

SEX, BODY SIZE, AND WINTER WEATHER EXPLAIN MIGRATION
STRATEGIES IN A PARTIAL MIGRANT POPULATION OF AMERICAN
KESTRELS (*FALCO SPARVERIUS*)

by

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DEDICATION

To my partner, Tanner. Thank you for your unwavering support since English class in high school.

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ABSTRACT

Partially migratory systems describe populations that consist of both individuals that migrate away from the breeding grounds for the winter, and others that remain resident near their nesting sites year-round. Partial migration is the most common type of migration across all animal taxa, but the evolution, maintenance, and consequences associated with different movement strategies are still poorly understood. Studying the factors that drive migratory strategies and the associated consequences of those decisions is important to understand how migratory animals may adapt to climate change. Partial migrant populations offer a great opportunity for which to study these questions because individuals with different movement strategies live in the same environment for a portion of their annual cycle. This allows researchers to directly compare individuals exhibiting both migration strategies in the same study area.

In our study, we examined the correlates, patterns, and consequences associated with migratory decisions in the American Kestrel (*Falco sparverius*), a small falcon species that exhibits partial migration tendencies across its range in North America. To investigate the factors associated with an individual's migratory strategy, and to assess the migratory patterns in a population of kestrels in southwestern Idaho, we used stable hydrogen isotope values (δD) extracted from talon tissues to distinguish migrant from resident kestrels during the 2013 – 2021 breeding seasons. We determined the migratory status for 349 birds with a previously unknown strategy and saw that males were more likely to migrate than females, and that in colder than average winters, smaller birds of

both sexes were more likely to migrate than larger birds. Additionally, kestrels can switch migration patterns on an annual basis, and the proportion of individuals with a migrant or resident strategy in the local southwestern Idaho population is not consistent over time. Broadly, these results offer support for the body size hypothesis in that larger individuals may be better equipped to withstand harsher winters compared to smaller-bodied individuals.

We also examined the consequences associated with an individual's movement strategy by comparing a bird's stable hydrogen isotope value to the date that they initiated breeding. For this work, we collaborated with project partners to collect talon samples from breeding kestrels across seven sites in Indiana, Kansas, Wisconsin, Wyoming, New York, Washington, and Saskatchewan, Canada; some of which were on Department of Defense lands. There was no significant association between an individual's isotope composition and lay date suggesting that individuals that wintered further south did not initiate breeding later than individuals that migrated shorter distances. Although these results contrast with what we predicted, they are consistent with results found in similar taxa.

Overall, this study elucidates the factors influencing migration decisions in American Kestrels and uncovers previously unknown phenomena in this species such as migration strategy switching. Lastly, we determined that extracting stable hydrogen isotope values from talon tissue is a viable option for researchers seeking to categorize individuals into discrete migratory strategies in studies of animal migration.

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LIST OF ABBREVIATIONS

δD	Stable hydrogen isotope value
km	Kilometer
m	Meter
USGS	United States Geological Survey
mm	Millimeter
μL	Microliter
mg	Milligram
CBS	Caribou keratin standard
KHS	Kudu keratin standard
RH-B	Chicken feather standard
TC/EA	Thermal Conversion Elemental Analyzer
VSMOW	Vienna Standard Mean Ocean Water
SLAP	Standard Light Antarctic Precipitation
LOOCV	Leave-one-out cross validation
GLM	Generalized linear model
SERDP	Strategic Environmental Research and Development Program
NSF	National Science Foundation
DoD	Department of Defense
GLMM	Generalized linear mixed model

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Abstract

Partially migratory breeding populations consist of individuals that either migrate or remain resident on the breeding grounds year-round. Given increasing evidence that climate change affects annual cycles of birds, it is important to understand mechanisms underlying the decision to migrate and how environmental changes might affect populations. We studied whether body size or competition for nest sites and mates (arrival time hypothesis) best explained migration decisions in a partially migratory population of American Kestrels (*Falco sparverius*) in southwestern Idaho, where both movement patterns and nesting phenology in kestrels are changing. Due to our limited knowledge of dominance hierarchies in kestrels, we were unable to assess the dominance hypothesis which is the third classic hypothesis often assessed in partially migratory systems. We used stable hydrogen isotope values (δD) extracted from talon tissues to distinguish migrant from resident kestrels during the 2013 – 2021 breeding seasons. Stable isotopic values of known migrants were significantly higher than those of known residents. We assigned migratory status to 349 birds with a previously unknown migration strategy and found that male kestrels were 1.7 times more likely to migrate than females, and that in colder than average winters, smaller birds of both sexes were more likely to migrate than larger birds. These results support the body size hypothesis

and are inconsistent with the arrival time hypothesis. Kestrels showed evidence of switching their migration strategies on an annual basis. There was no temporal trend in the proportion of migrants in the population, but proportions varied between years. Interestingly, winter weather did not explain patterns of interannual variation, suggesting that differential over-winter survival may play an important role in population composition. Overall, results suggest that costs of thermoregulation play an important part in migratory decisions of American Kestrels. Therefore, as winters continue to warm, fewer kestrels may migrate and more may remain resident on breeding grounds. Potential changes in migration patterns have important implications for monitoring kestrels at migration sites, and population resilience to climate change.

Introduction

Organisms across the world exhibit a variety of migration strategies to track seasonal changes in resources, ranging from extremely long-distance migrations to eruptive movements across the landscape (Chapman et al. 2011). The most common migration strategy is partial migration, which is when populations are composed of both individuals that migrate and others that remain resident on the breeding grounds year-round (Chapman et al. 2011). Despite the prevalence of partial migration, there are underexplored questions concerning the evolution and maintenance of this migration strategy across systems (Lundberg 1988). Further, recent studies show that migratory strategies (Rivalan et al. 2007), phenology (Koleček et al. 2020, Powers et al. 2021, Samplonius et al. 2018), and migration distances (Heath et al. 2012, Visser et al. 2009) may be changing in response to climate change. Therefore, understanding the mechanisms and consequences underlying migratory decisions is important for predicting

change in species distributions, annual cycles, and resilience (Buchan et al. 2020, Nilsson et al. 2006). Here, we studied the correlates of migratory strategies in a partially migratory population of American Kestrels (*Falco sparverius*), a small falcon that shows evidence of historic changes in migration distances and nesting phenology (Heath et al. 2012). Additionally, we examined whether the proportion of migrants in our study population has decreased over time as winters have warmed.

A similar phenomenon to partial migration, termed differential migration, describes when individuals in a population migrate at different times or at variable distances. Three classic differential migration hypotheses are commonly used to explain alternative migration strategies within a population: 1) the body size hypothesis, 2) the arrival time hypothesis, and 3) the dominance (or social status) hypothesis (Ketterson and Nolan 1976). The body size hypothesis predicts that smaller-bodied individuals are more likely to migrate than their larger-bodied conspecifics due to varying degrees of thermal tolerance when faced with harsh winter conditions (Chapman et al. 2011, Ketterson and Nolan 1976). The arrival time hypothesis suggests that, if a part of the population experiences more competition for a breeding resource than others, individuals within that group should arrive at the breeding grounds earlier, potentially through remaining resident year-round (Chapman et al. 2011, Ketterson and Nolan 1976). Finally, the dominance hypothesis predicts that subordinate individuals in a population are more likely to migrate than dominant individuals because dominant individuals exclude subordinates from limited resources during the winter (Chapman et al. 2011, Ketterson and Nolan 1976). Unfortunately, these hypotheses can be difficult to test in some systems because of confounding relationships between large body size, competition for breeding

resources, and dominance. In this context, raptors are excellent study systems for testing hypotheses because females are larger than males (reverse sexual-size dimorphism), but males are more likely to compete for nest sites and mates (Newton 1978).

