migratory connectivity, population change, and the impacts of climate change on the American Kestrel”, which will hopefully lead to insight on conservation actions that can be taken to reverse American Kestrel declines (Full Cycle Phenology Project 2017). Upon its completion, combining American Kestrel genoscape-based geographic assignments with those produced using $\delta^2\text{H}_f$ measurements could improve precision substantially, providing a powerful, cost effective method for determining the summer origins of American Kestrels in North America.

ACKNOWLEDGEMENTS

We thank numerous individuals for assistance with fieldwork and data collection. Additionally, we thank Jennifer L. Greenwood and Russell D. Dawson for providing access to some of the data used in the analysis.

Funding statement: Funding was provided by the Illinois Ornithological Society Grant Program and the Illinois State University School of Biological Sciences Collections Fund.

Ethics Statement: This work was conducted in accordance with the appropriate federal and state regulations, including the U.S. Fish & Wildlife Service Scientific Collecting permit #MB757495-1, Illinois Department of Natural Resources (IDNR) Scientific permit #NH16.5962, and Illinois State University Institutional Animal Care and Use Committee (IACUC) protocol #06-2015.

LITERATURE CITED

American Kestrel Partnership (2012). Declines of American Kestrel Populations

<https://kestrel.peregrinefund.org/decline>

American Kestrel Partnership (2017). American Kestrel Genoscape.

<https://kestrel.peregrinefund.org/index.php?action=genoscape>

Anker-Nilssen, T. and T. Aarvak (2009). Satellite telemetry reveals post-breeding movements of Atlantic puffins *Fratecula arctica* from Røst, North Norway. Polar Biology 32:1657-1664.

Asante, C. A., T. D. Jardine, S. L. Van Wilgenburg, and K. A. Hobson (2017). Tracing origins of waterfowl using the Saskatchewan River Delta: Incorporating stable isotope approaches in continent-wide waterfowl management and conservation. The Condor: Ornithological Applications 119:261-274.

- Atkinson, P. W., A. J. Baker, R. M. Bevan, N. A. Clark, K. B. Cole, P. M. Gonzalez, J. Newton, L. J. Niles, and R. A. Robinson (2005). Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. *Ibis* 147:738–749.
- Balgooyen, T. G. (1976). Behavior and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. *Univ. California Publ. Zool.* 103:1-83.
- Barron, D. G., J. D. Brawn, and P. J. Weatherhead (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1:180-187.
- Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* 75:451-458.
- Becker, B. H., S. H. Newman, S. Inglis, and S. R. Beissinger (2007). Diet-feather stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) fractionation in common murrelets and other seabirds. *The Condor* 109:451-456.
- Ben-David, M. and E. A. Flaherty (2012). Stable isotopes in mammalian research: A beginner's guide. *Journal of Mammalogy* 93:312-328.
- Berry, A. (2019). Athena completes her migration to Bernheim, reuniting with Harper. Bernheim Arboretum and Research Forest. <https://bernheim.org/athena-completes-her-migration-to-bernheim-reuniting-with-harper/>
- Betini, G. S., K. A. Hobson, L. I. Wassenaar, and D. R. Norris (2009). Stable hydrogen isotope (δD) values in songbird nestlings: Effects of diet, temperature, and body size. *Canadian Journal of Zoology* 87:767-772.

- Bird, D. M. and R. S. Palmer (1988). American Kestrel. In Handbook of North American Birds. Vol. 5: diurnal raptors (R. S. Palmer, Editor). Yale University Press, New Haven, CT, USA. pp. 253-290.
- Bird, D. M. (2009). The American Kestrel: From common to scarce? *Journal of Raptor Research* 43:261-262.
- Boslaugh, S. (2013). Statistics in a Nutshell, second edition (M. Treseler, Editor). O'Reilly Media Inc., Sebastopol, CA, USA.
- Bowen, G. J. (2010). Isoscapes: Spatial pattern in isotopic biogeochemistry. *Annual Review of Earth and Planetary Sciences* 38:161-187.
- Bowen, G. J. and J. Revenaugh (2003). Interpolating the isotopic composition of modern meteoric precipitation. *Water Resources Research* 39:1299. doi: [10.129/2003WR002086](https://doi.org/10.129/2003WR002086)
- Bowen, G. J., L. I. Wassenaar, and K. A. Hobson (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143:337-348.
- Bowen, G. J., Z. Liu, H. B. Vander Zanden, L. Zhao, and G. Takahasi (2014). Geographic assignment with stable isotopes in IsoMAP. *Methods in Ecology and Evolution* 5:201-206.
- Bowen G. J., J. B. West, C. C. Miller, L. Zhao, and T. Zhang (2019). IsoMAP: Isoscapes Modeling, Analysis and Prediction (version 1.0). The IsoMAP Project. <http://isomap.org>.
- Bowlin, M. S., P. Henningsson, F. T. Muijres, R. H. E. Vleugels, F. Liechti, and A. Hedenström (2010). The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution* 1:398-402.

