Assessing migration patterns of sharp-shinned hawks *Accipiter striatus* using stable-isotope and band encounter analysis

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Intraspecific migration patterns in birds have both spatial and temporal components. Two commonly reported spatial patterns are leap-frog and chain migration. Temporal migration patterns refer to the timing of migration of populations from different breeding latitudes. We investigated the spatial and temporal migration patterns of hatching-year (HY) sharp-shinned hawks *Accipiter striatus* of interior North America using stable-hydrogen isotope and band encounter analyses. Feather samples were collected from hawks migrating through New Mexico, USA and measured for their stable-hydrogen isotope ratios (δD) to distinguish individuals originating from relatively high and low natal latitudes. We then examined the relationship between feather δD values and passage dates through New Mexico, USA. We also gathered band encounter data from the Bird Banding Lab of the United States Geological Survey to determine the wintering latitudes of HY sharp-shinned hawks relative to their passage date through migration banding sites in interior North America. Combining these data, we found that during fall migration HY sharp-shinned hawks used a chain migration pattern, that is, hawks originating from lower latitudes wintered further south than those from higher latitudes. In addition, birds originating from lower latitudes passed through interior North America earlier than those from higher latitudes. We also found that hawks from higher latitudes were significantly larger than those from lower latitudes, and that females from higher latitudes had significantly higher estimated fat levels than females from lower latitudes.

Chain and leapfrog migration are two distinct latitudinal migration patterns reported in the literature (Swarth 1920, Salomonsen 1955, Lundberg and Alerstam 1986, Holmgren and Lundberg 1993, Bell 1996, Alerstam and Hedenström 1998). (So that our descriptions of migration patterns are consistent with others, we maintain a northern hemisphere perspective throughout this paper.) Chain migration (Nilsson 1858 in Alerstam and Hedenström 1998) occurs when northern and southern breeding populations keep the same latitudinal sequence on their breeding and wintering grounds. That is, northern breeding populations winter further north than southern breeding populations. In contrast, leapfrog migration (Palmeén 1874 in Alerstam and Hedenström 1998) occurs when the latitudinal sequence on the wintering quarters is opposite of that on the breeding grounds. In this case, the northern breeding populations migrate longer distances and winter further south than southern breeding populations. Along with a spatial component, migration patterns also have a temporal component. For example, Alerstam (1990) described one possible type of leapfrog migration where southern breeding populations of redshanks *Tringa totanus* arrived first on the northernmost portion of their wintering grounds, potentially causing later arriving northern breeding populations to travel to wintering grounds further south. Kelly et al. (2002) described another type of leapfrog migration for Wilson’s warblers *Wilsonia pusilla* where the northern breeders passed through their migration research site...
first and traveled the furthest to wintering grounds, while southern breeding populations passed through later and wintered furthest north.

Given these observations, we describe four migration scenarios that incorporate both spatial and temporal components. (1) Type I chain migration (Fig. 1a) occurs when northern and southern breeding populations keep the same latitudinal sequence on their breeding and wintering grounds, and southern breeding populations pass through migration sites before northern breeding populations. (2) Type II chain migration involves a chain migration spatial pattern with northern breeding populations passing through migration sites before southern populations (Fig. 1b). (3) Type I leap-frog migration occurs when the latitudinal sequence on the wintering quarters is opposite of that on the breeding grounds, and southern breeding populations pass through migration sites before the northern breeding populations (Fig. 1c). (4) Finally, type II leap-frog migration involves a leap-frog migration pattern with the northern breeding populations passing through migration sites before the southern breeding populations (Fig. 1d).

We were interested in learning the spatial and temporal migration patterns of hatching-year (HY) sharp-shinned hawks *Accipiter striatus* of interior North America during fall migration. Currently, little is known about their migration patterns. Understanding the migration patterns of sharp-shinned hawks can further our understanding of ecological interactions between populations of varying breeding latitudes. For example, Pienkowski et al. (1985) hypothesized that intraspecific competition could result in distinct migration patterns. Understanding migration patterns also has conservation implications. For example, knowing the natal origins, migration timing, and wintering quarters of bird populations can help natural resource managers design appropriate conservation efforts for distinct populations.