In addition to these three hypotheses, other studies have proposed alternate factors that may influence migration tendencies. Examples include evasion from predators (Skov et al. 2011), trophic polymorphism (Chapman et al. 2011), and sexual conflict (Grayson and Wilbur 2009). Additionally, given the heritability of migratory traits (Berthold and Querner 1981, Berthold et al. 1990, Helm and Visser 2010), genetics may influence whether an individual migrates (Pulido et al. 1996). Some animals that exhibit partially migratory tendencies can switch their migration strategy on an annual basis, however, suggesting that annual decisions can be modified by environmental conditions (Able and Belthoff 1998, Dale et al. 2019, Gillis et al. 2008, Ogonowski and Conway 2009, Palacín et al. 2011). Taken together, it is important to understand the factors— ecological, genetic, or both— that contribute to the expression of an individual’s migration strategy on an annual basis (Dale et al. 2019).

Whether an animal can adjust its migration strategy in response to internal or external conditions can have significant implications for the adaptive capacity of a population to climate change. This is because individual-level differences in migration strategies scale up to influence population-level patterns of migration, phenology, and demography. For example, in a study on Common Blackbirds (*Turdus merula*) in the Netherlands, researchers found that fewer individuals were migrating during the winter than documented historically, presumably due to a changing climate (van Vliet et al. 2009). These individual-level patterns initiated a population-level cascade such that the

proportion of migrating birds in the population decreased from 30% to 10% from 1955 to 1990 (van Vliet et al. 2009). Additionally, large-scale data across several avian taxa show that multiple bird species are overwintering at higher latitudes than seen previously, perhaps due to less harsh conditions for individuals to withstand during the winter (Fiedler et al. 2004). In extreme cases, species once thought to be entirely migratory are demonstrating transitions to the other end of the movement spectrum— complete residency. In a study of eight populations of White Storks (*Ciconia ciconia*), researchers found that one distinct population was in fact entirely resident due to human-mediated supplemental feeding (Flack et al. 2016). In consideration of the important roles that many migratory species play in the ecosystems of which they are a part, drastic changes in movement patterns can have significant consequences not only for the populations in consideration, but also for the complex systems that they contribute to.

American Kestrels (*Falco sparverius*) are a small falcon species that show reverse sexual-size dimorphism, with females being approximately 10% larger than males (Smallwood and Bird 2020). Additionally, kestrels exhibit a variety of migratory behaviors across their range, making them particularly valuable for assessing the correlates and patterns of migratory decisions. Most northern populations are fully migratory, most southern populations are fully resident, and mid-latitude populations are often partially migratory. American Kestrels migrate in “leap-frog” patterns, such that northern migrants migrate to lower latitudes than southern migrants and females migrate farther distances than males (Heath et al. 2012). In migratory populations, male kestrels typically arrive at the breeding grounds earlier to compete for access to territories and nesting sites (Smallwood and Bird 2020). Aborn (1989) suggested that females may be

dominant, but studies of social hierarchies have been equivocal (Smallwood and Bird 2020). American Kestrels may be migrating shorter distances as winters warm on breeding grounds (Heath et al. 2012, Paprocki et al. 2014). However, despite our knowledge of the factors influencing migration distance in kestrels, little is known about the correlates of migration strategies or whether individuals switch strategies between years.

We aimed to understand the mechanisms underlying migration strategies in American Kestrels, and whether the proportion of migrants was changing over time in our study population. We assigned individual kestrels to either the migrant or resident strategy based on stable hydrogen isotopes of talon tissue (δD ; D, or deuterium, is the more massive stable isotope of hydrogen). Stable isotope ratio analysis of tissues containing keratin has been used widely to study animal migration. Spatial variation in environmental δD values (food and water) results from differences in precipitation δD by location, and this spatially specific variation is often reflected in consumer tissues (Hobson 1999). Claw tissue regenerates every 3 – 4 months in avian species, so the δD value of the tissue collected from a breeding bird can proxy for the isotope composition of precipitation where that bird spent the winter (Fraser et al. 2008, Hopkins et al. 2013). We used δD values from known migrant and resident kestrels to assign migration strategies to unknown strategy individuals. We then tested whether the body size hypothesis or arrival time hypothesis explained migration strategies. Unfortunately, we were unable to assess the social dominance hypothesis because our knowledge of the characteristics of dominance hierarchies in American Kestrels is limited (Smallwood and Bird 2020). We included a variable for winter weather conditions as an interaction with

size because winter weather directly affects thermal tolerance. If the body size hypothesis explains kestrel migration strategies, males should migrate more often than females, and smaller-bodied birds should migrate more frequently than larger birds, particularly in cold winters. If the arrival time hypothesis explains migration strategies, females should migrate more often than males. In the case of recaptured birds, we assessed whether individual strategies were consistent between years, which may suggest that heritable factors outweigh environmental conditions. Finally, we examined the annual proportion of migrant to resident individuals to assess whether a temporal trend or winter weather explains population patterns.

Methods

During the breeding season, we hand-captured adult American Kestrels nesting in nest boxes over the months of April through July from 2013 – 2021 in rural portions of Ada and Canyon counties (Treasure Valley site), and Camas County (Camas Prairie Centennial Marsh site) in Idaho (Figure 1). These two study sites are ~150 km apart and the study site at Camas Prairie Centennial Marsh is at a higher elevation (1,542 m) than the Treasure Valley (832 m) site. Kestrels in the Treasure Valley are partial migrants. Many reside year-round, and individuals are routinely recaptured in both the breeding and winter seasons. Kestrels in Camas County are fully migratory. No kestrels are present at the Camas Prairie study site in winter (November – February), and the site has consistent snow cover throughout the winter. We trapped American Kestrels wintering at the Treasure Valley site over the months of November – February from 2013 – 15 and 2017 – 18 using a bal-chatri trap baited with a live mouse. Winter trapping helped to identify known residents (see below). Upon trapping breeding or wintering kestrels, we

fitted each bird with a unique United States Geological Survey (USGS) identification band (or noted the code of a preexisting band in the case of recaptures), collected morphometric measurements, and sexed birds based on plumage. We collected ~ 1 mm of claw tissue from the outermost talon on the right foot with small scissors and stored in microcentrifuge tubes at room temperature until further processing in the laboratory.

We used sex-adjusted mass to represent bird size because mass is a good estimate of size in kestrels (Heath et al. 2011). Sex-adjusted mass was calculated by subtracting the sex-specific mean mass from each individual and dividing the difference value by the standard deviation. Positive values represent larger than average birds and negative values represent smaller than average birds.

Winter weather conditions were recorded as site-specific winter minimum temperature anomalies. We created polygons with a 1 km buffer around the edge of the study site to define each site's spatial extent. Then we used Google Earth Engine (Gorelick et al. 2017) to access minimum temperature data from Daymet V3: Daily Surface Weather Data (Thornton et al. 2019). Anomalies were calculated by subtracting the average minimum minimum temperature in November – February, 1980 – 1995, from the minimum minimum temperature for each year that samples were collected.