- Bridge, E. L., J. F. Kelly, A. Contina, R. M. Gabrielson, R. B. MacCurdy, and D. W. Winkler (2013). Advances in tracking small migratory birds: A technical review of light-level geolocation. *Journal of Field Ornithology* 84: 121-137.
- Bub, H. (1991). *Bird Trapping and Bird Banding: A Handbook for Trapping Methods All Over the World* (F. Hamerstrom and K. Wuertz-Schaefer, Translators). Cornell University Press, Ithaca, N. Y., USA.
- Bustnes, J. O., A. Mosbech, C. Sonne, G. H. Syster (2010). Migration patterns, breeding, and moulting locations of king eiders wintering in north-eastern Norway. *Polar Biology* 33:1379-1385.
- Caccamise, D. F., L. M. Reed, P. M. Castellie, S. Wainright, and T. C. Nichols (2000). Distinguishing migratory and resident Canada Geese using stable isotope analysis. *Journal of Wildlife Management* 64:1084-1091.
- Cade, T. J. (1955). Experiments on winter territoriality of the American Kestrel, *Falco sparverius*. *The Wilson Bulletin* 67:5-17.
- Casper, R. M. (2009). Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour* 78:1477-1483.
- Chabot, A. A., K. A. Hobson, S. L. Van Wilgenburg, G. J. McQuat, and S. C. Loughheed (2012). Advances in linking wintering migrant birds to their breeding-ground origins using combined analyses of genetic and stable isotope markers. *PLOS One* 7:e43627. doi:10.1371/journal.pone.0043627
- Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. (1997). The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132-141.

- Coplen, T. B. and H. P. Qi (2012). USGS42 and USGS43: Human hair stable hydrogen and oxygen isotopic reference materials and analytical methods for forensic science and implications for published measurement results. *Forensic Science International* 214:135-141.
- Crossley, R., J. Liguori, and B. Sullivan (2013). American Kestrel (*Falco sparverius*). In *The Crossley ID Guide Raptors*. Princeton University Press, Princeton, NJ, USA. pp. 245-247.
- Cochran, W. W. and R. D. Lord, Jr. (1963). A radio-tracking system for wild animals. *Journal of Wildlife Management* 27:9-24.
- Dansgaard, W. (1964). Stable isotopes in precipitation. *Tellus* 16:436-468.
- De Ruyck, C., K. A. Hobson, N. Koper, K. W. Larson, and L. I. Wassenaar (2013). An appraisal of the use of hydrogen isotope methods to delineate origins of migratory Saw-whet Owls in North America. *The Condor* 115:366–374.
- Enderson, J. H. (1960). A population study of the Sparrow Hawk in East-Central Illinois. *The Wilson Bulletin* 72:222-231.
- Estep, M. F. and H. Dabrowski (1980). Tracing food webs with stable hydrogen isotopes. *Science* 209:1537-1538.
- Farmer, C. J. and J. P. Smith (2009). Migration monitoring indicates widespread declines of American Kestrels (*Falco sparverius*) in North America. *Journal of Raptor Research* 43:263-273.
- Farmer, G. C., K. McCarty, S. Robertson, B. Robertson, and K. L. Bildstein (2006). Suspected predation by Accipiters on radio-tracked American Kestrels (*Falco sparverius*) in Eastern Pennsylvania, U.S.A.. *Journal of Raptor Research* 40:294-297.

- Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, O. Robinson, S. Ligocki, B. Petersen, C. Wood, I. Davies, B. Sullivan, M. Iliff, S. Kelling (2019a). eBird Status and Trends, Version: November 2019. Cornell Lab of Ornithology, Ithaca, New York.
<https://doi.org/10.2173/ebirdst.2019>
- Fink, D., T. Auer, A. Johnston, V. Ruiz-Gutierrez, W. M. Hochachka, and S. Kelling (2019b). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications* 30:e02056. 10.1002/eap.2056
- Fraser, K. C., A. Shave, A. Savage, A. Ritchie, K. Bell, J. Siegrist, J. D. Ray, K. Applegate, and M. Pearman (2017). Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. *Journal of Avian Biology* 48:339-345.
- Fudickar, A. M., M. Wikelski, and J. Partecke (2012). Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution* 3:47-52.
- Full Cycle Phenology Project (2017). Full Cycle Phenology. <https://fullcyclephenology.com/>
- Fuller, M. R., W. S. Seegar, and L. S. Schuek (1998). Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the Western Hemisphere. *Journal of Avian Biology* 29:433-440.
- Gault, B. T., R. Ridgway, and A. A. Allen (1922). Check list of the birds of Illinois: Together with a short list of 200 commoner birds and Allen's key to bird's nests. Illinois Audubon Society, Chicago, IL, USA.
- Gill, F. B. (2007). Ornithology, third edition. W. H. Freeman and Company, New York, NY, USA.