Several methods have been used to determine intraspecific migration patterns. Field observations have been used to locate different races or subspecies at distinct breeding and/or wintering locations (Swarth 1920, Salomonsen 1955, Geller and Temple 1983, Summers 1994, Bell 1996). Band encounter data is also frequently used to examine migration patterns (Salomonsen 1955, Alerstam 1990, Schmutz et al. 1991, Summers 1994). More recently, researchers have used stable-isotope analyses of bird feathers to describe migration patterns (Kelly et al. 2002).
Here we used a combination of band encounter analysis (BEA) and stable-isotope analysis (SIA) to describe the migration patterns of HY sharp-shinned hawks of interior North America during fall migration. Combining BEA and SIA to study migrating sharp-shinned hawks promised to be more productive than any single traditional approach for several reasons. First, there are no geographically distinct races or subspecies of sharp-shinned hawks north of Mexico in interior North America that allow for differentiation of regional populations (Bildstein and Meyer 2000). Second, while there are abundant records of HY sharp-shinned hawk band encounters from the non-breeding season, there are few from the breeding grounds (Hoffman et al. 2002). Furthermore, band encounter records are nearly absent from vast, unpopulated areas of northern North America where sharp-shinned hawks are known to breed. Third, stable-isotope analysis of feathers grown on the breeding grounds provides information on latitudinal origins of migrating songbirds and raptors (Meehan et al. 2001, Wassenaar and Hobson 2001, Kelly et al. 2002), but provides no information regarding wintering quarters. Finally, sharp-shinned hawks are secretive and are found in relatively low densities on the breeding and wintering grounds (Bildstein and Meyer 2000). In contrast, they are easily studied during migration when they concentrate along ridge tops in large numbers and are easily captured with live lures (Kerlinger 1989). Thus, studying migration patterns of HY sharp-shinned hawks during migration allows for large sample sizes for BEA and SIA, relative to studies conducted on the breeding or wintering grounds.

Our approach involved three steps. (1) We used SIA to estimate the relative natal origins of migrating HY sharp-shinned hawks captured during their first southward migration, relative to their date of passage through a banding station in interior North America. (2) We used BEA to determine where HY sharp-shinned hawks were migrating to for their first winter, relative to their date of passage through banding stations in interior North America. (3) Finally, we determined migration patterns by linking relative natal origins and wintering latitudes using date of passage through banding stations in interior North America.

Methods

Stable-hydrogen isotope data collection

The stable-hydrogen isotope ratios (δD) found in precipitation vary systematically across North America and show a steadily decreasing δD value from the southeast to the northwest (Hobson and Wassenaar 1997, Araguas-Araguas et al. 2000). The δD values found in local precipitation are incorporated into local food webs and, subsequently, the diet of birds. When birds grow new feathers, the stable-hydrogen isotope ratios fixed in feather keratin are directly related to the δD values of the precipitation at the location where feathers are grown (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000a, Hobson et al. 2001, Meehan et al. 2001, Lott et al. 2003). Therefore, δD values of feathers are highly correlated to latitudes at which the feathers are grown (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Meehan et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002, Lott et al. 2003).

Feathers were collected during 2001 fall migration at HawkWatch International’s long-term raptor migration study site located in the Manzano Mountains in the Cibola National Forest of central New Mexico (34.71° N, 106.41° W; DeLong and Hoffman 1997). We captured migrating HY sharp-shinned hawks using three methods: dho-gazas, mistnets, and bow-nets (Bloom 1987). We baited traps with non-native, live lures: rock doves Columba livia, ringed turtle-doves Streptopelia risoria, and house sparrows Passer domesticus. We collected one, 1–2 cm clipping from a secondary flight feather from each individual for stable-hydrogen isotope analysis. In addition, we banded all captured birds with U.S. Fish and Wildlife Service bands and recorded sex, mass, and morphological measurements (wing chord, culmen length, tarsus length, hallux length; Hoffman et al. 1990).

We removed oils from feather samples by washing them with a 2:1 chloroform to methanol solution (Wassenaar and Hobson 2000b). After cleaning, feathers were air dried while exchangeable hydrogen (13–22%) was allowed to equilibrate with laboratory ambient moisture for two weeks. Our δD values represent both exchangeable and non-exchangeable hydrogen. See Wassenaar and Hobson (in press) for a description of new methods for attaining non-exchangeable hydrogen values for feathers using keratin lab standards. We then packed small clippings, weighing approximately 0.2 mg, into silver capsules (Costech 3.5 × 5 mm). Packaged feather samples were pyrolyzed using a Finnigan MAT TC-EA elemental analyzer and analyzed for their hydrogen isotope ratios using a DeltaPlus XL mass spectrometer in continuous flow mode. We conducted all stable-hydrogen isotope analysis at the Stable Isotope Laboratory at the University of New Mexico. Resulting δD values from this analysis were calculated using the following standard model: δD = [(hydrogen isotope ratio of sample/hydrogen isotope ratio of Vienna Standard Mean Oceanic Water, VSMOW) – 1] × 1,000. δD values are reported in parts per thousand (%). The precision of our analyses was δD ± 5‰ (1 SD), based on repeated measurements of biotite laboratory standards.
Band encounter data collection

We obtained band encounter records from the Bird Banding Lab (BBL) of the United States Geological Survey. These data included records of sharp-shinned hawks banded as HY birds at sites in interior North America during their first fall migration and encountered the following winter between the dates of 15 December and 15 February, when sharp-shinned hawks tend not to be migrating (Bildstein and Meyer 2000), and from the years 1942 to 2000. We also collected encounter data on sharp-shinned hawks banded as HY birds during their first fall migration and encountered on their breeding grounds after their first spring migration. These migrants were banded at the same locations as the winter band encounters and recovered during the years 1962 to 2000.

Data analysis

We used regression to model the relationship between the feather δD values of migrating sharp-shinned hawks and their passage dates through the Manzano Mountains. Regression was also used to model the relationship between winter and breeding band encounter latitudes and passage dates through migration sites in interior North America.