Laboratory Methods

All samples were prepared and analyzed in the Stable Isotope Laboratory, Department of Geosciences, Boise State University. We soaked each individual claw segment in ~ 300 μ l of 2:1 chloroform methanol solution for a minimum of 24 hours (but not exceeding 32 hours) to remove any lipids on the exterior of the sample prior to analysis (Chew et al. 2019). We then removed the chloroform methanol solution from the

sample vial, added a small amount of fresh 2:1 chloroform methanol to rinse the claw segment, then promptly removed the solution from the vial. We left each sample tube uncapped in a fume hood for approximately three hours to ensure all remaining solution had evaporated. The samples were left in uncapped tubes in the laboratory for a minimum of 48 hours to allow the samples to equilibrate to the ambient lab conditions. This equilibration step allows time for the exchangeable fraction of hydrogen in the keratin to match that of the standards; negating its effect on the measured isotopic composition in the non-exchangeable fraction of hydrogen in the unknown samples (Soto et al. 2017). We trimmed all individual claw samples to achieve a desired sample mass (0.3 – 0.4 mg) and encapsulated each sample into silver capsules in preparation for isotope analysis. When initial claw masses allowed, we trimmed the claws to create duplicate or triplicate samples. We prepared two standards– Caribou keratin (CBS), and Kudu keratin (KHS)– for instrument calibration, and one in-house laboratory control material, a chicken feather standard (RH-B; e.g., 50‰; McComb et al 2019), to assess machine performance. Samples and standards were analyzed using a Thermal Conversion Elemental Analyzer with a glassy carbon packed reactor operated at 1450°C (TC/EA, Thermo Fisher), coupled to a Thermo Fisher Delta V+, gas-source isotope ratio mass spectrometer (Qi and Coplen 2011). Unknown measurements were calibrated against CBS ($\delta D = -157.0$ ‰) and KHS ($\delta D = -35.3$ ‰) (Soto et al. 2017) and expressed in permil notation (‰) relative to Vienna Standard Mean Ocean Water (VSMOW), normalized to Standard Light Antarctic Precipitation (VSMOW-SLAP; Coplen 2011).

Migration Strategy Assignment

We identified kestrels in the dataset as known migrants, known residents, or as unknowns. We considered birds that were sampled during the breeding season and caught the preceding winter as residents of the Treasure Valley. Likewise, birds that were sampled in the winter and caught the preceding breeding season were also considered residents. We classified kestrels captured in Camas County as migrants. We used the δD values of individuals with known migration strategies to establish the distribution of isotope values for both the resident and migrant groups. Once we identified all individuals as either a known or unknown strategy bird, we used a likelihood assignment approach incorporating analytical error following the methods and scripts developed by Dale and colleagues (2019) to assign unknown individuals to the most probable migration strategy given the δD value of their talon sample (Royle and Rubenstein 2004, Wunder and Norris 2008). The estimated standard deviations for unknown claw samples were derived from analytical reproducibility of the two keratin standards and control keratin as determined by repeated sampling (Wunder and Norris 2008). We then performed a bootstrap analysis for each claw sample, where 10,000 simulations were drawn from a distribution with an average equivalent to each δD composition, and a standard deviation derived from the laboratory standards (Dale et al. 2019). We assigned each bird to either the migrant or resident group depending on where that bird received most of their assignments during the simulation. We included individuals in subsequent analyses if they were assigned as a migrant or resident with at least 80% confidence out of the 10,000 simulations (Bugajski et al. 2013, Dale et al. 2019). We assessed the efficacy of our bootstrapping assignment approach with leave-one-out-cross-validation (LOOCV) by

assigning individuals with a known migration strategy to either the resident or migrant groups (Bugajski et al. 2013, Dale et al. 2019, Franks et al. 2012).

Data Analysis

All analyses were conducted in R version 3.6.3, and all generalized linear models (GLM) were constructed using the package glmmTMB (Magnusson et al. 2020). We assessed standard assumptions of each statistical test and used non-parametric alternatives when assumptions were not met. Following the migration strategy assignment protocol, we first compared δD values between known migrant and known resident individuals using a nonparametric Wilcoxon Rank Sum test due to unequal variances between groups. We used a generalized linear mixed model with a binomial distribution and a logit link to assess the effects of sex, sex-adjusted mass, winter weather conditions and all possible interactions between explanatory variables to explore the potential correlates of migration strategies in American Kestrels. We included a random effect of year in the model to account for interannual variation in sampling efforts and other environmental conditions. Individuals with missing data (e.g. mass measurements) were not included in this analysis. Non-significant terms were removed from the full model until the final model contained only significant terms. Reported parameter estimates were based on the final model. In the case of recaptures, we compared each bird's assigned strategy to their previous migration strategy with a Fisher's exact test (due to small sample sizes) to assess if a bird's previous strategy influenced future migratory decisions.

We subset the data by year and calculated the proportion of residents in the population for each year sampled to assess any temporal trends in migration patterns in

the Treasure Valley. We ran a generalized linear model with a binomial distribution and a logit link with a numerical variable for year to assess the association between sampling year and the proportion of residents in the population. We also ran a generalized linear model with a binomial distribution and a logit link with a categorical variable for year to determine if the proportion of residents and migrants in the Treasure Valley significantly differed between years. Finally, we ran a generalized linear model with a binomial distribution and a logit link to assess the impact of winter weather conditions on the proportion of residents and migrants in the population.

Results

Of the 457 breeding kestrels and 54 wintering kestrels that we sampled between 2013 – 2021, 92 birds were identified as having a known migratory status – 38 residents, and 54 migrants. Migrants had significantly higher δD values (i.e. containing a higher proportion of the heavy hydrogen isotope, deuterium, relative to the light hydrogen isotope, protium) than residents ($W = 1956$, $p < 0.01$; Figure 2). We successfully assigned 77 (84%) of the individuals with a known strategy to the correct strategy, eight birds (8.7%) to the incorrect strategy, and we could not determine the migratory strategy for seven individuals (7.6%) with at least 80% confidence (Figure 3). Of the 457 breeding birds, 27 individuals were identified as known residents (88.9% correct assignment), and 54 individuals were identified as known migrants (81.5% correct assignment), leaving 376 of the sampled birds classified as unknowns. We assigned 349 (92.8%) of the unknown birds to either the migrant or resident group with at least 80% confidence (Figure 3).

In assessment of the factors correlating with migratory decisions in American Kestrels, we found that sex (Wald $\chi^2 = 4.6$, $p = 0.03$) and the interaction between size (sex-adjusted mass) and winter weather conditions (Wald $\chi^2 = 5.3$, $p = 0.02$) were significant factors in influencing individual-scale migration patterns (Table 1, Figure 4). Between sexes, males were 1.7 times more likely to migrate than females. In colder than average winters, smaller individuals of both sexes were more likely to migrate than larger individuals, which were more likely to remain resident on the breeding grounds (Table 1, Figure 5).

We recaptured 26 individuals in more than one year. Twenty-one individuals were caught in two consecutive years, four individuals were caught in two years with a one-year gap between successive captures, and one individual was captured in four consecutive years. We assigned migratory strategies to all recaptured individuals in each year that they were sampled. Of the recaptured individuals, 20 birds maintained a consistent migratory strategy across years. Six of the 26 recaptured individuals (23%) switched migration strategies (two of the six were sampled with one year in between sample collections). Of the individuals that switched strategies, three birds switched from the resident to the migrant strategy ($n = 1$ female, $n = 2$ males), and three birds switched from the migrant to the resident strategy ($n = 1$ female, $n = 2$ males). We did not find that an individual's previous strategy influenced their migration strategy in subsequent years (Fisher's Exact $\chi^2 = 7.5$, $p = 0.06$).

The proportion of residents in the population relative to the proportion of migrants varied widely across the years studied, from 30% in 2014 to nearly 86% in 2016 (Wald $\chi^2 = 54.8$, $p < 0.01$; Figure 6). There was no temporal trend in the proportion of residents

relative to migrants in the Treasure Valley (Wald $\chi^2 = 0.03$, $p = 0.87$). There were significantly more residents in 2015 ($\beta = 1.7$, $SE = 0.68$), 2016 ($\beta = 2.0$, $SE = 0.61$), and 2019 ($\beta = 2.0$, $SE = 0.65$) compared to the other years. Interestingly, winter weather did not affect the proportion of migrants and residents in the population (Wald $\chi^2 = 0.10$, $p = 0.75$).