- Goodrich, L. J., C. J. Farmer, D. R. Barber, and K. L. Bildstein (2012). What banding tells us about the movement ecology of raptors. *Journal of Raptor Research* 46:27-35.
- Greenwood, J. L. and R. D. Dawson (2011). Correlates of deuterium (δD) enrichment in the feathers of adult American Kestrels of known origin. *The Condor* 113:555-564.
- Groves, A., V. Berardi, P. Sweet, J. Sweet, A. P. Capparella, and R. G. Harper (2013). Influence of latitude on the winter abundance of Red-tailed Hawks (*Buteo jamaicensis*) and American Kestrels (*Falco sparverius*) in Illinois. *Journal of Raptor Research* 47:410-415.
- Haché, S., K. A. Hobson, M. A. Villard, and E. M. Bayne (2012). Assigning birds to geographic origin using feather hydrogen isotope ratios (δ^2H): Importance of year, age, and habitat. *Canadian Journal of Zoology* 90:722-728.
- Hallworth, M. T. and P. P. Marra (2015). Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Scientific Reports* 5:11069.
- Hawk Migration Association of North America (2019). HawkCount: Hawk Migration Association of North America's Raptor Migration Database. <http://hawkcount.org/>
- Heath, J. A., K. Steenhof, and M. A. Foster (2012). Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American Kestrels *Falco sparverius*. *Journal of Avian Biology* 43:376-384.
- Hinnebusch, D. M., J. F. Therrien, M. A. Valiquette, B. Robertson, S. Robertson, and K. L. Bildstein (2010). Survival, site fidelity, and population trends of American Kestrels wintering in southwestern Florida. *Wilson Journal of Ornithology* 122: 475–483.
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* 120:314-326.

- Hobson, K. A. (2003). Making migratory connections with stable isotopes. In *Avian Migration* (P. Berthold, E. Gwinner, and E. Sonnenschein, Editors). Springer-Verlag, Berlin, Germany. pp. 379-391.
- Hobson, K. A. (2005) Flying fingerprints: Making connections with stable isotopes and trace elements. In *Birds of Two Worlds: The Ecology and Evolution of Migratory Birds* (R. Greenberg and P.P. Marra, Editors). Johns Hopkins University Press, Washington, DC, USA. pp 235-246.
- Hobson, K. A. (2007). Isotope tracking of migrant wildlife. In *Stable Isotopes in Ecology and Environmental Science*, second edition (R. Michener and K. Lajitha, Editors). Blackwell Publishing, Boston, MA, USA. pp. 155-174.
- Hobson, K. A. (2011). Isotopic ornithology: A perspective. *Journal of Ornithology* 152:49-66.
- Hobson, K. A. and R. G. Clark (1992). Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. *The Condor* 94:181-188.
- Hobson, K. A. and L. I. Wassenaar (1997). Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142-148.
- Hobson, K.A., L. Atwell, and L. I. Wassenaar (1999a). Influence of drinking water and diet on the stable-hydrogen isotope ratios of animal tissues. *Proceedings of the National Academy of Sciences USA* 96:8003-8006.
- Hobson, K. A., L. I. Wassenaar, and O. R. Taylor (1999b). Stable isotopes (δD and $\delta^{13}\text{C}$) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* 120:397-404.

- Hobson, K. A., S. H. DeMent, S. L. Van Wilgenburg, and L. I. Wassenaar (2009). Origins of American Kestrels at two southern U.S. sites: An investigation using stable-isotope (δD , $\delta^{18}O$) methods. *Journal of Raptor Research* 43:325-337.
- Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson (2012). Linking hydrogen (δ^2H) isotopes in feathers and precipitation: Sources of variance and consequences for assignments to isoscapes. *PLOS One* 7:e35137.
- Hobson, K.A., K. P. McFarland, L. I. Wassenaar, C. C. Rimmer, and J. E. Goetz (2001). Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. *The Auk* 118:16–23.
- Hobson, K. A., G. J. Bowen, L. I. Wassenaar, Y. Ferrand, and H. Lormee (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Ecosystem Ecology* 141:477-488.
- Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, F. Moore, and J. Farrington (2007). Estimating origins of three species of Neotropical migrant songbirds at a gulf coast stopover site: combining stable isotope and GIS tools. *The Condor* 109:256-267.
- Hobson, K. A., L. I. Wassenaar, B. Milá, I. Lovette, C. Dingle, and T. B. Smith (2003). Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* 136:302–308.
- Howell, S. N. G. (2010). *Molt in North American Birds*. Houghton Mifflin Harcourt, New York, N. Y., USA.
- Hughes, J. M. (2009). *The Migration of Birds: Seasons on the Wing*. Firefly Books Ltd., Richmond Hill, ON, CA.