Results

Stable-hydrogen isotopes

We measured the δD values of feathers from 120 HY sharp-shinned hawks migrating through the Manzano Mountains. The feather δD values ranged from −36 to −148‰ VSMOW. Regression analysis indicated a negative relationship between feather values and passage dates (Fig. 2). The data were best fit ($r^2 = 0.50$) by a model with both linear (passage date, $t = 4.71$, $P < 0.001$) and quadratic (passage date$^2$, $t = -4.47$, $P < 0.001$) terms. Thus, birds with higher feather δD values (i.e., from relatively lower natal latitudes) passed through the New Mexico banding site earlier in the season than those with lower feather δD values (i.e., from relatively higher natal latitudes).

Band encounters

Forty-seven sharp-shinned hawk band encounter records obtained from the BBL met our criteria of being banded during fall migration in interior North America as HY birds and encountered that following winter on their wintering quarters. The locations of migration banding and sample size per location were as follows: Michigan, USA (n = 5); Wisconsin, USA (n = 19); Minnesota, USA (n = 11); Nevada, USA (n = 9) and Idaho, USA (n = 3). These birds were later encountered on the wintering grounds from 13.67° to 43.67° N. Lat. (central Nicaragua to central USA). We found a positive relationship between latitudes of winter band encounters and passage date through banding sites in interior North America (Fig. 3). This relationship was best fit ($r^2 = 0.41$) by a model with a linear term only (passage date, $t = 5.59$, $P < 0.001$). Thus, birds that passed through interior North America banding sites earlier wintered further south than those passing through later in the season.

Because we combined one year of isotope data from New Mexico with several years of band encounter data from Michigan, Wisconsin, Minnesota, Nevada, and Idaho, we used the breeding band encounter data to ensure migratory behavior was consistent over time and space. Although there were few encounters of breeding birds (n = 21), there was a marginally significant positive relationship ($r^2 = 0.18$, $t = 2.01$, $P = 0.06$) between breeding latitudes and passage date during the previous fall migration. These data provide support for the validity of combining isotope and band encounter data to generalize migratory timing of HY sharp-shinned hawks throughout interior North America and over the span of several years.
proposed hypotheses. It was beyond the scope of our data to evaluate the mechanisms driving HY sharp-shinned hawks’ use of a chain migration pattern.

One factor hypothesized to affect the evolution of migration patterns is intraspecific competition maintained through differential body size among regional populations (Pienkowski et al. 1985). Using our stable isotope data, we were able to compare body size of birds from relatively higher and lower natal latitudes. We used principle components analysis, combining three morphological measurements (mass, tarsus length and wing chord), to obtain a standardized summary variable for the size of birds with empty crops. We found that female (n = 39, $r^2 = 0.40$, t = 4.95, P < 0.001) and male (n = 30, $r^2 = 0.18$, t = 2.48, P = 0.02) HY sharp-shinned hawks with lower feather δD values (i.e., from relatively higher natal latitudes) were larger than those with higher feather δD values.

Another factor hypothesized to affect the evolution of migration patterns is the cost of migration. It is often assumed that distance traveled during migration is proportional to its cost (Pienkowski et al. 1985, Lundberg and Alerstam 1986). Such a cost, among others, can include the depletion of energy stores (Blem 1980). Using our stable isotope data we compared estimated total body fat of birds originating from higher and lower latitudes. DeLong and Gessaman (2001) developed models to estimate the total body fat for male and female Sharp-shinned hawks using morphological measurements. We used their models (equations 13 and 14; $r^2 = 0.86$) to estimate total body fat for migrants with empty crops captured in the Manzano Mountains. We found a negative relationship between feather δD values and estimated total body fat for females (n = 39, $r^2 = 0.20$, t = 3.07, P = 0.004), and no relationship between feather δD values and estimated total body fat for males (n = 30, $r^2 = 0.006$, t = 0.42, P = 0.68). Thus, females with lower feather δD values (i.e., from relatively higher natal latitudes) were carrying higher estimated fat loads than those with higher feather δD values. This analysis showed that longer distances traveled by HY sharp-shinned hawks does not have a net negative impact on fuel stores.

In conclusion, we found that (1) HY sharp-shinned hawks in interior North America migrated using a type I chain migration pattern, (2) HY sharp-shinned hawks from higher latitudes were larger than those from lower latitudes, (3) females migrating farther distances had higher estimated levels of body fat than those traveling shorter distances, (4) there was no relationship between distance traveled and estimated body fat for males, and (5) using a combined approach of stable-isotope and band encounter analysis was an effective means for assessing migration patterns of migrating HY sharp-shinned hawks. This method could be extended to other bird species that are easily sampled during migration and for which there are abundant winter band encounter records.
These new insights into the spatial and temporal migration patterns of sharp-shinned hawks have conservation implications. For example, knowing that birds from lower latitudes migrate through research sites earlier than those from higher latitudes can help natural resource managers partition migration counts into early and late season trends (Meehan et al. 2001). This will help elucidate regional variation in reproductive success. Furthermore, if certain populations were determined to need special attention, then conservation measures could be applied more efficiently.

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