Discussion

Migrant and resident δD values differ significantly – migrant kestrel compositions were, on average, less negative than for residents, as expected for birds overwintering at more southern latitudes (Dale et al. 2019). This result is consistent with patterns observed in other studies. For example, in Western Bluebirds (*Sialia Mexicana*), the samples collected from known migrant birds were less negative (higher) than samples collected from known resident birds (Dale et al. 2019). These observed patterns in isotope compositions between groups confirm that utilizing stable isotope values to infer relative geographic locations of tissue growth can be a useful method for studies of animal movement.

Additionally, we successfully assigned migration strategies to breeding kestrels, and found support for the body size hypothesis, but not the arrival time hypothesis, in explaining migratory strategies of individuals. Some kestrels switched migration strategies, suggesting that migration strategy is a flexible phenotype. Finally, there was no temporal trend in the proportion of resident and migrants at the Treasure Valley site, but the proportion did change from year to year. The annual proportions of migrants and residents were not explained by winter weather, suggesting that the factors that determine individual decisions may not scale-up to predict population patterns. Other factors that

are not accounted for in this study, such as differences in mortality risks between migrants and residents, may determine the proportion of alternate strategies in the breeding population.

Correlates of Migration Strategies

Sex and the interaction between size and winter weather significantly explain the likelihood of migratory behavior in kestrels. Smaller bodied males were more likely to migrate than females, and small-bodied birds of both sexes were more likely to migrate during colder winters compared to warmer winters. These results support the body size hypothesis, which predicts that smaller individuals are more likely to migrate than larger individuals to evade harsh winters on the breeding grounds due to limiting factors associated with thermal tolerance (Kendeigh 1969). Despite several studies investigating the mechanisms underlying partial migration across diverse taxa, few have found support for this hypothesis (Chapman et al. 2011). Conversely, the body size hypothesis does help explain differential migration in some avian species. For example, in a study of House Finches (*Haemorrhous mexicanus*) in the eastern United States, male finches overwintered farther north than females, likely because larger male body sizes promoted a higher thermal tolerance, and thus increased winter survival, compared to smaller-bodied females (Belthoff and Gauthreaux 1991). The limited empirical support for the body size hypothesis may reflect the difficulty in isolating different mechanisms contributing to partial migration. Thus, studies of the evolution and maintenance of partially migratory systems may not have found support for the body size hypothesis because of the limitations associated with partitioning individual drivers of migration.

Our results do not support the arrival time hypothesis, which predicts that male kestrels would be more likely to remain resident on the breeding grounds than females to compete for and obtain high quality nesting sites (Ketterson and Nolan 1976). This is surprising because female kestrels migrate farther than males (Heath et al. 2012) – a pattern that supports the arrival time hypothesis and is opposite of the predictions from the body size hypothesis (Aborn 1989, Heath et al. 2012). It is important to note that the factors influencing the characteristics of migration, such as initiation and distance, are likely to be more complex than a single mechanism (Chapman et al. 2011). To that end, findings of different drivers influencing migration strategy and distance may not be uncommon in systems that exhibit reverse sexual-size dimorphism where the smaller sex also competes for breeding resources, such as in many raptor species. Taken together, these results suggest that the mechanisms associated with migration distance in American Kestrels may be distinct from the mechanisms influencing whether an individual migrates. To our knowledge, this is the first report of different mechanisms underlying migration strategy and distance and is a topic for future research in other systems.

Migration Strategy Switching

In the assessment of the birds that we captured in more than one breeding season, some individuals were assigned to different migration strategies on an annual basis, suggesting that migration is a flexible phenotype, and that American Kestrels do not demonstrate an obligate predisposition to migrate or to remain resident. We found that of the six individuals that switched strategies, an equal number switched from migrant-to-resident as from resident-to-migrant. An individual's prior migration strategy also did not influence migratory decisions in subsequent years; a finding that could be due to a limited

number of recaptured individuals that exhibited strategy switching in this study. Migration strategy transition in American Kestrels was previously unknown, but other species also show migration strategy switching including Lesser Kestrels (*Falco naumanni*; Buchan et al. 2021), Great Bustards (*Otis tarda*; Palacín et al. 2011), Western Bluebirds (*Sialia mexicana*; Dale et al. 2019), and Burrowing Owls (*Athene cunicularia*; Ogonowski and Conway 2009). In the closely related Lesser Kestrel, Buchan et al. (2021) found that across the 25 recaptured birds in their study, four individuals switched migration strategies: one bird transitioned from resident to migrant, and three individuals switched from migrants to residents. Bidirectional migration strategy switching also occurs in Great Bustards and is likely associated with an individual's breeding success in the season preceding migration (Palacín et al. 2011). However, unlike American Kestrels, Lesser Kestrels, and Great Bustards, migration strategy switching in Western Bluebirds, Burrowing Owls, and European Blackbirds (*Turdus merula*) occurs in only a single direction (Dale et al. 2019, Ogonowski and Conway 2009, Schwabl 1983). Unidirectional changes from migrant to resident suggests that changes in age or social status may contribute to migration decisions (Ogonowski and Conway 2009), whereas birds that switch between the two strategies may be responding to environmental conditions. For example, in the present work, we found that small-bodied kestrels were more likely to migrate during colder winters.

Migration and Climate

The ability for kestrels to switch migration strategies suggests potential in this species to adapt to climate change. However, despite a warming trend in winters, we did not detect a significant temporal trend in the proportion of migrants to residents over the

nine years of our study. Further, although we found a significantly higher proportion of residents in the Treasure Valley population in some years compared to others, winter weather did not correlate with this annual variation. This was surprising because winter temperatures influenced individual decisions, but not population-level patterns. Further, kestrels in the Treasure Valley show several other responses to warming weather such as earlier nesting (Smith et al. 2017) and shorter migration distance (Heath et al. 2012). We may not have detected a temporal trend in the proportion of migrants because our study spans only nine years. Alternatively, there may be other factors along their migratory routes or on the wintering grounds that affect survival of migratory birds in those years. Some examples include collisions with anthropogenic structures, poaching, distance to wildfires, and air quality conditions (Cheng et al. 2019, Klaassen et al. 2014, Yang et al. 2021). However, disentangling the different drivers and potential causes of mortality in migratory birds is difficult and is a topic for further research. Additional study is also needed in other portions of the kestrel's annual cycle, particularly during fall and spring migration, to further elucidate these potential threats.

Although we did not detect a relationship between winter weather and the proportion of migrants in the population, we did see a relationship between kestrel body size and winter weather. This result has interesting implications for the impacts of future climate change. If smaller birds are able to withstand future projected milder winters, fewer individuals may need to leave the breeding grounds during the winter months to survive, leading to changes in population dynamics such as intraspecific competition (Pulido and Berthold 2010, Resano-Mayor et al. 2020, Singh et al. 2012). Additionally, if fewer birds migrate, annual migration counts – an accepted proxy for population health in

migratory birds – may not reliably inform population trends (Bednarz et al. 1990, Farmer et al. 2007, Titus and Fuller 1990).

Future Stable Isotope Research

Although using δD to assign migratory status to individual birds succeeded for the scope of this research project, limitations to using this method in migration studies warrant further discussion. In our work, we aimed only to distinguish between migrant and resident individuals and did not attempt to determine the specific geographical origins of migratory birds. Lott and Smith (2006) found that the relationships between stable hydrogen isotope compositions derived from animal tissues and from local precipitation are not consistent across geographic regions in raptors. This inconsistency makes it difficult to assign migratory individuals to discrete geographic regions reliably (Lott and Smith 2006). Additionally, studies have found variation in stable hydrogen isotope values derived from multiple feathers collected simultaneously from a single bird, and within a single feather (Smith and Dufty 2005, Smith et al. 2008). Similarly, in our study, we often observed variation between duplicate and triplicate samples derived from the same initial claw sample. As such, the underlying mechanisms that define stable hydrogen isotope compositions in different tissues is limited, so researchers should proceed with caution when deducing migratory origins from isotopic compositions alone. However, in the case of broadly categorizing individuals according to their most likely migratory strategy, using known residents and known migrants for comparison, stable hydrogen isotope analysis proved highly effective.