- Inger, R. and S. Bearhop (2008). Applications of stable isotope analyses to avian ecology. *Ibis* 150:447-461.
- Kanai, Y., M. Nagendran, M. Ueta, Y. Markin, J. Rinne, A. G. Sorokin, H. Higuchi, and G. W. Archibald (2002). Discovery of breeding grounds of a Siberian Crane *Grus leucogeranus* flock that winters in Iran, via satellite telemetry. *Bird Conservation International* 12:327-333.
- Kelly, J. F., K. C. Ruegg, and T. B. Smith (2005). Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications* 15:1487-1494.
- Kingsbury, B. A. and N. J. Robinson (2016). Movement patterns and telemetry. In *Reptile Ecology and Conservation: A Handbook of Techniques* (C. K., Dodd, Jr., Editor). Oxford University Press, Oxford, United Kingdom. pp. 110-121.
- Lament, J. J. (2005). Banding Together. Ducks Unlimited. <https://www.ducks.org/conservation/waterfowl-research-science/banding-together>
- Langin, K. P., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe (2007). Hydrogen isotopic variation in migratory bird tissues of known origin: Implications for geographic assignment. *Oecologia* 152:449-457.
- Layne, J. N. (1982). Analysis of Florida-related banding data for the American Kestrel. *North American Bird Bander* 7:94-99.
- Lott, C. A. and J. P. Smith (2006). A geographic-information-system approach to estimating the origin of migratory raptors in North America using stable hydrogen isotope ratios in feathers. *The Auk* 123:822-835.

- Macías-Duarte, A. and C. J. Conway (2014). Spatial patterns in hydrogen isotope ratios in feathers of Burrowing Owls from western North America. *The Auk: Ornithological Advances* 132:25-36.
- Marquiss, M., L. Newton, K. A. Hobson, and Y. Kolbeinsson (2012). Origins of irruptive migrations by common crossbills *Loxia curvirostra* into northwestern Europe revealed by stable isotope analysis. *Ibis* 154:400-409.
- Martell, M. S., C. J. Henny, P. E. Nye, and M. J. Solensky (2001). Fall migration routes, timing, and wintering sites of North American ospreys as determined by satellite telemetry. *The Condor* 103:715-724.
- Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and R. D. Norris (2007). Optimal conservation of migratory species. *PLOS One* 8:e751. doi: [10.1371/journal.pone.0000751](https://doi.org/10.1371/journal.pone.0000751)
- Martinez del Rio, C. and B. O. Wolf (2005). Mass balance models for animal isotopic ecology. In *Physiological and Ecological Adaptations to Feeding in Vertebrates* (M. A. Starck and T. Wang, Editors). Science Publishers, Enfield, NH, USA. pp. 141-174.
- Mazerolle, D. F., K. A. Hobson, and L. I. Wassenaar (2005). Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of white-throated sparrows at a migration monitoring station. *Oecologia* 144:541-549.
- McClure, C. J. W., S. E. Schulwitz, R. V. Buskirk, B. P. Pauli, and J. A. Heath (2017). Commentary: Research recommendations for understanding the decline of American Kestrels (*Falco sparverius*) across much of North America. *Journal of Raptor Research* 51:455-464.

- McKechnie, A. E., B. O. Wolf, and C. Martínez del Río (2004). Deuterium stable isotope ratios as tracers of water resource use: An experimental test with rock doves. *Oecologia* 140:191-200.
- McMahon, C. R., N. Collier, J. K. Northfield, and F. Glen (2011). Taking the time to assess the effects of remote sensing and tracking devices on animals. *Animal Welfare* 20:515-521.
- Meehan, T. D., R. N. Rosenfield, V. A. Atudorei, J. Bielefeldt, L. J. Rosenfield, A. C. Stewart, W. E. Stout, and M. A. Bozek (2003). Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's Hawks. *The Condor* 105:567-572.
- Meehan, T. D., J. T. Giermakowski, and P. M. Cryan (2004). GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental Health and Studies* 40:291-300.
- NABCI (2020). Bird Conservation Regions Map. <https://nabci-us.org/resources/bird-conservation-regions-map/>
- National Audubon Society (2019). American Kestrel. <https://www.audubon.org/field-guide/bird/american-kestrel>
- Nelson, D. M., M. Braham, T. A. Miller, A. E. Duerr, J. Cooper, M. Lanzone, J. Lemaître, and T. Katzner (2015). Stable hydrogen isotopes identify leapfrog migration, degree of connectivity, and summer distribution of Golden Eagles in eastern North America. *The Condor: Ornithological Applications* 117:414-429.
- Paprocki, N., J. A. Heath, and S. J. Novak (2014). Regional distribution shifts help explain local changes in wintering raptor abundance: Implications for interpreting population trends. *PLOS One* 9:e86814. doi:10.1371/journal.pone.0086814