Conclusion

Stable hydrogen isotope analysis and the assignment methods developed by Dale et al. (2019) determined (or verified, in the case of known-strategy birds) the migration status for 417 of the 457 individuals (91.2%) sampled during the breeding season in Idaho. The δD values allowed us to assess individual correlates and population-level patterns of migratory decisions in American Kestrels. The results from this study help explain how partial migration operates in American Kestrels, and how ecological conditions may interact to influence migration patterns and phenology of migratory birds. These results could have relevant implications for patterns in other partially migratory animals as well, particularly in other species with similar life histories or behavioral traits. Future research could assess other potential drivers of migration such as the dominance hypothesis (when advances in our understanding of social hierarchies in kestrels allow), the potential effect of predation vulnerability, or sexual conflict (Chapman et al. 2011). Despite a growing body of research regarding the factors that influence individual decisions about migration across diverse taxa, additional research is needed to understand how all factors— genetic, physiological, environmental, or some combination— contribute to population-level patterns in migration. This is especially important to predict population trends of migratory animals during current rapid environmental change, and to inform and implement management strategies appropriately.

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TABLES AND FIGURES

Table 1. Explanatory variables (and the associated parameter estimates and standard errors) included in the final model to assess the potential correlates of migration decisions in American Kestrels.

Variable	Estimate	Standard Error
Sex (Male)	0.52*	0.24
Size	-0.63*	0.20
Winter Minimum Temperature Anomaly	-0.001	0.08
Size : Winter Minimum Temperature Anomaly	0.07*	0.03

*Indicates that the variable was statistically significant at a threshold of $\alpha = 0.05$.

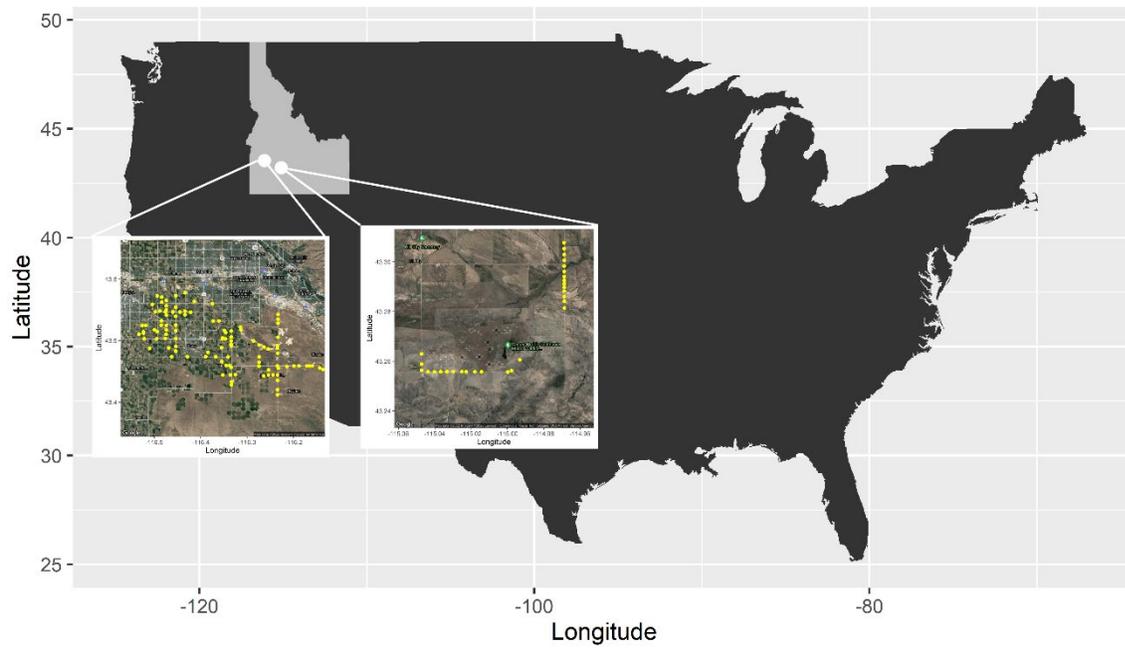


Figure 1 A map demonstrating the locations of the two Idaho study sites utilized in this study: the Treasure Valley site (left panel) and the Camas Prairie Centennial Marsh site (right panel). The two sites are approximately 150 km apart.

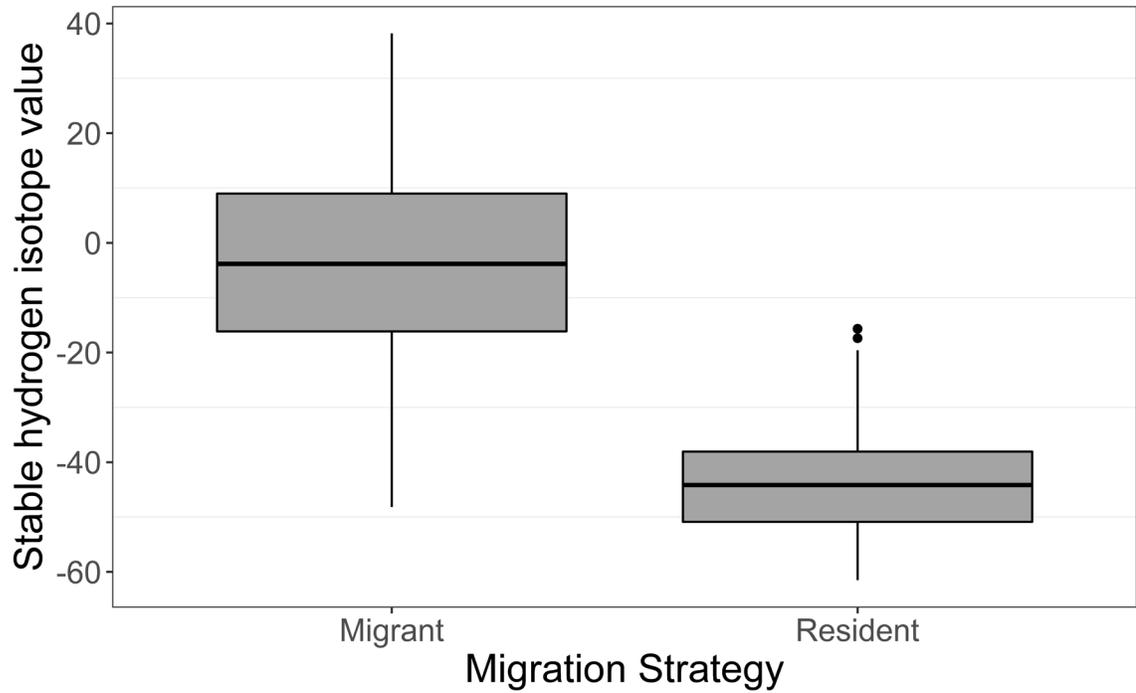


Figure 2 Box plots demonstrating stable hydrogen isotope values (δD) for known migrant ($n = 54$) and known resident ($n = 38$) American Kestrels. Lines represent medians and filled circles indicate outliers. Average δD differed significantly between groups ($W = 1956, p < 0.01$).