- Paprocki, N., D. Oleyar, D. Brandes, L. Goodrich, T. Crewe, and S. W. Hoffman (2017). Combining migration and wintering counts to enhance understanding of population change in a generalist raptor species, the North American Red-tailed Hawk. *The Condor: Ornithological Applications* 119:98-107.
- Paritte, J. M. and J. F. Kelly (2009). Effect of cleaning regime on stable-isotope ratios of feathers in Japanese Quail (*Coturnix japonica*). *The Auk* 126:165-174.
- Pearson, S. F., D. J. Levey, C. H. Greenberg, and C. Martínez del Río (2003). Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Ecophysiology* 135:516-523.
- Peixoto, J. P. and A. H. Oort (1983). The atmospheric branch of the hydrological cycle and climate. In *Variations in the Global Water Budget* (A. Street-Perrott, M. Beran, R. Ratcliffe, Editors). D. Reidel Publishing Company, pp. 5-65.
- Pérez, G. E. and K. A. Hobson (2007). Feather deuterium measurements reveal origins of migratory western Loggerhead Shrikes (*Lanius ludovicianus excubitorides*) wintering in Mexico. *Diversity and Distributions* 13:166-171.
- Powell, L. A. and K. A. Hobson (2006). Enriched feather hydrogen isotope values for Wood Thrushes sampled in Georgia, USA, during the breeding season: Implications for quantifying dispersal. *Canadian Journal of Zoology* 84:1331-1338.
- Rocque, D. A., M. Ben-David, R. P. Barry, and K. Winker (2006). Assigning birds to wintering and breeding grounds using stable isotopes: Lessons from two feather generations among three intercontinental migrants. *Journal of Ornithology* 147:395-404.
- Roest, A. I. (1957). Notes on the American Sparrow Hawk. *The Auk* 74:1-19.

- Rohrbaugh Jr., R. W. and R. H. Yahner (1997). Effects of macrohabitat and microhabitat on nest-box use and nestling success of American Kestrels. *Wilson Bulletin* 109:410-423.
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, P. P. Marra (2019). Decline of the North American avifauna. *Science* 366:120-124.
- Royle, J. A. and D. R. Rubenstein (2004). The role of species abundance in determining the Breeding origins of migratory birds using stable isotopes. *Ecological Applications* 14:1780-1788.
- Rozanski K., L. Araguas-Araguas, and R. Gonfiantini (1993). Isotopic patterns in modern global precipitation. In *Climate Change in Continental Isotopic Records* (P. K. Swart, K. C. Lohmann, J. McKenzie, and S. Savin, Editors). American Geophysical Union, Washington, D. C., USA pp. 1-36.
- Ruegg, K. C., E. C. Anderson, K. L. Paxton, V. Apkenas, S. Lao, R. B. Siegel, D. F. Desante, F. Moore, and T. B. Smith (2014). Mapping migration in a songbird using high-resolution genetic markers. *Molecular Ecology* 23:5726–5739.
- Sarasola, J. H., J. J. Negro, K. A. Hobson, G. R. Bortolotti, and K. L. Bildstein (2008). Can a ‘wintering area effect’ explain population status of Swainson’s Hawks? A stable isotope approach. *Diversity and Distributions* 14:686–691.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link (2014). The North American Breeding Bird Survey, results and analysis 1966 - 2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

- Schell, D. M., S. M. Saupe, and N. Haubenstock (1988). Natural isotope abundance in Bowhead Whale (*Balaena mysticetus*) baleen: Markers of aging and habitat usage. In Stable Isotopes in Ecological Research (P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, Editors). Ecological Studies 68, Springer- Verlag, BER, DE. pp. 260-269.
- Seegar, W. S., N. C. Protagoras, M. R. Fuller, J. J. Suter, V. Bhatnagar, and J. G. Wall (1996). Fifteen years of satellite tracking development and application to wildlife research and conservation. Johns Hopkins APL Technical Digest 17:401-411.
- Şekercioğlu, C. H. (2006). Increasing awareness of avian ecological function. Trends in Ecology and Evolution 22:464-471.
- Şekercioğlu, C. H., G. C. Daily, and P. R. Ehrlich (2004). Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences USA 101:18042-18047.
- Sherman, A. R. (1913). The nest life of the Sparrow Hawk. The Auk 30:406-418.
- Siegel, R. B., R. Taylor, J. F. Saracco, L. Helton, S. Stock (2016). GPS-tracking reveals non-breeding locations and apparent molt migration of a Black-headed Grosbeak. Journal of Field Ornithology 87:196-203.
- Smallwood, J. A. (1988). A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida. The Auk 105:36-46.
- Smallwood, J. A. (1989). Age determination of American Kestrels: A revised key. Journal of Field Ornithology 60:510-519.
- Smallwood, J. A. and P. J. Wargo (1997). Nest site habitat structure of American Kestrels in northwestern New Jersey. Bulletin of the New Jersey Academy of Science 42:7-10.

- Smallwood, J. A. and D. M. Bird (2002). American Kestrel (*Falco sparverius*), version 2.0. In The Birds of North America Online (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bna.602>
- Smallwood, J. A., M. F. Causey, D. H. Mossop, J. R. Klucsarits, B. Robertson, S. Robertson, J. Mason, M. J. Maurer, R. J. Melvin, R. D. Dawson, G. R. Bortolotti, J. W. Parish, Jr., et al. (2009). Why are American Kestrel (*Falco sparverius*) populations declining? Evidence from nest-box programs. *Journal of Raptor Research* 43:274-282.
- Smith, A. D. and A. M. Dufty Jr. (2005). Variation in the stable-hydrogen isotope composition of Northern Goshawk feathers: Relevance to the study of migratory origins. *The Condor* 107:547-558.
- Smith, A. D., K. Donohue, and A. M. Dufty Jr. (2008). Intrafeather and intraindividual variation in the stable-hydrogen isotope (δD) content of raptor feathers. *The Condor* 110:500–506.
- Smith, E. L., M. W. Reudink, P. P. Marra, A. E. Mckellar, S. L. Van Wilgenburg (2019). Breeding origins and migratory connectivity at a northern roost of Vaux's Swift, a declining aerial insectivore. *The Condor: Ornithological Applications* 121:duz034. <https://doi.org/10.1093/condor/duz034>
- Smith, R. J. (2009). Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology* 140:476-486.
- Steenhof, K. and B. E. Peterson (2009). American Kestrel reproduction in southwestern Idaho: Annual variation and long-term trends. *Journal of Raptor Research* 43:283-290.

- Studds, C. E., K. P. McFarland, Y. Aubry, C. C. Rimmer, K. A. Hobson, P. P. Marra, and L. I. Wassenaar (2012). Stable-hydrogen isotope measures of natal dispersal reflect observed population declines in a threatened migratory songbird. *Diversity and Distributions* 18:919-930.
- Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev (2009). Tracking long-distance songbird migration by using geolocators. *Science* 323:896.
- Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. (2009). eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142: 2282-2292.
- Sulzman, E. W. (2007). Stable isotope chemistry and measurement: a primer. In *Stable Isotopes in Ecology and Environmental Science*, second edition (R. Michener and K. Lajitha, Editors). Blackwell Publishing, Boston, MA, USA. pp. 1-21.
- Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12:art.8.
- The Migratory Connectivity Project (2017a). Geolocators (E. Bridge, Editor). <http://www.migratoryconnectivityproject.org/geolocators/>
- The Migratory Connectivity Project (2017b). Radio telemetry (D. Kesler and N. Cooper, Editors). <http://www.migratoryconnectivityproject.org/vhf-radios/#top>
- Thomson, D. L., P. Monaghan, and R. W. Furness (1998). The demands of incubation and avian clutch size. *Biological Reviews* 73:293-304.

- USGS Patuxent Wildlife Research Center (2018). North American Breeding Bird Survey, Route Map. <https://www.pwrc.usgs.gov/bbs/RouteMap/Map.cfm>
- van Dijk, J. G. B., W, Meissner, and M. Klaassen (2014). Improving provenance studies in migratory birds when using feather hydrogen stable isotopes. *Journal of Avian Biology* 45:103-108.
- Van Wilgenburg, S. L. and K. A. Hobson (2011). Combining stable-isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecological Applications* 21:1340-1351.
- Van Wilgenburg, S. L., K. A. Hobson, K. R. Brewster, and J. M. Welker (2012). Assessing dispersal in threatened migratory birds using stable hydrogen isotope (δD) analysis of feathers. *Endangered Species Research* 16:17-29.
- Walsberg, G. E. and K. A. Voss-Roberts (1983). Incubation in desert-nesting doves: mechanisms for egg cooling. *Physiological Zoology* 56:88-93.
- Wassenaar, L. I. and K. A. Hobson (2000). Stable-carbon and hydrogen isotope ratios reveal breeding origins of Red-winged Blackbirds. *Ecological Applications* 10:911-916.
- Wassenaar, L. I. and K. A. Hobson (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39:211-217.
- Wassenaar, L. I. and K. A. Hobson (2006). Stable-hydrogen isotope heterogeneity in keratinous materials: Mass spectrometry and migratory wildlife tissue subsampling strategies. *Rapid Communications in Mass Spectrometry* 20:2505-2510.