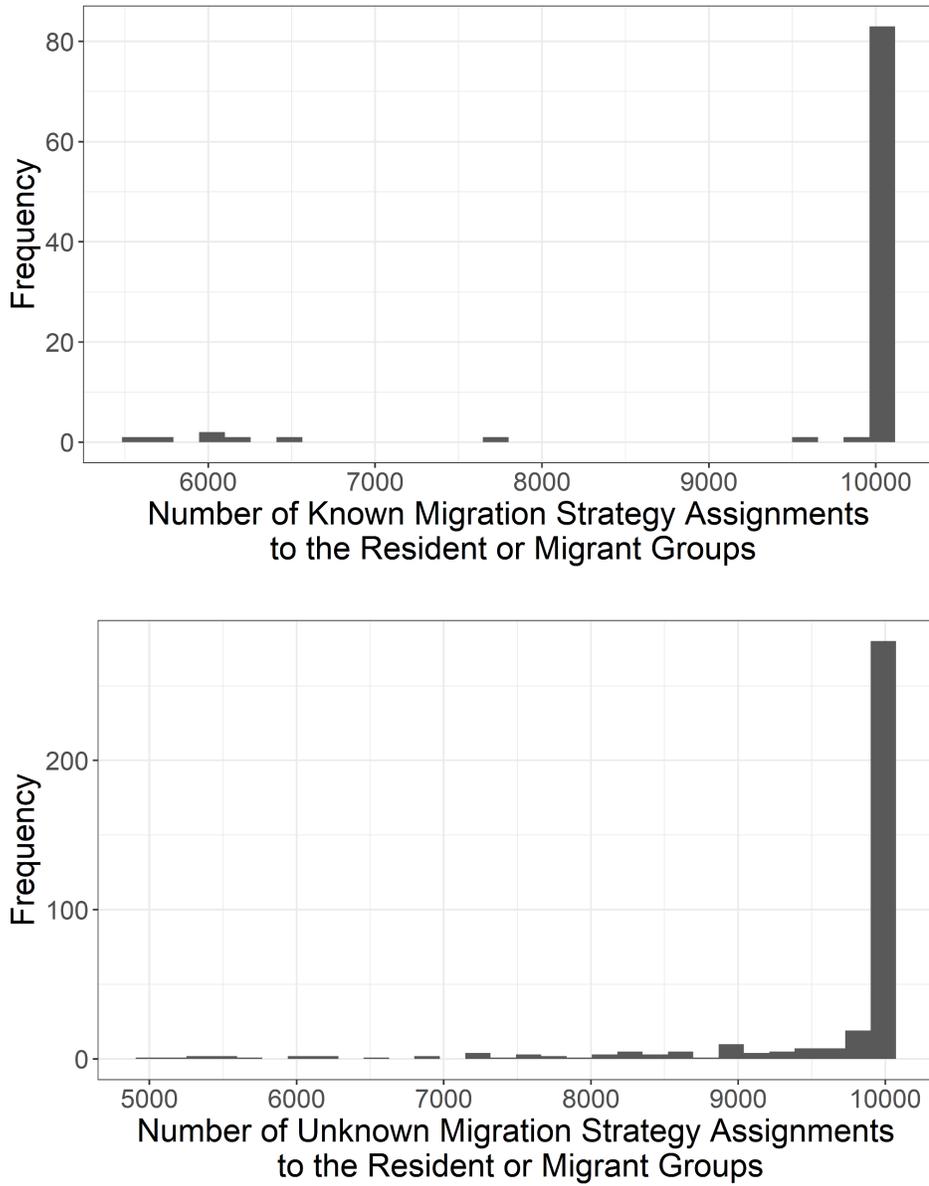


Figure 3 The frequency at which bootstrapping assigned individuals with a known (top) or unknown (bottom) migration strategy to either the migrant or resident groups (method of Dale et al. 2019).

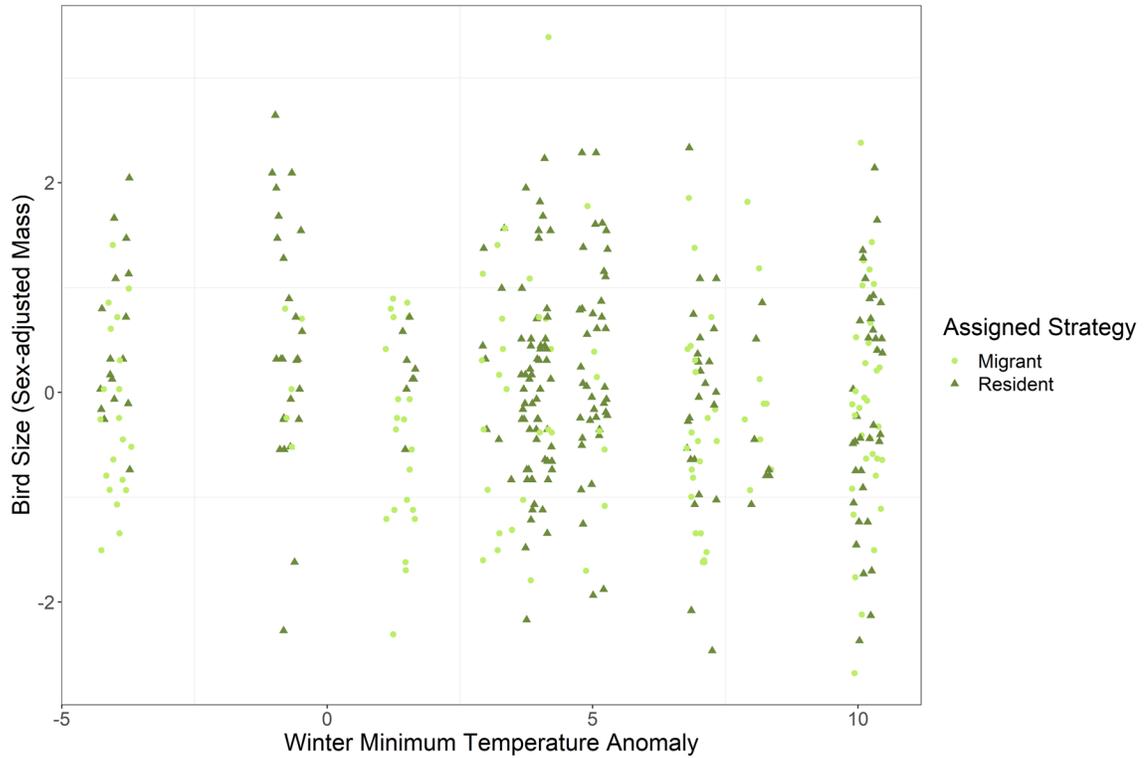


Figure 4 A scatterplot demonstrating migration strategy assignments and body sizes of adult American Kestrels across winters of varying severity. If the body size hypothesis influences individual migration strategies, then smaller individuals should migrate more often than larger individuals, particularly in colder winters.