- Webster, M. S. and P. P. Marra (2005). The importance of understanding migratory connectivity and seasonal interactions. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Editors). John Hopkins University Press, Baltimore, MD, USA. pp. 199-209.
- West, J. B., G. J. Bowen, T. E. Cerling, and J. R. Ehleringer (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution* 21:408-414.
- Williams J. B. (1996). Energetics of Avian Incubation. In *Avian Energetics and Nutritional Ecology* (C. Carey, Editor). Chapman and Hall, New York, NY, USA. pp. 375-416.
- Wilsey, C., B. Bateman, L. Taylor, J. X. Wu, G. LeBaron, R. Shepherd, C. Koseff, S. Friedman, and R. Stone (2019). *Survival by Degrees: 389 Bird Species on the Brink*. National Audubon Society, NY, USA.
- Willoughby, E. J. (1966). Wing and tail molt of the Sparrow Hawk. *The Auk* 83:201-206.
- Willoughby, E. J. and T. J. Cade (1964). Breeding behavior of the American Kestrel (Sparrow Hawk). *Living Bird* 3:75-96.
- Wittenberg, S. R., S. E. Lehnen, and K. Smith (2013). Use of stable isotopes of hydrogen to predict natal origins of juvenile Merlins and Northern Harriers migrating through the Florida Keys. *The Condor* 115:451-455.
- Wolf, B. O. and C. Martínez del Río (2000). Use of saguaro fruit by White-winged Doves: isotopic evidence of a tight ecological association. *Oecologia* 124:536-543.
- Wolf, B. O. and C. Martínez del Río (2003). How important are columnar cacti as sources of water and nutrients for desert consumers? A review. *Isotopes in Environmental and Health Studies* 39:53-67.

- Wunder, M. B. (2007). Geographic structure and dynamics in Mountain Plover. Ph.D. dissertation, Colorado State University, Fort Collins.
- Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In *Tracking Animal Migration with Stable Isotopes* (K. A. Hobson and L. I. Wassenaar, Editors). Academic Press, San Diego, CA, USA. pp. 251-280.
- Wunder, M. B. (2012). Determining geographic patterns of migration and dispersal using stable isotopes in keratins. *Journal of Mammalogy* 93:360-367.
- Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye (2005). A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia* 144:607-617.
- Zigler, R. (2017). Connecting the Dots. *BirdWatching* 31(5):16-20.

APPENDIX

Table 2. IsoMAP-derived amount-weighted mean annual $\delta^2\text{H}_p$ model summary (job 73439 at

<https://isomap.rcac.purdue.edu/isomap/>).

Geostatistical Model

ANOVA

Variable	df	SS	MS	F-value	P-value
Elevation	1	18303.8	18303.8	35.08	3.30E-08
Latitude ²	1	24110.5	24110.5	46.21	4.87E-10
Error	116	60527.3	521.787		
Total	118	18303.8			

Parameter Values

Matern Correlation Function Used

Estimate of Correlation Parameter is: 0.91

Estimate of Scale Parameter is: 1003.43

Variable	Estimate	SE	t-value	P-value
Intercept	7.52	15.573	0.48	0.63
Elevation	-0.01	0.002	-5.98	2.56E-08
Latitude ²	-0.03	0.005	-6.80	4.87E-10

Aging Individuals Based on $\delta^2\text{H}_f$ Values

Greenwood and Dawson (2011) found that the $\delta^2\text{H}_f$ distribution of juvenile and adult American Kestrels did not overlap in their study area. Under the assumption that this pattern is true across North America, the measured $\delta^2\text{H}_f$ values of the American Kestrels sampled during our winter field season can provide a suggestion of their age. Our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape was converted to a juvenile and adult American Kestrel $\delta^2\text{H}_f$ isoscape using the established calibration functions and the raster calculator tool in ArcMAP. Three individual birds sampled had body plumage and flight feather characteristics that were supportive, but nondefinitive of being adults. Additionally, these 3 individuals had enriched $\delta^2\text{H}_f$ values also suggestive of them being adults, for when they were treated as juveniles, their predicted summer origins were south of where they were wintering. Furthermore, these birds had a $\delta^2\text{H}_f$ value that was more enriched than the upper bound juvenile American Kestrel $\delta^2\text{H}_f$ value produced by the 90% prediction interval at their respective wintering locations (using the $\delta^2\text{H}_p$ value at these locations). On this basis, we felt confident treating these individuals as adults.