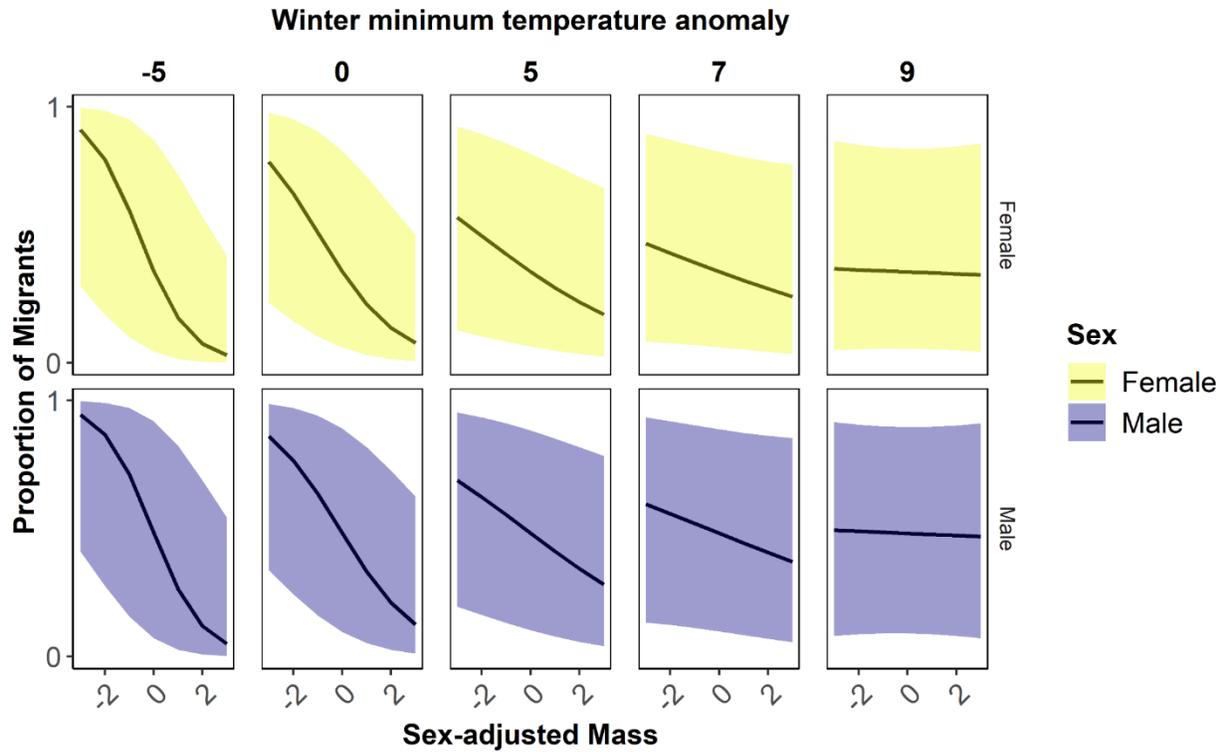


Figure 5 The relationship between size (sex-adjusted mass) and winter minimum temperature anomaly on the proportion of migrants in female (top) and male (bottom) American Kestrels. Male kestrels are more likely to migrate than females (Wald $\chi^2 = 4.6$, $p = 0.03$). In colder than average winters, larger individuals are less likely to migrate than smaller individuals (Wald $\chi^2 = 5.3$, $p = 0.02$).

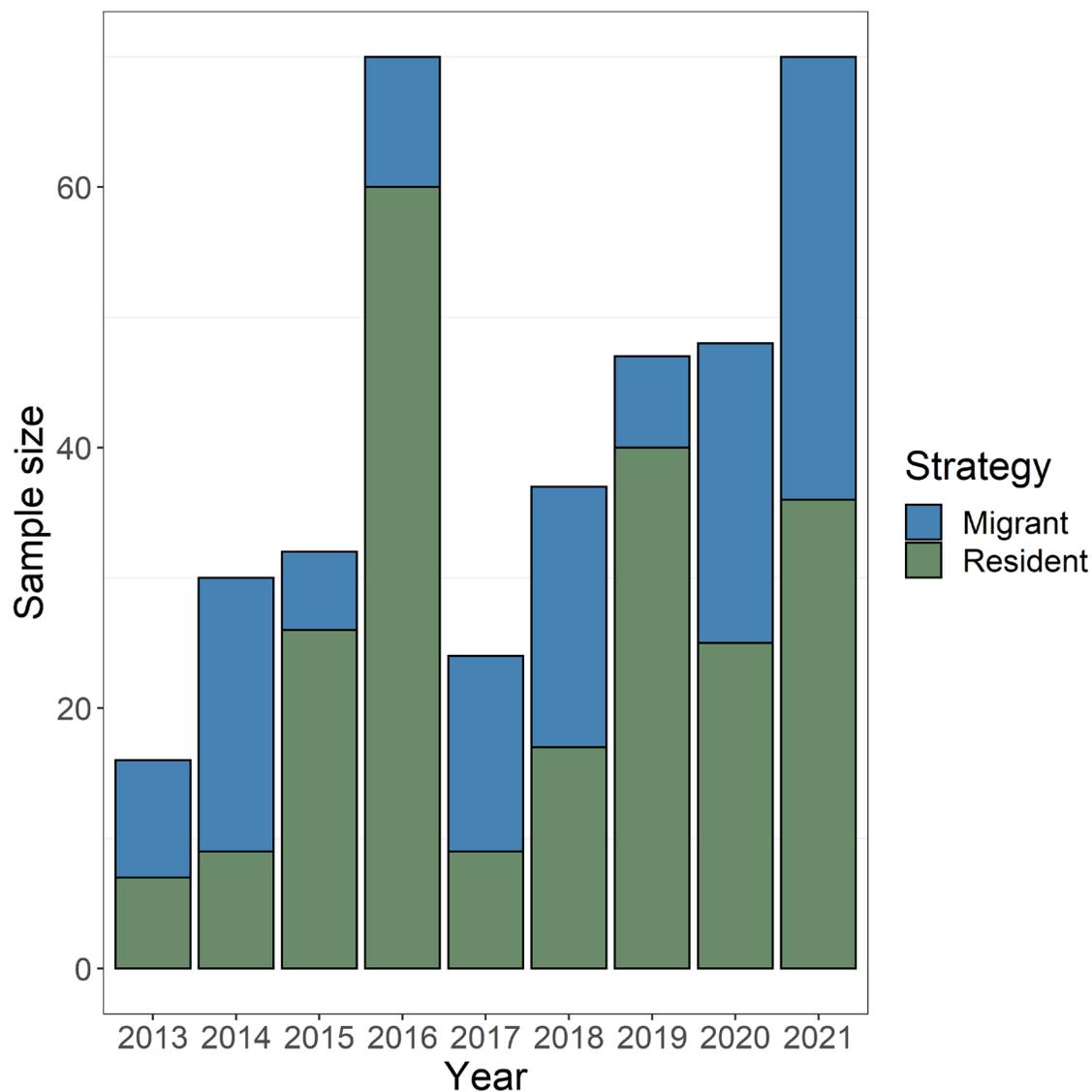


Figure 6 A stacked bar chart demonstrating no temporal trend in the proportion of migrants to residents in the Treasure Valley (Wald $\chi^2 = 0.03$, $p = 0.87$). There were significantly more residents than migrants in the years 2015 ($\beta = 1.7$, $SE = 0.68$), 2016 ($\beta = 2.0$, $SE = 0.61$), and 2019 ($\beta = 2.0$, $SE = 0.65$). Winter weather conditions did not affect the proportion of migrants and residents (Wald $\chi^2 = 0.10$, $p = 0.75$).

APPENDIX

**Assessing the consequences of individual migration patterns in the American
Kestrel (*Falco sparverius*)**

Introduction

Carryover effects of one life cycle stage on other major life events is a phenomenon that has been documented across various taxa (Harrison et al. 2011, Stanley et al. 2012, Norris et al. 2004, Norris 2005). One example is the effect of recurring animal movements on the timing and success of other important events, like reproduction and subsequent migrations. Migration is known to pose costs to the organisms that exhibit it, with some documented consequences being a decrease in body condition (Newton 2006), metabolic costs associated with sustained natural flight and stopovers (Wikelski et al. 2003), limited or difficult to access resources along the migratory route (Newton 2006), or extreme environmental conditions that may ultimately lead to mortality (Newton 2006). In our study, we aimed to assess the association between the relative distance traveled during migration and the initiation of an important life event, reproduction, in the American Kestrel (*Falco sparverius*). Kestrels are a generalist species that are widespread across their range in North America, they exhibit a range of migratory strategies, and are relatively easy to study due to their tendencies to nest in artificial nesting structures. Taken together, these characteristics make them a suitable model species for this investigation (Smallwood and Bird 2002). We predict that kestrels that travel further distances during migration initiate reproduction later than individuals that migrate shorter distances or remain resident on the breeding grounds.

Methods

Field Methods

For this analysis, we hand-trapped breeding American Kestrels across four sites on Department of Defense (DoD) lands from 2018-2020 as part of the Full Cycle

Phenology Project (<https://fullcyclephenology.com/>). Samples included in this analysis were collected from DoD sites located in Indiana, Kansas, New York, and Washington. Upon trapping, we placed a unique United States Geological Survey (USGS) identification band, or noted the code on an existing band in the case of recaptures, recorded a variety of morphometric measurements, collected four feather samples for genetic analysis, and a small ~ 1mm claw segment for isotope analysis. We also utilized claw samples that were contributed by project partners from Wisconsin in the 2017-2019 breeding seasons, from Wyoming in the 2015 breeding season, and from the 2019 breeding season in Saskatchewan, Canada. Because we were interested in the effect of migration on the initiation of reproduction, we omitted individuals that were captured and sampled at sites where the population is resident year-round, including birds sampled in California, North Carolina, and New Mexico. Lay dates were determined through the use of remote cellular camera tracking, or through back calculation based on estimated nestling ages.

Laboratory Methods

To gauge the relative distance that kestrels traveled during migration, we used stable hydrogen isotope values (δD) from claw samples of breeding birds. Hydrogen stable isotope values vary spatially (according to latitude and elevation, chiefly), and this spatial variation is often retained in consumer tissues (Hobson 1999). In other avian species, claw tissue regenerates every 3-4 months, so the isotope value in the claw of a breeding bird reflects the precipitation patterns of where the individual overwintered (Fraser et al. 2008, Hopkins et al. 2013).

We processed the claw samples according to the same methodology described in the first chapter of this thesis. Briefly, we soaked all claw segments in a solution of 2:1 chloroform methanol solution for approximately 24 hours (Chew et al. 2019). Following the washing step, samples were left to dry and equilibrate to laboratory conditions for at least 48 hours before they were weighed and encapsulated in silver capsules. Samples were analyzed using a Thermal Conversion Elemental Analyzer with a glassy carbon packed reactor operated at 1450°C (TC/EA, Thermo Fisher), coupled to a Delta V+, gas-source isotope ratio mass spectrometer (Qi and Coplen 2011). We prepared two standards– Caribou keratin (CBS), and Kudu keratin (KHS)– for instrument calibration, and one in-house laboratory control material, a chicken feather standard (RH-B; e.g., 50‰; McComb et al. 2019), to assess machine performance. Unknown measurements were calibrated against CBS ($\delta D = -157.0$ ‰) and KHS ($\delta D = -35.3$ ‰; Soto et al. 2017) and expressed in permil notation (‰) relative to Vienna Standard Mean Ocean Water (VSMOW), normalized to Standard Light Antarctic Precipitation (VSMOW-SLAP; Coplen 2011).

Data Analysis

All analyses were conducted in R version 3.6.3, and generalized linear mixed models (GLMM) were built using the package glmmTMB (Magnusson et al. 2020). We utilized a GLMM with a gamma distribution and a log link to model the relationship between an individual's stable hydrogen isotope value (δD) and the date they initiated a nest attempt (lay date). We also included random effects of both sampling location and sampling latitude in the model.

Results and Discussion

We found no significant association between an individual's isotopic value and lay date (Wald $\chi^2 = 0.54$, $p = 0.46$). In other words, we did not find that individuals who overwintered at southern latitudes initiated nesting later than individuals that remained on the breeding grounds or migrated shorter distances (Figure A1). This result is in contrast to what we predicted based on other research that found that birds migrating longer distances nested later than birds that remained closer to the breeding grounds (Gow et al. 2019, Lok et al. 2017). However, in a study on Black-tailed Godwits (*Limosa limosa*) wintering either north or south of the Sahara Desert, researchers found that the individuals that traveled further distances during migration actually arrived at the breeding grounds earlier and initiated reproduction earlier than their shorter-distance migrant counterparts, perhaps due to a difference in habitat quality on the breeding and wintering grounds (Alves et al. 2012, Gunnarsson et al. 2006, Kentie et al. 2017). Additionally, in a recent study by Buchan et al. 2021, they did not find an association between distance traveled during migration and lay date in Lesser Kestrels (*Falco naumanni*), a similar species to our focal subject in our study. In all, these studies combined with our results suggest that the distance between the breeding and wintering grounds is not always a driving factor in the initiation of reproduction. Future studies could be done to investigate if other factors, such as the habitat quality of an individual's overwintering site, may impact when kestrels initiate reproduction.

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Appendix Figures

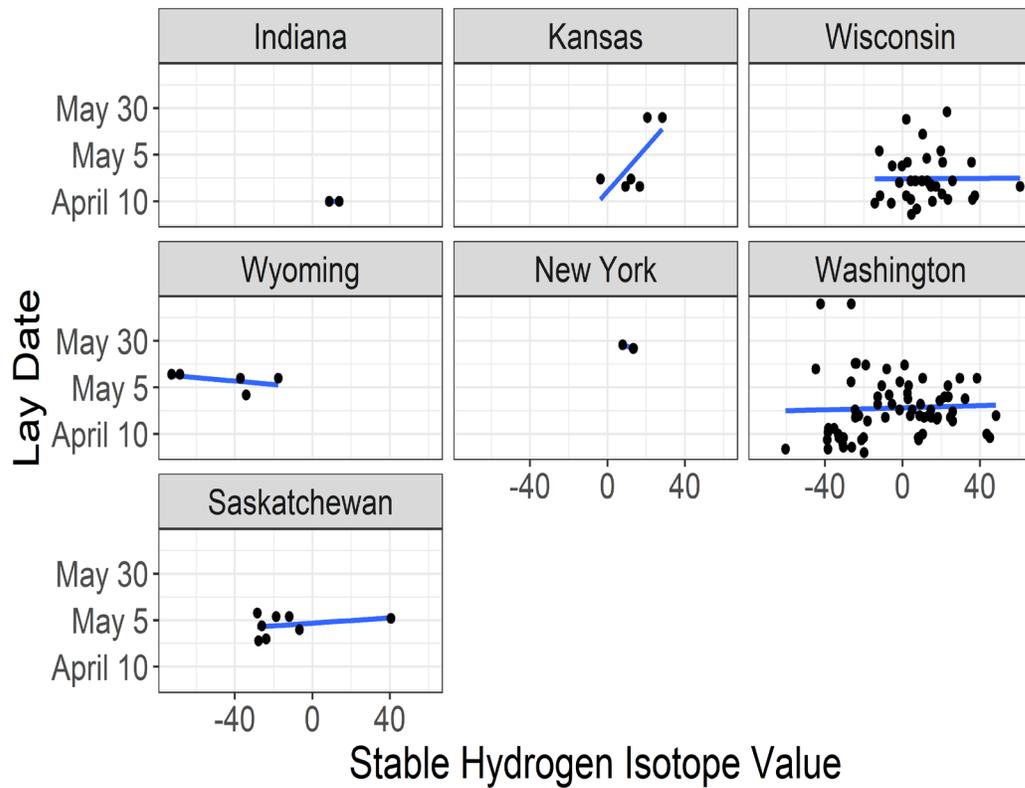


Figure A1 The association between stable hydrogen isotope values (δD) and lay date in American Kestrels (*Falco sparverius*) across seven sites in order of increasing latitude. Isotope values do not significantly predict lay date in this species (Wald $\chi^2 = 0.54$, $p = 0.46$).