Table 3. American Kestrels of unknown origin sampled in Illinois during the winter of 2015-16.

Location	Age		Adult		Unknown Age		IL Division	Total
	Juvenile							
	♂	♀	♂	♀	♂	♀		
Cook	-	-	1	-	-	-	Northern	1
DeKalb	1	1	2	-	1	-	Northern	5
DeWitt	-	2	1	4	1	-	Central	8
Ford	-	1	1	1	-	1	Central	4
Kane	2	-	1	-	1	1	Northern	5
Livingston	-	-	1	1	-	-	Central	2
Logan	-	-	1	1	-	-	Central	2
Macon	-	1	1	2	-	-	Central	4
McLean	1	7	3	6	11	2	Central	30
Morgan	-	1	-	2	5	1	Central	9
Tazewell	-	1	1	1	-	-	Central	3
Woodford	-	-	1	2	2	-	Central	5
Total	4	14	14	20	21	5	N:11, C:67	78

RMA Calibration Functions

When using $\delta^2\text{H}_p$ values from our amount-weighted mean annual $\delta^2\text{H}_p$ isoscape and $\delta^2\text{H}_f$ values of the known origin juvenile American Kestrels from the Lott and Smith (2006) dataset ($n = 41$) and a subset of the Greenwood and Dawson (2011) dataset ($n = 5$), the juvenile RMA calibration function characterizing the relationship between $\delta^2\text{H}_p$ and $\delta^2\text{H}_f$ was: $\delta^2\text{H}_f = 45.21 + 1.30 * \delta^2\text{H}_p$ (df = 1 and 44, $P < 0.001$, $r^2 = 0.65$). The standard deviation of the regression residuals was 14.92‰. After adjusting this by the age-related $\delta^2\text{H}_f$ adjustment factor (58.55‰), the adult RMA calibration function was $\delta^2\text{H}_f = 103.76 + 1.30 * \delta^2\text{H}_p$.

Figure 5. Expected geographic distribution of mean $\delta^2\text{H}_f$ (‰) for juvenile American Kestrels derived from ordinary least squares regression (OLS) of the known origin juvenile American Kestrel $\delta^2\text{H}_f$ values from the Lott and Smith (2006) and Greenwood and Dawson (2011) datasets and $\delta^2\text{H}_p$ values from our IsoMAP derived amount-weighted mean annual $\delta^2\text{H}_p$ isoscape.

Figure 6. Expected geographic distribution of mean $\delta^2\text{H}_f$ (‰) for adult American Kestrels derived from adjusting the expected geographic distribution of mean $\delta^2\text{H}_f$ for juvenile American Kestrels by the age-related $\delta^2\text{H}_f$ adjustment factor.

Figure 7. Comparison of the predicted summer origins for an individual when utilizing the upper 20% and upper 30% of the grid cell values from the IsoMAP-based probability of origin surfaces.

TABLES

Table 1. Ratio of resident to migrant American Kestrels in the Northern and Central Divisions of Illinois during the 2015-16 winter when including only the individuals able to be aged (scenario 1), aged individuals and individuals unable to be aged treated as juveniles (scenario 2), and aged individuals and individuals unable to be aged treated as adults (scenario 3).

IL Division	Resident to migrant ratio		
	Scenario 1	Scenario 2	Scenario 3
Northern	5:3	8:3	5:6
Central	26:18	43:24	26:41
Total	31:21	51:27	31:47

FIGURES

Figure 1. Location of the feather clipping collected from (A) P4 of a male American Kestrel and (B) P4 of a female American Kestrel. A small piece of feather vane was clipped from the area indicated by the dashed rectangle.

Figure 2. Ordinary least squares (OLS) regression modelling the relationship between δ^2H_p from our amount-weighted mean annual δ^2H_p isoscape and δ^2H_f values of the known origin juvenile American Kestrels from the Lott and Smith (2006) dataset ($n = 41$) and a subset of the Greenwood and Dawson (2011) dataset ($n = 5$).

Figure 3. Likely summer origin for an individual American Kestrel based on the upper 20% of the grid cell values from its IsoMAP probability of origin surface and the refinements made by including only geographic areas within the North American breeding range of the American Kestrel, by removing grid cells containing unlikely breeding habitat, and by excluding grid cells representing unlikely summer origins based on known movement patterns.

Figure 4. The refined summer origin predictions (based on the upper 20% of grid cells) for the migrant American Kestrels able to be aged definitively ($n = 21$) that wintered in the Northern and Central Divisions of Illinois during the 2015-16 winter. Numbers and their corresponding color indicate the number of migrant Kestrels' extents that overlap in an area (i.e. the number of migrant Kestrels for which a grid cell is a predicted summer origin).